Class DINOPHYCEAE F.E. Fritsch *in* West & Fritsch 1927, pp 23, 392

Pascher (1914, pp 151, 153, 158) used the name "Dinophyceae" for one of his "Algenreihen". The following typified names are available for this class: Peridiniophyceae Knoblauch *in* Warming 1890, p. 9 ("Peridinea"); Dinophyceae T. A. Christensen 1978, p. 65 (typified by *Dinococcus* Fott)

For a description of dinoflagellate features see **Chap. 2**.

Order 1. DESMOMASTIGALES Fott 1959, p. 347

Proposed as a typified name to replace the descriptive name Desmomonadales Pascher (1914, pp 148, 158)

Cells with two band-shaped flagella emerging from the apical end, no furrows. Nucleus large, typical for dinoflagellates (dinokaryon). No amphiesmal plates.

Family 1. Desmomastigaceae Fott *ex* A. R. Loeblich 1970, p. 881, 906

With the characters of the order.

Genus 1. ***Desmomastix*** Pascher 1914, p. 160

Type species: *Desmomastix globosa* Pascher

Cells naked, elliptic, in apical view circular. Two parietal chloroplasts. Two band-shaped apical flagella. One flagellum beats with wave-like movements.
Only 1 species known. It has apparently not been observed since the original find a century ago.

1. *Desmomastix globosa* Pascher 1914, p. 160 (**Fig. 7**)

With excentrical pyrenoid. Cell length 10–15 µm, width 8–14 µm. Spherical cysts surrounded by cellulosic wall. Cell division takes place in both the motile stage and the cyst stage.
Ecology: only known from oxbows of the river Vltava near Prague.
Geographical distribution: Czech Republic.

Ø. Moestrup, A. J. Calado, *Süßwasserflora von Mitteleuropa, Bd. 6 – Freshwater Flora of Central Europe, Vol. 6: Dinophyceae*, Süßwasserflora von Mitteleuropa,
https://doi.org/10.1007/978-3-662-56269-7_7

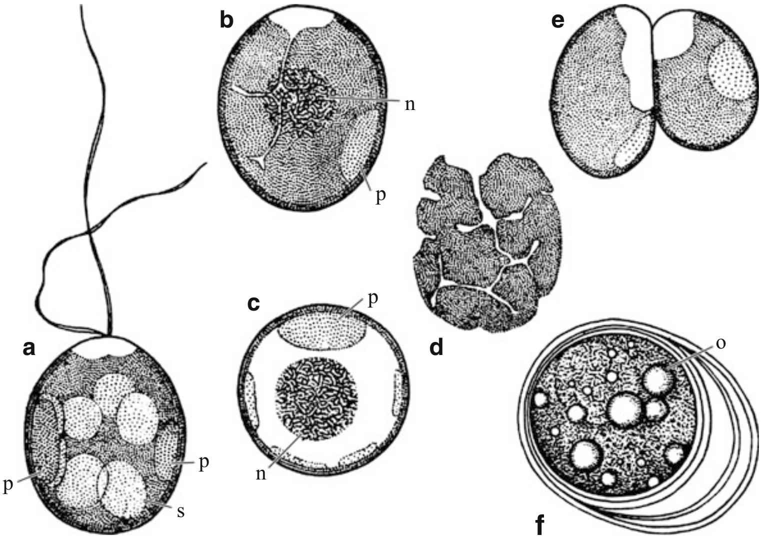

Fig. 7 *Desmomastix globosa* Pascher (after Pascher *in* Schiller 1931). **a** lateral view of cell showing apically inserted flagella, the chloroplast with pyrenoids (p) and starch (s) reserves; **b** lateral view of cell, with pyrenoid (p) and nucleus (n) indicated; **c** cross section of cell showing nucleus (n), chloroplast lobes and pyrenoid (p); **d** incised outline of chloroplast; **e** recently divided cells; **f** cyst (resting stage) with oil droplets (o)

Order 2. DINAMOEBIDIALES Fott 1960, p. 144

Proposed as a typified name to replace the descriptive name Rhizodiniales Pascher (1931, p. 326, *nom. nud.*); Rhizodiniales was validated by Schiller (1937, p. 481) who provided a description.

Dinoflagellates with both gymnodinioid and amoeboid motile stages, and a walled resting stage. All stages with a single typical dinoflagellate nucleus (dinokaryon). Originally described as lacking chloroplasts (but see the species described below).

Family 1. Dinamoebidiaceae Fott 1959, p. 361

Nomenclatural synonym: Dinamoebaceae Pascher 1916a, p. 135

With the characters of the order.

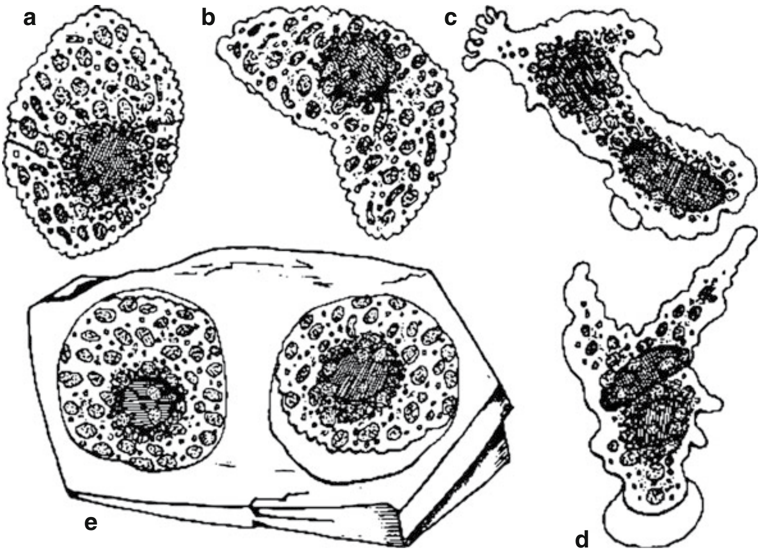

Fig. 8 *Dinamoebidium coloradense* Bursa (after Bursa 1970). **a** ventral view; **b** dorsal view; **c** amoeboid cell with a pseudopodium forming papillae; **d** amoeboid cell with different shape; **e** discoid cysts attached to sand grain

Genus 1. ***Dinamoebidium*** Pascher 1916b, p. 31, *nom. cons.*

Type species: *Dinamoebidium varians* (Pascher) Pascher 1916b, p. 31 (marine) ≡ *Dinamoeba varians* Pascher 1916a, p. 118, text-fig. 5, pl. 10
Nomenclatural synonym: *Dinamoeba* Pascher 1916a, p. 118, *nom. rej.*

Cells amoeboid, forming short, blunt pseudopodia. Feeds on flagellates, diatoms, green algae and cyanobacteria. Chloroplasts absent in the type species. Cell division not observed. The cell may transform into thick-walled, bipolar, sausage-shaped resting stage (cysts), in which the cell contents divides into 4–8 gymnodinioid zoospores of somewhat irregular shape. The transverse flagellum of zoospores has been clearly observed, but not the longitudinal. Epicone usually slightly larger than the hypocone. The epicone rounded, the hypocone conical. Cingulum incomplete, very variable in appearance. Sulcus also variable in appearance (longitudinal flagellum not observed). The zoospores develop into new amoebae. Feeds on flagellates, diatoms, green algae and cyanobacteria.

Note: the species below differs from the type species in possessing chloroplasts.

1. *Dinamoebidium coloradense* Bursa 1970, p. 146, figs 1–8 (**Fig. 8**)

Nomenclatural synonym: *Dinamoeba coloradensis* (Bursa) Carty 2014, pp 45, 222 (“*coloradense*”), incorrect name (combination with rejected generic name)

Cells polymorphic, with irregularly scalloped periplast and equatorial girdle-like groove (cingulum?). Many small plate-shaped chloroplasts. Cytoplasm contains sausage-shaped brown structure of unknown nature and numerous lipid droplets, especially around the centrally located nucleus. Eyespot absent. Flagella not observed. Cells are free-swimming or attached, when attached changing into amoeboid cells with pseudopodia. Amoebae mixotrophic, phagocytizing other algae. Cell length 20–39 µm, width 13–23 µm, amoeboid cells 28–47 µm long.
Ecology: attached to rocks and grains intermingled with mosses, mainly *Fontinalis*, in creek in Colorado, in September 1968.
Geographical distribution: USA, CO (Bursa).

Note: the identity of this organism is very uncertain. Dinoflagellate?

Order 3. AMPHIDINIALES Moestrup & Calado *ordo nov.*

Cells without amphiesmal plates. Cingulum located near the anterior end of the cell, typically V-shaped on the ventral side. Cell division by longitudinal or oblique division of the motile cell or by cells ceasing swimming and the cytoplasm dividing into two, occasionally more, new cells, which leave the parent cell cover when fully formed.

Family 1. Amphidiniaceae Moestrup & Calado *fam. nov.*

Epicone finger or crescent-like, much smaller than hypocone.

Genus 1. *Amphidinium* Claparède & J. Lachmann 1859, p. 410

Type species: *Amphidinium operculatum* Claparède & J. Lachmann 1859, p. 410, pl. 20, figs 9, 10 (marine)

Cells dorsoventrally compressed. Epicone deflected to the left.

1. *Amphidinium steinii* (Lemmermann) Kofoid & Swezy 1921, p. 152 (**Fig. 9**)

Basionym: *Amphidinium operculatum* var. *steinii* Lemmermann 1910, p. 616, figs 1–7 (on p. 580); based on Stein 1883, pl. XVII, figs 7–20 (as *A. operculatum*)

Cells rounded rectangular. With central pyrenoid from which radiate few to many strap-shaped chloroplasts. Nucleus posterior. Eyespot absent. Cingulum descending, the ends displaced 2–4 µm. The sulcus starts close to the right end of the cingulum, initially deep and wide, but becoming less distinct when approaching the antapex. Size of cells collected in freshwater: length 19–22 µm, width 10–14 µm, thickness 7–10 µm.

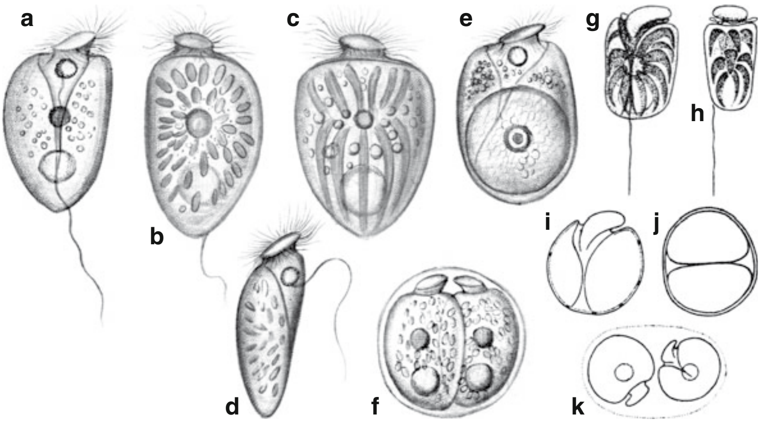

Fig. 9 *Amphidinium steinii* (Lemmermann) Kofoid & Swezy (**a**–**f** after Stein 1883; **g**–**k** after Thompson 1951). **a** ventral view, with central starch body (produced by central pyrenoid) and posteriorly located nucleus; **b**, **c** dorsal views, in **c** showing chloroplast lobes radiating from central pyrenoid; **d** lateral view; **e** ventral view of cell with large inclusion body; **f** division cyst; **g**, **h** ventral and lateral views, respectively, with chloroplast lobes radiating from central pyrenoid; **i**–**k** stages in cell division

Ecology and geographical distribution: reported from marine and brackish water areas in Australia, USA, and Germany (Flø Jørgensen *et al.*). Reported from freshwater swamp in small pond, Drum Point, MD, USA (Thompson, as *A. klebsii*).

Order 4. GYMNODINIALES Apstein 1909, p. 4 ("Gymnodiniaceae")

Unarmored flagellates, in which the cells are surrounded by numerous amphiesmal vesicles not arranged in any clear pattern (see more detailed description under Gymnodiniaceae). The three known families, Actiniscaceae, Gymnodiniaceae and Gyrodiniaceae, comprise both heterotrophic and autotrophic species, but whether they are phylogenetically related remains presently unknown.

Key to the families of Gymnodiniales:

1a Cells typically with internal skeleton .... 1. Actiniscaceae
1b Cells typically without internal skeleton 2
2a Cells with or without chloroplasts, not longitudinally striated ....
.... 2. Gymnodiniaceae
2b Cells without chloroplasts, longitudinally striated .... 3. Gyrodiniaceae

Note: the enigmatic genus *Pseudoactiniscus*, which very much resembles *Actiniscus*, is interpreted as a member of the Actiniscaceae that has secondarily lost the internal skeleton.

Family 1. Actiniscaceae Kützing 1844, pp 130, 139 ("Actinisceae")

Cells naked, typically with internal skeleton of two silicified stellate spicules (often called pentasters) enclosing the nucleus (secondary lost in *Pseudoactiniscus*). A thick fibrous layer of lamin, perhaps accompanied by extranuclear membranes (Hansen 1993) typically confer a capsulate appearance to the nucleus. In the motile cells the flagellar bases are connected to the nucleus with a so-called nuclear connector, as in the genus *Gymnodinium* and *Polykrikos*, indicating phylogenetic relationship.

Key to the genera of Actiniscaceae occurring in fresh water:
1a Cells with internal silicious skeleton .... 1. *Actiniscus*
1b Cells lacking internal skeleton .... 2. *Pseudoactiniscus*

Genus 1. *Actiniscus* (Ehrenberg) Ehrenberg 1843, p. 103

Basionym: *Dictyocha* "Gruppe" *Actiniscus* Ehrenberg 1840, p. 147 (taken as an unranked subdivision of a genus)
Type species: *Actiniscus pentasterias* (Ehrenberg) Ehrenberg 1844, p. 68 (marine) (see Downie & Sarjeant 1965)

Cells without chloroplasts. Each amphiesmal vesicle with very thin membranous sheet. A group of complex ejectisomes (docidosomes) located near the nucleus in *Actiniscus pentasterias* (Hansen 1993). Nucleus and ejectisomes surrounded by the pentasters (with 4–6 arms). Nucleus with distinct sheath (capsule). *Actiniscus* is a genus of mainly extinct marine dinoflagellates but three different taxa have been reported from Arctic Canada, some believed to having adapted to freshwater habitats. The pentasters in some of the freshwater forms are more or less rudimentary or absent.

Key to taxa of *Actiniscus* reported from fresh water:
1a With 1–8 large and 14 rudimentary pentasters ... 1. *A. pentasterias* var. *arcticus*
1b With rudimentary pentasters only .... 2. *A. canadensis*

1. *Actiniscus pentasterias* var. ***arcticus*** Bursa *ex* Moestrup & Calado *var. nov.* (**Fig. 10**)

Originally described by Bursa (1969, p. 412, figs 1–14), but not validly published for lack of type designation and Latin diagnosis. Type: Bursa 1969, *J. Protozool.* **16**, figs 1–3, from unspecified lacustrine origin. We arbitrarily select Keyhole Lake (69°23′N 106°14′W) as the type locality.

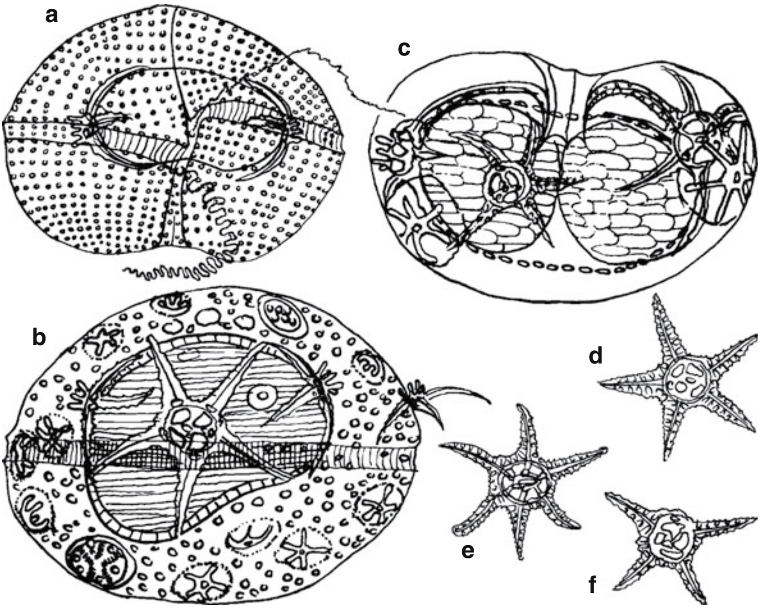

Fig. 10 *Actiniscus pentasterias* var. *arcticus* Bursa *ex* Moestrup & Calado (after Bursa 1969). **a** ventral view showing rows of inclusions on the cell cover and two pentasters flanking the nucleus; **b** optical section, with nuclear capsule surrounded by three pentasters, numerous small pentasters along the periphery and one pentaster emerging from the cell; **c** antapical view, with sulcus (upward on the image) flanked by special, bent arms of pentasters; **d** regular pentaster; **e**, **f** variant morphologies of pentasters, from a marine sample

Cells spherical or elliptical. The cingulum descending, the cingular ends displaced up to *ca.* 2.5 cingulum widths. Sulcus reported to extend to the apex. Parallel rows of small inclusions are present beneath the amphiesma. Cells contain 1–8 large and 14 peripheral rudimentary pentasters. Cytoplasm with spherical inclusions, oil droplets, etc. Nucleus surrounded by distinct nuclear capsule. Cell diameter 28–63 µm.
TEM of nominal species: Hansen (1993).
Ecology: phagotrophic, feeding on cryptomonads, chrysophytes and other dinoflagellates. A marine taxon, which has been found also in some oligotrophic arctic lakes, *e. g.*, Great Bear Lake, and Keyhole Lake.
Geographical distribution: Arctic Canada.

2. *Actiniscus canadensis* Bursa *ex* Carty 2014, p. 221, fig. 16 (**Fig. 11**)

Originally described by Bursa (1969, p. 414, figs 15–18, 20–22), but invalidly published for lack of type designation and Latin diagnosis.

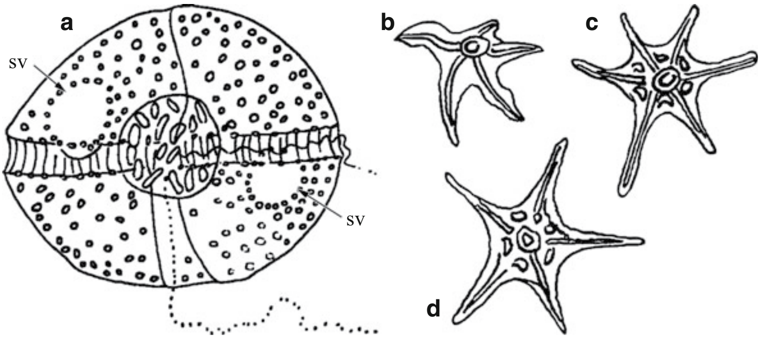

Fig. 11 *Actiniscus canadensis* Bursa *ex* Carty (after Bursa 1969). **a** ventral view with central nucleus and two secretory vesicles (sv), stated to form the pentasters; **b**–**d** pentasters

Cells spherical or subspherical, epicone and hypocone of equal size. Cingulum ends opposite or cingulum very slightly descending. Cells very similar to the preceding species but differing in having only rudimentary pentasters or lacking pentasters altogether. Cell diameter 28–43 μm.
Ecology: found in Great Bear Lake, an oligotrophic arctic lake; interpreted as an originally marine organism adapted to fresh water, resulting in atrophy of the pentasters (Bursa 1969).
Geographical distribution: Arctic Canada.

Genus 2. *Pseudoactiniscus* Bursa *ex* Carty 2014, p. 222

Originally described by Bursa (1969, p. 414), but invalidly published for lack of a Latin diagnosis.

Very similar to *Actiniscus*, from which it differs essentially in totally lacking pentasters.

1. *Pseudoactiniscus apentasterias* Bursa *ex* Carty 2014, p. 222, fig. 34 (**Fig. 12**)

Originally described by Bursa (1969, p. 414, fig. 19) but invalidly published for lack of a Latin diagnosis.

Cells spherical or subspherical, divided into epi- and hypocone of equal size. Sulcus described to extend to the apex as a narrow line. With radial rows of trichocysts. Pentasters missing. Nucleus central. Cytoplasm with spherical inclusions, lipid droplets, colored bodies. Some cells reportedly with diffuse yellowish-green chloroplasts. Cells 26–53 μm in diameter. Spherical cysts (not figured) formed in autumn.
Ecology: phagotrophic, ingesting mainly cryptomonads and dinoflagellates. Found at 1–11 ˚C in Keyhole Lake, Northwest Territories, Arctic Canada, a small, oligotro-

a

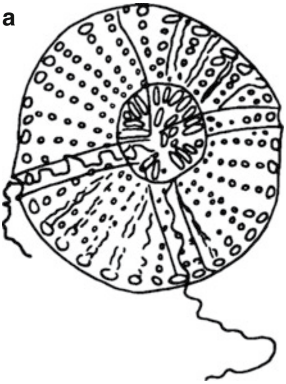

Fig. 12 *Pseudoactiniscus apentasterias* Bursa *ex* Carty (after Bursa 1969). **a** ventral view showing central nucleus and (presumably) radiating rows of inclusions on the amphiesma

phic, up to 6 m deep lake 3 km from the coast. Maximum concentration 1520 cells per liter in August. Considered a marine relict adapted to fresh water (Bursa 1969). Geographical distribution: Arctic Canada.

Family 2. Gymnodiniaceae Lankester 1885, p. 859 ("Gymnodinida")

The Gymnodiniaceae comprises most of the so-called "naked" dinoflagellates, whose cells are lined beneath the cell membrane by amphiesmal vesicles that appear empty or almost so, or which contain very thin plate-like structures, too thin to be visible under the light microscope. As presented below, it is not a monophyletic family, but our general knowledge is insufficient to allow us to present a stable, alternative classification, based on both morphological and molecular data.
The taxonomy of *Gymnodinium* is presently in a state of chaos. Following the precise circumscription of *Amphidinium*, *Katodinium* and *Gyrodinium*, several species were left in these genera after removal of the type species and related species. These we have transferred to *Gymnodinium*, pending further studies. *Gymnodinium*, as the generic name is used in the present account, is not a natural (monophyletic) genus but a conglomerate of species, of which the large majority has been seen only a few times and are in need of detailed studies. In this respect it does not differ from the old circumscriptions of *Gymnodinium*, *Gyrodinium*, *Amphidinium* and *Katodinium*, none of which were monophyletic. Ultrastructural and molecular data will almost certainly result in *Gymnodinium* being divided up into several genera. In fact, two species were recently transferred to the marine genus *Spiniferodinium* on the basis of molecular data, a transfer which was not supported by morphological evidence and which we have not followed. Problems also persist at

the species level, as many species have been described in a very incomplete way and their identity is difficult to ascertain.

Key to the genera of Gymnodiniaceae:

1a Cells typically with blue-green or green chloroplast-like endosymbionts 2
1b Cells colorless or with yellowish-brown chloroplasts .... 1. *Gymnodinium*
2a Cells typically with green endosymbionts .... 3. "*Katodinium*"
2b Cells typically with blue-green endosymbionts .... 2. *Nusuttodinium*

Genus 1. *Gymnodinium* F. Stein 1878, pp 89, 90, 91, 95, 97

Type species: *Gymnodinium fuscum* (Ehrenberg) F. Stein 1878 (see Chatton 1912)

Cell cover with very thin amphiesmal plates or lacking plates. With or without chloroplasts. The position of the cingulum variable, from being located in the anterior part of the cell (formerly the genus *Amphidinium*) to the posterior part (formerly *Katodinium*). Cingulum usually circular or descending (formerly *Gymnodinium* and *Gyrodinium*). Anterior end of the cell with apical groove, forming an anticlockwise loop.

Cell division described in detail by Thompson (1951) in *Gymnodinium fuscum*: division is oblique, starting from the posterior end while the cell is still moving. The hypocone broadens and then splits. Fission continues apically, the cell coming to rest when the cingulum becomes involved. When fission is nearly complete, but with a portion of the two epicones still attached, the two cells have developed independent flagellation and swimming activity is resumed. Cingulum and sulcus are formed on the new individuals as fission progresses.

Sexual reproduction known in several species.

Identification of *Gymnodinium* species can be difficult. It may not be possible to identify a single cell in a water sample, since species-specific features such as presence or absence of chloroplasts and eyespot may sometimes be difficult to see. Chloroplast number and structure may be seen with certainty in a fluorescence microscope, in which the chlorophyll fluoresces red when illuminated with violet-ultraviolet light. More difficult to handle is the increasing number of cases in which heterotrophic species have been found to retain prey chloroplasts as functional chloroplasts for longer or shorter periods before digesting them. This is a feature of the genus *Nusuttodinium*, where ingested cells (often blue cryptomonads) are retained for longer periods, but it is likely that such cases will be found also in *Gymnodinium*. Thus some species described as having chloroplasts may in fact be heterotrophs (or mixotrophs) with recently ingested prey. Another source of confusion is the eyespot, which may be confused with lipid droplets of the same color. However, the dinoflagellate eyespot is, with few described exceptions (Tamura *et al.* 2009, Iwataki *et al.* 2010), located in the proximal end of the sulcus (and connected within the cell to the flagellar apparatus by a microtubular root that is not usually visible in the light microscope). Lipid droplets may occur anywhere in the cell.

We have recognized 92 species of *Gymnodinium* and divided them into four groups, characterized by the presence or absence of chloroplasts and eyespot. Two additional species of "*Katodinium*" with specific epithets unavailable in *Gymnodinium*

have been included in these groups and in the identification keys to avoid creating new names at this point:
Chloroplasts and eyespot present .... Group I
Chloroplasts present, eyespot absent .... Group II
Chloroplasts absent, eyespot present .... Group III
Chloroplasts absent, eyespot absent .... Group IV

Group I. Chloroplasts and eyespot present

With 15 species, this is the second-smallest group. An eyespot has been found only in 20 % of the species with chloroplasts.

G. baumeisteri	*G. hyperxanthum*	*G. pusillum*
G. caudatum	*G. mazuricum*	*G. schuettii*
G. elongatum	*G. paradoxum*	*G. vierae*
G. huber-pestalozzii	*G. partitum*	*“Katodinium” viride*
G. hyperxanthoides	*G. purpureum*	*G. wawrikae*

Key to species of *Gymnodinium* with chloroplasts and eyespot:
1a Epicone twice the length of the hypocone or more 2
1a Epicone slightly larger, equal in size or smaller than hypocone 6
2a Sulcus extends far up on the ventral side of the epicone 3
2b Sulcus does not extend onto the epicone 4
3a Sulcal extension on the epicone straight, pointing towards the apex ....
.... 31. *G. hyperxanthum*
3b Sulcal extension on the epicone long and curved, pointing back ....
.... 30. *G. hyperxanthoides*
4a Epi- and hypocone of the same width .... 57. *G. partitum*
4b Epicone wider than hypocone 5
5a Epicone slightly wider than hypocone, the edges hanging over the hypocone
.... *“Katodinium” viride*
5b Epicone much wider than hypocone .... 46. *G. mazuricum*
6a Cells over 100 µm long, with pointed “tail” .... 14. *G. caudatum*
6b Cells less than 100 µm long, hypocone not tail-like 7
7a Hypocone much longer than epicone 8
7b Epi- and hypocone almost equal in length or epicone longer 9
8a Cingulum circular .... 74. *G. schuettii*
8b Cingulum strongly descending .... 66. *G. pusillum*
9a Cells spherical or very slightly elongate, ends rounded 10
9b Cells elongate, epicone typically conical 12
10a Cells red (red pigments in the cytoplasm) .... 65. *G. purpureum*
10b Cells brownish or yellowish 11
11a Cells more than 30 µm in diameter .... 56. *G. paradoxum*
11b Cells less than 30 µm in diameter .... 91. *G. wawrikae*
12a Sulcus extends at least halfway up the epicone 10
12b Sulcus extends less than halfway up the epicone .... 88. *G. vierae*

13a Sulcus extends to the apex or very nearly so 14
13b Sulcus extends *ca.* halfway up the epicone .... 28. *G. huber-pestalozzii*
14a Epicone twice the length of the hypocone, many chloroplasts ....
.... 10. *G. baumeisteri*
14b Epi- and hypocone of equal size, 4–6 chloroplasts .... 22. *G. elongatum*

Group II. Chloroplasts present, but eyespot absent

With 53 species, more than half the number of *Gymnodinium* species in fresh water, this is by far the largest group. To simplify identification, we have divided the species into two groups, comprising species whose cells are either larger or smaller than 25 µm. Species with overlapping dimensions are included in both keys.

G. alaskense	*G. kesslitzii*	*G. posthiemale*
G. albulum	*G. lacustre*	*G. pseudomirabile*
G. arenicola	*G. lalitae*	*G. radiatum*
"Katodinium" auratum	*G. limitatum*	*G. ruttneri*
G. baicalense	*G. limneticum*	*G. saginatum*
G. bogoriense	*G. lividum*	*G. sanctipaulense*
G. bohemicum	*G. luteofaba*	*G. simile*
G. chiastosporum	*G. mirabile*	*G. sphagnicola*
G. christenii	*G. mirum*	*G. tatricum*
G. cnecoides	*G. obesum*	*G. thomasii*
G. cryophilum	*G. oligoplacatum*	*G. triceratium*
G. danubiense	*G. palustre*	*G. tylotum*
G. discoidale	*G. palustriforme*	*G. undulatum*
G. fontinale	*G. paradoxiforme*	*G. varians*
G. fuscum	*G. pavlae*	*G. vernum*
G. hippocastanum	*G. peisonis*	*G. viridaliut*
G. impatiens	*G. planum*	*G. wigrense*
G. inversum	*G. poculiferum*	

Key to species of *Gymnodinium* with chloroplasts and without eyespot, and more than 25 µm in length:

1a Epicone twice or more the length of the hypocone 2
1b Epicone less than twice the length of the hypocone 3
2a Cells 24–27 µm long, strongly flattened dorsoventrally ....
.... *"Katodinium" auratum*
2b Cells 40–60 µm long, slightly flattened dorsoventrally .... 53. *G. palustre*

3a Hypocone pointed-conical 4
3b Hypocone rounded or rectangular 5
4a Cells 75–100 µm long and 47–60 µm wide .... 1. *G. fuscum*
4b Cells rarely longer than 50 µm and wider than 32 µm. Under the ice .... 9. *G. baicalense*
5a Hypocone at least twice the length of the epicone 6
5b Hypocone less than twice the length of the epicone 8
6a Hypocone nearly twice the width of the epicone .... 35. *G. kesslitzii* var. *sanctipaulense*
6b Hypocone less than twice the width of the epicone 7
7a Hypocone subcylindrical, chloroplasts parietal .... 19. *G. cryophilum*
7b Hypocone broadly rounded, chloroplasts radiating from cell center .... 67. *G. radiatum*
8a Cingulum descending at least one cingulum width 9
8b Cingulum circular or descending less than one cingulum width 17
9a Cingular ends displaced 10 µm or more .... 61. *G. poculiferum*
9b Cingular ends displaced less than 10 µm 10
10a Cingular ends displaced more than one cingulum width 11
10b Cingular ends displaced *ca.* one cingulum width 13
11a Cingular ends displaced at least 3 cingulum widths, sulcus very oblique, extending to the left on epicone .... 16. *G. christenii*
11b Cingular ends displaced 2–3 cingulum widths, sulcus does not enter the epicone 12
12a Epicone much smaller than hypocone, cells globular, not compressed .... 76. *G. sphagnicola*
12b Epicone slightly longer than hypocone, cells oval, strongly compressed .... 44. *G. lividum*
13a Cells ovoid, epicone slightly smaller than hypocone, right rim of hypocone undulate .... 85. *G. undulatum*
13b Right rim of hypocone not undulate; sulcus extends onto the epicone 14
14a Sulcal extension onto the epicone directed anteriorly 15
14b Sulcal extension directed towards the cell's left .... 51. *G. obesum*
15a Sulcal extension reaches the apex, cells convex-concave .... 3. *G. alaskense*
15b Sulcal extension on the epicone short, cells barely flattened dorsoventrally .... 34. *G. inversum*
16a Cells circular in ventral view, red-colored (red pigment in the cytoplasm) .... 65. *G. purpureum*
16b Cells circular, ovoid or elongate, brown, yellow or greenish in color 17
17a Hypocone with an excavated antapex 18
17b Hypocone rounded or flat at the antapex, sometimes with short tooth 19
18a Cells 31–36 µm long, epi- and hypocone of equal length .... 64. *G. pseudomirabile*
18b Cells 48–77(–90) µm long, epicone larger than hypocone .... 47. *G. mirabile*
19a Sulcus extends onto the epicone 20
19b Sulcus does not, as far as can be surmised from the often rather incomplete published drawings, extend onto the epicone 27
20a Sulcal extension on the epicone directed towards the cell's left when leaving the cingulum 21

20b Sulcal extension directed towards the cell apex 22
21a Numerous small chloroplasts covering the nucleus .... 48. *G. mirum*
21b Elongate, radiating chloroplasts .... 42. *G. limitatum*
22a Sulcal extension half the way to the apex or more 23
22b Sulcal extension shorter 25
23a Epicone shorter than hypocone, planktonic species 24
23b Epi- and hypocone of equal size, benthic species from sand ... 6. *G. arenicola*
24a Cells egg-shaped or spherical .... 43. *G. limneticum*
24b Cells elongate, very slim .... 92. *G. wigrense*
25a Epicone rounded, conical 26
25b Epicone rounded, hemispherical or bell-shaped 27
26a Numerous discoid chloroplasts in the cell periphery .... 84. *G. tylotum*
26b Many radiating chloroplasts filling the cell .... 9. *G. baicalense*
27a Epicone larger than hypocone .... 54. *G. palustriforme*
27b Epicone shorter than hypocone .... 27. *G. hippocastanum*
28a Many elongate chloroplasts radiating from cell center .. 55. *G. paradoxiforme*
28b Numerous discoid chloroplasts in the cell periphery 29
29a Chloroplasts yellow-brown, disc-shaped; tropical India .... 37. *G. lalitae*
29b Chloroplasts dark green, shortly band-shaped; Austria .... 89. *G. viridaliut*

Key to species of *Gymnodinium* with chloroplasts and without eyespot, and up to 25 µm in length:

1a Hypocone with three short “horns” .... 82. *G. triceratium*
1b No horns on the hypocone 2
2a Cells blood-red or carmine red .... 78. *G. tatricum*
2b Cells brownish, yellowish or greenish 3
3a Epicone twice or more the length of the hypocone 4
3b Epicone less than twice the length of the hypocone, sometimes smaller than hypocone 8
4a Cells strongly dorsoventrally flattened 5
4b Cells not or only slightly flattened 6
5a Epi- and hypocone of almost equal width, epicone not overhanging; hypocone rectangular, concave at the antapex .... 60. *G. planum*
5b Epicone wider than hypocone, overhanging; hypocone rounded .... 87. *G. vernum*
6a Epicone 3× the length of the hypocone .... 72. *G. sanctipaulense*
6b Epicone 2× the length of the hypocone 7
7a Cells 8–9 µm long, epicone elongate-ovoid .... 25. *G. fontinale*
7b Cells 10–16 µm long, epicone oval to hemispherical .... 13. *G. bohemicum*
8a Hypocone 2–3× the length of the epicone 9
8b Hypocone of the same size as the epicone or slightly larger 12
9a Epicone broadly hemispherical; five chloroplasts, cells 7–14 µm long .... 35. *G. kesslitzii*
9b Epicone flattened hat-shaped, much broader than long; more than 5 chloroplasts, cells 16–25 µm long 10
10a Sulcus extends onto the epicone .... 67. *G. radiatum*
10b Sulcus does not extend onto the epicone 11

11a Epicone v-shaped, extending into sulcus .... 70. *G. ruttneri*
11b Epicone ventrally not v-shaped, not extending into sulcus ..... 59. *G. peisonis*
12a Cells strongly dorsoventrally compressed, discoid .... 21. *G. discoidale*
12b Cells not discoid 13
13a Cingular ends displaced less than 1 cingulum width 14
13b Cingular ends displaced one or more cingulum widths .... 42. *G. limitatum*
14a Sulcus extends onto the epicone for half the length of the epicone or longer 15
14b Sulcus extends for a shorter distance on the epicone or not at all 16
15a Cells pentagonal, with excavation at the antapex, hypocone 50 % larger than epicone .... 20. *G. danubiense*
15b Cells spherical or elliptic, epi- and hypocone both bell-shaped, epi- and hypocone of the same size .... 58. *G. pavlae*
16a The epicone extends as a small triangular structure into the upper part of the sulcus 17
16b The epicone does not extend as a triangular structure into the sulcus 21
17a Epi- and hypocone both bell-shaped, cells 18–21 µm .... 32. *G. impatiens*
17b Cells cylindrical or ovoid, sometimes more or less conical 18
18a Cells cylindrical, 9–25 µm long .... 4. *G. albulum*
18b Cells ovoid 19
19a Cells 20–24 µm long .... 12. *G. bogoriense*
19b Cells shorter than 20 µm 20
20a Cells with many disc-shaped chloroplasts .... 79. *G. thomasii*
20b Cells with one chloroplast in each cell half .... 75. *G. simile*
21a The sulcus forms an indentation or an extension in the epicone 22
21b The sulcus does not enter the epicone, the anterior edge of the cingulum is even or, if the cingulum descends slightly, very slightly undulate 24
22a Hypocone indented slightly at the antapex .... 52. *G. oligoplacatum*
22b Antapex flat or convex 23
23a Cells ovoid, sulcus extends onto the epicone .... 27. *G. hippocastanum*
23b Cells globular, sulcus forms a bulge in the epicone (extending further?) .... 71. *G. saginatum*
24a 1–2 chloroplasts 25
24b More than 2 chloroplasts 26
25a Epi- and hypocone equal in length or hypocone longer, 1–2 chloroplasts, when two one in each cell half .... 17. *G. cnecoides*
25b Epicone longer than hypocone, single chloroplast in the hypocone .... 45. *G. luteofaba*
26a Chloroplasts radiating from cell center 27
26b Numerous parietal chloroplasts 28
27a Cells 8–17 µm long, cell shape variable, hypocone often longer than epicone .... 86. *G. varians*
27b Cells 20–44 µm long, epi- and hypocone of equal size 55. *G. paradoxiforme*
28a Epicone smaller than hypocone .... 15. *G. chiastosporum*
28b Epi- and hypocone of equal size or epicone larger 29
29a Winterform, also under ice .... 62. *G. posthiemale*
29b Summer form .... 36. *G. lacustre*

Group III. Chloroplasts absent, eyespot present

The five species of this very small group are well separated. Future studies, using modern technology, are likely to show that they belong in other genera. They are all in need of study.

G. aeschrum	*G. intermedium*	*G. titubans*
G. hyalinum	*G. rarum*	

Key to species of *Gymnodinium* with eyespot, but without chloroplasts:

1a Epicone much wider than hypocone, the cell toadstool-like ... 2. *G. aeschrum*
1b Epicone not notably wider than hypocone 2
2a Cingulum descending, the ends displaced several cingulum widths .... 29. *G. hyalinum*
2b Cingulum circular or very slightly descending 3
3a Epicone much smaller than hypocone .... 68. *G. rarum*
3b Epi- and hypocone of equal or nearly equal size 4
4a Cell longer than wide, sulcus extends wide up into the epicone 81. *G. titubans*
4b Cell length and width equal or nearly so, sulcus extension in the epicone minute, triangular .... 33. *G. intermedium*

Group IV. Chloroplasts absent, eyespot absent

A total of 22 species. None of these have been studied in culture and the range of variation reported is therefore based on material observed in nature. Species can be difficult to identify, especially those in the latter part of the key, and it seems likely that once species are brought into culture and studied carefully, better circumscription of the species will become possible. Most species are probably phagotrophic and the size and shape therefore probably depends somewhat on whether the cells have been feeding recently. In addition, features now considered important for identification, such as details of the intersection of cingulum and sulcus, are sometimes given rather cursorily if at all in the older descriptions.

G. albulum	*G. granii*	*G. rhinophoron*
G. alsiophilum	*G. lantzschii*	*G. schilleri*
G. astigmatum	*G. latum*	*G. spirodinioides*
G. austriacum	*G. legiconveniens*	*G. thompsonii*
G. blax	*G. leptostauron*	*G. tridentatum*
G. colymbeticum	*G. mitratum*	*G. waltzii*
G. eufrigidum	*G. mucicola*	
G. eurytopum	*G. pratense*	

Key to species of *Gymnodinium* without chloroplasts and without eyespot:

1a Sulcus sigmoid, turning left on the hypocone .... 50. *G. mucicola*
1b Sulcus straight or nearly so 2
2a Sulcus extends to half the length of the epicone or more 3
2b Sulcus barely extends onto the epicone or not at all 9
3a Sulcus extends to the apex or very nearly so 4
3b Sulcus extends to *ca.* half or 3/4 the length of the epicone, tiny anterior spines sometimes present 6
4a Cingulum circular (ends at same level) .... 26. *G. granii*
4b Cingulum distinctly descending 5
5a Cingular ends displaced several cingulum widths .... 80. *G. thompsonii*
5a Cingular ends displaced *ca.* one cingulum width .... 41. *G. leptostauron*
6a Sulcal extension on the epicone directly above sulcus on the hypocone, anterior spines sometimes present 7
6b Sulcal extension on the epicone shifted towards the left, no anterior spines ... . 18. *G. colymbeticum*
7a Tiny anterior spines present .... 83. *G. tridentatum*
7b No anterior spines 8
8a Epicone larger and wider than hypocone, cell length 6–11 µm ..... 11. *G. blax*
8b Epi- and hypocone of equal size and shape, cell length 40–41 µm .... 8. *G. austriacum*
9a Wing from epicone and right side of hypocone extends over the central area .... 69. *G. rhinophoron*
9b No wing present 10
10a Antapical end very oblique .... 77. *G. spirodinioides*
10b Antapical end more or less symmetrical 11
11a Epicone at least twice the length of the hypocone, wider than hypocone .... 63. *G. pratense*
11b Epicone less than twice the length of the hypocone, often more or less equal 12
12a Cells distinctly flattened dorsoventrally 13
12b Cells not or barely flattened dorsoventrally 14
13a Epicone bell-shaped .... 7. *G. astigmatum*
13b Epicone conical .... 73. *G. schilleri*
14a Apex pointed, sometimes with spines 15
14b Apex rounded, epicone conical or hemispherical 16
15a Cells pentagonal, 40–45 µm long, 34–38 µm wide .... 39. *G. latum*
15b Epicone conical, hypocone hemispherical, cells 25–30 µm long, 20–23 µm wide .... 5. *G. alsiophilum*
16a Epicone conical .... 38. *G. lantzschii*
16b Epicone hemispherical 17
17a Epicone smaller and less wide than hypocone, cytoplasm pink .... 23. *G. eufrigidum*
17b Epicone and hypocone of approximately same width, or epicone wider, cytoplasm not pink 18
18a Epicone ventrally even, without indentations or extensions 19
18b Epicone with a small triangular indentation or extension ventrally 20
19a Cells cylindrical, cell length 9–25 µm .... 4. *G. albulum*

19b Cells ovoid, cell length 32–35 µm .... 49. *G. mitratum*
20a Epicone with very small triangular extension ventrally .. 40. *G. legiconveniens*
20b Epicone with indentation from the sulcus 21
21a Nucleus in the hypocone .... 24. *G. eurytopum*
21b Nucleus in the epicone .... 90. *G. waltzii*

1. *Gymnodinium fuscum* (Ehrenberg) F. Stein 1878, p. 95 (**Fig. 13**)

Basionym: *Peridinium fuscum* Ehrenberg 1834, p. 270

Cells with rounded or dome-shaped epicone and conical hypocone. Hypocone extends posteriorly into a very short tip. Cingulum median, descending, displaced *ca.* one cingulum width. Sulcus short, extending for a very short distance onto the epicone. A very delicate horseshoe-shaped apical furrow extends from the sulcal extension onto the epicone and is usually not visible in the light microscope. Numerous small, elongate chloroplasts scattered throughout the cell. Nucleus in the epicone. Numerous mucilage-producing vesicles (mucocysts) in the cell, which may produce copious amounts of mucilage, forming colony-like aggregates, in which the cells do not move or move very slowly. Cells *ca.* 75–100 µm long and *ca.* 47–60 µm wide. Resting cysts spherical, colorless except for a dark red, central body, *ca.* 40 µm in diameter, with distinct ridges in a roughly hexagonal pattern.
SEM: Hansen *et al.* (2000), Hansen & Flaim (2007).
TEM: Dodge & Crawford (1969), Hansen *et al.* (2000).
DNA data: Daugbjerg *et al.* (2000).
Ecology: common and widespread in peat bogs and acid, oligotrophic waters, sometimes forming blooms. Occurs both in brown and clear water. Höll (1928) gives pH *ca.* 6 as optimum. Reported a single time from brackish water in Belgium (Conrad 1926).
Geographical distribution: from Great Britain (Harris; Lewis & Dodge) and Portugal (Nauwerck) in western Europe to Poland (Wołoszyńska) and Ukraine (Krakhmalny *et al.*) in eastern Europe. USA, MD (Thompson), TX (Carty). Brazil (Cunha; Bicudo & Skvortsov). Japan (Senzaki & Horiguchi); Australia, Tasmania (Ling *et al.*).

var. *minus* Villeret 1953, p. 71 ("*minor*")
Differs in the smaller size of the cells: cell length 52–62 µm, width 32–35 µm.
Ecology: oligotrophic waters in Bretagne, France.

Note: material from Maryland, USA, bridges the difference between this variety and the type: 46–77 µm long and 32–45 µm wide (Thompson 1947). Additional studies are required to determine the variation in cell size of this species and the variety *minus*.

2. *Gymnodinium aeschrum* (T. M. Harris) Moestrup *comb. nov.* (**Fig. 14**)

Basionym: *Amphidinium aeschrum* T. M. Harris 1940, *Proc. Linn. Soc. London* **152** (1), p. 18, fig. 6

Cells oval, compressed dorsoventrally. Epicone much smaller than hypocone, but strongly overhanging, toadstool-like. Cingulum oblique, the ends displaced about

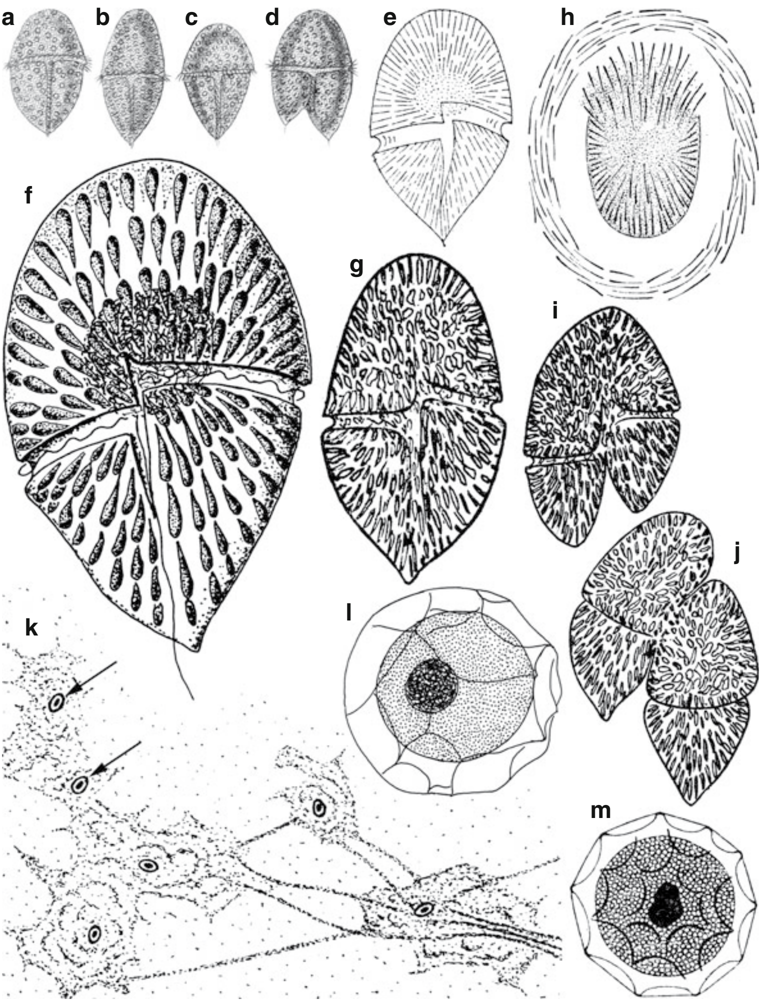

Fig. 13 *Gymnodinium fuscum* (Ehrenberg) F. Stein (**a**–**d** after Ehrenberg 1838; **e**, **h**, **m** after Wołoszyńska 1924; **f**, **l** after Bourrelly 1970; **g**, **i**, **j** after Geitler 1928a; **k** after Lindemann 1929). **a**–**d** Ehrenberg's illustrations (as *Peridinium fuscum*), with rows of cilia, instead of flagella, represented in the furrows (**d** division stage); **e**–**g** ventral views; **h** radial arrangement and discharge of mucocysts in saline solution; **i**, **j** stages in cell division; **k** immobile stage, with cells (arrows) in mucilage envelopes connected by mucilage strands (the dots represent ink used to evidence the mucilage); **l**, **m** resting cysts, with a wide, colorless wall provided with ridges, and a dark red, central body

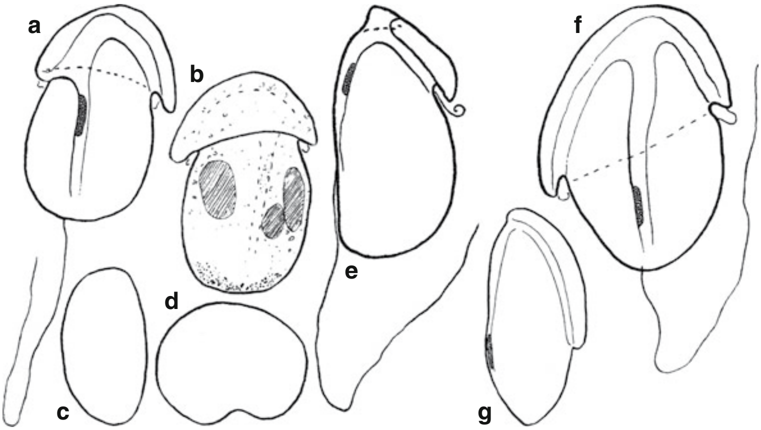

Fig. 14 *Gymnodinium aeschrum* (T. M. Harris) Moestrup (after Harris 1940). **a**–**d** four views of the same specimen (dark bodies in **b** represent food material); **e** another specimen in side view; **f**, **g** ventral and lateral views of large specimen with unusually long epicone (**g** slightly reduced)

two cingulum widths. On the ventral side, the right side of the cingulum descends, traversing the dorsal side more or less transversely, and on the left-ventral side ascends toward the sulcus. Sulcus restricted to the hypocone, but without reaching the antapex. Chloroplasts absent. Elongate eyespot in the sulcus. With food vacuoles and other vacuoles in the cell. Longitudinal flagellum as long as the cell. Cell length 20 µm, width 18 µm, thickness 12 µm.
Ecology: in eutrophic lock of the River Thames, June 1936.
Geographical distribution: England (Harris).

3. ***Gymnodinium alaskense*** Bursa *ex* Moestrup & Calado *sp. nov.* (**Fig. 15**)

Originally described as "*Gymnodinium alaskensis* Bursa 1963, p. 252, fig. 6", a designation not validly published (no Latin diagnosis). Type: Bursa 1963, *Arctic* **16**, fig. 6 (here designated).

Cells ellipsoidal, flattened dorsoventrally. The ventral surface slightly concave, the dorsal side convex. Epicone variable in size, in some cells only slightly longer than hypocone, in others up to twice as long. The epicone hemispherical or conical, with distinct triangular extension in the sulcus, the hypocone hemispherical or slightly angular. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus extends from apex to antapex. Longitudinal flagellum 1.5× the cell length. Numerous ribbon-shaped chloroplasts, greenish- or yellowish-brown. Nucleus in the epicone. With cubic crystals in the cytoplasm. Cell length in large individuals 40–54 µm, in smaller ones 28–31 µm. Cell width 30–35 µm. Palmella stages also observed.

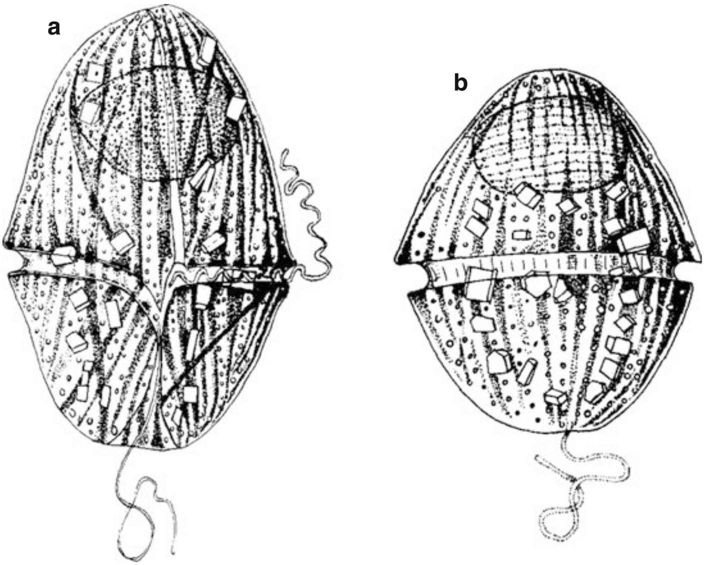

Fig. 15 *Gymnodinium alaskense* Bursa *ex* Moestrup & Calado (after Bursa 1963). **a** ventral view of long form, showing chloroplasts, nucleus, flagella and scattered crystals; **b** dorsal view of short form with crystals arranged in a circle

Fig. 16 *Gymnodinium albulum* Er. Lindemann (**a**, **b** after Lindemann 1928c; **c**–**e** after Schiller 1932; **f**–**j** after Schiller 1955). **a**, **b** ventral and side views; **c**–**j** shape variation (**d** top view), sometimes interpreted as different species (**c**, **d**, *G. profundum*; **e**, *G. submontanum*; **f**, *G. achroum*; **g**, *G. absumens*; **h**, *G. devorans*; **i**, **j**, *G. knollii*)

Ecology: in lake west of Barrow Base, Alaska, July–September 1954, in brackish as well as freshwater parts of the lake, most common on the lake bottom.
Geographical distribution: USA, AK (Bursa).

4. *Gymnodinium albulum* Er. Lindemann 1928c, p. 292, figs 8–10 (**Fig. 16**)

Taxonomic synonyms: *Gymnodinium profundum* J. Schiller 1932, p. 399, fig. 416; *Gymnodinium achroum* J. Schiller 1955, p. 30, pl. II, fig. 18; *Gymnodinium absumens* J. Schiller 1955, p. 34, pl. III, fig. 27; *Gymnodinium devorans* J. Schiller

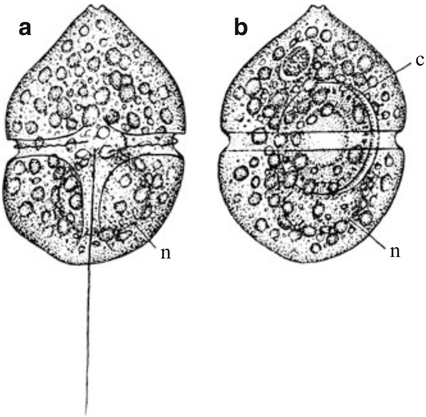

Fig. 17 *Gymnodinium alsiophilum* Skuja (after Skuja 1964). **a**, **b** ventral and dorsal views, respectively (c ingested *Cyclotella*; n nucleus)

1955, p. 32, pl. III, fig. 23; *Gymnodinium knollii* J. Schiller 1955, p. 32, pl. III, fig. 22; *Gymnodinium submontanum* J. Schiller 1955, p. 29 (illustrated in Schiller 1933, fig. 333c–d, as *G. albulum*)

Cells cylindrical with rounded apices, not compressed or rarely somewhat dorso-ventrally compressed. Cingulum circular. Sulcus restricted to the hypocone, running completely or incompletely to the antapex. Epicone as wide as or wider than hypocone. Relative size of epicone and hypocone variable. Epicone extends as a triangular structure into the sulcus. Nucleus oval. Chloroplasts yellowish-brown to green, discoidal, parietal, occurring 3–5 together, sometimes absent. Eyespot absent. Orange or red globules sometimes present. Cell length 9–25 μm, width 9–11 μm.
Ecology: described in a very incomplete way from a saltwater pond in Greifswald, Germany, but subsequently found in fresh water: Lake Attersee and Lake Neusiedl, Austria, both in winter and summer. Described in more detail from Maryland by Thompson (1947), occurring in February and March.
Geographical distribution: Austria (Schiller); Germany (Lindemann). USA, MD (Thompson).

Note 1: the absence or presence of chloroplasts indicates a mixotrophic species. If the chloroplast-containing and chloroplast-lacking forms turn out to be different species, then *G. albulum* will be available for the chloroplast-lacking forms and *G. profundum* for the chloroplast-containing forms.

Note 2: Additional work is required to determine whether cells occurring in winter belong to a separate species, for which the name *G. absumens* would then be available.

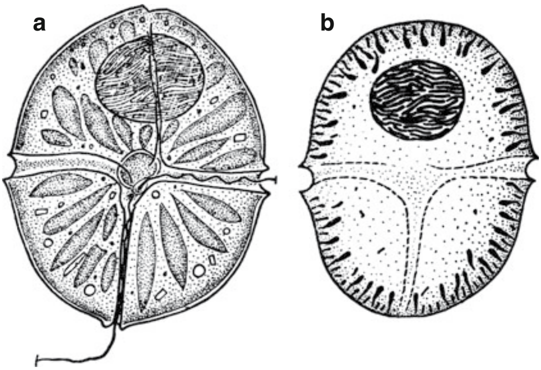

Fig. 18 *Gymnodinium arenicola* Dragesco (after Dragesco 1965). **a** ventral view of live cell, showing nucleus, chloroplasts and flagella; **b** cell stained with basic fuchsin, with peripheral trichocysts (rod-like) and mucocysts (inner part inflated)

5. *Gymnodinium alsiophilum* Skuja 1964, p. 350, pl. LXVII, figs 5, 6 (**Fig. 17**)

Cells rounded hexangular, barely compressed dorsoventrally. Epicone rounded-conical with two minute apical spines, of the same size as the hemispherical hypocone. Cingulum circular. Sulcus extending very slightly onto the epicone, on the hypocone reaching the antapex, widening antapically. Cytoplasm colorless, chloroplasts absent. Eyespot absent. Nucleus in the hypocone. Described with many food vacuoles containing centric diatoms and green algae. Cell length 25–30 µm, width 20–23 µm.
Ecology: under the ice in Lake Torneträsk, North Sweden.
Geographical distribution: Sweden (Skuja).

6. *Gymnodinium arenicola* Dragesco 1965, p. 109, text-fig. 16; pl. II, fig. 2 (“*arenicolus*”) (**Fig. 18**)

Cells oval, dorsoventrally flattened. Epi- and hypocone equal in size. Cingulum circular. Sulcus extends on the epicone almost to the apex, on the hypocone to the antapex. Numerous elongate, greenish-brown chloroplasts extend from a central pyrenoid. Nucleus in the epicone. Numerous trichocyst-like structures present in the cell, discharging into muciferous filaments. Cell length 30–70 µm.
Ecology: in sandy littoral in both marine and fresh water, considered to be euryhaline.
Geographical distribution: France, Switzerland (Dragesco).

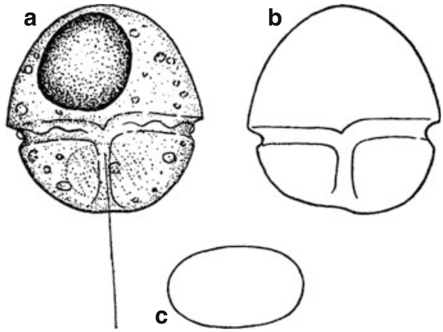

Fig. 19 *Gymnodinium astigmatum* Moestrup & Calado (after Christen 1959b). **a**, **b** two cells in ventral view; **c** cross section

7. *Gymnodinium astigmatum* Moestrup & Calado *sp. nov.* (**Fig. 19**)

Originally described as "*Katodinium astigmatum* Christen 1959b, p. 183, 187, fig. 8", a designation not validly published (no type designation). See Latin description in Christen (1959b, p. 187). Type: Christen 1959b, *Mitt. Naturwiss. Ges. Winterthur* **29**, fig. 8a (here designated).

Cells usually as long as wide, distinctly dorsoventrally flattened. Epicone as large as the hypocone or slightly larger, rounded. Hypocone sometimes slightly narrower than epicone, symmetrically rounded or somewhat oblique. The ends of the cingulum not displaced. The anterior rim of the cingulum not overhanging. Sulcus extending to the antapex, which is often very slightly indented, but not extending onto the epicone. Nucleus in the hypocone, eyespot lacking. Chloroplasts absent. Often several food vacuoles in the epicone. Cell length 18–20 µm, width 15–17 µm, thickness 11–13 µm.
Ecology: lake plankton, both in the epilimnion and above the bottom sediment, among detritus. Spring, summer and autumn, Switzerland.
Geographical distribution: Andelfingen, Hausersee and Rootsee, Luzern, Winterthur, Switzerland (Christen).

8. *Gymnodinium austriacum* J. Schiller 1932, p. 336, fig. 340 (**Fig. 20**)

Cells symmetrical, both epi- and hypocone conical or rounded-conical and equal in size, not dorsoventrally compressed. Cingulum circular, the upper rim somewhat overhanging. Sulcus on both halves of the cell, narrow, extending for half to 3/4 the length of both epi- and hypocone. Nucleus mostly centrally located. Cytoplasm colorless, sometimes with yellowish food vacuoles. Cell length 40–41 µm, width 25–26 µm.
Ecology: observed in the upper 5 m of the Austrian Lake Attersee, in August.
Geographical distribution: Austria (Schiller); Czech Republic (Popovský).

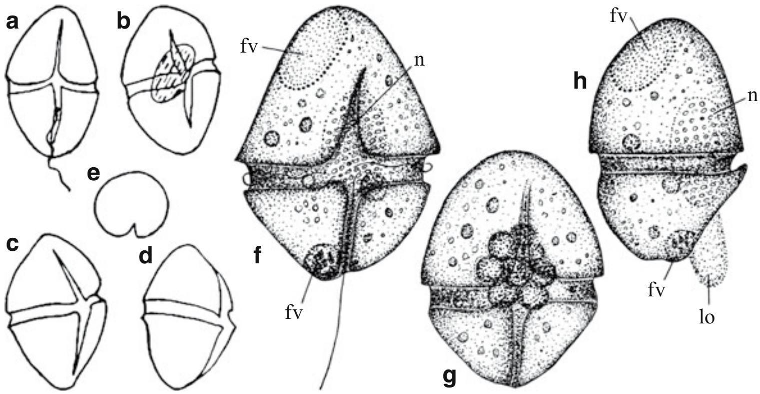

Fig. 20 *Gymnodinium austriacum* J. Schiller (**a**–**e** after Schiller 1932; **f**–**h** after Popovský 1985). **a**–**d** ventral and lateral outlines; **e** cross section; **f**–**h** ventral and lateral views of cells with contents (group of spheres in the middle of cell **g** represent ingested *Sphaerocystis* colony; fv, food vacuole; lo, lobopod; n nucleus)

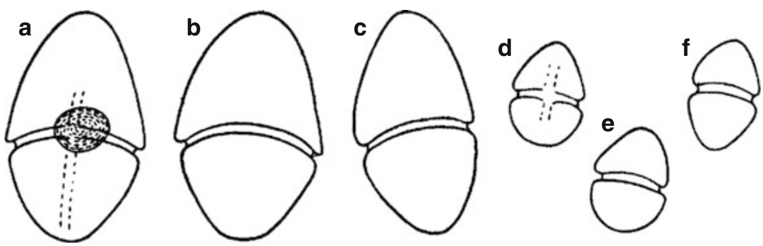

Fig. 21 *Gymnodinium baicalense* N. L. Antipova (after Antipova 1955). **a**–**c** shape variation of typical form; **d**–**f** variation of small-sized form (originally as *G. baicalense* var. *minus*)

9. *Gymnodinium baicalense* N. L. Antipova 1955, p. 325, fig 1, I (Fig. 21)

Taxonomic synonym: *Gymnodinium baicalense* var. *minus* N. L. Antipova 1955, p. 326, fig. 1, II ("*minor*")

Cells variable in shape, usually oval, not dorsoventrally compressed but ventral side slightly flattened. Epicone dome-shaped or rounded conical, of about the same size as the hemispherical, broadly hemispherical or sometimes conical hypocone. Cingulum circular with prominent anterior rim. Sulcus weakly developed, extending slightly onto the epicone, and in the hypocone reaching the antapex. Chloroplasts arranged radially in the cell center, filling large part of the cell. Chloroplast color varies from dark-brown to light-brown or yellow. Nucleus oval, in the mid-region

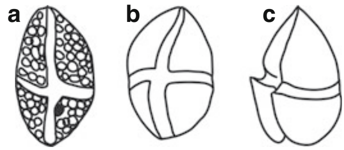

Fig. 22 *Gymnodinium baumeisteri* J. Schiller (after Schiller 1955). **a**, **b** ventral views (chloroplasts and eyespot shown in **a**); **c** left view

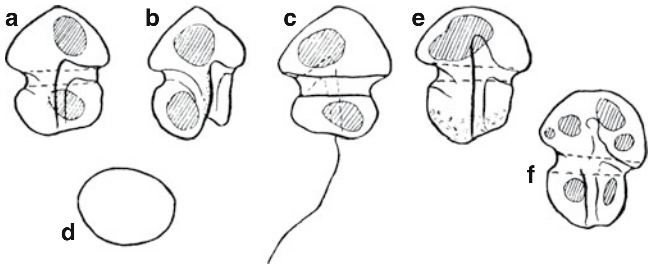

Fig. 23 *Gymnodinium blax* T. M. Harris (after Harris 1940). **a**–**d** different views of the same cell; **e**, **f** two different cells in ventral view. Shaded bodies represent ingested items

of the cell. Eyespot absent. Cell length: 28–50(–90) μm, width 16–32(–45) μm. Cells reproduce sexually by isogamy but the hypnozygote has not been described. DNA data: Annenkova *et al.* (2009, 2011).
Ecology: very common in Lake Baikal; develops in February–March under the ice, spreading into deeper water. Disappears in May after the ice has melted. In April 1954 the maximum number of cells recorded was 3.5×10^6 per liter, in April 2008 1.7×10^6 per liter (biomass 30 mg/l). Holes in the ice turned tea-brown during the bloom (Antipova 1955, Annenkova *et al.* 2009).
Geographical distribution: Russia.

Note 1: there is no mention of chloroplast arrangement in the original description. The radial arrangement of the chloroplasts was mentioned by Kobanova (2009).

Note 2: based on what is presently known, *G. baicalense* appears very similar in morphology to *G. tylotum*.

10. *Gymnodinium baumeisteri* J. Schiller 1955, p. 38, pl. IV, fig. 35A (**Fig. 22**)

Cells elongate-elliptic, slightly asymmetrical. Dorsal side convex, ventral side concave. Epicone *ca.* twice the length of the hypocone, conical with convex sides. Hypocone likewise conical with convex sides. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus extends from apex to antapex, becoming narrower towards the apex. Many yellow-green, oval, disc-shaped chloroplasts. Small eyespot in the sulcus. Cells 21–22 μm long, 12–13 μm wide.

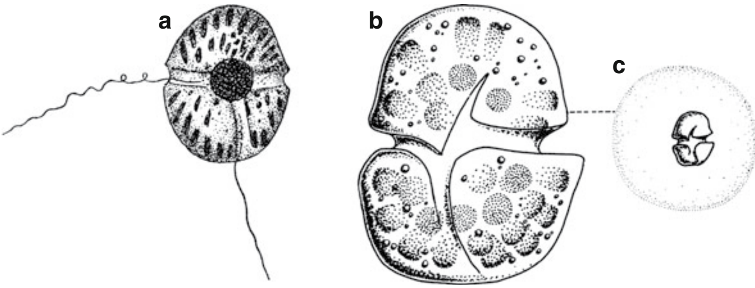

Fig. 24 *Gymnodinium bogoriense* G. A. Klebs (**a** after Klebs 1912; **b**, **c** after Javornický 1965). **a** flagellated cell showing the central nucleus and radiating chloroplasts; **b**, **c** two views of a cell without flagella, enveloped in mucilage

Ecology: reported at 18 ˚C in Ruster Canal, Lake Neusiedl, May 1950.
Geographical distribution: Austria.

11. *Gymnodinium blax* T. M. Harris 1940, p. 6, figs 1A–F (**Fig. 23**)

Cells oval, slightly dorsoventrally compressed. Epi- and hypocone of the same length or epicone slightly longer. Epicone rounded conical, hypocone broad, rectangular, the left side often slightly shorter than the right side. Cingulum slightly descending, the distal end apparently curved somewhat towards the antapex. Sulcus extends for a short distance onto the epicone, and on the hypocone continues to the antapex. Chloroplasts absent. Eyespot absent. Longitudinal flagellum equals the cell in length. Cell length 6–11 µm, width 7 µm, thickness 6 µm.
Ecology: slow swimmer in a ditch near Playhatch, Reading, England.
Geographical distribution: England.

12. *Gymnodinium bogoriense* G. A. Klebs 1912, p. 397, 439, text-fig. 7C, D (**Fig. 24**)

Cells ovoid, dorsoventrally compressed. Epicone barely larger than hypocone. Epicone rounded, hypocone slightly elongate rounded. Cingulum very slightly descending, the ends displaced less than or almost one cingulum width. Sulcus extends from the cingulum to the antapex. It continues on the epicone, deflected towards the cell's left. The right side of the extension forms a triangular structure in the sulcus (Javornický 1965). Many elongate, radially disposed chloroplasts. Eyespot absent. Length 20–24 µm, width 16–18 µm, thickness 12 µm.
Ecology: in pond in the Botanical Garden at Buitenzorg, Indonesia, and at *ca.* 16 ˚C in the shallow, slightly acid, clear-water Lake Flosek, Poland.
Geographical distribution: Poland (Javornický). Indonesia (Klebs).

Note: "*Gymnodinium deformabile* J. Schiller 1955, p. 34, pl. III, fig. 28", a provisional and therefore invalidly published designation, was described as differing in not being dorsoventrally flattened and in occurring in cold water (in a park in Vienna, Austria).

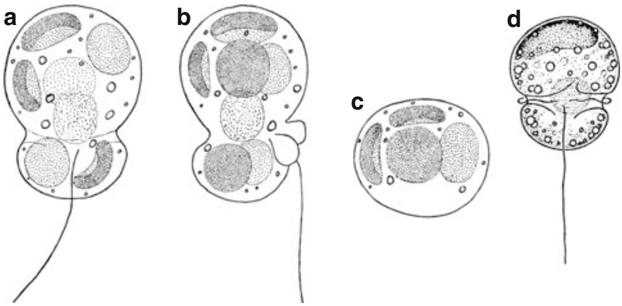

Fig. 25 *Gymnodinium bohemicum* Fott (**a**–**c** after Fott 1938; **d** after Thompson 1951). **a** ventral view with the longitudinal flagellum in the indistinct sulcus; **b** cell viewed from the right showing all chloroplasts (those on the back with thinner dots), the central nucleus and two bag-shaped pseudopods with hyaline cytoplasm; **c** apical view, the ventral side of the cell without chloroplasts and grains; **d** ventral view

The ecological difference suggests "*G. deformabile*" may be a different species, but this needs to be examined further.

13. *Gymnodinium bohemicum* Fott 1938, p. 102, fig. 1 (**Fig. 25**)

Nomenclatural synonym: *Katodinium bohemicum* (Fott) Litvinenko *in* Matvienko & Litvinenko 1977, p. 205

Cells ovoid, not or barely compressed dorsoventrally. Epicone ovoid, twice or more the length of the hypocone. Hypocone hemispherical, narrower than epicone. Cingulum circular, the ends not displaced. Sulcus indistinct. Longitudinal flagellum about the length of the cell. Pseudopodia seen to extend from the cingulum, indicating mixotrophy. Two to 8 brown or yellow-green chloroplasts. Cell length 10–16 µm, width 6–7 µm. The cells round off quickly under the coverslip.
Ecology: in Bohemian (Czech Republic) oligotrophic mountain lake (Fott 1938) and peat bog (Popovský 1968), in pond just after ice melt (Kansas, USA), in a swamp (New Zealand).
Geographical distribution: Czech Republic (Fott; Popovský). USA, KS (Thompson). New Zealand (Thompson).

14. *Gymnodinium caudatum* Prescott 1944, p. 371, pl. 4, figs 14–16 (**Fig. 26**)

Cells ovoid to inversely conical or top-shaped, broadly rounded anteriorly, narrowing and extending into a narrow tail posteriorly. Strongly flattened. Cingulum in the middle, descending. Sulcus short, extending for a short distance onto the epicone. Chloroplasts golden-brown, numerous, plate-like, ovoid or elongate, arranged radially. Eyespot present near the sulcus. Cells 104–118 µm long and 65–70 µm wide.
Ecology: in ponds and acid bogs.

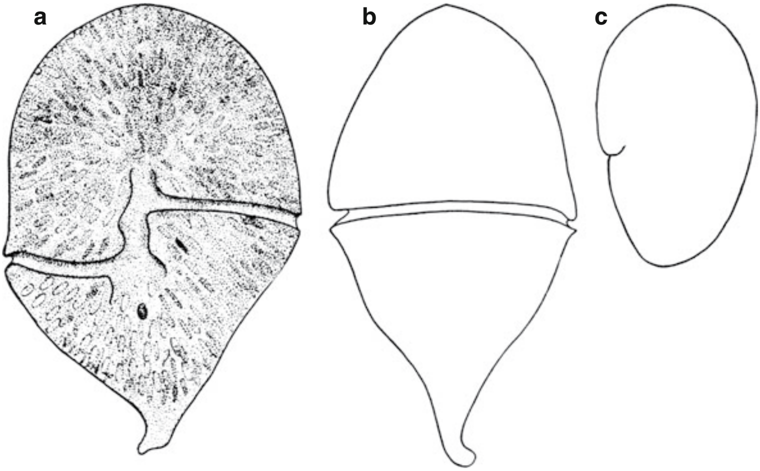

Fig. 26 *Gymnodinium caudatum* Prescott (after Prescott 1944). **a** ventral view showing the radial arrangement of the chloroplasts and a small eyespot; **b** dorsal view; **c** cross section

Geographical distribution: Denmark (Nygaard). USA, WI (Prescott, Graham & Wilcox).

Note: this species is closely related to *G. fuscum* but differs in its larger size, distinct posterior tail-like extension (always curved to the cell's right according to Nygaard 1996), more flattened cells and the presence of an eyespot.

15. *Gymnodinium chiastosporum* (T. M. Harris) Cridland 1958, p. 287. (**Fig. 27**)

Basionym: *Tetradinium chiastosporum* T. M. Harris 1940, p. 25, figs 9A–J
Nomenclatural synonym: *Dinastridium chiastosporum* (T. M. Harris) Starmach 1974, p. 448

Cells ovoid, slightly dorsoventrally compressed. Epicone slightly shorter than hypocone. Cingulum circular or very slightly descending, wide. Sulcus does not reach the antapex. Many disc-shaped chloroplasts, eyespot absent. Cells 12–25 µm long, 10–12 µm wide. Cysts squarish, with two short spines at each corner, 13–25 µm long and 13–40 µm wide.
Ecology: pools and ponds; first described from a tub of fresh water, Reading University, England.
Geographical distribution: Reading, England (Harris).

Note 1: the unusual type of resting cyst indicates that the species does not belong in *Gymnodinium* or, since cysts and motile cells are known only from wild samples, that the cyst described does not belong in the life cycle of *G. chiastosporum*. Studies based on pure cultures are needed.

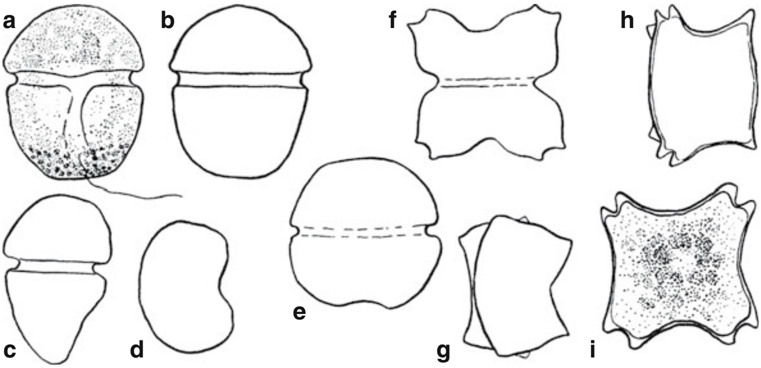

Fig. 27 *Gymnodinium chiastosporum* (T. M. Harris) Cridland (after Harris 1940). **a**–**d** ventral, dorsal, lateral and vertical views of the same cell; **e**–**g** stages in cyst formation (**f** and **g** are different views of a late, but still motile, stage); **h**, **i** two aspects of a mature (non-motile) cyst

Note 2: *Tetradinium chiastosporum* var. *armatum* Wawrik (1981, p. 805, figs 8a–f, "*armata*") is a related form, which differs in the motile cells possessing an eyespot, the resting spore having additional spines and in occurring during ice break in Steinbruchlacke, a pond in Waldviertel, Lower Austria. It needs to be examined in detail.

16. *Gymnodinium christenii* Thessen, D. J. Patterson & Sh. Murray 2012, p. 12, 28 ("*christenum*") (**Fig. 28**)

Replaced synonym: *Gymnodinium irregulare* Christen 1959b, p. 179, 187, fig. 6, *nom. illeg.* (non *Gymnodinium irregulare* B. Hope 1954, p. 152, figs 1g–j)

Cells elongate ovoid in ventral view, strongly dorsoventrally compressed. Both ends rounded. Epi- and hypocone approximately equal in size. Left side of hypocone thicker than right side. Cingulum descending, the ends displaced *ca.* 3× the cingulum width. Sulcus oblique, extending from the left-hand side of the epicone, halfway from the apex, and continuing to the right side of the antapex. With elongate radial, yellow-brown chloroplasts. Eyespot absent. Cell length 34–37 µm, width 21–24 µm.
Ecology: Schützenweiher (Hunter's meadow) near Winterthur, Switzerland, a shallow, relatively eutrophic pond dominated by macrophytes, scattered in spring and autumn.
Geographical distribution: Switzerland.

Note: Popovský (1968, p. 253–255, pl. IX, fig. 10; 1971, p. 278, pl. 35, fig. 7) described a similar taxon under the name *Gymnodinium uberrimum* var. *rotundatum* (G. A. Klebs) Popovský, showing the same exceptionally oblique path of the sulcus on the epicone, but differing in size (length 40–45 µm, width 35–37 µm). It may be a variety of *G. christenii* or perhaps a separate species. However, *Gymnodinium rotundatum* G. A. Klebs, on

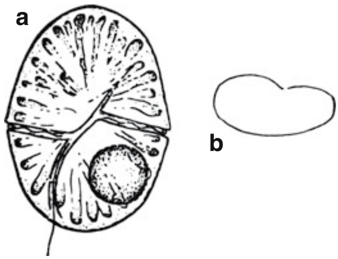

Fig. 28 *Gymnodinium christenii* Thessen, D. J. Patterson & Sh. Murray (after Christen 1959b). **a** ventral view showing radiating chloroplasts and the nucleus; **b** cross section of the hypocone

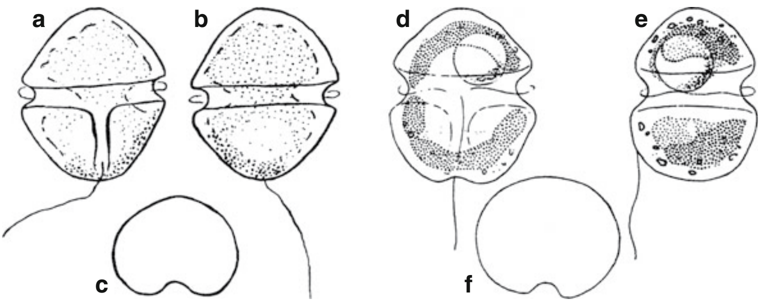

Fig. 29 *Gymnodinium cnecoides* T. M. Harris (**a**–**c** after Harris 1940; **d**–**f** after Javornický 1957). **a**–**c** ventral, dorsal and cross-section views of the same cell; **d**–**f** ventral, lateral and cross-section views (the spherical bodies in the epicone in **d** and **e** represent the nucleus)

which Popovský's varietal name is based, shows affinity with *Cystodinium* rather than with *Gymnodinium* (see further under *Cystodinium unicorne*).

17. *Gymnodinium cnecoides* T. M. Harris 1940, p. 9, figs 2A–D (**Fig. 29**)

Cells round, barely compressed dorsoventrally. Epi- and hypocone both rounded, of the same size. Cingulum circular. Sulcus extends from the cingulum to the antapex. One or two pale yellow chloroplasts. Eyespot absent. Cell length *ca.* 9 µm (up to 14 µm), width *ca.* 8 µm (up to 11 µm).
Ecology: pond with macrophytes and many other flagellates; temporary pools and peat bogs.
Geographical distribution: Czech Republic (Javornický); England (Harris); Ukraine (Krakhmalny).

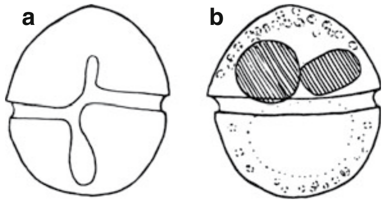

Fig. 30 *Gymnodinium colymbeticum* T. M. Harris (after Harris 1940). **a**, **b** ventral and dorsal views of the same cell (shaded bodies in the epicone represent ingested food)

Note: in the Czech material the epicone is somewhat shorter than the hypocone (5.5 µm versus 7 µm) and the ventral view shows the hypocone indented at the antapex (Javornický 1957).

18. *Gymnodinium colymbeticum* T. M. Harris 1940, p. 8, figs 1G, H (**Fig. 30**)

Cells nearly spherical. Epi- and hypocone of same length or the epicone barely longer. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus continues onto the epicone displaced towards the cell's left. On the hypocone it extends towards but does not reach the antapex. Chloroplasts absent. Eyespot absent. Cell diameter 16 µm.
Ecology: rapid swimmer found in March and April 1937 in tub of water at Reading University, England.
Geographical distribution: England.

19. *Gymnodinium cryophilum* (G. J. Wedemayer, L. W. Wilcox & L. E. Graham) Gert Hansen & Moestrup *in* Daugbjerg *et al.* 2000, p. 305 (**Fig. 31**)

Basionym: *Amphidinium cryophilum* G. J. Wedemayer, L. W. Wilcox & L. E. Graham 1982, p. 14, figs 1–10

Cells pointed ovoid. Epicone conical with convex sides, half the size of the elongate rounded hypocone. Ventral side at times slightly flattened. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus extends onto the epicone, turning towards the cell's left upon approaching the apex, almost reaching the apex. In the hypocone it extends for only half the length of the hypocone. Amphiesmal plates with scattered papillae. Peduncle extending from the junction between cingulum and sulcus. Numerous golden-yellow chloroplasts, mainly in the cell periphery, the chloroplasts being spherical to elongate to somewhat irregular. Eyespot absent. Refractile bodies scattered in the cytoplasm. Nucleus in the hypocone, just below the cingulum. Cell length 33 µm, width 22 µm. Cell division in the motile stage, oblique.
SEM: Wedemayer *et al.* (1982).
TEM: Wilcox *et al.* (1982), Wilcox & Wedemayer (1991).
DNA data: Daugbjerg *et al.* (2000).

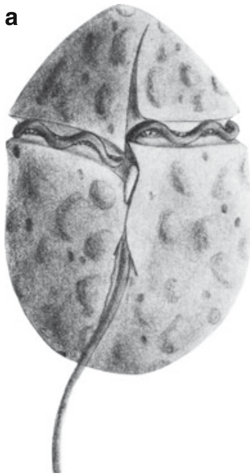

Fig. 31 *Gymnodinium cryophilum* (G. J. Wedemayer, L. W. Wilcox & L. E. Graham) Gert Hansen & Moestrup (after Wedemayer *et al.* 1982). **a** ventral view, partly based on SEM observations (reproduction of the holotype)

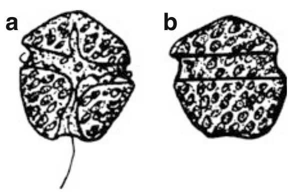

Fig. 32 *Gymnodinium danubiense* J. Schiller (after Schiller 1955). **a**, **b** ventral and dorsal views

Ecology: cold-water species in pond in Wisconsin, occurring from November till melting of ice in early spring, under 40-cm thick layer of ice and snow in numbers of up to 3.5 × 10^6 cells per liter. Apparently does not grow at temperatures above 10 ˚C. The species is mixotrophic, and was shown to feed on other dinoflagellates by means of a temporary tubular appendix, the phagopod, formed on the cell antapex (Wilcox & Wedemayer 1991).
Geographical distribution: USA, WI.

20. *Gymnodinium danubiense* J. Schiller 1955, p. 34, pl. III, fig. 26 (**Fig. 32**)

Cells more or less pentagonal, dorsoventrally flattened. Epicone in ventral view triangular, hypocone trapezoidal and invaginated at the antapex. Length of hypocone 1.5× the epicone. Cingulum wide, more or less circular. Sulcus extends on the

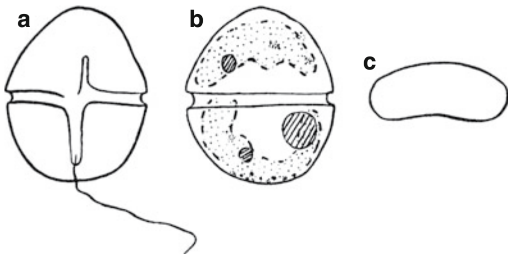

Fig. 33 *Gymnodinium discoidale* T. M. Harris (after Harris 1940). **a**–**c** ventral, dorsal and cross-section views of the same cell (shaded areas represent ingested food; stippled areas represent pale yellow chloroplasts)

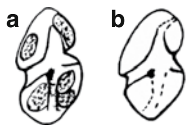

Fig. 34 *Gymnodinium elongatum* (J. Schiller) Moestrup & Calado (after Schiller 1955). **a**, **b** ventral view (chloroplasts shown in **a**)

epicone to near the apex, on the hypocone reaches the antapex, widening distally. Numerous yellow-green chloroplasts. Eyespot absent. Cell length 15–16 µm, width 13–15 µm.
Ecology: Vienna, Alte Donau, autumn 1926.
Geographical distribution: Austria.

21. ***Gymnodinium discoidale*** T. M. Harris 1940, p. 9, figs 2G–I (**Fig. 33**)

Cells oval, strongly compressed dorsoventrally, dorsal side convex, ventral side slightly concave. Epicone rounded conical or hemispherical in ventral view, hypocone hemispherical. Cingulum circular, the ends not displaced. Sulcus extends to about half the length of the epicone and to nearly the antapical end of the hypocone. Apparently two pale-yellow chloroplasts, one in each half of the cell. Eyespot absent. Longitudinal flagellum as long as the cell. Cell length 12–16 µm, width 10–14 µm, thickness 5–7 µm.
Ecology: in roadside ditch near Reading, England, in January 1939.
Geographical distribution: Czech Republic? (Popovský); England (Harris).

22. ***Gymnodinium elongatum*** (J. Schiller) Moestrup & Calado *comb. nov.* (**Fig. 34**)

Basionym: *Gyrodinium elongatum* J. Schiller 1955, *Wiss. Arbeiten Burgenland* **9**, p. 48, pl. VIII, fig. 45

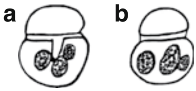

Fig. 35 *Gymnodinium eufrigidum* J. Schiller (after Schiller 1955). **a** ventral view; **b** dorsal view

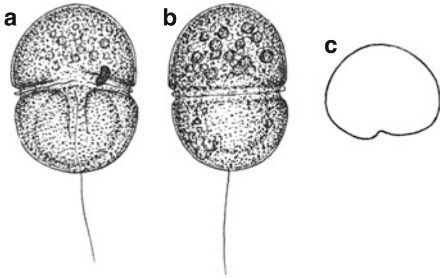

Fig. 36 *Gymnodinium eurytopum* Skuja (after Skuja 1948). **a**, **b** ventral and dorsal views; **c** cross section outline

Cells elongate ovoid, dorsoventrally slightly compressed. Epi- and hypocone both rounded conical, of equal length. Cingulum descending, oblique, the ends not displaced. Sulcus extends almost to the apex, curving towards the left near the apex. On the hypocone it is difficult to see, probably reaching the antapex. Cell with 4–6 oval, yellow-brown chloroplasts. Eyespot small. Cell length 17–20 µm, width 9 µm.
Ecology: Lake Neusiedl, Austria, June 1952, at 18–20 ˚C.
Geographical distribution: Austria.

23. ***Gymnodinium eufrigidum*** J. Schiller 1955, p. 28, pl. II, fig. 14 (**Fig. 35**)

Cells rounded-oval, slightly flattened dorsoventrally. Epicone and hypocone both hemispherical, epicone narrower than hypocone. Hypocone 1.4× the length of the epicone. Cingulum circular, narrow. Sulcus extends on the hypocone halfway to the antapex. Chloroplasts absent. Cytoplasm light pink, commonly with 2–3 yellowish bodies of various size. Cell length *ca.* 9 µm, width 6 µm.
Ecology: winter form, Vienna, Alte Donau, very common.
Geographical distribution: Austria.

24. ***Gymnodinium eurytopum*** Skuja 1948, p. 368, pl. XXXVIII, figs 35, 36 (**Fig. 36**)

Cells elliptical, barely compressed dorsoventrally. Epi- and hypocone of approximately the same size, both hemispherical. Epicone sometimes with two tiny apical spines. Cingulum circular. Sulcus mainly confined to the hypocone. Chloroplasts

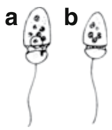

Fig. 37 *Gymnodinium fontinale* (C. E. M. Bicudo & Skvortsov) Moestrup (after Bicudo & Skvortsov 1970). **a**, **b** two unspecified longitudinal views (sulcus not observed)

absent. Eyespot absent. Nucleus large, filling most of the hypocone. Longitudinal flagellum as long as the cell length or slightly longer. Cell length 18–22 µm, width 15–18 µm, thickness 12–14 µm.
Ecology: in Lake Erken, Sweden, in Lapland and in several lakes in Latvia.
Geographical distribution: Latvia (Skuja); Portugal (Nauwerck); Sweden (Skuja).

25. *Gymnodinium fontinale* (C. E. M. Bicudo & Skvortsov) Moestrup *comb. nov.* (**Fig. 37**)

Basionym: *Katodinium fontinale* C. E. M. Bicudo & Skvortsov 1970, *Rickia* **5**, p. 15, figs 14, 15 ("*fontinalis*")

Cells asymmetrical, ovoidal in dorsal view, elliptical in top view. Epicone subovoid, approximately twice the length of the subglobose hypocone. Cingulum straight or oblique. Sulcus not observed. Numerous disc-shaped yellowish-brown chloroplasts in the epicone. Cell length 8–9 µm, width 4 µm.
Ecology: among *Tribonema* in small temporary pool in park in São Paulo, Brazil.
Geographical distribution: Brazil.

26. *Gymnodinium granii* J. Schiller 1955, p. 42, pl. VIII, fig. 41a–g (marked 41A in the legend, p. 63) (**Fig. 38**)

Cells broadly elliptic. Epicone not flattened dorsoventrally, smaller than the ventrally flattened or concave hypocone. Epicone hemispherical, hypocone elongate hemispherical. Cingulum wide, circular. Sulcus extending from the apex to the antapex, on the epicone narrow, especially near the apex, on the hypocone wide and reaching the antapex, which is notched. Chloroplasts absent, eyespot absent. Cytoplasm with large lipid droplets and light refractile larger bodies. Cell length 19–21 µm, width 14–19 µm.
Ecology: Lake Neusiedl and pond in nursery, Rust, Austria, October 1954, at 4–6 ˚C, pH 8.3. Information on phagotrophy given by Schiller (1955, p. 9–11).
Geographical distribution: Austria.

27. *Gymnodinium hippocastanum* Cridland 1958, p. 285, fig. 1 (**Fig. 39**)

Cells ovoid, epicone slightly smaller than the hypocone. Epicone broadly rounded. Hypocone often dorsoventrally compressed. Cingulum very slightly descending, the sulcus extending onto the epicone. Numerous yellow, ovoid chloroplasts. Often 2–3 brown bodies in the cytoplasm. Eyespot absent. Longitudinal flagellum twice

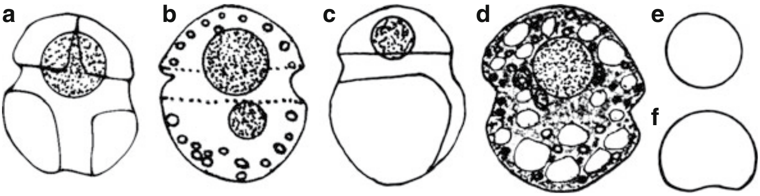

Fig. 38 *Gymnodinium granii* J. Schiller (after Schiller 1955). **a**–**c** ventral, dorsal and lateral views of cells with normal appearance; **d** cell somewhat deformed due to the ingested algae (one ingested, round cyanobacterial cell in **a**, **b** and **d** two in **b**); **e**, **f** cross section of the epi- and hypocone, respectively

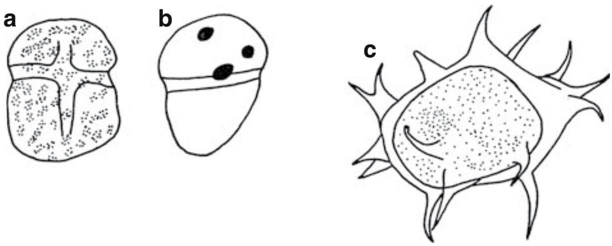

Fig. 39 *Gymnodinium hippocastanum* Cridland (after Cridland 1958). **a** ventral view, chloroplasts indicated by stippling; **b** lateral view with three brown bodies; **c** mature cyst (resting stage)

the length of the cell. Cells 25 µm long, 15 µm wide. Division by equal fission while cells are actively swimming.

Resting spore ovoid or nearly hexahedral, not compressed. Wall thick, bearing about 10 spines around the edges and others of the spore faces. Spines often curved and forked, sometimes in pairs. Spore length 40 µm, width 25 µm excluding the spines, which are up to 13 µm long. Spores accumulate at the bottom of culture vessel. During spore formation the furrows slowly disappear, the cells sink to the bottom and spines develop.

Ecology: in winter in shallow pond on acid gravel soil, persisting till the pond dried out during summer. The pond contained rotting beech and oak leaves.

Geographical distribution: near Reading, England.

Note: the very unusual type of resting spore indicates that this taxon belongs in a separate, new genus.

28. *Gymnodinium huber-pestalozzii* J. Schiller 1955, p. 39, pl. V, fig. 37 (Fig. 40)

Cells conically elliptic, angular, dorsoventrally compressed, in transverse section flattened elliptic. Epicone conical with almost straight sides, hypocone trapezoid with slight depression at the antapex. Epi- and hypocone of equal size. Cingulum

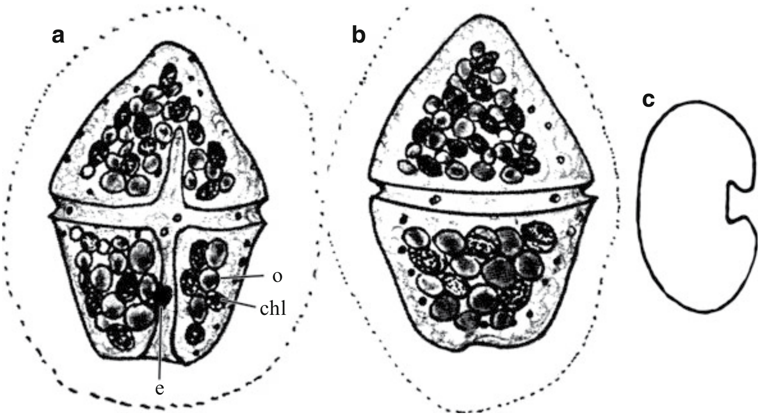

Fig. 40 *Gymnodinium huber-pestalozzii* J. Schiller (after Schiller 1955). **a**, **b** ventral and dorsal views of cells enveloped in mucilage (o oil droplet; chl, cloroplast; e eye-spot); **c** cross section

circular or very slightly descending. Sulcus reaches the middle part of the epicone, on the hypocone extends to the retuse antapex. Chloroplasts parietal, yellow-brown, ovoid or elliptic. Eyespot large, in the sulcus. Cytoplasm with lipid bodies. In the cell periphery irregular lumps of material. Cells 40–54 µm long, 30–32 µm wide, surrounded by narrow layer of mucilage.
Ecology: Vienna-Alte Donau, February, March.
Geographical distribution: Austria.

Note: the mucilage around the cells indicates a non-motile stage; flagella were not reported.

29. *Gymnodinium hyalinum* A. J. Schilling 1891a, p. 279, pl. X, fig. 14 (**Fig. 41**)

Nomenclatural synonyms: *Spirodinium hyalinum* (A. J. Schilling) Lemmermann 1900b, p. (116) ≡ *Gyrodinium hyalinum* (A. J. Schilling) Kofoid & Swezy 1921, p. 311

Cells broadly oval, asymmetric. Epicone smaller than hypocone. Epicone conical-rounded, hypocone broadly rounded, sac-like. Cingulum descending, displaced several cingulum widths. Cingulum starts close to the apex and spirals over the dorsal side to terminate in the mid-ventral region; the sulcus extends from here to the antapex. A narrowly horseshoe-shaped eyespot is present near the anterior part of the sulcus. Chloroplasts absent. Food vacuoles common, with remains of *Chlamydomonas*, *Pandorina* and other organisms. Food uptake was described by Schilling (1891b) to involve formation of pseudopodia. Cell length 24–31 µm, width 21–23 µm.

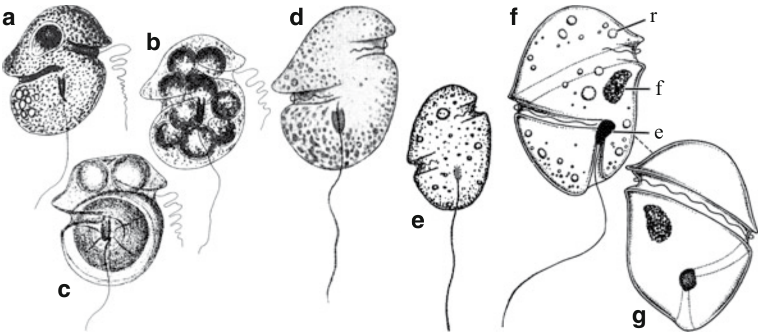

Fig. 41 *Gymnodinium hyalinum* A. J. Schilling (**a**–**c** after Schilling 1981b; **d** after Schilling 1913; **e** after Nygaard 1945; **f**, **g** after Javornický 1967). **a**–**e** ventral views (**a**–**c** with various numbers of ingested *Chlamydomonas*, in **c** also young *Pandorina* colony); **f**, **g** ventral-right and dorsal views (r, reserve material; f ingested food; e eyespot)

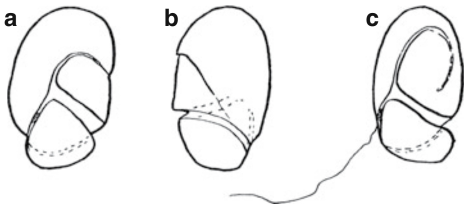

Fig. 42 *Gymnodinium hyperxanthoides* (T. M. Harris) Moestrup (after Harris 1940). **a**–**c** different views of the same cell

Ecology: among vegetation in ponds and bogs (originally from basin in Botanical Garden); also in the plankton of reservoirs (Javornický 1967).
Geographical distribution: Czech Republic (Javornický); Denmark (Nygaard); Switzerland (Schilling). Japan (Senzaki & Horiguchi); Manchuria? (Skvortsov).

Note: *Gyrodinium steinii* Skvortsov (1968, p. 91, pl. II, fig. 14) resembles a small *G. hyalinum* (length 14–15 μm, width 8 μm).

30. *Gymnodinium hyperxanthoides* (T. M. Harris) Moestrup *comb. nov.* (**Fig. 42**)

Basionym: *Massartia hyperxanthoides* T. M. Harris 1940, *Proc. Linn. Soc. London* **152** (1), p. 16, figs 5G–I
Nomenclatural synonym: *Katodinium hyperxanthoides* (T. M. Harris) A. R. Loeblich 1965, p. 16

Cells oval, somewhat dorsoventrally compressed. Epicone much larger than hypocone. Cingulum spiral-shaped (?). Sulcus extends onto the epicone, forming a U-

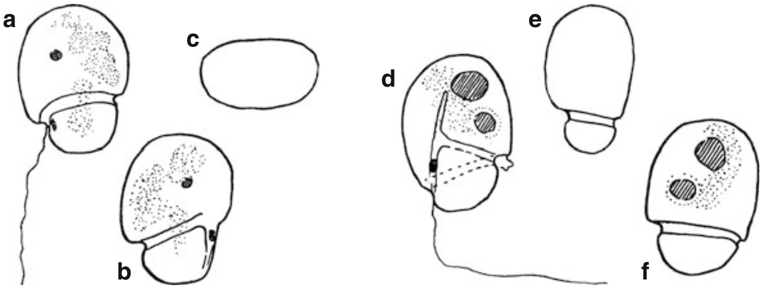

Fig. 43 *Gymnodinium hyperxanthum* (T. M. Harris) Moestrup (after Harris 1940). **a**–**c** three views of one cell; **d**–**e** three views of another cell (shaded bodies represent ingested food; lightly stippled areas represent chloroplasts)

shaped curve toward the cell's left, on the hypocone reaches the antapex. With two, very pale-yellow chloroplasts, small cells appearing nearly colorless. Eyespot small. Longitudinal flagellum of cell length. Cell typically *ca.* 15 µm long, but often smaller.
Ecology: in eutrophic trough near Reading, England, in August 1936. Swamp in New Zealand. Originally described as mixotrophic.
Geographical distribution: England (Harris). New Zealand (Thompson).

Note: it is difficult to understand, from the original description, the exact paths of the furrow system, which appear to be very unusual.

31. ***Gymnodinium hyperxanthum*** (T. M. Harris) Moestrup *comb. nov.* (**Fig. 43**)

Basionym: *Massartia hyperxantha* T. M. Harris 1940, *Proc. Linn. Soc. London* **152** (1), p. 16, figs 5A–F
Nomenclatural synonym: *Katodinium hyperxanthum* (T. M. Harris) A. R. Loeblich 1965, p. 16

Cells oval, often dorsoventrally flattened. Epicone longer and wider than hypocone, both rounded. Cingulum descending, the ends displaced more than two cingulum widths. Sulcus extends widely into the epicone, and in the hypocone apparently reaches the antapex. One-two lobed, pale-yellow chloroplasts. Eyespot in the sulcus. Longitudinal flagellum longer than cell length. Cell length 12–14 µm, width 10 µm, thickness 7 µm. Swims with rotating and hesitating movements.
Ecology: in eutrophic cow-trough near Reading, England, in July 1935. Originally described as mixotrophic.
Geographical distribution: England.

32. ***Gymnodinium impatiens*** Skuja 1964, p. 349, pl. LXVI, figs 30–34 (**Fig. 44**)

Cells oval or elliptical. Cells barely compressed dorsoventrally. Epicone slightly larger than hypocone, both epi- and hypocone bell-shaped. Cingulum circular, both ends curving towards and continuing into the sulcus. Sulcus mainly restricted to

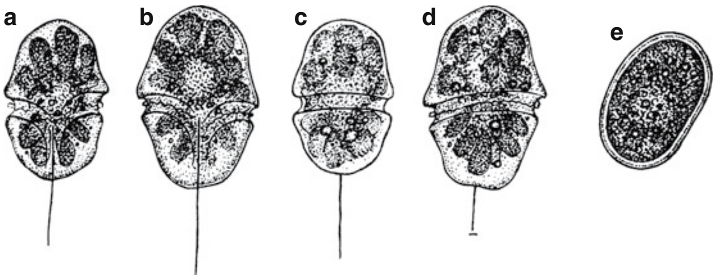

Fig. 44 *Gymnodinium impatiens* Skuja (after Skuja 1964). **a**, **b** ventral views; **c**, **d** dorsal views; **e** cyst (resting stage)

the hypocone, on the epicone only a very shallow extension. The sulcus does not appear to reach the antapex. Numerous disc-shaped, yellow-brown chloroplasts, partly parietal partly radially arranged. Eyespot absent. Nucleus in the epicone. Cell length 18–21 µm, width 11–14 µm. Cyst cylindrical-ellipsoidal, about the size of the vegetative cells, with moderately thick, colorless and smooth, layered wall.
Ecology: in various ponds and pools in Northern Sweden (Abisko).
Geographical distribution: Sweden.

33. *Gymnodinium intermedium* Moestrup & Calado *sp. nov.* (**Fig. 45**)

Originally described as "*Katodinium intermedium* Christen 1959b, p. 184, 188, fig. 9", a designation not validly published (reported from the Schützenweiher, Winterthur, Switzerland, and from the Hausersee, Austria, hence no type designation). See Latin description in Christen (1959b, p. 188). Type: Christen 1959b, *Mitt. Naturwiss. Ges. Winterthur* **29**, fig. 9a (here designated).
Cells rounded-conical. Epicone almost hemispherical or somewhat rounded-conical, about the size of the hypocone, which is broadly rounded, the left side of-

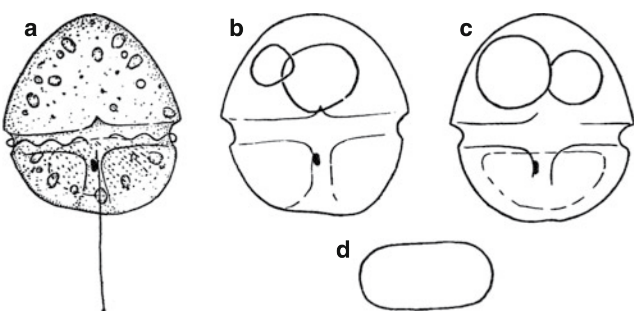

Fig. 45 *Gymnodinium intermedium* Moestrup & Calado (after Christen 1959b). **a**–**c** three cells in ventral view; **d** cross section

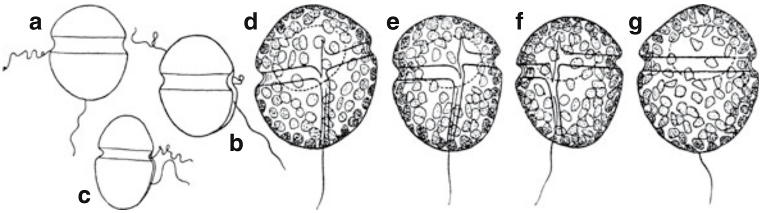

Fig. 46 *Gymnodinium inversum* Nygaard (**a**–**c** after Nygaard *in* Berg & Nygaard 1929; **d**–**g** after Nygaard 1950). **a**–**c** dorsal and lateral outlines of cells; **d**–**f** ventral views; **g** dorsal view

ten slightly longer than right side. Cell usually dorsoventrally flattened. Cingulum circular. Sulcus extends very slightly onto the epicone, forming a small triangle here. On the hypocone the sulcus extends to the antapex, becoming wider near the antapex. Chloroplasts absent. A small eyespot is present in the sulcus. Cell length 10–13 μm, width 9–11 μm.
Ecology: plankton in macrophyte-rich shallow ponds and in lakes in spring and autumn.
Geographical distribution: Austria; Switzerland.

Note: this species is morphologically close to *Nusuttodinium hiemale*, which was, however, described as a colder water species that maintains symbiotic cyanobacteria in the cytoplasm (perhaps as kleptochloroplasts) (Schiller 1954a).

34. *Gymnodinium inversum* Nygaard *in* Berg & Nygaard 1929, p. 294, pl. V, figs 28–36 (**Fig. 46**)

Cells elliptic, dorsoventrally slightly compressed. Epicone and hypocone both broadly rounded, hypocone considerably larger than epicone. Cingulum descending, the two ends displaced *ca.* one cingulum width. Sulcus extends for a short distance onto the epicone, on the hypocone reaching the antapex. A triangular process extends from the epicone ventrally at the right-side termination of the cingulum. Numerous chloroplasts, round to oblong, elongated or somewhat irregular. Eyespot absent. Nucleus broadly oval, mainly on the epicone. Cell length 27–36 μm, width 22–29 μm, thickness 20–27 μm. According to Lewis & Dodge (2002) the cyst is dumbbell-shaped with knob-like appendages at the corners, apex and antapex, 42 μm long, 26 μm wide.
Ecology: in plankton in eutrophic lakes, February–May, at 1–12 ˚C, pH 7.8–9.4.
Geographical distribution: Denmark.

Note: the current concept of the species is mainly based on the improved description provided by Nygaard (1950, p. 160–162, fig. 98).

var. *elongatum* Nygaard 1950, p. 162, fig. 99 (**Fig. 47**)
Epicone conical, hypocone hemispherical, of equal size. Chloroplasts reddish-brown. Cells longer than wide, cell length 39–50 μm, width 23–34 μm.

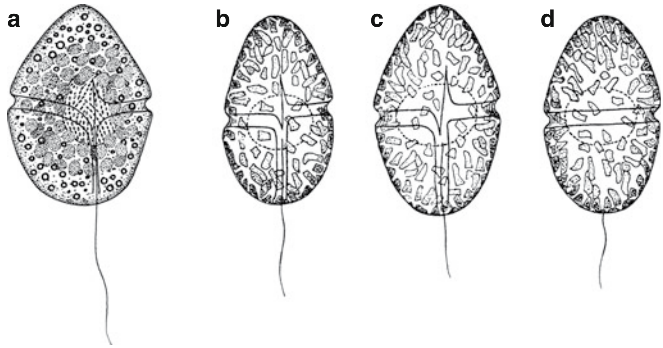

Fig. 47 *Gymnodinium inversum* var. *elongatum* Nygaard (after Nygaard 1950). **a**–**c** ventral views; **d** dorsal view

Ecology: in two eutrophic lakes in Denmark at 5–6 ˚C in March and May, rare.
Geographical distribution: Denmark (Nygaard), United Kindgom (Lewis & Dodge).

35. *Gymnodinium kesslitzii* (J. Schiller) Moestrup *comb. nov.* (**Fig. 48**)

Basionym: *Amphidinium kesslitzii* J. Schiller 1928, *Arch. Protistenk.* **62**, p. 135, text-fig. 11; pl. 5, fig. 12 ("*Kesslitzi*")

Epicone spherical, hypocone ovoid, much longer than the epicone. Hypocone wider than epicone. Cells not dorsoventrally compressed. Cingulum circular. Sulcus short, does not reach the antapex. Longitudinal flagellum 2.5× the cell length. Usually 5 yellow-green disc-shaped chloroplasts scattered in the cell. Cell length 7–14 µm, width 4–7 µm.
Ecology: marine plankton, also claimed to occur in fresh water.
Geographical distribution: Adriatic Sea in summer and autumn (Schiller). However, Bicudo & Skvortsov (1970) claimed to having found it in a lake and in two

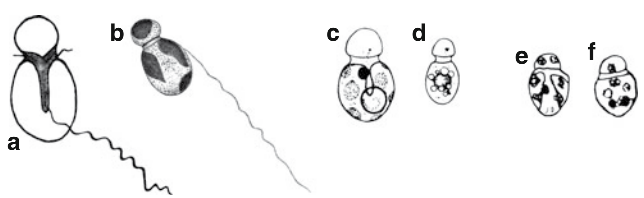

Fig. 48 *Gymnodinium kesslitzii* (J. Schiller) Moestrup (**a**, **b** after Schiller 1928; **c**, **d** after Bicudo & Skvortsov 1970; **e**, **f** after Schiller 1955). **a**, **b** ventral and nearly dorsal view of cells from the marine environment (**b** from an colored original); **c**, **d** ventral and dorsal (?) view of cells from freshwater pool; **e**, **f** *Amphidinium pusillum* J. Schiller, ventral and dorsal views

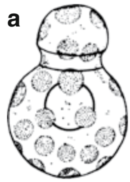

Fig. 49 *Gymnodinium kesslitzii* var. *sanctipaulense* (C. E. M. Bicudo & Skvortsov) Moestrup (after Bicudo & Skvortsov 1970). **a** dorsal (?) view

temporary pools in a park in São Paulo, Brazil. The Brazilian material differed by having numerous granular or disc-shaped green chloroplasts.

var. *sanctipaulense* (C. E. M. Bicudo & Skvortsov) Moestrup *comb. nov.* (**Fig. 49**)
Basionym: *Amphidinium kesslitzii* var. *sanctipaulense* C. E. M. Bicudo & Skvortsov 1970, *Rickia* **5**, p. 12, fig. 7

Cells somewhat ovoidal, epicone much smaller than hypocone, slightly dorsoventrally compressed. Epi- and hypocone both subspheroidal. Cingulum circular. Sulcus extending to the antapex. Numerous disc-shaped brown chloroplasts. Cell length 26 µm, width 18 µm.
Ecology: in pools, São Paulo, Brazil.
Geographical distribution: Brazil.

Note: *Amphidinium pusillum* J. Schiller (1955, p. 20, pl. I, fig. 1) appears to differ only in that the sulcus extends all the way to the antapex. Further observations are needed to clarify its affinities.

36. *Gymnodinium lacustre* J. Schiller 1932, p. 374, fig. 383 (**Fig. 50**)

Cells elliptical, symmetrical or slightly asymmetrical, not dorsoventrally compressed. Epicone semi-ovoid, hypocone hemispherical. Epi- and hypocone of nearly the same length, or epicone slightly larger. Cingulum circular. Sulcus does not extend onto the epicone, on the hypocone reaches halfway to the antapex. With many light-yellow polygonal chloroplasts. Cell length 18–20 µm, width 10–13 µm.

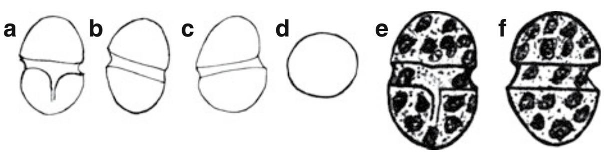

Fig. 50 *Gymnodinium lacustre* J. Schiller (**a**–**d** after Schiller 1932; **e**, **f** after Schiller 1955). **a**–**d** cell outline in different views; **e**, **f** ventral and dorsal views

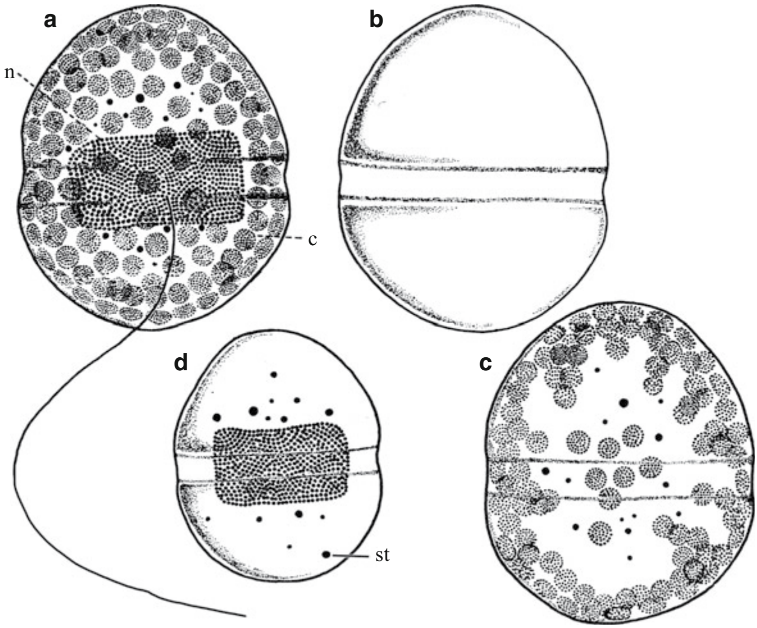

Fig. 51 *Gymnodinium lalitae* Sarma & Shyam (after Sarma & Shyam 1974). **a** ventral view; **b**–**d** dorsal views, shape variations (c chloroplast; n nucleus; st, storage product)

Ecology: in Lake Attersee, Austria, in summer at 10–30 m depth, and in eutrophic concrete basin, Vienna.
Geographical distribution: Austria (Schiller).

37. *Gymnodinium lalitae* Sarma & Shyam 1974, p. 21, figs 4–8 (**Fig. 51**)

Cells globular or oval, dorsoventrally flattened. Both epi- and hypocone hemispherical, hypocone slightly smaller. Cingulum wide, circular. Sulcus not observed. Numerous small yellow-brown discoid chloroplasts, mostly in the cell periphery but some elsewhere in the cell. Eyespot absent. Nucleus in the cell center, rectangular. Longitudinal flagellum twice the cell length. Cell length 28–37 µm, width 22–25 µm. Cell division in the motile state.
Ecology: in temporary pond in Varanasi and in roadside pond in Mirzapur, Uttar Pradesh, India, July and October.
Geographical distribution: India.

Note: cells of this tropical species are morphologically similar to *Gymnodinium viridaliut*, known from Austria, differing in chloroplast color and shape (dark-green, shortly band-shaped in *G. viridaliut* and yellow-brown disc-shaped in *G. lalitae*). Whether they are separate species cannot be ascertained based on the available evidence.

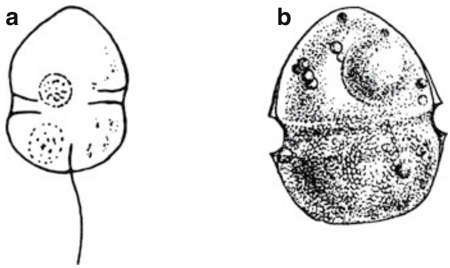

Fig. 52 *Gymnodinium lantzschii* Utermöhl (**a** after Lantzsch 1914; **b** after Litvinenko 1963). **a** ventral view; **b** *Gymnodinium macronucleum* Litvinenko, typical cell in dorsal view

38. *Gymnodinium lantzschii* Utermöhl 1925, p. 407 (**Fig. 52**)

Substitute name for *Gymnodinium minimum* Lantzsch (1914, p. 642, fig. 2B), *nom. illeg.* (non *Gymnodinium minimum* G. A. Klebs 1912, p. 396, 439, text-figs 7A, B)
Nomenclatural synonym: *Glenodinium minimum* H. Bachmann 1923, p. 153, pl. III, figs 14–19 (here taken as nomen novum under Art. 58 of the ICBN)

Cells ovoid. Epicone rounded-conical, hypocone flattened-rounded, slightly shorter or slightly longer than epicone. Cingulum descending, the ends displaced very slightly. Nucleus central. Chloroplasts absent. Cell length 14 µm, width 12 µm.
Ecology: cold water species occurring mainly in late winter and early spring. Early reports from Zugersee, Switzerland (Lantzsch 1914) and several lakes in Holstein, Germany (Utermöhl 1925; up to 150 cells/ml in eutrophic Hemmelsdorfer See).
Geographical distribution: Austria (Schiller); Germany (Utermöhl); Switzerland (Lantzsch).

Note 1: the difference between this species and *G. albulum* needs to be clarified.

Note 2: Bachmann (1923) reported the species both with and without chloroplasts.

Note 3: *Gymnodinium macronucleum* Litvinenko (1963, p. 76, 80, figs 1: 1–6), a cold-water species described from near Kharkiv, Ukraine, differs in having the nucleus in the hypocone but appears otherwise very similar to *G. lantzschii*.

39. *Gymnodinium latum* Skuja 1948, p. 369, pl. XXXVIII, figs 42–45 (**Fig. 53**)

Cells rounded-pentagonal. Epicone pointed hemicircular, hypocone obliquely rectangular, the left side slightly longer than the right side. Epicone slightly longer than hypocone, with two tiny apical spines. Cells only slightly compressed dorso-ventrally. Cingulum very distinct (3 µm wide), with upper sharp edge and lower rounded edge. Cingulum circular, the ends not displaced. Sulcus mainly restricted to the hypocone, becoming wider and more shallow near the antapex. Chloroplasts absent. Nucleus in the epicone. Cytoplasm colorless or peach-colored. Cell length 40–45 µm, width 34–38 µm, thickness 30–34 µm.

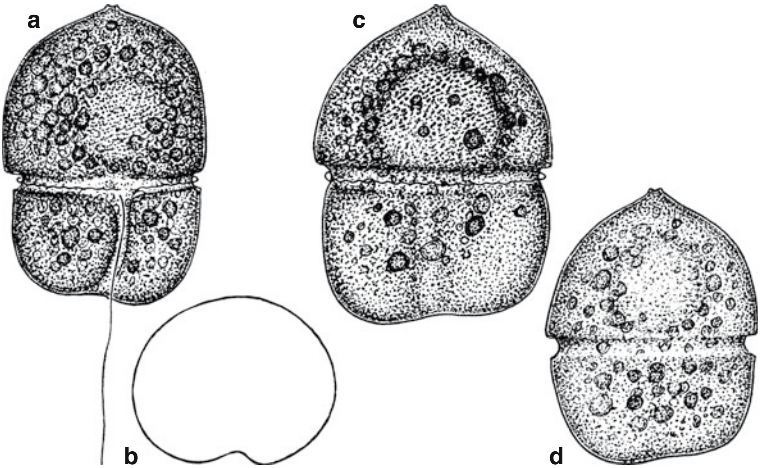

Fig. 53 *Gymnodinium latum* Skuja (after Skuja 1948). **a** ventral view; **b** cross section outline; **c**, **d** dorsal views

Ecology: in Lake Erken and Lake Valloxen near Uppsala, Sweden, Aug-Sept.
Geographical distribution: Portugal (Pandeirada *et al.*); Sweden (Skuja).

40. *Gymnodinium legiconveniens* J. Schiller 1955, p. 33, pl. III, fig. 24 (**Fig. 54**)

Cells pointed egg-shaped, barely compressed dorsoventrally. Epi- and hypocone of equal size. The epicone rounded conical, the hypocone hemispherical. Cingulum wide, circular, the sulcus wide, narrowing posteriorly but reaching the antapex. Epicone ventrally with a small, triangular extension. Chloroplasts absent. Eyespot absent. Cytoplasm sometimes with several brown bodies (lipids?) and food-vacuoles, including whole or parts of *Pseudopedinella*. Cell length 19–20 μm, width 9–10 μm.
Ecology: Ruster Canal, Lake Neusiedl, during spring, at 10–15 ˚C.
Geographical distribution: Austria.

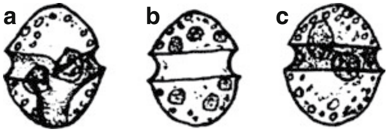

Fig. 54 *Gymnodinium legiconveniens* J. Schiller (after Schiller 1955). **a** ventral view; **b**, **c** dorsal views

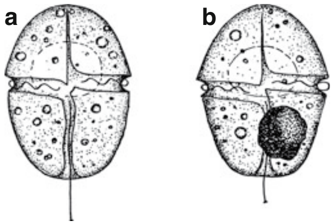

Fig. 55 *Gymnodinium leptostauron* Moestrup & Calado (after Christen 1959a). **a**, **b** two different cells

41. *Gymnodinium leptostauron* Moestrup & Calado *sp. nov.* (**Fig. 55**)

Originally described as "*Gymnodinium autumnale* Christen 1959a, p. 76, fig. 13", a designation not validly published for lack of type designation. Type: Christen 1959a, *Schweiz. Z. Hydrol.* **21**, fig. 13a (here designated).

Epicone hemispherical, hypocone elongate-rounded, slightly longer than epicone. Cells not compressed dorsoventrally. Cingulum descending, the ends displaced less than one cingulum width. Sulcus extends on the epicone almost to the cell apex and on the hypocone to the antapex, widening slightly posteriorly, forming a thin cross with the cingulum ("*leptostauron*"). Chloroplasts absent. Eyespot absent. Cell length 21–33 µm, width 17–18 µm.
Ecology: plankton in the Hausersee area, Switzerland, autumn.
Geographical distribution: Switzerland (Christen).

42. *Gymnodinium limitatum* Skuja 1956, p. 356, pl. LXI, figs 29–31 (**Fig. 56**)

Cells ovoid, both epi- and hypocone rounded. Epi- and hypocone of nearly the same size. Cells somewhat flattened dorsoventrally. Cingulum slightly descending, the ends curved towards the antapical end displaced *ca.* one cingulum width. The sulcus narrow, extends to the left on the epicone, reaching up to 2/3 the length of the epicone. On the hypocone it reaches the antapex. Longitudinal flagellum about twice the length of the cell. With numerous yellowish-brown, elongate chloroplasts radiating from the cell center. Nucleus in the epicone, elliptic or nearly spherical, often more or less lateral. The surface of the nucleus with pattern resembling more or less parallel rod-shaped bacteria (Skuja 1956) or pearl-like (Javornický 1965). Eyespot absent, but 1–3 orange droplets often present in the hypocone. With large vacuole centrally in the cell. Division both in the motile stage and in non-motile stage, in which the cell is surrounded by mucilage. Cell length 24–38 µm, width 20–34 µm.
Ecology: in lakes in Sweden (especially in late summer) and northern Poland (June).
Geographical distribution: Poland (Javornický); Sweden (Skuja).

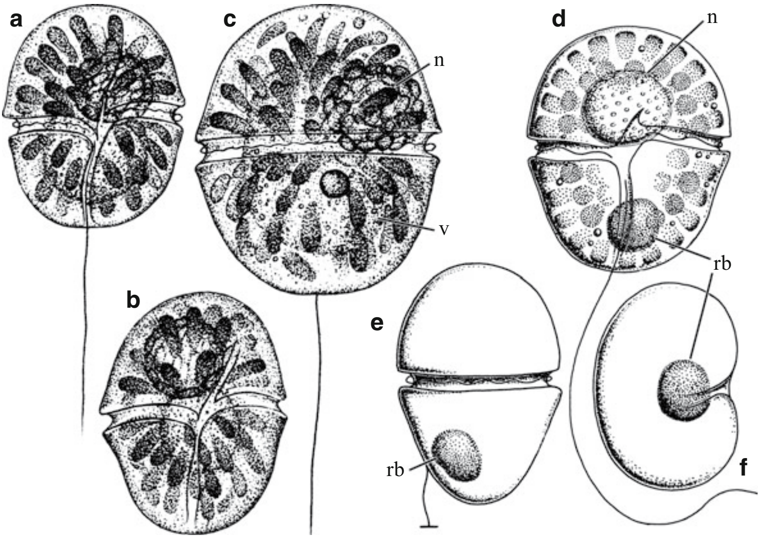

Fig. 56 *Gymnodinium limitatum* Skuja (**a**–**c** after Skuja 1956; **d**–**f** after Javornický 1965). **a**, **b** ventral views; **c** dorsal view; **d**–**f** ventral, lateral and antapical views of the same specimen (n nucleus; rb, red body; v, vacuole)

43. *Gymnodinium limneticum* Wołoszyńska 1936, p. 3, 9, text-figs 1–5, pl. 1, figs 1–11 (**Fig. 57**)

Nomenclatural synonym: *Spiniferodinium limneticum* (Wołoszyńska) Kretschmann & Gottschling *in* Kretschmann *et al.* 2015, p. 629

Cells more or less egg-shaped or spherical, somewhat asymmetric, slightly dorsoventrally compressed, but cell shape variable. Epicone hemispherical or more or less cone-shaped with convex sides, sometimes rounded apically, smaller than hypocone. Hypocone rounded or sometimes indented at the antapical end. Cingulum circular but the ends curved towards the antapex on the ventral side. Sulcus extends to the middle of the epicone. From this region an apical horseshoe-shaped furrow encircles the apical end. On the hypocone the sulcus extends to the antapex. Nucleus spherical to elongate, located centrally. Eyespot not observed. Chloroplasts numerous, darkish-brown or olive-green. Starch grains may be numerous, sometimes covering the nucleus. Cell length 30–40(–50) µm, width 25–38 µm.
Movement of cells usually slow. When conditions deteriorate, cells rapidly shed the flagella and become surrounded by a thick layer of mucilage, cell including mucilage reaching up to 420 um in diameter and sometimes visible to the naked eye. The cingulum and sulcus remain present in this stage. Cells regain motility by reformation of the flagella and shedding of the mucilaginous cover. Coccoid stage

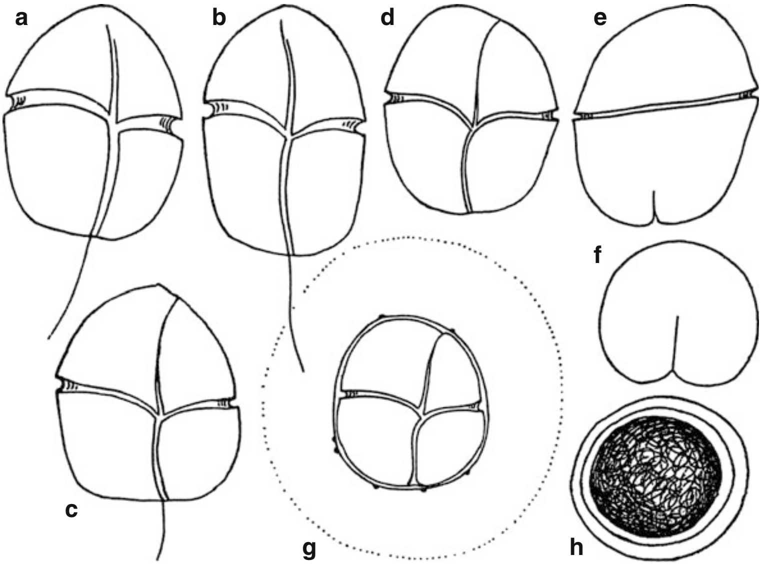

Fig. 57 *Gymnodinium limneticum* Wołoszyńska (after Wołoszyńska 1936). **a**-**c** swimming cells in ventral view (slightly lateral in **a**); **d**-**f** ventral, dorsal and antapical views of non-motile cells; **g** non-motile cell enveloped in mucilage; **h** cyst (enveloping mucilage not shown)

lacking mucilaginous layer also observed in culture. Cell division occurs in both the motile and the non-motile stage.
Cells that were interpreted by Wołoszyńska as cysts rounded, also surrounded by layer of mucilage.
SEM: Kretschmann *et al.* (2015).
DNA data: Kretschmann *et al.* (2015).
Ecology: in the plankton of lakes in summer, the non-motile stage apparently the most common, also occurring in the plankton. The swimming stage is very sensitive and readily changes into the non-motile stage.
Geographical distribution: Tatra Mountains, Poland (Wołoszyńska; Kretschmann *et al.*).

Note: *Gymnodinium limneticum* was recently obtained in culture from the Tatra Mountains and studied by Kretschmann *et al.* (2015). Based on molecular data, *G. limneticum* and *G. palustre* were in the article transferred to *Spiniferodinium* T. Horiguchi & Chihara 1987, a genus of benthic marine dinoflagellates from the Pacific (Kretschmann *et al.* 2015). As mentioned by Kretschmann *et al.* (2015), the phylogenetic relationship between the two species and *Spiniferodinium* is not a close one, based on molecular data, and morphologically the two species, as presently known, share little resemblance to the two species of *Spiniferodinium* presently described. While there is no doubt that the two

a


Fig. 58 *Gymnodinium lividum* Moestrup & Calado (after Schiller 1955). **a** ventral view

species will eventually be removed from *Gymnodinium*, it is not clear to which genus or genera they will eventually be moved to.

44. *Gymnodinium lividum* Moestrup & Calado *nom. nov.* (**Fig. 58**)

Replaced synonym: *Gyrodinium pallidum* J. Schiller 1955, *Wiss. Arbeiten Burgenland* **9**, p. 47, pl. VIII, fig. 44 (in *Gymnodinium*, the epithet *pallidum* is unavailable because of the existence of *Gymnodinium pallidum* Skuja 1939, p. 152, pl. X, figs 32–34, described from brackish water)

Cells broadly oval, strongly compressed dorsoventrally. Epicone broadly rounded, obliquely hat-shaped, slightly wider than hypocone. Hypocone rounded conical. Cingulum descending, the ends displaced *ca.* 1/4 the length of the cell, or 2–3× the cingulum width. Sulcus extends from the cingulum to the antapex which may or may not be slightly retuse. Chloroplasts oval, pale-yellow, difficult to see in the cytoplasm, which is filled with pale lipid droplets. Cell length 28–30 µm, width 20–21 µm, thickness 7 µm.
Ecology: Lake Neusiedl, Austria, February 1952, at 6–8 ˚C.
Geographical distribution: Austria.

45. *Gymnodinium luteofaba* Javornický 1965, p. 56, figs 8–11 (**Fig. 59**)

Cells ovoid, not dorsoventrally compressed. Epicone rounded-conical, hypocone rounded, smaller than epicone. The ends of the cingulum almost opposite, sulcus not reported to continue onto the epicone. Single yellow, bean-shaped chloroplast. Nucleus in epicone. Longitudinal flagellum *ca.* 1.5× the cell length. Cells 10–11 µm long, 8.5 µm wide.
Ecology: found at 15 ˚C among *Sphagnum*-associated filamentous algae in Lake Flosek, Masuria, Poland, in June 1963. The lake was apparently oligotrophic and weakly acid.
Geographical distribution: Poland.

46. *Gymnodinium mazuricum* (Javornický) Moestrup *comb. nov.* (**Fig. 60**)

Basionym: *Katodinium mazuricum* Javornický 1965, *Phycologia* **5**, p. 54, figs 1–7

Cells mushroom-shaped, the epicone three times as long and twice as wide as the hypocone. Cells somewhat flattened dorsoventrally, the ventral side flat, the dorsal

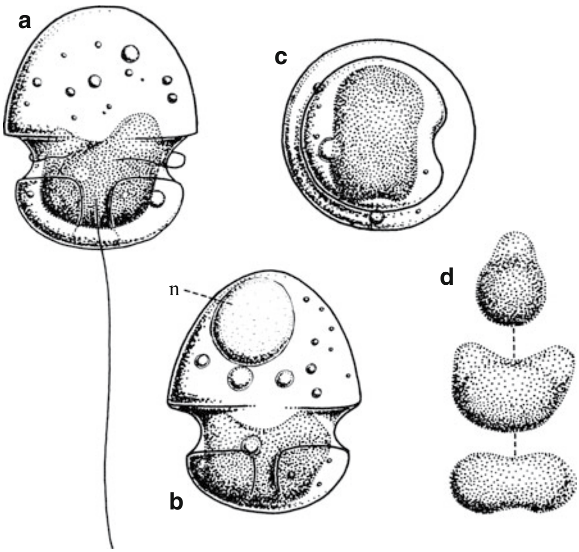

Fig. 59 *Gymnodinium luteofaba* Javornický (after Javornický 1965). **a**, **b** ventral views (n nucleus); **c** antapical view; **d** chloroplast in three different views

side convex. Hypocone thinner than epicone. The cingulum incomplete ventrally, sometimes descending, the two ends slightly displaced. The sulcus does not extend onto the epicone. Single bright-yellow parietal chloroplast shaped like an irregular plate, covering most of the cell surface. The chloroplast is deeply indented on the left side above the cingulum. A large rectangular eyespot present near the sulcus. Cytoplasm hyaline, containing spherical inclusions. Nucleus located in the lower left side of the epicone, in the indentation of the chloroplast. Cells *ca.* 13 µm long, 12 µm wide.
Ecology: in littoral plankton of small forest lake (data from September 1950: depth 3 m, pH 6.1, transparency to the bottom, 15.5 ˚C), in June 1963, Masuria, Poland.
Geographical distribution: Poland.

47. *Gymnodinium mirabile* Penard 1891, p. 56, pl. V, figs 1–7 (**Fig. 61**)

Taxonomic synonyms: *Gymnodinium mirabile* var. *rufescens* Penard 1891, p. 57, pl. V, figs 8, 9 ≡ *Gymnodinium rufescens* (Penard) Lemmermann 1900b, p. (116)

Cells ovoid, somewhat variable. Epicone rounded, hemispherical, elongate, or bell-shaped. Hypocone usually smaller than the epicone, rounded or with slight indentation at the antapex, the hypocone becoming broadly hemispherical. Cells dorsoventrally compressed, the hypocone particularly so. Cingulum narrow, circular or very slightly descending. Sulcus narrow, extending onto the epicone and reaching the apical groove near the front end of the cell. Apical groove nearly circular. Chloro-

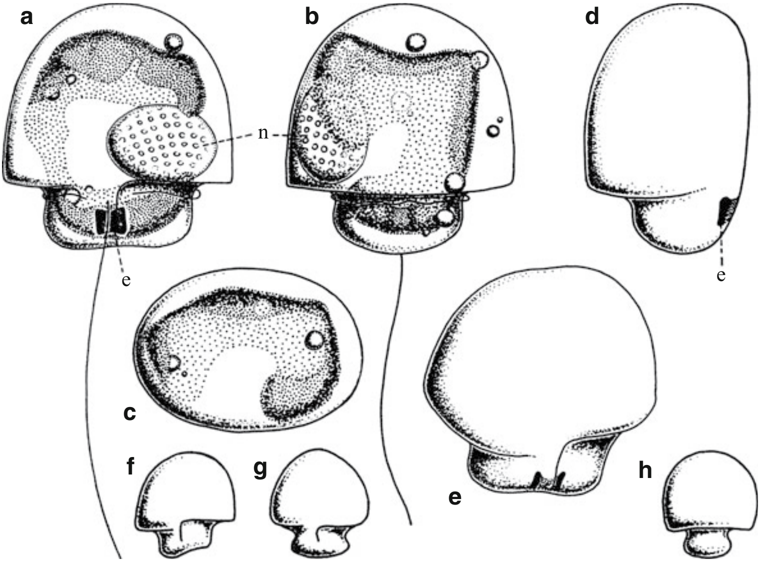

Fig. 60 *Gymnodinium mazuricum* (Javornický) Moestrup (after Javornický 1965). **a**-**c** ventral, dorsal and apical views, showing the chloroplast, the nucleus (n) and the eyespot (e); **d** lateral view with the eyespot indicated (e); **e** oblique-ventral view; **f**-**h** variability in cell shape (**f**, **g** ventral, **h** dorsal views)

plasts yellowish-green to brown, radiating from the center but often without reaching the cell surface (chloroplasts retract toward the center in high light intensity), leaving a more or less wide hyaline border along the periphery. A small, circular vesicle (pusule?) in the cell middle. Eyespot absent. Cells often occur together in chain-like pairs and the nucleus is located in the hypocone in the anterior cell of a pair, in the epicone in the posterior cell. Cell length 48–77 μm, width 46–62 μm. (Original length reported by Penard up to 90 μm.)
SEM: Hansen & Flaim (2007).
Ecology: apparently a summer-autumn species, restricted to alpine and temperate, oligotrophic to mesotrophic lakes.
Geographical distribution: Italy (Hansen & Flaim); Germany (Lemmermann, Utermöhl); Sweden (Skuja); Switzerland (Penard). Brazil (Cavalcante *et al.*). Japan (Senzaki & Horiguchi).

Note: the name *G. mirabile* is given in several floras as a synonym of *Gymnodinium uberrimum* (G. J. Allman) Kofoid & Swezy. However, the original description of *Peridinium uberrimum* G. J. Allman, on which *G. uberrimum* was based, shows several aspects that suggest a woloszynskioid rather than a species of *Gymnodinium* (Hansen & Flaim 2007; Pandeirada *et al.* 2013).

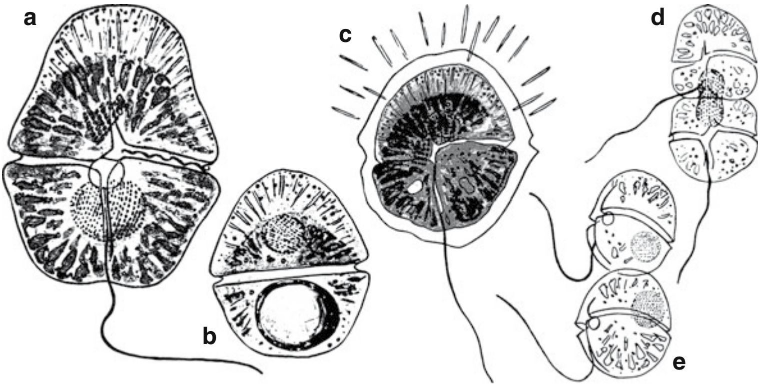

Fig. 61 *Gymnodinium mirabile* Penard (after Penard 1891). **a** ventral view; **b** dorsal view; **c** ventral view of cell in glycerine, with discharged hyaline rods (mucocysts); **d**, **e** dividing cells (as *G. mirabile* var. *rufescens*)

48. *Gymnodinium mirum* Utermöhl 1923a, p. 6, figs 1–10 (*sensu* Utermöhl 1925, p. 407, 408, fig. 35) (**Fig. 62**)

"*Woloszynskia mira* (Utermöhl) Kisselev 1954, p. 128" intended as a new combination, but not validly published for lack of full and direct reference to place of publication of basionym.

Cells elliptic or ovoid. Cingulum slightly descending, sulcus reaches the antapex, becoming slightly wider near the antapical end. Sulcus extends onto the epicone as an oblique line directed towards the cell's left, and continues as a narrow furrow in anticlockwise direction around the cell apex. Numerous small chloroplasts which obscure the nucleus. Eyespot absent. Cell length 34–45 µm, width 28–33 µm, young cells smaller. Great plasticity and aberrant cell shapes reported by Utermöhl (1925).
According to Gert Hansen (pers. comm.) the cingulum is incomplete, terminating on the ventral side a short distance before reaching the sulcus (may be difficult to see in the light microscope).

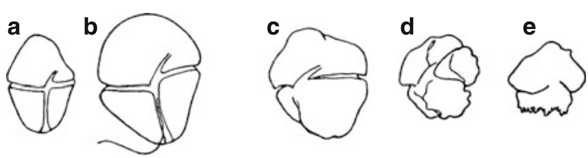

Fig. 62 *Gymnodinium mirum* Utermöhl (after Utermöhl 1925). **a** typical shape (more elliptic); **b**, a more oval shape; **c**-**e** aberrant shapes

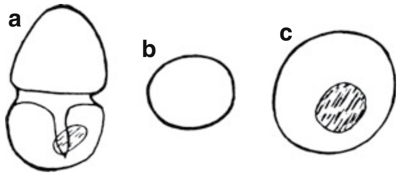

Fig. 63 *Gymnodinium mitratum* J. Schiller (after Schiller 1932). **a** ventral view; **b** apical view; **c** antapical view showing the nucleus

Ecology: in lake plankton, during the warmer part of the year (Kleine Ukleisee, Germany), with up to 10^3 cells/ml in August 1922 (Utermöhl 1925). The cells appear to perform vertical migrations.
Geographical distribution: Attemose, Denmark (Gert Hansen, unpublished); Germany (Utermöhl).

Note: the species concept presented here is based on Utermöhl (1925, p. 408), because more than one species seems to have been included in the variations described by Utermöhl (1923a).

49. *Gymnodinium mitratum* J. Schiller 1932, p. 386, fig. 396 (**Fig. 63**)

Cells oval, barely compressed dorsoventrally. Epicone ovoid or hemispherical, larger or equal in size to the hemispherical hypocone, symmetrical. Cingulum circular, the ends not or very slightly displaced. Sulcus restricted to the hypocone, but does not reach the antapex. Nucleus in the hypocone. Chloroplasts absent. Eyespot absent. Cell division reported to take place both in the motile and the non-motile stage. Cell length 32–35 µm, cell width 15–16 µm.
Ecology: in deep, cold parts of alpine lakes, also in melting snow.
Geographical distribution: Austria.

50. *Gymnodinium mucicola* (W. Conrad) Moestrup *comb. nov.* (**Fig. 64**)

Basionym: *Amphidinium mucicola* W. Conrad 1941, *Bull. Mus. Roy. Hist. Nat. Belgique* **17** (46), p. 1, figs A–E ("*mucicolum*")

Cell elongate, spindle-shaped, not compressed dorsoventrally. Epicone much smaller than hypocone, ovoid or slightly pentagonal in ventral view, concave on the ventral side. Hypocone elongate ellipsoidal to ovoid, gradually tapering towards the antapex, which is rounded. Cingulum circular but on the dorsal side closer to the apex than on the ventral side. Sulcus sigmoid, extending in a left-hand curve towards the antapex. Chloroplasts absent. Eyespot absent. Nucleus nearly central. Cells 14–19 µm long, 5–7 µm wide.
Ecology: in experimental garden pond, in or on the mucilage of the red alga *Batrachospermum*, at 10 °C, pH 7.1. It seemed to be mainly benthic and was rarely seen swimming.
Geographical distribution: Belgium.

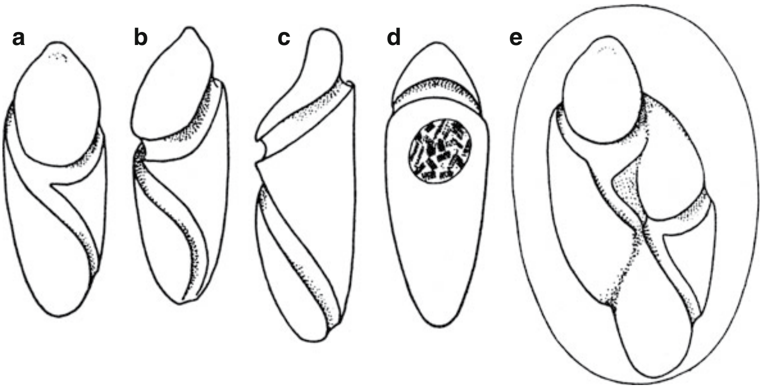

Fig. 64 *Gymnodinium mucicola* (W. Conrad) Moestrup (after Conrad 1941). **a**-**c** respectively ventral, ventral-left and left views; **d** dorsal view showing nucleus; **e** cell division

51. ***Gymnodinium obesum*** J. Schiller 1932, p. 391, fig. 405 (**Fig. 65**)

Cell ovoid with median descending cingulum that is displaced *ca.* one cingulum width. Sulcus narrow, reaching only halfway down the hypocone. Sulcus extends onto the epicone, deflecting towards the left and making a slight sigmoid bend before continuing in the apical groove. Nucleus in the epicone or central. Chloroplasts oblong, evenly distributed in the cell or concentrated in the center. Eyespot absent. Cell length 27–37 µm, width 22–30 µm.
SEM: Hansen & Flaim (2007).
Ecology: lake plankton, apparently a summer species.
Geographical distribution: Austria (Schiller); Denmark, Italy (Hansen & Flaim).

52. ***Gymnodinium oligoplacatum*** Skuja 1956, p. 358, pl. LXI, figs 33–34 (**Fig. 66**)

Cells spherical to bipyramidal, barely compressed dorsoventrally, epi- and hypocone of almost equal length. Epicone conical with convex sides, hypocone hemispherical with retuse antapex. Cingulum circular, sulcus extends slightly onto the epicone, on the hypocone reaching the antapex. Chloroplasts olive to dark-yellow,

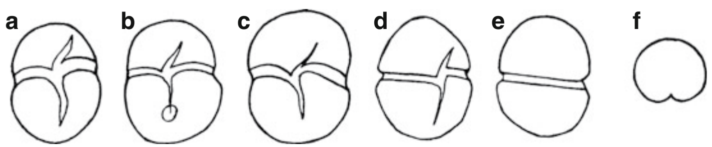

Fig. 65 *Gymnodinium obesum* J. Schiller (after Schiller 1932). **a**-**d** variations in outline of cell and furrows (ventral views); **e** dorsal outline; **f** cross section

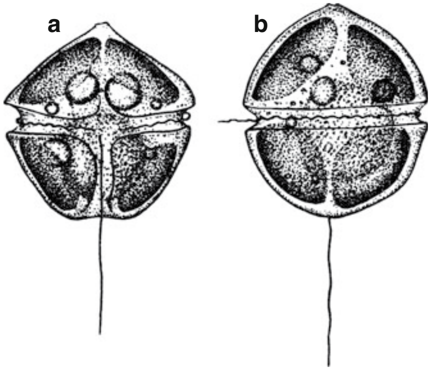

Fig. 66 *Gymnodinium oligoplacatum* Skuja (after Skuja 1956). **a** ventral view; **b** dorsal view

parietal, rather large, disc-shaped, 2-3 in each cell half. Eyespot absent. Nucleus rather large, in the center of the hypocone. Cell length 16–20 µm, width 13–19 µm.
Ecology: in lakes in central Sweden, May and June (Gärdefjärden, Västerbotten, Åsgarn, Dalarna).
Geographical distribution: Sweden.

53. *Gymnodinium palustre* A. J. Schilling 1891a, p. 277, pl. X, fig. 11 (**Fig. 67**)

Nomenclatural synonym: *Spiniferodinium palustre* (A. J. Schilling) Kretschmann & Gottschling *in* Kretschmann *et al.* 2015, p. 630
Taxonomic synonym: *Gymnodinium zachariasii* Lemmermann 1900b, p. (116) ("*Zachariasi*") (validated by reference to Zacharias 1899a, p. 141, figs 1–9 and Zacharias 1899b, p. 136, figs 1–9)

Cells elongate elliptical, somewhat compressed dorsoventrally. Epicone much longer than hypocone. Epicone elongate bell-shaped, hypocone short and wide, often asymmetrical, left side sometimes slightly larger. Antapical end slightly indented or rounded. Cingulum ends hardly displaced. Sulcus narrow, extending onto the epicone, on the hypocone widening near the antapex. With numerous yellow to dark brown peripheral chloroplasts. Eyespot absent. Nucleus central. Pseudopodia illustrated by Zacharias (1899a,b), extending from the ventral side. Cell length 40–60 µm, width 27–32 µm, thickness 16 µm. With fish-hook shaped apical groove (Gert Hansen, *pers. comm.*). Cysts spherical. The species readily forms mucilage and may form resting stages surrounded by mucilage.
Ecology: summer species found in slightly acid (pH 6.5-6.9), oligotrophic localities (Höll 1928).
Geographical distribution: Denmark (Calado, Gert Hansen); Germany (Schilling, Zacharias); Poland (Höll).

Note 1: *Gymnodinium carinatum* A. J. Schilling (1891a, p. 278, pl. X, fig. 12) was described based on a few cells but has apparently not been reported again. It differs from

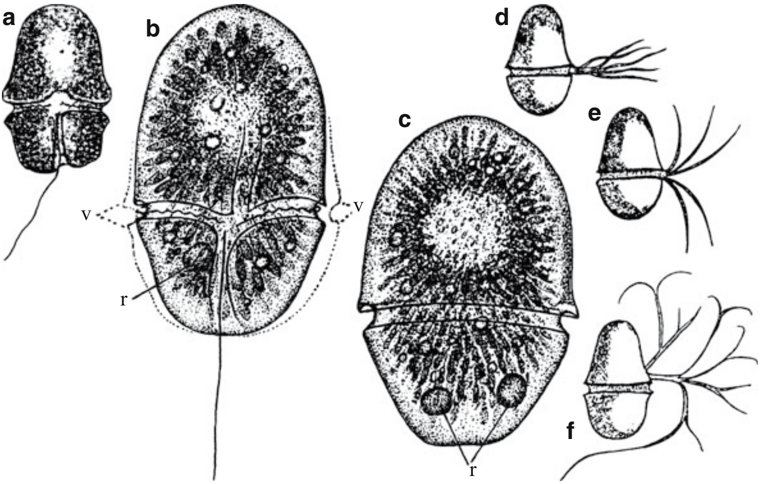

Fig. 67 *Gymnodinium palustre* A. J. Schilling (**a** after Schilling 1891a; **b**, **c** after Skuja 1964; **d**-**f** after Zacharias 1899b). **a** ventral view; **b** ventral view with outline variation indicated by dotted line (v); **c** dorsal view (r, red carotenoid body); **d**-**f** lateral views of cells with pseudopods emerging from the mid-ventral area

G. palustre in possessing a ridge along the left side of the sulcus. Its identity is uncertain, the ridge may be interpreted as part of a food-uptake apparatus.

Note 2: Regarding transfer to *Spiniferodinium*, see note to *Gymnodinium limneticum*.

54. *Gymnodinium palustriforme* Gert Hansen & Flaim 2007, p. 113, figs 6A–D (holotype: figs 6B, C) (**Fig. 68**)

Cells elliptical or ovoid, dorsoventrally flattened. Epicone bell shaped, longer than the hemispherical hypocone. Cingulum circular or descending less than one cingulum width. Sulcus narrow, widening slightly before reaching the antapex. Sulcus extends onto the epicone and continues into the fish-hook-shaped apical groove, which partly encircles the apex. Chloroplasts yellowish green, radiating from the central part of the cell towards the cell surface. Nucleus rounded, in the epicone. Eyespot absent. Cell length *ca.* 35 µm, width *ca.* 25 µm but smaller cells (*ca.* 22 × 17 µm) also occur.
SEM: Hansen & Flaim (2007).
Ecology: cold water plankton species that did not grow above 12 ˚C. In Lake Tovel, Italy, only, a lake situated on limestone.
Geographical distribution: Italy (Hansen & Flaim).

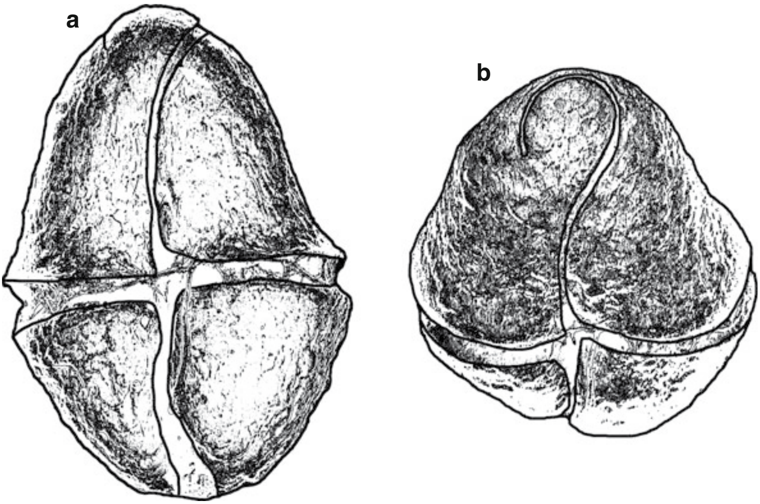

Fig. 68 *Gymnodinium palustriforme* Gert Hansen & Flaim (original images, prepared from Hansen & Flaim 2007, figs 6C and 6D, both SEM micrographs). **a** ventral view; **b** apical-ventral view showing complete path of the hook-like, anticlockwise-turning apical extension of the sulcus

55. *Gymnodinium paradoxiforme* J. Schiller 1955, p. 41, pl. VII, figs 41a-g; pl. VIII, figs 41h, i (**Fig. 69**)

Cells rounded-ovoid, barely compressed dorsoventrally. Epi- and hypocone both hemispherical, of equal size. Cingulum circular. Sulcus without sharp edges and difficult to see. Eyespot absent. With red or reddish-brown, round bodies of different size. Chloroplast light yellow to yellowish-brown, radially arranged. Cell length 20–44 µm, width 22–36 µm. Cysts reported to be spherical.

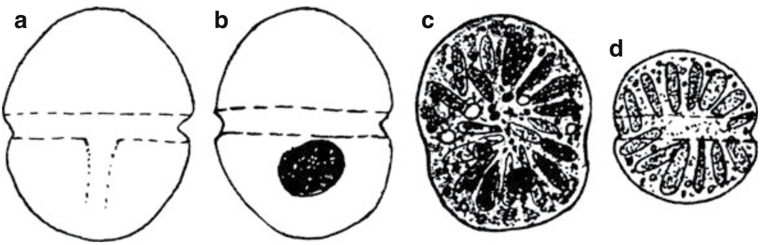

Fig. 69 *Gymnodinium paradoxiforme* J. Schiller (after Schiller 1955). **a**, **b** ventral and dorsal outlines; **c**, **d** different cells showing chloroplast arrangement

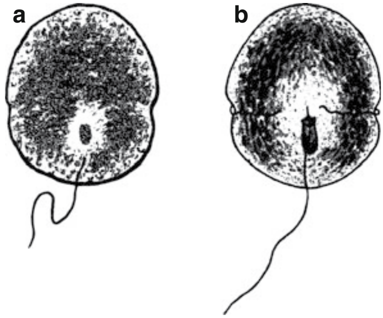

Fig. 70 *Gymnodinium paradoxum* A. J. Schilling (**a** after Schilling 1891a; **b** after Schilling 1913). **a**, **b** ventral views

Ecology: in concrete basin in park in Vienna, July–October, at 20–28 ˚C.
Geographical distribution: Austria.

56. *Gymnodinium paradoxum* A. J. Schilling 1891a, p. 278, pl. X, fig. 13 (**Fig. 70**)

Cell spherical, epicone slightly larger than hypocone. Cingulum circular, sulcus not observed. Chloroplasts dark red-brown, in the cell middle. Eyespot in the sulcus. Cell length 37 µm, width 35 µm. Described to be characterized by its very slow swimming.
Ecology: Neudorfer swamp, Baden, and lakes in central Sweden.
Geographical distribution: Germany (Schilling); Sweden (Skuja).

Note: the very incomplete original description of this species is a major obstacle to identification.

var. *majus* Lemmermann *in* West & G. S. West 1906, p. 91 ("*major*")
Cells oval, length 66–75 µm, width 61–67 µm.
Ecology: plankton, Irish lakes.
Geographical distribution: Ireland.

57. *Gymnodinium partitum* (Perty) Moestrup *comb. nov.* (**Fig. 71**)

Basionym: *Monas partita* Perty 1849b, *Mitth. Naturf. Ges. Bern* **1849**, p. 168
Nomenclatural synonyms: *Peridinium monadicum* Perty 1852, p. 162 (pl. VII, fig. 15), *nom. illeg.* (*Monas partita* is cited as a synonym, rendering *P. monadicum* superfluous) ≡ *Glenodinium monadicum* Diesing 1866, p. 392, *nom. illeg.* ≡ *Gymnodinium monadicum* Kent 1881, p. 443, *nom. illeg.* ≡ *Katodinium monadicum* Javornický 1970, p. 297, *nom. illeg.*
Taxonomic synonym: *Katodinium polyplastidum* Popovský 1968, p. 256, pl. X, figs 6, 7

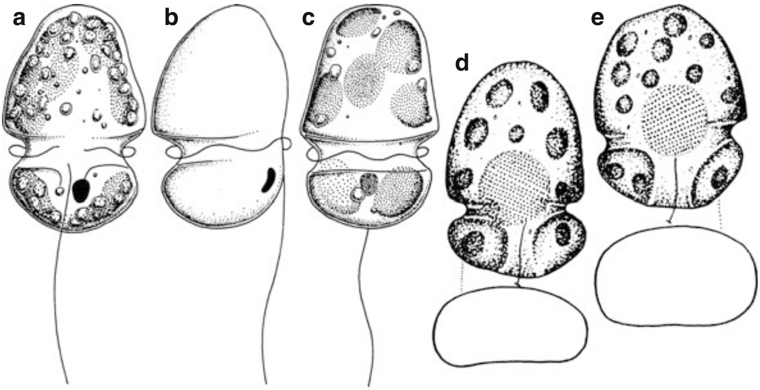

Fig. 71 *Gymnodinium partitum* (Perty) Moestrup (**a**-**c** after Javornický 1970; **d**, **e** after Popovský 1968). **a**-**c** respectively ventral, lateral and dorsal views; **d**, **e** ventral views and apical outlines of two cells

Cells elongate ellipsoidal with bluntly conical epicone and flatly rounded hypocone. Epicone 2–3× the length of the hypocone. Epicone slightly wider than hypocone. Cells slightly compressed dorsoventrally. Cingulum wide, circular. Sulcus does not reach the antapex. With several disc-shaped, yellow-green, parietal chloroplasts. Distinct eyespot near the sulcus. Nucleus central. Cell size 15–26 µm, width 9–15 µm, thickness *ca.* 10 µm.
Ecology: in pool in the Alps (Perty 1849b), in shallow oligotrophic swamp in Abisko, Sweden (Javornický 1970), in peat bog in Bohemia (Popovský 1968).
Geographical distribution: Czech Republic (Popovský); Sweden (Javornický); Switzerland (Perty).

Note: the current concept of *G. partitum* is the one described by Javornický (1970, p. 297, figs 1a-c; as *Katodinium monadicum*).

58. *Gymnodinium pavlae* Popovský 1990, p. 8, pl. II, fig. 11 (**Fig. 72**)

Cells nearly spherical to ellipsoid, not flattened dorsoventrally. Epicone and hypocone similar in size, both bell-shaped. Cingulum circular or very slightly descending. Sulcus extends to half the length of the epicone, the anteriormost end deflecting to the left. Chloroplasts numerous, oval, parietal. Eyespot absent. Numerous refractile bodies present. Cells move very quickly. Cell length 12–20 µm, width 10–19 µm.
Ecology: peat bog in Česká Lípa Distric, Czech Republic, in April 1966.
Geographical distribution: Czech Republic.

59. *Gymnodinium peisonis* J. Schiller 1955, p. 36, pl. IV, fig. 33 (**Fig. 73**)

Cells shortly cylindrical, rounded at the ends, barely compressed dorsoventrally. Epicone flattened-convex, almost as wide as the hypocone, which is hemispherical and 2–3× the length of the epicone. Cingulum wide, circular. Sulcus also wide, re-

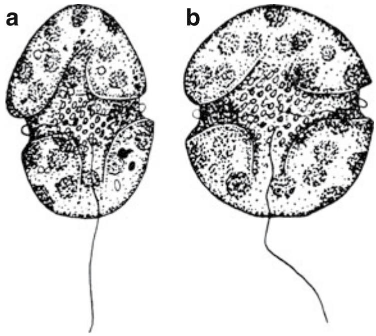

Fig. 72 *Gymnodinium pavlae* Popovský (after Popovský 1990). **a**, **b** shape variation

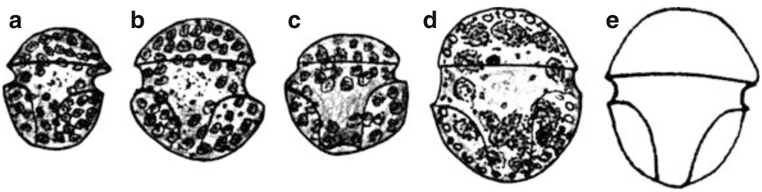

Fig. 73 *Gymnodinium peisonis* J. Schiller (after Schiller 1955). **a**-**e** ventral views of cells showing shape variation (**e** outline)

stricted to the hypocone, becoming narrower towards the antapex. Numerous small greenish-yellow chloroplasts, rounded disc-shaped. Eyespot absent. Cell length 19–22 μm, width 16–22 μm.
Ecology: Ruster Kanal, Lake Neusiedl, spring.
Geographical distribution: Austria.

60. *Gymnodinium planum* (Fott) Moestrup *comb. nov.* (**Fig. 74**)

Basionym: *Massartia plana* Fott 1938, *Stud. Bot. Čechoslov.* **1**, p. 103, fig. 2
Nomenclatural synonym: *Katodinium planum* (Fott) A. R. Loeblich 1965, p. 16

Cells widely ovoid, strongly flattened dorsoventrally. Epicone 3× the length of the hypocone, rounded-elongate. Hypocone flat, as wide as the epicone, slightly concave. Cingulum ends not displaced. Sulcus extends onto the epicone, but on the hypocone does not reach the antapex. With two golden-yellow chloroplasts, one in the epicone and one in the hypocone. Eyespot absent. Nucleus centrally in the epicone. Longitudinal flagellum of the same length as the cell. Cell length 16–20 μm, width *ca.* 13–14 μm. The cells round off quickly when examined under a coverslip.
Ecology: among surface plankton in oligotrophic mountain lake in Bohemia.
Geographical distribution: Czech Republic (Fott).

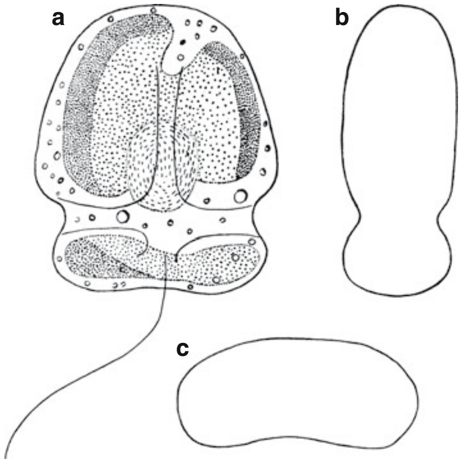

Fig. 74 *Gymnodinium planum* (Fott) Moestrup (after Fott 1938). **a** ventral view, showing the chloroplast and the centrally located nucleus; **b** lateral outline; **c** apical outline

61. *Gymnodinium poculiferum* Skuja 1956, p. 360, pl. LXII, figs 1–3 (**Fig. 75**)

Cells more or less circular or broadly elliptical in ventral view, somewhat compressed dorsoventrally. Epi- and hypocone both hemispherical, of equal size, rounded. Cingulum descending, the ends displaced 10–15 µm. Sulcus narrow, extending to half the length of the epicone and to the antapex of the hypocone. With

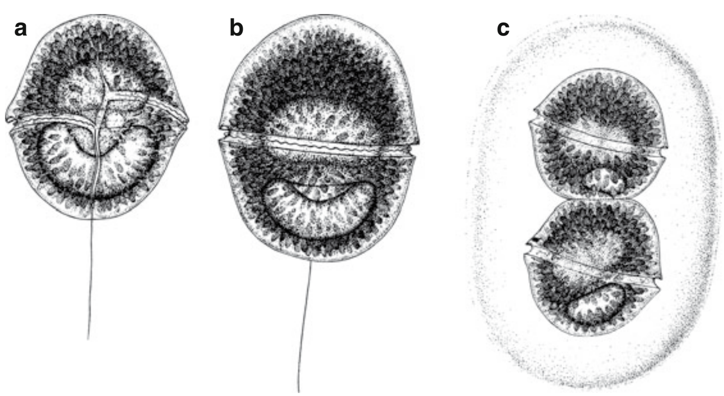

Fig. 75 *Gymnodinium poculiferum* Skuja (after Skuja 1956). **a** ventral view; **b** dorsal view of another cell; **c** division stage

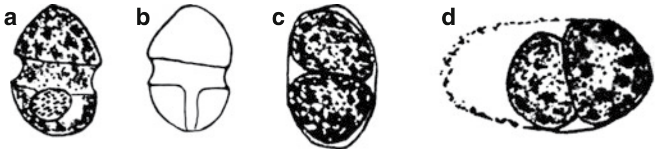

Fig. 76 *Gymnodinium posthiemale* J. Schiller (after Schiller 1955). **a** cell with contents, showing nucleus and chloroplasts; **b** cell outline in ventral view; **c**, **d** division stages (old cell cover breaking up in **d**)

numerous more or less parietal, partly radial, shortly elongated, olive, dark-yellow chloroplasts. Eyespot absent. Nucleus transversely elongated, in the cell middle or in the epicone. A large, cup-shaped refractile body present in the hypocone, brownish-red or colorless. Cell length 60–82 µm, width 60–76 µm, thickness 40–55 µm. Cell division oblique, in the motile as well as in the non-motile stage, in the latter case cells surrounded by copious mucilage.
Ecology: lakes in central Sweden (Gärdefjärden, Västerbotten, Högfjärden).
Geographical distribution: Sweden.

62. *Gymnodinium posthiemale* J. Schiller 1955, p. 35, pl. III, fig. 29 (**Fig. 76**)

Cells elongate ovoid, not compressed dorsoventrally. Epicone more or less conical, somewhat longer than the hemispherical hypocone. Cingulum circular. Sulcus restricted to the hypocone, does not extend to the antapex. With numerous yellowish-green, disc-shaped chloroplasts. Eyespot absent. With numerous small grains in the cytoplasm, indicating mixotrophy. Nucleus in the hypocone. Cell division by transverse division, seemingly in the non-motile state. Cells 18–20 µm long, 14–16 µm wide.
Ecology: in winter (February, March), also under the ice, in park in Vienna, Austria.
Geographical distribution: Austria.

Note: this species appears to differ from *G. lacustre* only in the latter occurring in summer. The two taxa may be conspecific.

63. *Gymnodinium pratense* (Baumeister) Moestrup *comb. nov.* (**Fig. 77**)

Basionym: *Massartia pratensis* Baumeister 1943a, *Arch. Protistenk*. **96**, p. 332, fig. 1

Epicone large, bell-shaped, hypocone very small, less than 1/3 the length of the epicone and much narrower, measuring only about 2/3 the width of the epicone. Hypocone flattened. Cingulum descending, on the ventral side the two ends displaced *ca.* half a cingulum width and forming an inverted V. Sulcus very short and indistinct. Nucleus fills a large part of the epicone. Chloroplasts absent. Eyespot absent. Cells with food vacuoles containing variously colored material. Cell length 17–18 µm, width 16–17 µm. Cells swim constantly, without resting.
Ecology: in snow-filled grassy hollows, at pH 4-7.7.
Geographical distribution: Germany.

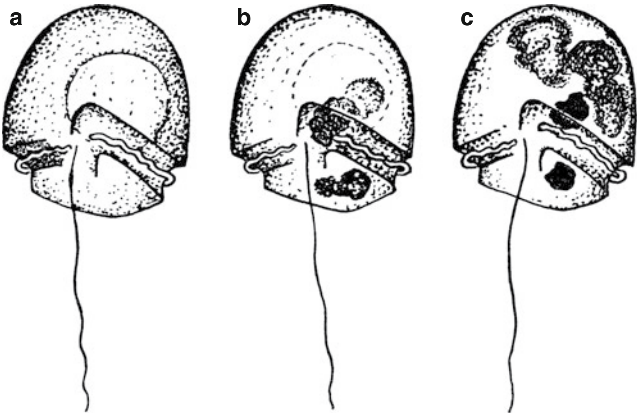

Fig. 77 *Gymnodinium pratense* (Baumeister) Moestrup (after Baumeister 1943a). **a** colorless form; **b** cell with green and yellowish inclusions; **c** cell with yellow, green and red inclusions

Note 1: the species somewhat resembles *Opisthoaulax vorticella*, differing in particular in lacking an eyespot.

Note 2: *Katodinium parvulum* Litvinenko (1963, p. 79, 80, figs 1: 7, 8) described from cold water in Kharkiv, Ukraine, appears to differ in size only, measuring 11–12 µm in length and 8–9 µm in width.

64. *Gymnodinium pseudomirabile* Gert Hansen & Flaim 2007, p. 114, figs 7A–G (holotype: fig. 7F) (**Fig. 78**)

Cells ovoid, slightly dorsoventrally compressed. Epi- and hypocone both hemispherical, the latter with slight antapical indentation. Cingulum median, not displaced. Sulcus narrow, does not reach the antapex. Sulcus extends for *ca.* 2/3 onto the epicone and continues into the fish hook-shaped apical groove. Nucleus rounded, central, premedian. Numerous greenish-brown chloroplasts radiate from the cell center. Eyespot absent. Division cysts and cell pairs observed. Cell length 31–36 µm, width 28–31 µm.
SEM: Hansen & Flaim (2007).
Ecology: autumn or winter species, but grows in culture at 15 °C. In Lake Tovel (Tretino, Italy), a lake located on limestone.
Geographical distribution: Italy (Hansen & Flaim).

65. *Gymnodinium purpureum* Skuja 1956, p. 357, pl. LXI, figs 39–42 (**Fig. 79**)

Cells circular in ventral view, more or less dorsoventrally flattened. Epicone hemispherical, larger than or equal in size to the broadly rounded hypocone. Cingulum circular or somewhat descending. Sulcus extends onto the epicone, on the hypo-

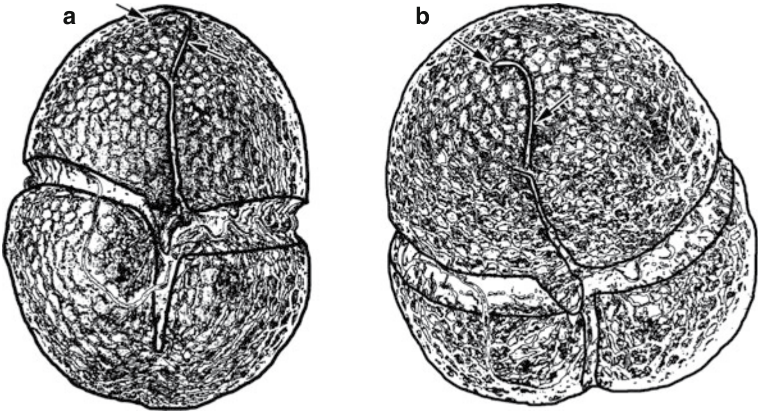

Fig. 78 *Gymnodinium pseudomirabile* Gert Hansen & Flaim (original images, prepared from Hansen & Flaim 2007, figs 7F and 7G, both SEM micrographs). **a** ventral view; **b** apical-ventral view. The arrows point to the apical groove

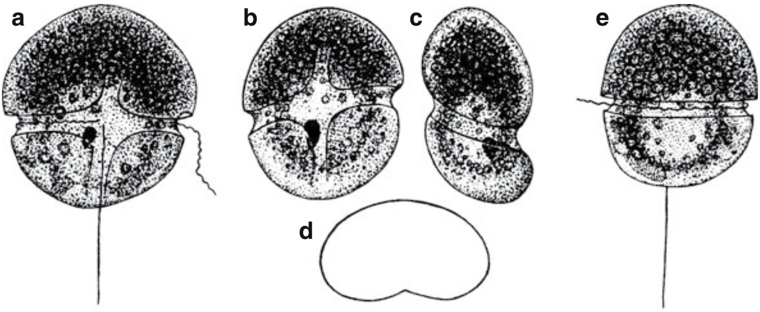

Fig. 79 *Gymnodinium purpureum* Skuja (after Skuja 1956). **a** ventral view; **b**-**d** ventral, lateral and cross-section views of one cell; **e** dorsal view

cone reaches the antapex. Chloroplasts yellow-brown, relatively large, disc-shaped, more or less parietal. Elongate eyespot in the sulcus. Nucleus large, spherical or elliptic, filling most of the antapical end of the cell. Cell with numerous grains of pink or purple-red pigments, particularly in the epicone. The pigment is sometimes present in sufficiently large amounts to render the cell more or less red. Cell length 23–29 μm, width 18–25 μm, thickness 13–20 μm.
Ecology: in lakes in central Sweden (May, June).
Geographical distribution: Sweden.

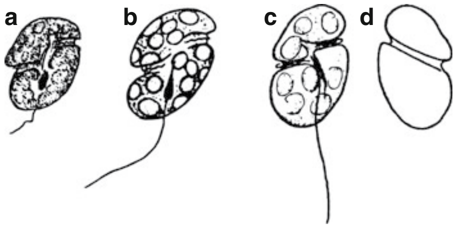

Fig. 80 *Gymnodinium pusillum* A. J. Schilling (**a** after Schilling 1891a; **b** after Schilling 1913; **c**, **d** after Thompson 1947). **a**-**c** ventral views; **d** dorsal view

66. *Gymnodinium pusillum* A. J. Schilling 1891a, p. 279, pl. X, fig. 15 (**Fig. 80**)

Nomenclatural synonyms: *Spirodinium pusillum* (A. J. Schilling) Lemmermann 1900b, p. (116) ≡ *Gyrodinium pusillum* (A. J. Schilling) Kofoid & Swezy 1921, p. 329

Cells elongate-oval, asymmetric. Epicone bell-shaped or kidney-shaped, usually smaller than the hypocone, which is obliquely sack-shaped. The cingulum emerges in the mid-area of the cell, extends obliquely forward and on the dorsal side extends obliquely towards side of the cell. On the ventral side it extends upwards toward the proximal part of the sulcus, and meets it with displacement of 1.5 cingulum widths. Sulcus shallow, broadening toward the antapex (Thompson 1947). Several disc-shaped, green or golden-brown, parietal chloroplasts. Eyespot elongate, in the anterior part of the sulcus. Flagellum 1–1.5× the cell length. Moves rapidly, rotating around the longitudinal axis. Cell length 13–32 µm, width 15–18 µm, thickness 14–15 µm. Cysts with resistant wall reported by Conrad (1926).
Ecology: in vegetation-rich ponds. Also in a peat bog (Popovský 1990); in brackish water (Conrad 1926, nice colored illustration in fig. 31); and in fresh water near Bush River Estuary, Maryland, in January (Thompson 1947).
Geographical distribution: Belgium (Conrad); Czech Republic (Popovský); Switzerland (Schilling). USA, MD (Thompson).

Note: *Gyrodinium hiemale* Skvortsov (1968, p. 91, pl. II, figs 11–13), described from Manchuria, shows some similarity, but the description is insufficient to determine its identity.

var. *minus* (Skuja) Moestrup *comb. nov.* (**Fig. 81**)
Basionym: *Spirodinium pusillum* var. *minus* Skuja 1956, *Nova Acta Regiae Soc. Sci. Upsal., ser. IV*, **16** (3), p. 361, pl. LXI, fig. 35 ("*minor*")

Smaller than the species type and usually with only two parietal, yellowish chloroplasts (one in the epi-, the other in the hypocone). Eyespot as in the species type, elongate and in the sulcal area. Nucleus nearly central. Length 7–9 µm, width 4–6 µm.

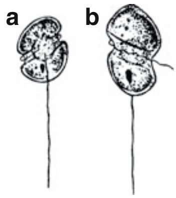

Fig. 81 *Gymnodinium pusillum* var. *minus* (Skuja) Moestrup (after Skuja 1956). **a** ventral view; **b** dorsal view

Ecology: in the plankton of Lake Gärdefjärden, NW Sweden (Skuja 1956) and in oligotrophic mountain lake in Portugal (Nauwerck 1962).
Geographical distribution: Portugal (Nauwerck); Sweden (Skuja).

67. ***Gymnodinium radiatum*** (Javornický) Moestrup & Calado *comb. nov.* (**Fig. 82**)

Basionym: *Amphidinium radiatum* Javornický 1957, *Univ. Carol. Biol.* **3**, p. 260, fig. 7b, d

Cells broadly ovoid, slightly compressed dorsoventrally. Epicone much smaller than hypocone. Both epi- and hypocone broadly rounded. Cingulum wide, circular. Sulcus wide, extending onto the epicone, on the hypocone not reaching the antapex. Several yellowish-brown, club-shaped chloroplasts radiate from a hyaline center towards the periphery of both epi- and hypocone. Small regular granular bodies present. Eyespot absent. Large round nucleus in the epicone. Cell length 25 µm (epicone 7.5 µm, hypocone 17.5 µm), width of epicone 17 µm, width of hypocone 20 µm.

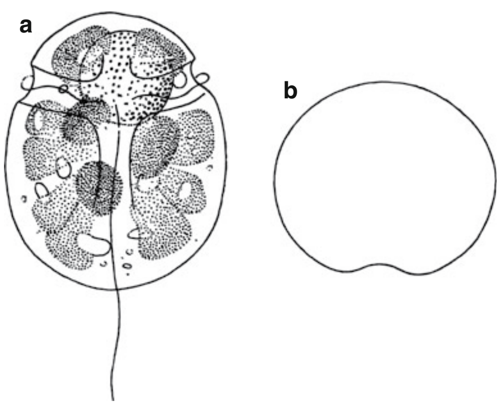

Fig. 82 *Gymnodinium radiatum* (Javornický) Moestrup & Calado (after Javornický 1957). **a** ventral view; **b** cross section

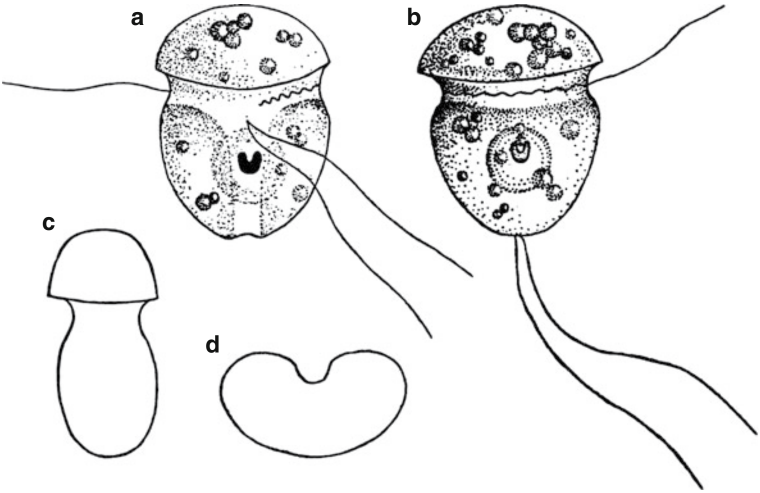

Fig. 83 *Gymnodinium rarum* Litvinenko (after Litvinenko 1963). **a** ventral view showing horseshoe-shaped eyespot in the sulcus; **b** dorsal view; **c** lateral outline; **d** cross section

Ecology: in red-brown water in swamp in Bohemia, at pH 5.3.
Geographical distribution: Czech Republic.

Note: this species is very similar to *Gymnodinium sphagnicola*, and the two taxa may prove to belong to the same species. They appear to differ mainly in the development of the sulcus.

68. *Gymnodinium rarum* Litvinenko 1963, p. 79, 80, fig. 2 (**Fig. 83**)

Cells obovoid, dorsoventrally compressed, in cross-section bean-shaped. Epicone broadly rounded, lid-like, smaller than the elongated hypocone. Cingulum very slightly descending. Sulcus does not extend onto the epicone, on the hypocone extending to the antapex. Amphiesma thin, without visible structure. Cytoplasm transparent, chloroplasts absent. Nucleus globose, located in the center of the hypocone or slightly closer to the cingulum. Eyespot horseshoe-shaped, bright red. The longitudinal flagellum up to 40 μm long. Movement smooth. Cell length 18 μm, width 14 μm, thickness 10 μm.
Ecology: in spring (March) plankton of temporary water bodies or under the ice.
Geographical distribution: Ukraine.

Note 1: Litvinenko's original illustrations show cells with two longitudinal flagella, a feature typical of planozygotes.

Note 2: *Gymnodinium aestivale* Skvortsov (1968, p, 86, pl. I, fig. 11), described from Manchuria, may be the same species. Skvortsov's drawing is reminiscent of *Gymno-*

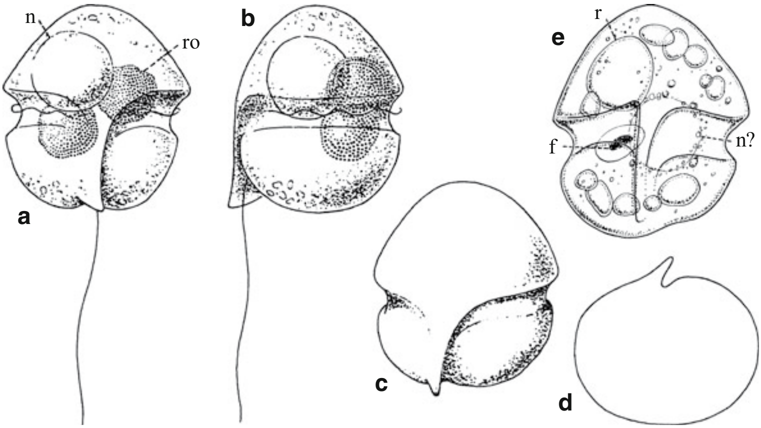

Fig. 84 *Gymnodinium rhinophoron* (Javornický) Litvinenko (**a**-**d** after Javornický 1957; **e** after Javornický 1967). **a**, **b** ventral and lateral views, with the flagella, nucleus (n) and red oil droplets (ro); **c** ventral morphology; **d** cross section; **e** ventral view with ingested food (f), reserve material (r) and the possible location of the nucleus (n)

dinium rarum, showing an epicone much smaller than the hypocone. However, his description does not agree with his figure, as he states that epi- and hypocone are of almost the same size.

69. *Gymnodinium rhinophoron* (Javornický) Litvinenko *in* Matvienko & Litvinenko 1977, p. 241 (**Fig. 84**)

Basionym: *Gymnodinium lantzschii* var. *rhinophoron* Javornický 1957, p. 262, 265, 267, fig. 8a, b, d, e

Epicone rounded conical, longer and wider than hypocone, which is broadly rounded with an invagination at the antapex. Cell barely compressed dorsoventrally. A thin wing or carina extends on the ventral side from the right side of the sulcus and the left side of the epicone to cover the sulcus area and the flagellar bases. At the cell's antapex the wing terminates as a triangular "nose". Cingulum circular. Longitudinal flagellum twice the length of the cell. Chloroplasts absent. Eyespot absent. Nucleus in the epicone. The cytoplasm contains 1-4 large red lipid bodies. Cell length 15–18 μm, width 14–15 μm, thickness 13–14 μm. Cell division in the motile stage.
Ecology: massive development in diluted waste water during spring, in Prague (Javornický 1957).
Geographical distribution: Czech Republic (Javornický).

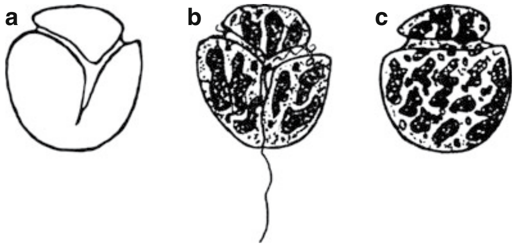

Fig. 85 *Gymnodinium ruttneri* (J. Schiller) Moestrup (after Schiller 1955). **a** outline of cell in ventral view; **b** ventral view; **c** dorsal view

70. *Gymnodinium ruttneri* (J. Schiller) Moestrup *comb. nov.* (**Fig. 85**)

Basionym: *Amphidinium ruttneri* J. Schiller 1955, *Wiss. Arbeiten Burgenland* **9**, p. 28, pl. II, fig. 13

Cells more or less circular in ventral view. Epicone flattened hat-shaped, on the ventral side pointed triangular, hypocone hemispherical. Epicone half the length of the hypocone. Cingulum circular, the ends directed towards the antapex. Sulcus short, narrow, reaching halfway to the antapex. Numerous irregularly band-shaped chloroplasts. Eyespot absent. Lipid bodies near the chloroplasts and free in the cytoplasm. Cell length 16–18 µm, width 15–17 µm.
Ecology: Vienna, Alte Donau, June 1926.
Geographical distribution: Austria.

71. *Gymnodinium saginatum* T. M. Harris 1940, p. 11, figs 2E, F (**Fig. 86**)

Cells ovoid or globular, barely compressed dorsoventrally. Epi- and hypocone both hemispherical, equal in size. Cingulum circular or slightly ascending. Sulcus forms a very slight indentation in the epicone, on the hypocone extends to the antapex. Single pale yellow chloroplast. Eyespot absent. Cell with brown droplets of lipid and larger bodies of unknown nature. Cell length 18–23 µm, width 18–20 µm.

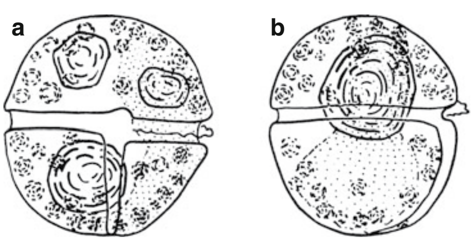

Fig. 86 *Gymnodinium saginatum* T. M. Harris (after Harris 1940). **a** ventral view; **b** lateral view (the large stippled body represents the chloroplast; other bodies are protoplasmic granules and food reserve)

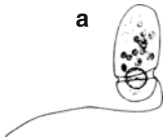

Fig. 87 *Gymnodinium sanctipaulense* (C. E. M. Bicudo & Skvortsov) Moestrup (after Bicudo & Skvortsov 1970). **a** lateral (or perhaps dorsal) view

Ecology: in acid, oligotrophic pool and in peaty pools near Reading, in autumn and winter.
Geographical distribution: England.

72. *Gymnodinium sanctipaulense* (C. E. M. Bicudo & Skvortsov) Moestrup *comb. nov.* (**Fig. 87**)

Basionym: *Katodinium sanctipaulense* C. E. M. Bicudo & Skvortsov 1970, *Rickia* **5**, p. 14, fig. 13

Cells elliptical to subcylindrical, subcircular in transverse section. Epicone semi-elliptical, about 3× the length of the sub-hemispherical hypocone. Cingulum oblique, sulcus not observed. Numerous yellowish to golden, granular chloroplasts, restricted to the epicone. Cell length 13–16 µm, width 6–8 µm.
Ecology: among *Spirogyra* in permanent pool in park in São Paulo, Brazil.
Geographical distribution: Brazil.

73. *Gymnodinium schilleri* (Wołoszyńska) Moestrup *comb. nov.* (**Fig. 88**)

Basionym: *Massartia schilleri* Wołoszyńska 1937, *Arch. Hydrobiol. Rybactwa* **10**, p. 191, pl. IX, fig. 9
Nomenclatural synonym: *Katodinium schilleri* (Wołoszyńska) A. R. Loeblich 1965, p. 16
Cells in ventral view with conical epicone and smaller, narrower hypocone. Cells strongly compressed dorsoventrally, almost disc-shaped. Epicone *ca.* twice the length of the hypocone, and much wider than the latter. Hypocone short and wide,

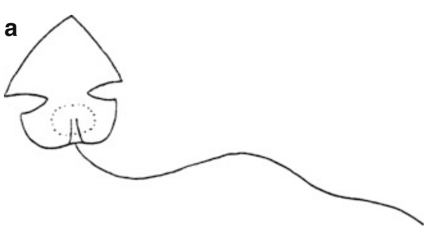

Fig. 88 *Gymnodinium schilleri* (Wołoszyńska) Moestrup (after Wołoszyńska 1937). **a** ventral view (nucleus outlined with dots)

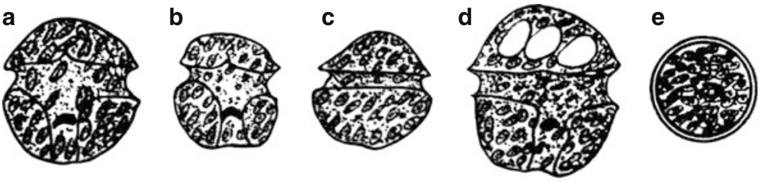

Fig. 89 *Gymnodinium schuettii* J. Schiller (after Schiller 1955). **a**–**d** shape variation, partly the result of the observation conditions (**c** dorsal view; **d**, 3 carotenoid bodies in the epicone); **e** cyst

weakly concave at the antapex. Cingulum very wide. Longitudinal flagellum very long, 2–3× the cell length. Nucleus in the hypocone. No chloroplasts and no eyespot. Cells *ca.* 15 µm long.
Ecology: in winter plankton under the ice in Lake Morskie Oko, Tatra Mountains.
Geographical distribution: Poland (Wołoszyńska).

74. *Gymnodinium schuettii* J. Schiller 1955, p. 32, pl. II, fig. 21 (**Fig. 89**)

Cell rounded-elliptic, somewhat flattened dorsoventrally. Epicone flattened-rounded, much smaller than the hemispherical hypocone. Cingulum circular. Sulcus indented into the epicone, on the hypocone continuing to the antapex, which is slightly retuse. Numerous elliptic, golden-yellow chloroplasts. Eyespot semilunate. Epicone often with 1–3 yellowish-brown lipid droplets. Cell length 13–18 µm, width 10–12 µm. Cysts more or less spherical, yellowish-brown because of the chloroplasts, with lipid droplets of variable size.
Ecology: Alte Donau (common in late June), Lake Neusiedl.
Geographical distribution: Austria.

75. *Gymnodinium simile* Skuja 1956, p. 359, pl. LXI, figs 36–38 (**Fig. 90**)

Cells in ventral view oval to elliptic, flattened dorsoventrally. Epicone rounded conical, hypocone hemispherical, equal in size to the epicone or slightly smaller. Epicone ventrally with triangular extension in the sulcal area. Antapex often

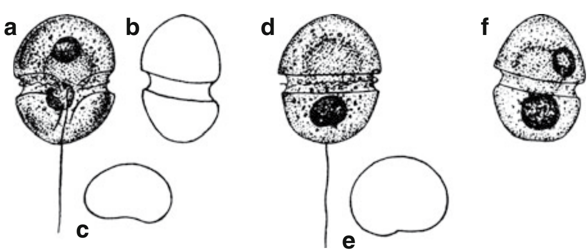

Fig. 90 *Gymnodinium simile* Skuja (after Skuja 1956). **a**–**c** ventral view and lateral and cross-section outlines of one cell; **d**, **e** dorsal view and cross-section outline of one cell; **f** dorsal view

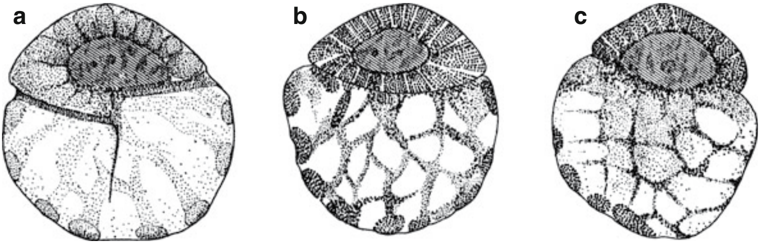

Fig. 91 *Gymnodinium sphagnicola* (W. Conrad) Moestrup & Calado (after Conrad 1943). **a** ventral view, surface; **b**, **c** optical sections

oblique. Cingulum wide, descending, the ends displaced less than one cingulum width and curved slightly towards the antapex. Two parietal yellow chloroplasts, which may be indistinct or even lacking. Eyespot absent. Nucleus central, mostly in the epicone. Cell with food vacuoles containing remains of green algae, detritus, etc. Cell length 13–16 µm, width 9–12 µm, thickness 6–9 µm.
Ecology: lakes in central Sweden, mainly in spring (April–May).
Geographical distribution: Portugal (Nauwerck); Sweden (Skuja).

76. ***Gymnodinium sphagnicola*** (W. Conrad) Moestrup & Calado *comb. nov.* (**Fig. 91**)

Basionym: *Amphidinium sphagnicola* W. Conrad 1943, *Bull. Mus. Roy. Hist. Nat. Belgique* **19** (41), p. 2, text-fig. 1; pl. 1, fig. 3 ("*sphagnicolum*")

Cells globular, slightly longer than wide, not compressed dorsoventrally. Epicone much smaller than hypocone. Cingulum descending, the ends displaced at least two cingulum widths. Sulcus thin and short, does not reach the antapex. With numerous brown chloroplasts, in the epicone arranged in a ring, in the hypocone reticulate, appearing discoid along the cell periphery. Large nucleus in the epicone. Cells moves slowly and trembling. It is fragile, readily loses the flagella, stops and dies. Cell length 28–33 µm, width 25–27 µm.
Ecology: apparently sphagnophilic, collected by squeezing *Sphagnum rubellum* north of Dochamps, Belgium, in November 1942.
Geographical distribution: Belgium.

Note: see comment under *Gymnodinium radiatum*.

77. ***Gymnodinium spirodinioides*** Moestrup & Calado *sp. nov.* (**Fig. 92**)

Originally described as "*Katodinium spirodinioides* Christen 1961, p. 332, fig. 17", a designation not validly published (no type designation). See Latin description in Christen (1961, p. 333). Type: Christen 1961, *Schweiz. Z. Hydrol.* **23**, fig. 17a (here designated).

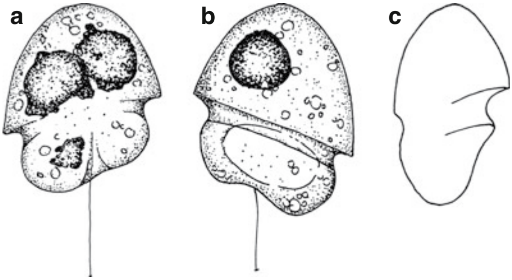

Fig. 92 *Gymnodinium spirodinioides* Moestrup & Calado (after Christen 1961). **a**, **b** ventral and dorsal views; **c** lateral outline

Cells distinctly flattened dorsoventrally. Epicone bell-shaped, wider than the obliquely truncate hypocone, which is rounded laterally and indented at the antapex. Right side of the epicone therefore much higher than left side. Epicone twice the length of the hypocone. Cingulum distinct on the dorsal side, difficult to see on the ventral side, descending, but because of the oblique shape of the cell, the two ends of the cingulum are not displaced. Sulcus very indistinct proximally, becoming more distinct near the antapex. Chloroplasts and eyespot absent. Often larger or smaller food vacuoles in the cytoplasm. Cell length 12–15 µm, width 9–10 µm. Swims very quickly.
Ecology: spring and autumn in peat bogs, shallow ponds, grassy hollows etc., in Cantons Zürich and Jura.
Geographical distribution: Switzerland.

78. *Gymnodinium tatricum* Wołoszyńska 1919a, p. 318; 1919b, p. 198 (**Fig. 93**)

Cells oval, somewhat flattened dorsoventrally, the hypocone more so than the epicone, with broadly rounded epi- and hypocone. Epicone bell-shaped, larger than hypocone. Cingulum circular or descending, but little displaced. Nucleus oval,

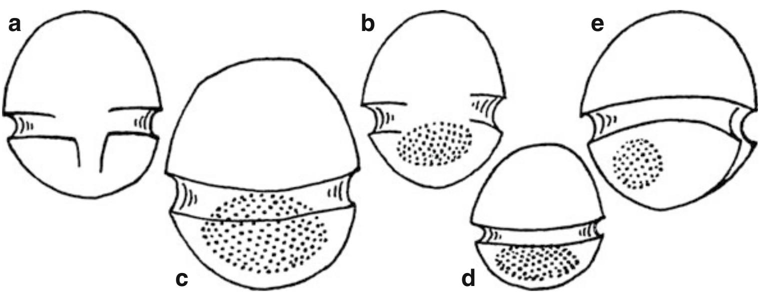

Fig. 93 *Gymnodinium tatricum* Wołoszyńska (after Wołoszyńska 1936). **a**, **b** ventral views; **c**, **d** dorsal views; **e** ventral-right view

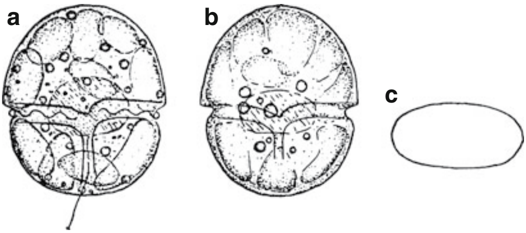

Fig. 94 *Gymnodinium thomasii* Christen (after Christen 1959b). **a**, **b** two cells in ventral view; **c** cross section

dorsally in the hypocone. Cells blood-red or carmine-red due to red pigmentation which obscures the olive-green chloroplasts. Cells without the red pigment not known. Epicone dark-red, hypocone lighter due to the presence of the nucleus. Cell length 20–25(–35) µm, width 24–30 µm. Cysts bright red, spherical with smooth, colorless or yellowish, not very thick wall. Survives freezing in the ice (Wołoszyńska 1937).
Ecology: in several lakes of the Tatra mountains in summer, in small numbers; probably also in other cool, oligotrophic lakes in the area but absent from dystrophic lakes. Also in Lake Neusiedl, Austria.
Geographical distribution: Austria (Schiller); Poland (Wołoszyńska).

79. ***Gymnodinium thomasii*** Christen 1959b, p. 179, 187, fig. 7 ("*Thomasi*") (**Fig. 94**)

Cells broadly ovoid, dorsoventrally distinctly compressed. Epi- and hypocone almost hemispherical, of almost equal length. Cingulum descending, the ends very slightly displaced. Sulcus restricted to the hypocone, almost extending to the antapex. Epicone with small triangular extension ventrally aligned with the sulcus. Many yellow-green, plate-like chloroplasts and strongly refractile spheres. Nucleus in the hypocone. Eyespot absent. Cell length 16–17 µm, width 10–12 µm.
Ecology: Schützenweiher (hunter's meadow pond) near Winterthur, Switzerland, a shallow, relatively eutrophic pond dominated by macrophytes in spring, summer and autumn.
Geographical distribution: Switzerland.

Note: specimens identified as belonging to this species were reported from Nagano Prefecture, Japan (Senzaki & Horiguchi 1994); they differed from Christen's type by being only slightly compressed and having a nucleus occupying most of the epicone, and may represent an independent species.

80. ***Gymnodinium thompsonii*** Kisselev *ex* Moestrup & Calado *nom. nov.* (**Fig. 95**)

Replaced synonym: *Gymnodinium cruciatum* R. H. Thompson 1951, *Lloydia* **13**, p. 282, figs 103, 104, *nom. illeg.* [non *Gymnodinium cruciatum* (Massart) J. Schiller 1932, p. 350]

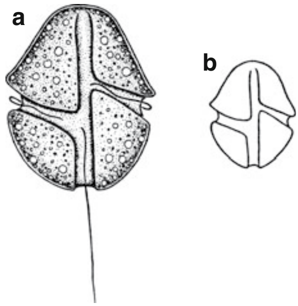

Fig. 95 *Gymnodinium thompsonii* Kisselev *ex* Moestrup & Calado (after Thompson 1951). **a**, **b** ventral view and general outline of the same cell

"*Gymnodinium Thompsonii* Kisselev 1954, p. 114" intended as a *nom. nov.*, but not validly published for lack of full and direct reference to place of publication of replaced name.

Cell ovoid. Epi- and hypocone of same size. Epicone rounded conical, hypocone hemispherical with indentation at the antapex. The sulcus extends from apex to antapex. Cingulum descending, the ends displaced several cingulum widths. Cells without chloroplasts. Eyespot absent. Cytoplasm with granular contents and sometimes a few large food vacuoles. Cell length 19–21 µm, width 14–16 µm.
Ecology: in Horseshoe Lake, a small lake in Lawrence, Kansas.
Geographical distribution: USA, KS (Thompson).

81. ***Gymnodinium titubans*** Christen 1958b, p. 70, fig. 3 (**Fig. 96**)

Cells longer than wide, more or less elongate bell-shaped, barely flattened dorsoventrally. Epicone broadly rounded, hypocone with slightly converging sides, antapex oblique. Cytoplasm colorless, chloroplasts absent. Cingulum slightly descending, the two ends barely displaced. Sulcus extends onto the epicone as a short narrow fissure, which is directed anteriorly. On the hypocone it is narrow but it widens antapically. Nucleus in the epicone. Very small eyespot in the hypotheca, sometimes not visible (true eyespot?). Food vacuoles present. Cells 17–20 µm long, 13–15 µm wide.
Ecology: plankton, Lake Hausersee (Switzerland), in September. Cells swim rather quickly, but irregularly. They appear to be fragile and soon die under the coverslip.
Geographical distribution: Switzerland.

82. ***Gymnodinium triceratium*** Skuja 1939, p. 153, pl. X, figs 35–38 (**Fig. 97**)

Taxonomic synonyms: *Gyrodinium asymmetricum* Wołoszyńska 1937, p. 192, pl. IX, figs 7, 8 (in *Gymnodinium*, the epithet *asymmetricum* is unavailable because of the existence of *Gymnodinium asymmetricum* Massart 1920, p. 133, fig 22 ["*asy-*

Fig. 96 *Gymnodinium titubans* Christen (after Christen 1958b). **a** ventral view

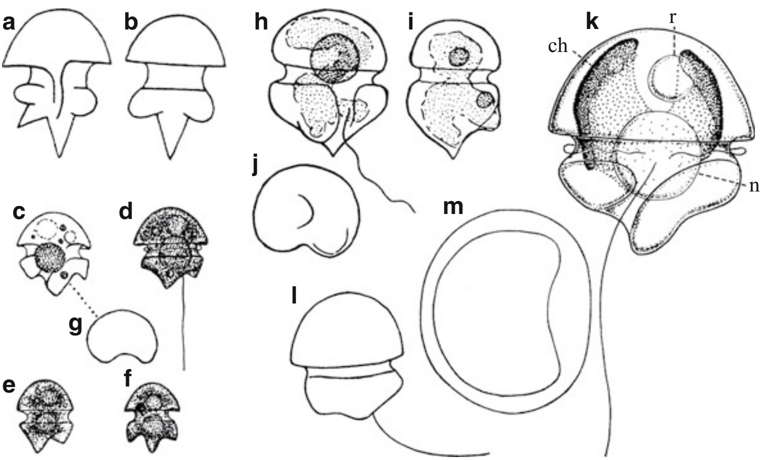

Fig. 97 *Gymnodinium triceratium* Skuja (**a**, **b** after Wołoszyńska 1937; **c**–**g** after Skuja 1939; **h**–**j** after Harris 1940; **k**–**m** after Javornický 1967). **a**, **b** ventral and dorsal outlines of two cells; **c** ventral view; **d**–**f** dorsal views; **g** cross section; **h**–**j** ventral, lateral and antapical views; **k**–**m** ventral, dorsal and antapical views (ch, chloroplast; n nucleus; r, reserve material)

metricum"]); *Gymnodinium impar* T. M. Harris 1940, p. 9, figs 2J–L; *Gymnodinium armoricanum* Villeret 1953, p. 71, fig. 2

Cells very slightly dorsoventrally compressed, epi- and hypocone of almost equal size. Epicone nearly hemispherical, longer and slightly wider than hypocone. Hypocone asymmetric, with two short bulges to the left and right and two longer

pointed extensions, one extending from the right dorsal side, the other and longer approximately at the antapex. Cingulum descending, displaced *ca.* half the cingulum width. Sulcus extends along the right side of the middle horn to the posterior cell margin. On the epicone it forms a shallow impression. Posterior flagellum 1.5–2× cell length. Cell surface smooth, without visible ornamentation. Three to five parietal, plate-like, irregular chloroplasts of yellow-brown color. Eyespot not observed but the epicone sometimes contains 1–2 red, eyespot-like bodies. Nucleus relatively large, located below the cell middle. Swimming rapid and jumping or a more slow rotation. A peduncle-like structure has been seen to emanate from the cingular region. Apparently mixotrophic. Cells 10–17 μm long, 6–13 μm wide and 7–10 μm thick.
Ecology: ponds in forest, peat bogs and other humic waters; winter and spring at 10–15 ˚C. Also reported from a swimming pool in Prague (Popovský 1990).
Geographical distribution: Czech Republic (Javornický; Popovský); Denmark (Nygaard); England (Harris); France (Villeret); Latvia (Skuja); Poland (Wołoszyńska). USA, MD (Thompson).

Note: cells were maintained in crude cultures for some time by Wołoszyńska and multiplied in the culture, the cell morphology remaining unchanged. Cultures were also obtained by Villeret.

83. *Gymnodinium tridentatum* J. Schiller 1932, p. 422, fig. 443 (**Fig. 98**)

Cells pointed ovoid, not compressed dorsoventrally. Epicone of the same size or somewhat longer than the hypocone. Epicone rounded conical, the sides terminating into 3 anterior teeth, of which the middle tooth is the longest. Hypocone ovoid to conical. Cingulum deep, the anterior edge somewhat overhanging, the two ends of the cingulum hardly or only very slightly displaced relative to each other. Sulcus extends onto the epicone but does not reach the apex. On the hypocone the sulcus is V-shaped, and does not reach the antapex. Chloroplasts and eyespot absent. Cytoplasm colorless. Cell length 35–41 μm, width 25–30 μm.
Ecology: in lake Attersee, Austria, in August–September 1930, from surface to 30-m depth.
Geographical distribution: Austria.

Note 1: *Gymnodinium austriacum* is similar in general morphology but does not show the apical "trident".

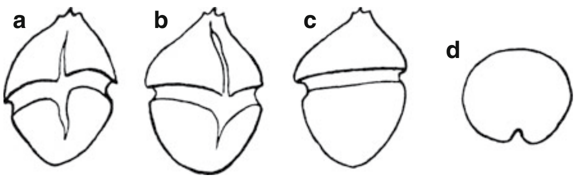

Fig. 98 *Gymnodinium tridentatum* J. Schiller (after Schiller 1932). **a**, **b** ventral views; **c** dorsal view; **d** cross section

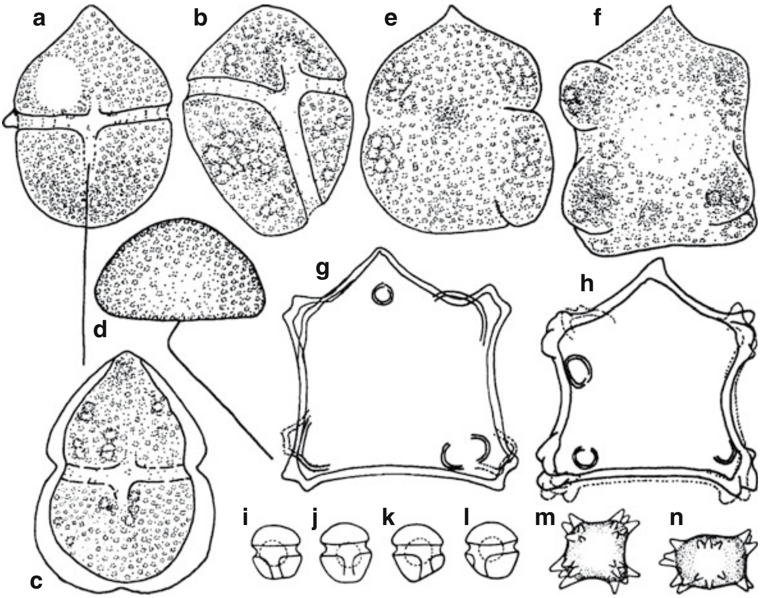

Fig. 99 *Gymnodinium tylotum* Mapletoft, M. Montgomery, J. Waters & P. Wells (**a**–**h** after Mapletoft *et al.* 1966; **i**–**n** after Nygaard 1950). **a** ventral view of motile cell; **b** ventral view of cell with spiraling cingulum; **c** plasmolyzed cell; **d** antapical view; **e**, **f** two stages in cyst formation; **g**, **h** mature cysts; **i**–**n** *Gymnodinium paradoxum* f. *astigmosum* Nygaard, vegetative cells (**i**–**l**) and two views of cyst (**m**, **n**)

Note 2: although the cingulum ends are not strongly displaced this species shows some similarities with the genus *Gyrodinium*, the anterior teeth suggesting the elliptical apical furrow and the central ridge typical of that genus. The long extension of the sulcus onto the epicone is another character of *Gyrodinium*, which differs, however, by having longitudinally striated cells.

84. *Gymnodinium tylotum* Mapletoft, M. Montgomery, J. Waters & P. Wells 1966, p. 54, fig. 1 (**Fig. 99**)

Nomenclatural synonym: *Woloszynskia tylota* (Mapletoft, M. Montgomery, J. Waters & P. Wells) B. T. Bibby & J. D. Dodge 1972, p. 95

Cells ovoid, epicone slightly smaller than hypocone. Epicone conical, hypocone rounded. Hypocone often dorsoventrally compressed towards the posterior end. Cingulum circular or very slightly descending. Sulcus extends onto the epicone but details unknown. Numerous yellow-brown discoid chloroplasts in the cell periphery. Vacuole (nucleus?) in the epicone. Brown body often present. Eyespot absent.

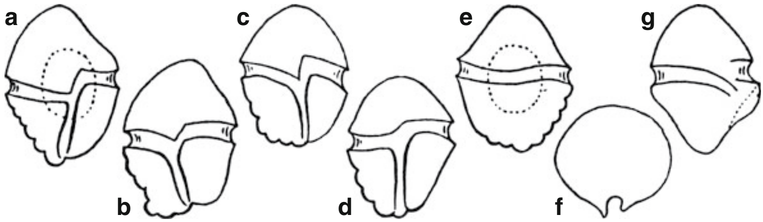

Fig. 100 *Gymnodinium undulatum* Wołoszyńska (after Wołoszyńska 1925). **a**–**d** ventral views; **e** dorsal view; **f** apical view; **g** right-ventral view

Longitudinal flagellum nearly the same length as the cell. Cell length 30–35 µm, width 25–30 µm.
Resting spore square in face view, 40–50 µm wide, thickness about 2/3 of the width. All corners with two short spines, variable, sometimes knobbed, sometimes somewhat bilobed. With a simple short spine on one side, formed by the apex of epicone of the motile cell. Corners on the opposite side occasionally with more than two lobes. Spore wall transparent and colorless, *ca.* 5 µm thick. During spore formation the planozygote gradually enlarges and becomes broader, then square with a pointed top.
Ecology: in pools in Berkshire, England, in late January and February in large numbers causing brown water, forming hypnospores. The cells had disappeared in early May.
Geographical distribution: England; Austria? (see note 3).

Note 1: the morphology of the resting spore indicates that this interesting species does not belong in *Gymnodinium* but in a separate genus, perhaps together with *Gymnodinium chiastosporum*. The taxon described as *Gymnodinium paradoxum* f. *astigmosum* Nygaard (1945, p. 52, "*astigmosa*") may belong in the same group; its cysts were described as flatly cubiform with 3 obtuse, short spines at each of the 8 edges (Nygaard 1950).

Note 2: the resting spores illustrated by Bibby & Dodge (1972) are very different, indicating that the species identified by these authors as *G. tylotum* is different, and perhaps represents a species of *Tovellia* without an eyespot.

Note 3: cysts from Waldviertel, Austria, illustrated by Wawrik (1986, fig. 7) and identified as *Woloszynskia veris*, appear to be identical to *Gymnodinium tylotum*.

85. *Gymnodinium undulatum* Wołoszyńska 1925b, p. 54, 62, figs 3E–K (**Fig. 100**)

Cells ovoid elongate. Epicone somewhat smaller than hypocone, slightly pointed or rounded. Hypocone strongly dorsoventrally compressed, in lateral view pyramidal with concave sides. Right side of the hypovalve strongly undulated. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus on the hypocone only, extending to the antapex. Sulcus is bounded by lists on each side, the list on the left side largest. Chloroplasts brown. Structure of periplast unknown. Cell length *ca.* 35 µm, width *ca.* 22 µm.

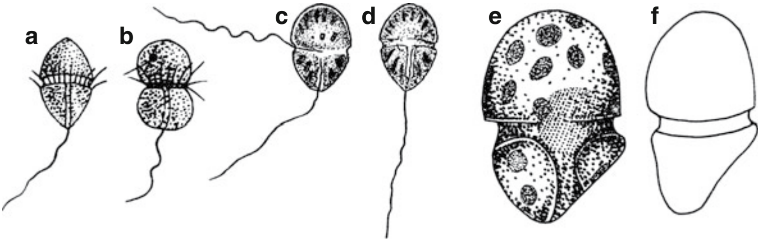

Fig. 101 *Gymnodinium varians* Maskell (**a**, **b** after Maskell 1888; **c**, **d** after Klebs 1912; **e**, **f** after Popovský 1971). **a** common shape; **b** more usual shape; **c**, **d** two swimming cells (as *Gymnodinium minimum* G. A. Klebs); **e** ventral view; **f** lateral view

Ecology: ponds, reported only on one occasion. Winter form.
Geographical distribution: Ukraine (Wołoszyńska).

Note: according to Huber-Pestalozzi (1950) and Schiller (1954a) this description was possibly based on teratological specimens. In contrast, Pochmann (1957) regarded the undulated surface as a good character.

86. *Gymnodinium varians* Maskell 1888, p. 7, pl. I, fig. 9 (**Fig. 101**)

Taxonomic synonym: *Gymnodinium minimum* G. A. Klebs 1912, p. 396, 439, text-fig. 7A, B (not *Gymnodinium minimum* Lantzsch 1914)

Cells ovoid or somewhat cone-shaped. Epicone semicircular, hypocone larger, conical. Cells slightly compressed dorsoventrally. Ends of cingulum little displaced. Sulcus does not extend onto the epicone. Chloroplasts not mentioned but cells are green (Maskell) or dark brown (Klebs) and Klebs's drawings show cell structures that seem to be radiating chloroplasts. Eyespot absent. Cell length 8–17 µm, width 6–8 µm. Cyst oval or spherical.
Ecology: pond in Botanical Garden, Indonesia; drinking-water reservoir in Bohemia.
Geographical distribution: Czech Republic (Popovský). Indonesia (Klebs); North Island, New Zealand (Maskell).

Note: the New Zealand material is the largest (17 µm) while the Indonesian and Czech materials are smaller (8–12 µm long and 6–8 µm wide in Indonesia, 9 µm long and 5 µm wide in the Czech material; Popovský 1971b).

87. *Gymnodinium vernum* Moestrup *nom. nov.* (**Fig. 102**)

Replaced synonym: *Katodinium vernale* Christen 1961, *Schweiz. Z. Hydrol.* **23**, p. 334, fig. 20 (non *Gymnodinium vernale* Skvortsov)

Epicone bell-shaped, flattened-rounded, 2–3× the length of the narrower hypocone. Cells strongly compressed dorsoventrally. Cingulum descending, the ends very slightly displaced. Sulcus does not extend onto the epicone. Several small or

Fig. 102 *Gymnodinium vernum* Moestrup (after Christen 1961). **a** ventral view, with chloroplasts and ingested food

medium-large, disc-shaped, inconspicuous chloroplasts, which are green or yellowish-green. Eyespot absent. Nucleus in the hypocone or somewhat lateral in the cell. Cell length 14–17 µm, width 11–16 µm.
Ecology: shallow rainwater pools near Hausersee, Switzerland, at pH 4–5.5.
Geographical distribution: Switzerland.

Note: material from Maryland (Thompson 1947, as *Massartia musei*) agrees in size (19 µm long, 18 µm wide, 11 µm thick) and in the lack of an eyespot. It also agrees in cell shape. However, Thompson reported the presence of many dark-brown chloroplasts, and his material may therefore belong to another species.

88. ***Gymnodinium vierae*** (Javornický) Moestrup *comb. nov.* (**Fig. 103**)

Basionym: *Katodinium vierae* Javornický 1970, *Svensk Bot. Tidskr.* **64**, p. 300, figs 1D–G

Cells ovoid or obovoid, epicone rounded mitra-shaped, hypocone obliquely cut, indented centrally. Epicone slightly larger than hypocone. Cells not flattened dorsoventrally. Cingulum slightly oblique, but the ends not displaced. Two-three green-yellow parietal chloroplasts, one or two in the epicone and one in the hypocone. Distinct eyespot underneath the sulcus. Cells 14 µm long and 9 µm wide.
Ecology: oligotrophic pools.
Geographical distribution: Denmark (Ettl); Northern Sweden (Javornický).

89. ***Gymnodinium viridaliut*** J. Schiller 1955, p. 38, pl. IV, fig. 36 (**Fig. 104**)

Cells roundish to elliptic-ovoid, round to elliptic in cross section. Epicone hemispherical, as wide as or slightly narrower than hypocone. Epi- and hypocone of nearly equal size. Cingulum circular, the ends curving towards the antapex. Sulcus restricted to the hypocone, extending to the antapex, here becoming very narrow. Chloroplasts dark green, elongate, parallel, covering the entire cell surface. Eyespot absent. Cells 28–42 µm long, 23–32 µm wide. Cells multiply by transverse division and apparently also by formation of (8?) spores within the cell.

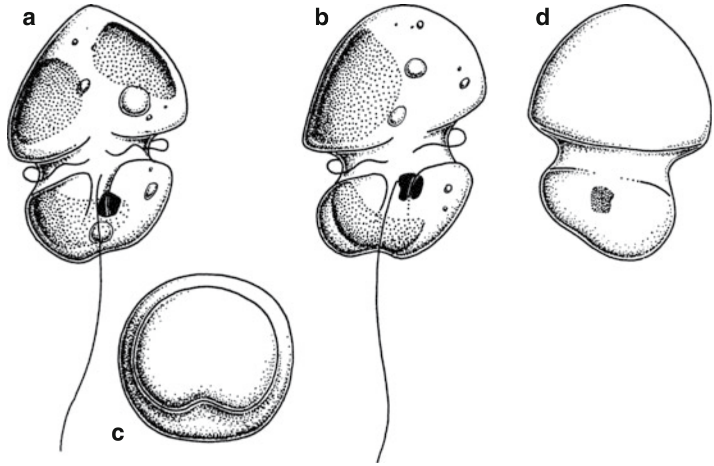

Fig. 103 *Gymnodinium vierae* (Javornický) Moestrup (after Javornický 1970). **a**, **b** ventral views; **c** antapical view; **d** dorsal outline, with the position of the eyespot marked

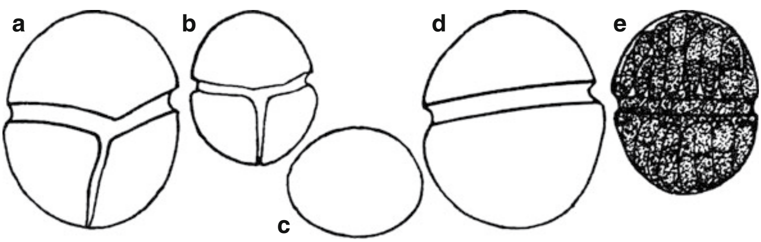

Fig. 104 *Gymnodinium viridaliut* J. Schiller (after Schiller 1955). **a**, **b** ventral views; **c** cross section; **d**, **e** dorsal views, with chloroplasts represented in **e**

Ecology: in highly eutrophic ponds near Lake Neusiedl, Austria, January, also under the ice.
Geographical distribution: Austria.

90. ***Gymnodinium waltzii*** Baumeister 1957a, p. 2, 18, Abb. 2, fig. 7 ("*Waltzi*") (**Fig. 105**)

Cells ovoid, the epicone bell-shaped and 1/3 longer than the hemispherical hypocone. Cell dorsoventrally compressed, bean-shaped in transverse section. Sulcus apparently forming a triangle in the epicone. Nucleus in the epicone. Cell contains orange grains and colorless crystals, but apparently no chloroplasts. Eyespot not

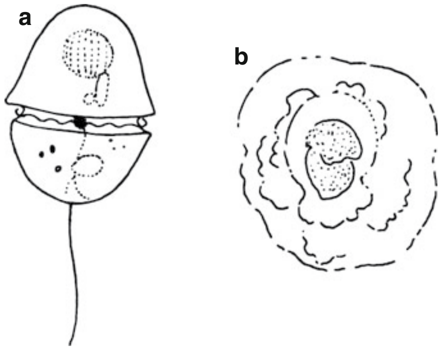

Fig. 105 *Gymnodinium waltzii* Baumeister (after Baumeister 1957a). **a** swimming cell, dorsal view (?); **b** cell surrounded by abundant mucilage (dying cell?)

reported. Cell length 34–36 µm, width 25–28 µm. Dying cells were observed surrounded by copious amounts of mucilage.
Ecology: together with characeans in lake in Bavaria.
Geographical distribution: Germany.

Note: this very incompletely described species appears to differ from *Gymnodinium mitratum* mainly in the position of the nucleus.

91. *Gymnodinium wawrikae* J. Schiller 1955, p. 36, pl. IV, fig. 32 (**Fig. 106**)

Taxonomic synonym: *Gymnodinium amphiconicoides* J. Schiller 1955, p. 33, pl. III, fig. 25

Cells rounded-spherical, barely compressed dorsoventrally. Epicone broadly rounded-very slightly conical, equal in size to the hemispherical or slightly conical hypocone. Cingulum circular, wide, the ventral side of the epicone forming a small tooth in the cingulum. Sulcus equally wide. Chloroplasts yellowish- to greenish-brown, disc-shaped. Oval eyespot in the sulcus. Cell length 15–24 µm, width 15–22 µm.
Ecology: Ruster Kanal, Lake Neusiedl, May 1950, 1951 (Schiller 1955); swamp-pools among vegetation and in fishponds in Czech Republic (Javornický 1967); small water reservoir (Senzaki & Horiguchi 1994).
Geographical distribution: Austria (Schiller); Czech Republic (Javornický). Japan (Senzaki & Horiguchi).

92. *Gymnodinium wigrense* Wołoszyńska 1925b, p. 54, 62, figs 3A–D (**Fig. 107**)

Cells elongate, very slim, almost twice as long as wide. Epicone smaller than hypocone, conical, at the apex often somewhat oblique and thickened. Hypocone wider than epicone, with almost parallel sides. At the antapex often a tiny tooth. Cingulum very slightly descending. Sulcus deep and narrow, on the epicone reaching

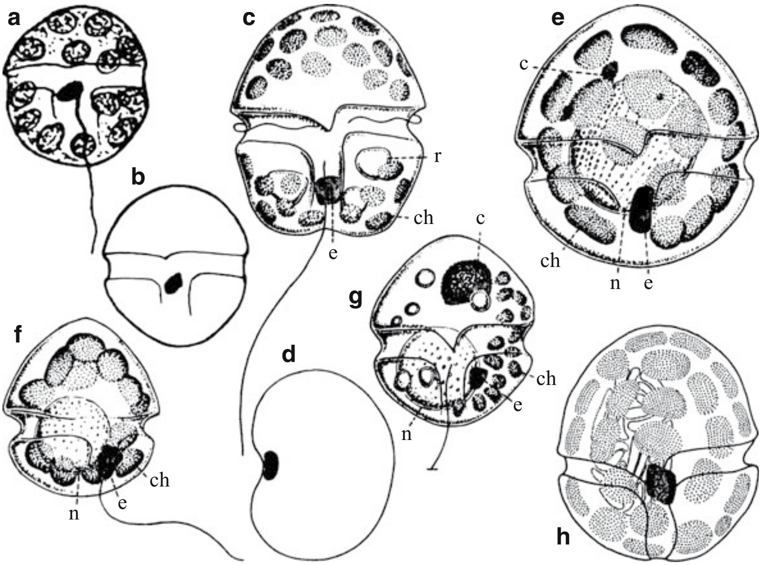

Fig. 106 *Gymnodinium wawrikae* J. Schiller (**a**, **b** after Schiller 1955; **c**–**g** after Javornický 1967; **h** after Senzaki & Horiguchi 1994). **a** ventral view; **b** ventral outline; **c**, **d** ventral view and cross section of hypocone of the same cell; **e**–**h** ventral views (c carotenoid corpuscle; ch, chloroplast; e eyespot; n nucleus; r, reserve material)

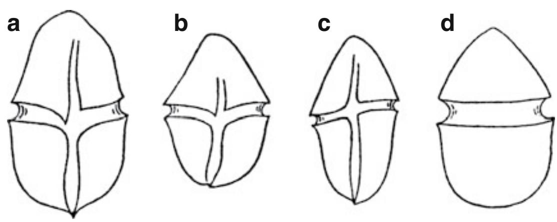

Fig. 107 *Gymnodinium wigrense* Wołoszyńska (after Wołoszyńska 1925). **a**–**c** ventral views; **d** dorsal view

halfway to the apex or more, on the hypocone reaching the antapex. Cell cover very thin. Chloroplasts light brown or light reddish brown. Nucleus in the cell center, short and thick, almost kidney shaped. Eyespot absent. Cells often surrounded by layer of mucilage. Form and size of the cells highly variable. Cell length 35–40 µm, width 22 µm, but cells often smaller. Temporary cysts surrounded by mucilage, resting cysts unknown.
Ecology: in winter and spring in the plankton of Lake Wigry, Poland.
Geographical distribution: Poland.

Genus 2. *Nusuttodinium* Y. Takano & T. Horiguchi *in* Takano *et al.* 2014, p. 773

Type species: *Nusuttodinium latum* (M. Lebour) Y. Takano & T. Horiguchi *in* Takano *et al.* 2014, p. 773 (marine)

Permanent chloroplasts absent but blue-green (rarely brown or yellow-brown) chloroplast-like bodies usually present, derived from phagocytosis of blue-green (rarely brown or yellow) cryptomonads (kleptochloroplasts). Starving cells colorless. Cell size very variable, depending on the amount of prey present. Well-fed cells with up to 20 food vacuoles are larger than the numbers given below. This variation makes definition of species difficult and future studies will most likely find some of the species names included below to be synonymous. With fishhook-shaped apical groove running in an anticlockwise direction around the cell apex (usually visible only in the electron microscope). In a recently described marine species, kleptochloroplastidy has been lost and the cells are permanently colorless. Cells differ internally from *Gymnodinium* by the nucleus having typical eukaryotic nuclear pores rather than pores leading from the nucleoplasm into nuclear chambers. A palmelloid stage has been described in some species, the cells being spherical or ovoid and surrounded by mucilaginous material. Cell division may take place in the motile stage and in the palmelloid stage. Species of *Nusuttodinium* were formerly included in *Amphidinium* and *Gymnodinium*.

Key to species of *Nusuttodinium* occurring in fresh water:

1a Epicone twice the length of the hypocone or longer 2
1b Epicone less than twice the length of the hypocone 4
2a Epicone three times the length of the hypocone, wider than hypocone .... 8. *N. crassifilum*
2b Epicone twice the length of the hyposone, of similar width 3
3a Cell length *ca.* 13 µm, nucleus central, epicone bell-shaped, eyespot absent . ... 7. *N. campaniforme*
3b Cell length 16–20 µm, nucleus in the epicone, epicone hemispherical, eyespot present .... 15. *N. montanum*
4a Hypocone at least twice the length of the epicone 10
4b Hypocone less than twice the length of the epicone 5
5a Cells longer than 18 µm 6
5b Cells shorter than 16 µm 8
6a Cells light-green, eyespot present; cells 29–39 µm long .... 18. *N. viride*
6b Cells blue-green, eyespot absent; cells 18–49 µm long 7
7a Cells rounded posteriorly .... 2. *N. aeruginosum*
7b Cells pointed posteriorly .... 1. *N. acidotum*
8a Cells *ca.* 9 µm long .... 9. *N. cyaneum*
8b Cells 11–16 µm long 9
9a Under the ice, cold-water species .... 11. *N. hiemale*
9b Tropical species (India) .... 12. *N. indicum*
10a Cells less than 10 µm long 11
10b Cells at least 14 µm long 13

11a Sulcus terminates into two spine-like wings .... 4. *N. bidentatum*
11b Antapex rounded, no wings present 12
12a Hypocone 3× the length of the epicone, eyespot present ...... 16. *N. oculatum*
12b Hypocone twice the length of the epicone, eyespot absent .. 5. *N. caerulescens*
13a Epicone half the width of the hypocone and much shorter .. 17. *N. phthartum*
13b Epi- and hypocone equally wide or epicone slightly narrower than hypocone 14
14a The ends of the cingulum curve towards the antapex .... 13. *N. lacunarum*
14b The cingulum more or less transverse 15
15a Hypocone conical, rounded at the end .... 10. *N. eucyaneum*
15b Hypocone hemispherical, elongate or polygonal, sometimes excavate 16
16a Sulcus extends onto the epicone .... 3. *N. amphidinioides*
16b Sulcus does not extend onto the epicone 17
17a Cells excavate at the antapex, as long as wide .... 6. "*Amphidinium caerulescens*"
17b Cells not excavate, longer than wide .... 14. *N. limneticum*

1. *Nusuttodinium acidotum* (Nygaard) Y. Takano & T. Horiguchi *in* Takano *et al.* 2014, p. 773 (**Fig. 108**)

Basionym: *Gymnodinium acidotum* Nygaard 1950, p. 155, fig. 95

Epi- and hypocone similar in length, or epicone slightly smaller than hypocone. Cells barely (original description) or somewhat dorsoventrally flattened, in dorsal or ventral view pear-shaped. Epicone rounded-conical, hypocone acuminate with short, bulb-like antapical projection. Late in the season or in old cultures cells lose the projection. Sulcus reaches the antapex and extends for one half to 2/3 the length of the epicone and continues to the apical groove. The ends of the cingulum not displaced, or displaced up to one cingulum width. Nucleus central. Originally described from natural collections to possess 4–7 discoid (klepto-) chloroplasts, but

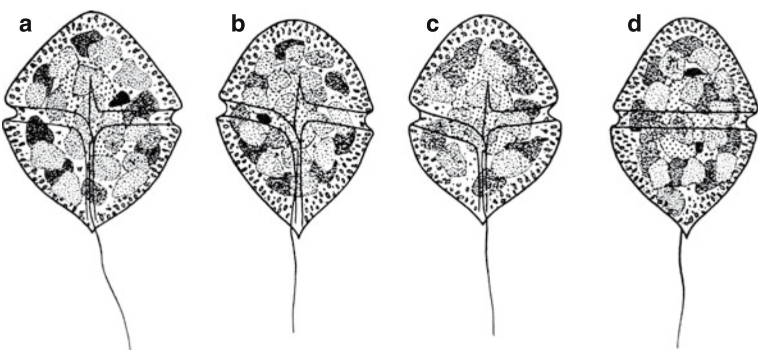

Fig. 108 *Nusuttodinium acidotum* (Nygaard) Y. Takano & T. Horiguchi (after Nygaard 1950). **a**–**c** ventral views; **d** dorsal view

starved cells from Missouri became colorless in culture and could only be maintained in culture by feeding with the cryptomonad *Chroomonas* (Fields & Rhodes 1991). Eyespot absent. Cell length 25–40 µm, width 20–30 µm.
Rounded cysts described from cultures in Missouri. Germination of cysts from soil samples resulted in colorless cells which remained motile for a few days and then disappeared. Both colored and colorless cells positive phototactic (Fields & Rhodes 1991).
SEM: Farmer & Roberts (1990b).
TEM: Farmer & Roberts (1990a, 1990b).
DNA data: Takano *et al.* (2014).
Ecology: described from a eutrophic, plankton-rich, bird-polluted pond in central Jutland, Denmark, in September 1944 (pH 8.5) and subsequently in Lake Sockton, Missouri, 1987 and 1989, in an area where flocks of Canada geese and pelicans were conspicuous. Colorless cells from the latter collections remained colorless in culture and died in less than a week, while pigmented cells grew for 10 days and then declined. The cells ingested *Chroomonas* spp but not *Cryptomonas ovata* or *C. ozolini*.
Geographical distribution: very commonly mixed up with *N. aeruginosum*, from which it differs in its distinctly pointed hypocone. Cells with pointed hypocone have presently been reported from Denmark (Nygaard), USA, MO (Fields & Rhodes), LA, (Farmer & Roberts), and Japan (Xia *et al.*; Takano *et al.*).

2. *Nusuttodinium aeruginosum* (F. Stein) Y. Takano & T. Horiguchi *in* Takano *et al.* 2014, p. 773 (**Fig. 109**)

Basionym: *Gymnodinium aeruginosum* F. Stein 1883, pl. II, figs 19–22
Taxonomic synonyms: *Gymnodinium p-dohrnii* Wawrik 1956, pp 292, 293, Abb. 1, figs a–e and 1–5 ("*P. Dohrni*"); *Gymnodinium autumnale* Skvortsov 1968, p. 88, pl. II, fig. 2 ≡ *Gymnodinium manchuriense* Thessen, D. J. Patterson & Sh. Murray 2012, p. 28 ("*manchuriensis*"), *nom. illeg.* (superfluous)

Cells elongate ovoid, strongly (in the original illustrations) or somewhat dorsoventrally flattened. Epi- and hypocone of almost the same length, rounded-campanulate. Hypocone also campanulate, the antapex sometimes slightly indented. The ends of the cingulum not or only very slightly displaced. Sulcus extends onto the epicone for *ca.* half the length of the epicone, followed by the apical groove. On the hypocone it reaches one half to 2/3 the length of the hypocone. Eyespot absent. Nucleus situated in the anterior or central part of the cell. Often immobile, surrounded by mucilage. Cell length 18–49 µm, width 12–36 µm. Resting cysts ellipsoidal to slightly bean-shaped reported by Wawrik (1956) from Austria, surrounded by fine to firm mucilaginous material.
SEM: Hansen & Flaim (2007).
TEM: Wilcox & Wedemayer (1984), Schnepf *et al.* (1989).
DNA data: Takano *et al.* (2014).
Ecology: Typically in macrophyte- and humus-rich ponds but also in clearwater lakes. Prefers organic compounds and high concentrations of chloride, sulphate and phosphate. Often in dystrophic waters (Skuja 1948), pH optimum given as 7.2 by Höll (1928), but also present at higher pH (8.5) and in slightly acid ponds.

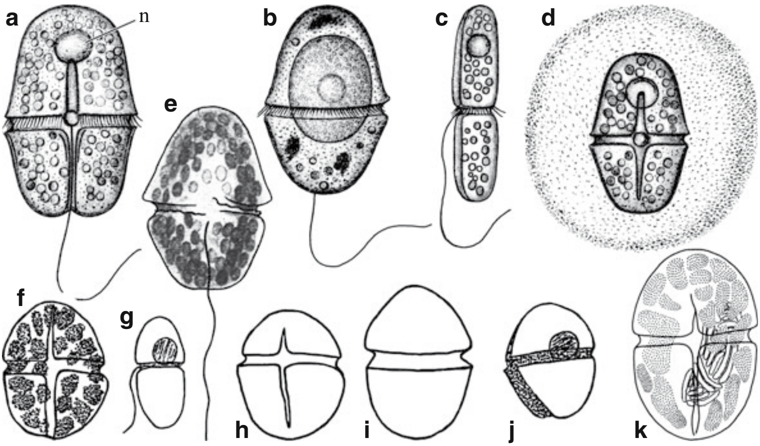

Fig. 109 *Nusuttodinium aeruginosum* (F. Stein) Y. Takano & T. Horiguchi (**a**–**d** after Stein 1883; **e** after Schilling 1913; **f**–**j** after Wawrik 1956, as *Gymnodinium p-dohrnii*; **k** after Senzaki & Horiguchi 1994). **a**–**c** ventral, dorsal and lateral views, respectively (n nucleus); **d** immobile cell enveloped in mucilage; **e** ventral view; **f** ventral view; **g** lateral view; **h**–**j** ventral, dorsal and left ventral–lateral views; **k** ventral view

Geographical distribution: Austria (Wawrik); Czech Republic (Stein); Denmark (Nygaard); England (Lewis & Dodge); Finland (Levander); Germany (Schnepf *et al.*); Italy (Barsanti *et al.*; Hansen & Flaim), Sweden (Skuja). USA, MD (Thompson). Brazil (Cavalcante *et al.*). Manchuria, China (Skvortsov); Japan (Takano et al.). Australia, New South Wales (Playfair), Tasmania (Ling *et al.*), Queensland (McLeod *in* Ling. *et al.*). New Zealand (Thompson).

Note 1: the most commonly reported blue dinoflagellate from fresh water and usually identified as *G. aeruginosum* or *G. acidotum*. The cells vary somewhat in morphology and it has been suggested that *N. aeruginosum*, *N. acidotum* and *N. eucyaneum* belong to the same species. This question is still open and the species concept is presently uncertain. It therefore also applies to information about ecology and geographic distribution. When first illustrated by Stein from the Czech Republic, Stein included as one of his four figures a cell which is extremely dorsoventrally flattened. Cells resembling this figure have subsequently been reported from Austria (Wawrik 1956, as *Gymnodinium p-dohrnii*), Toscana, Italy (Barsanti *et al.* 2009, as *G. acidotum*), and perhaps Manchuria, China (Skvortsov 1968, as *G. autumnale*). Lewis & Dodge (2002) also mention that cells of this species are strongly dorsoventrally flattened.

Note 2: in many reports of "*Gymnodinium aeruginosum*" identification to species level is not possible. This includes Finland (Levander 1894), Australia (Playfair 1920), Sweden (Skuja 1948, 1964).

Note 3: the material from Maryland, USA, identified as *G. aeruginosum* by Thompson (1951) differs in the epicone being much smaller than the hypocone (as in *N. eucya-*

neum). During cell division in the American material the cell stopped swimming and secreted a thick gelatinous envelope. Two or four daughter cells were produced by divisions within the gel.

3. *Nusuttodinium amphidinioides* (Geitler) Y. Takano & T. Horiguchi *in* Takano *et al.* 2014, p. 773 (**Fig. 110**)

Basionym: *Gymnodinium amphidinioides* Geitler 1924, p. 110, figs a–f
Nomenclatural synonyms: *Amphidinium amphidinioides* (Geitler) J. Schiller 1932, p. 278 ≡ *Amphidinium geitleri* Huber-Pestalozzi 1950, p. 105, *nom. illeg.* (superfluous substitute name)
Taxonomic synonyms: *Amphidinium vigrense* Wołoszyńska 1925a, pp 3, 8, fig. 1; *Amphidinium coprosum* Baumeister 1943a, p. 337, figs 3b, 3c; *Amphidinium bourrellyi* Wawrik 1983, p. 790, figs 7e, 7f

Cells elongate-elliptic, up to 2 1/2× as long as wide. Epicone less than 1/3 the length of the hypocone, rounded-conical, hypocone with parallel sides and rounded antapex. Barely flattened dorsoventrally. Cingulum weakly descending or ends not displaced. Sulcus extends to about halfway up the epicone. On the hypocone it widens posteriorly but does not reach the antapex. Cells colorless or with blue-green or yellow-brown chloroplasts, separated from the cytoplasm by a hyaline layer (kleptochloroplasts). Eyespot sometimes reported to be present. Nucleus at the level of the cingulum. Cell length 15–35 µm, epicone 11–14 µm wide, hypocone 15–22 µm wide, the epicone sometimes slightly narrower than the hypocone, thickness 10–13 µm. Immotile stage of spherical or ovoid cells, surrounded by thick mucilaginous material.
SEM: Takano *et al.* (2014).
TEM: Wilcox & Wedemayer (1985; but see note 1 below).
DNA data: Takano *et al.* (2014).
Ecology: in calcareous ponds and bogs. In peat-bog in Czech Republic. Phagotrophy of blue-green or brown cryptophytes demonstrated (Takano *et al.* 2014), the cells therefore containing blue or brown food vacuoles or both colors.
Geographical distribution: Austria (Geitler); Czech Republic (Javornický); Denmark (Takano *et al.*, late September); Latvia (Skuja); Poland (in shallow water, probably associated with the bottom sediment, late autumn, winter and spring, often a few days after the ice had melted; Wołoszyńska); Portugal (associated with marginal sediment in shallow pond; Calado *et al.*, unpublished); Sweden (Skuja); Switzerland (Christen; Preisig). Brazil (Bicudo & Skvortsov). Japan (Takano *et al.*).

Note 1: material from Wisconsin, USA (Wilcox & Wedemayer 1985), identified as *A. vigrense* (“*A. wigrense*”), had blue-green chloroplasts surrounded by 3 membranes, indicating permanent chloroplasts rather than kleptochloroplasts. Its possible conspecificity with the European material needs to be examined.

Note 2: *Gymnodinium glaucum* W. Conrad (1926, p. 80, pl. 1, figs 13–15), from brackish water in Belgium, is slightly larger, measuring 32–40 µm in length, and in width 15–20 µm (epicone) and 20–26 µm (hypocone). It formed resting stages in which the cells were surrounded by large amounts of mucilage. It is closely related or identical to *N. amphidinioides*.

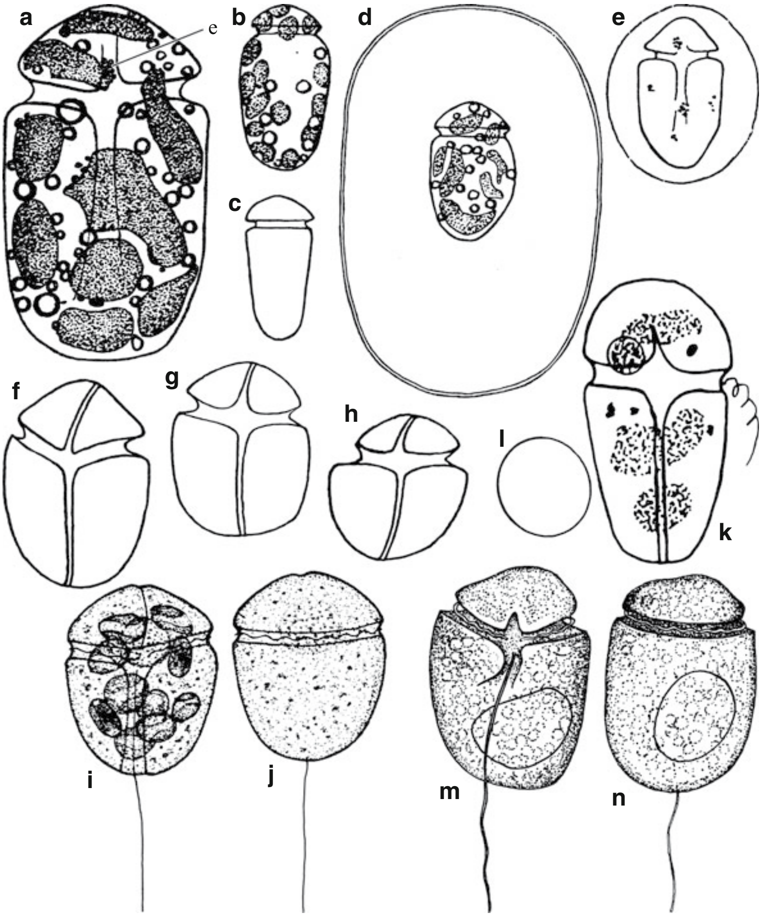

Fig. 110 *Nusuttodinium amphidinioides* (Geitler) Y. Takano & T. Horiguchi (**a**–**e** after Geitler 1924; **f**–**h** after Wołoszyńska 1925a; **i**, **j** after Preisig 1979; **k**, **l** after Wawrik 1983; **m**, **n** after Baumeister 1943a). **a** ventral view with kleptochloroplasts and eyespot (e); **b** dorsal view; **c** lateral view; **d**, **e** cells enveloped in mucilage; **f**–**h** ventral views (as *Amphidinium vigrense*); **i**, **j** ventral and dorsal views, respectively (as *A. vigrense*); **k**, **l** ventral view and cross section, respectively (as *Amphidinium bourrellyi*); **m**, **n** ventral and dorsal views, respectively (as *Amphidinium coprosum*)

Note 3: *Gymnodinium glaucum* J. Schiller (1955, p. 35, pl. III, fig. 30), *nom. illeg.* (*non* Conrad 1926) is a cold-water taxon from Austria, which appears to differ from *N. amphidinioides* in having a relatively shorter hypocone and a sulcus that extends to the antapex.

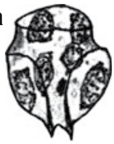

Fig. 111 *Nusuttodinium bidentatum* (J. Schiller) Moestrup & Calado (after Schiller 1955). **a** ventral view

Note 4: since starved cells of *N. gymnodinioides* are colorless, it appears likely that the colorless *Amphidinium coprosum* Baumeister represents such cells.

4. *Nusuttodinium bidentatum* (J. Schiller) Moestrup & Calado *comb. nov.* (**Fig. 111**)

Basionym: *Amphidinium bidentatum* J. Schiller 1955, *Wiss. Arbeiten Burgenland* **9**, p. 21, pl. I, fig. 3

Cells elliptic, somewhat dorsoventrally compressed. Epicone narrower than hypocone, flat, 2–2.3 µm high. Hypocone rounded-elongate, *ca.* 6 µm long. Cingulum circular, wide. Sulcus extends from the cingulum to the antapex, the edges raised, extending behind the cell into two short wings (spines). Six disc-shaped, somewhat irregular, blue-green chloroplasts. With small eyespot. Cell length 8–9 µm, width 7–8 µm.
Ecology: Lake Neusiedl, summer and autumn.
Geographical distribution: Austria.

5. *Nusuttodinium caerulescens* (J. Schiller) Moestrup & Calado *comb. nov.* (**Fig. 112**)

Basionym: *Gymnodinium caerulescens* J. Schiller 1955, *Wiss. Arbeiten Burgenland* **9**, p. 30, pl. II, fig. 17

Cells elongate, dorsoventrally little compressed. Epicone distinctly narrower than hypocone. Hypocone nearly twice the length of the epicone. Epicone broadly hemispherical, hypocone hemispherical. Cingulum circular, wide. Sulcus wide proxi-

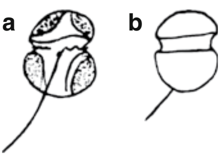

Fig. 112 *Nusuttodinium caerulescens* (J. Schiller) Moestrup & Calado (after Schiller 1955). **a** ventral view with chloroplasts; **b** dorsal view

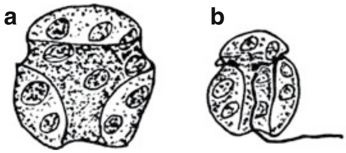

Fig. 113 "*Amphidinium caerulescens*" J. Schiller (after Schiller 1955). **a**, **b** ventral views; **c** outline of cross-section

mally, becoming narrower towards the antapex. Four bluish, rather large chloroplasts, two in each half of the cell, parietal. Cells 8–9 µm long, 7 µm wide.
Ecology: Ruster Kanal, Lake Neusiedl, in winter.
Geographical distribution: Austria.

6. "*Amphidinium caerulescens*" J. Schiller 1955, p. 27, pl. I, fig. 12 (**Fig. 113**)

Cells rounded-ovoid, dorsoventrally somewhat compressed. Cell length 14 µm, width 13 µm. Epicone half the length of the hypocone. Epicone beret-shaped, hypocone trapezoidal, excavated at the antapex. Cingulum circular. With 7–9 blue-gray, oval, sometimes yellowish chloroplasts.
Ecology: Ruster Kanal, Lake Neusiedl, February–March 1953, common at temperatures of 1–9 ˚C.
Geographical distribution: Austria.

Note: the transfer of the previous species to *Nusuttodinium* renders the epithet *caerulescens* unavailable for this species. As the species affinities are not completely clear we refrain from creating a new name at this time.

7. *Nusuttodinium campaniforme* (Popovský) Moestrup & Calado *comb. nov.* (**Fig. 114**)

Basionym: *Gymnodinium campaniforme* Popovský 1971b, *Arch. Protistenk.* **113**, p. 279, pl. 35, fig. 13

Fig. 114 *Nusuttodinium campaniforme* (Popovský) Moestrup & Calado (after Popovský 1971b). **a** ventral view, with central nucleus and several chloroplasts

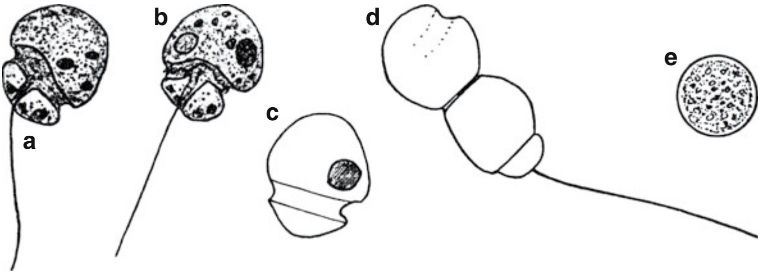

Fig. 115 *Nusuttodinium crassifilum* (J. Schiller) Moestrup & Calado (after Schiller 1954a). **a** ventral view of cell with cyanelles only; **b** ventral view, cyanelles, ingested chlorophyte (left) and oil droplet (right) present; **c** dorsal view, with ingested chlorophyte; **d** final stage of cell division; **e** cyst

Cells ellipsoid. Epicone bell-shaped, approximately twice the length of the conical hypocone. The cingulum circular, rarely a slight spiral. The sulcus does not extend onto the epicone, on the hypocone it proceeds to the antapex. Not dorsoventrally compressed. Four-six wedge-shaped to elongate ellipsoid green chloroplasts. Nucleus central. Cells 13 µm long and 9 µm wide.
Ecology: in drinking-water reservoir Lázský Pond in Bohemia, Czech Republic.
Geographical distribution: Czech Republic.

8. *Nusuttodinium crassifilum* (J. Schiller) Moestrup & Calado *comb. nov.* (**Fig. 115**)

Basionym: *Massartia crassifilum* J. Schiller 1954a, *Oesterr. Bot. Z.* **101**, p. 263, fig. 21
Nomenclatural synonym: *Katodinium crassifilum* (J. Schiller) A. R. Loeblich 1965, p. 15

Cells rounded ovoid, very slightly flattened. Epicone shaped like half an egg. Hypocone somewhat narrower. Epicone *ca.* 3× the length of the hypocone. Cingulum circular, the anterior rim somewhat overhanging. Sulcus does not extend onto the epicone, on the hypocone reaches the antapex. Longitudinal flagellum nearly the length of the cell. Eyespot in the sulcus. Cell division oblique. Cell length 15–16 µm, width 12–13 µm.
Ecology: pond near Lake Neusiedl, Austria, winter form, also under ice.
Geographical distribution: Austria.

9. *Nusuttodinium cyaneum* (J. Schiller) Moestrup & Calado *comb. nov.* (**Fig. 116**)

Basionym: *Gymnodinium cyaneum* J. Schiller 1955, *Wiss. Arbeiten Burgenland* **9**, p. 30, pl. II, fig. 16

This species differs from *N. aeruginosum* only in its smaller size (9 µm long, 6 µm wide) but is otherwise identical.
Ecology: Lake Neusiedl, winterform.
Geographical distribution: Austria.

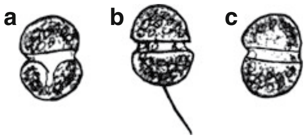

Fig. 116 *Nusuttodinium cyaneum* (J. Schiller) Moestrup & Calado (after Schiller 1955). **a** ventral view; **b**, **c** dorsal views

Note: the species appears very closely related to *N. caerulescens*, which differs in the epicone being slightly narrower than the hypocone and the sulcus being wider than in *N. cyaneum*. Both are winterforms found in the same area.

10. *Nusuttodinium eucyaneum* (H. J. Hu) Moestrup & Calado *comb. nov.* (**Fig. 117**)

Basionym: *Gymnodinium eucyaneum* H. J. Hu 1983, *Chin. J. Oceanol. Limnol.* **1**, p. 198, fig. 1
The designation "*Gymnodinium cyaneum* H. J. Hu" in Hu *et al.* (1980) was invalidly published (no Latin diagnosis). The epithet *cyaneum* is unavailable in *Gymnodinium* because of *G. cyaneum* J. Schiller.

Cells ovoid, epicone a little less than half the size of the hypocone. With many discoidal blue-green chloroplasts. Cells 29–45 μm long, 16–19 μm wide, 13–15 μm thick.
Ecology: fishponds. Cells are phototactic (Hu *et al.* 1980).
Geographical distribution: China (Hu *et al.*).

Note: the identity of this taxon is uncertain. It may be considered a synonym of *N. acidotum* (as by Takano *et al.* 2014), or it may be considered a separate species characterized by its very short epicone.

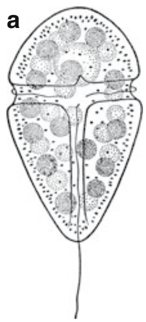

Fig. 117 *Nusuttodinium eucyaneum* (H. J. Hu) Moestrup & Calado (after Hu 1983). **a** ventral view

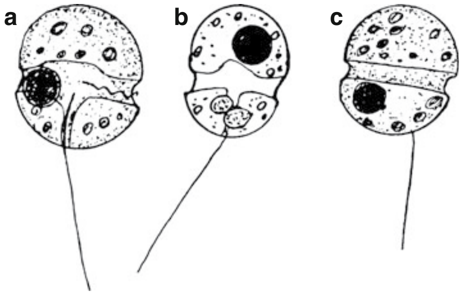

Fig. 118 *Nusuttodinium hiemale* (J. Schiller) Moestrup & Calado (after Schiller 1954a). **a**, **b** ventral views; **c** dorsal view. Oval bodies represent cyanelles; round, dotted bodies in **b** represent ingested chlorophytes; black bodies represent oil

11. *Nusuttodinium hiemale* (J. Schiller) Moestrup & Calado *comb. nov.* (**Fig. 118**)

Basionym: *Massartia hiemalis* J. Schiller 1954a, *Oesterr. Bot. Z.* **101**, p. 264, fig. 22
Nomenclatural synonyms: *Katodinium hiemale* (J. Schiller) A. R. Loeblich 1965, p. 16 ≡ *Gymnodinium hiemale* (J. Schiller) Popovský 1990, p. 6, *nom. illeg.* (*non* Wołoszyńska 1917)

Cells ovoid, dorsoventrally barely flattened. Epi- and hypocone both hemispherical, the epicone slightly longer. Cingulum circular, wide. Sulcus narrower than cingulum, the area of the epicone opposite the sulcus slightly excavate. With parietal "cyanelles", probably kleptochloroplasts. Eyespot very inconspicuous. Cell length 14–15 µm, width 11–12 µm.
Ecology: Lake Neusiedl, December–March, under ice.
Geographical distribution: Austria.

12. *Nusuttodinium indicum* (Shyam & Sarma) Moestrup & Calado *comb. nov.* (**Fig. 119**)

Basionym: *Gymnodinium indicum* Shyam & Sarma 1976, *Pl. Syst. Evol.* **124**, p. 210, figs 10–15, 21

Cells subspherical to broadly ellipsoidal, slightly dorsoventrally compressed. Epi- and hypocone of the same length or the hypocone slightly longer. Cingulum circular, shallow, wide. Sulcus extends for 3/4 the length of the hypocone. With 6–10 green to blue-green, angular chloroplasts. Eyespot absent. Nucleus centrally located in the hypocone. Cells 11–16 µm long and 8–14 µm wide. Cell division in the motile state.
Ecology: in temporary pond, Botanical Garden, Banaras Hindu University, Varanasi, India.
Geographical distribution: India.

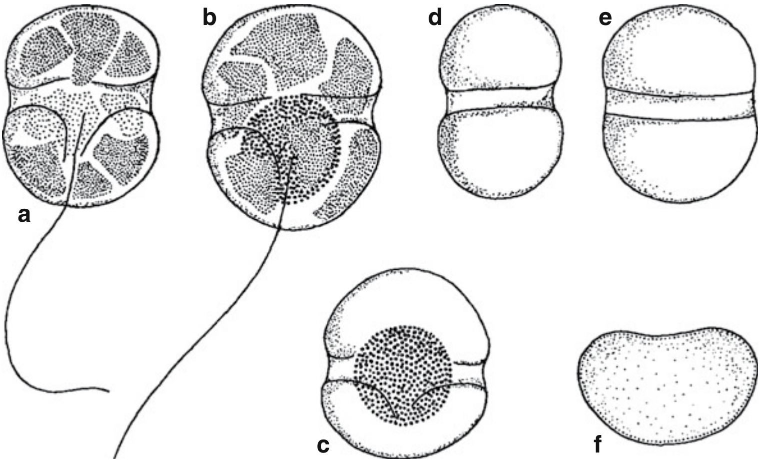

Fig. 119 *Nusuttodinium indicum* (Shyam & Sarma) Moestrup & Calado (after Shyam & Sarma 1976). **a**, **b** ventral views showing chloroplasts (nucleus approximately central in **b**); **c** ventral view showing central nucleus; **d** lateral view; **e** dorsal view; **f** antapical view

13. *Nusuttodinium lacunarum* (Skuja) Moestrup & Calado *comb. nov.* (**Fig. 120**)

Basionym: *Amphidinium lacunarum* Skuja 1964, *Nova Acta Regiae Soc. Sci. Upsal., ser. IV*, **18** (3), p. 347, pl. LXVI, figs 28, 29

Cells elliptical, barely compressed dorsoventrally. Epicone hemispherical, 1/3–1/4 the cell length. Hypocone elongate-rounded, slightly excavate at the antapex. Cingulum almost horizontal dorsally, on the ventral side curving downwards to continue in the wide sulcus, which extends to the antapex. Cytoplasm containing 6–10 blue-green disc-shaped or band-shaped chloroplasts (kleptochloroplasts?). Nucleus mainly in the epicone. Cell length 25–30 µm, width 17–20 µm, thickness 15–17 µm.
Ecology: in pools and lagoons connected to Lake Torneträsk, Northern Sweden.
Geographical distribution: Sweden.

14. *Nusuttodinium limneticum* Moestrup & Calado *nom. nov.* (**Fig. 121**)

Replaced synonym: *Gymnodinium limneticum* Lackey 1936, *Biol. Bull. Mar. Biol. Lab. Woods Hole* **71**, p. 497, pl. I, figs 8, 9, *nom. illeg.* (non *G. limneticum* Wołoszyńska 1936) [Re-use of the epithet under Art. 58.1 of the ICN.]
"*Gymnodinium lackeyi* Kisselev 1954, p. 108" intended as a *nom. nov.*, but not validly published for lack of full and direct reference to place of publication of replaced name.

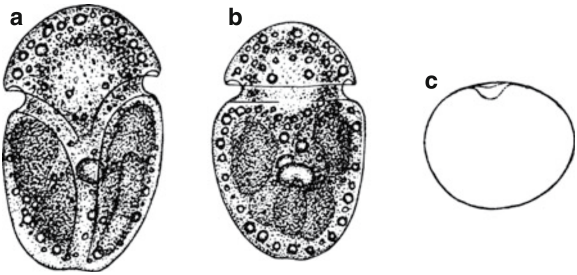

Fig. 120 *Nusuttodinium lacunarum* (Skuja) Moestrup & Calado (after Skuja 1964). **a** ventral view; **b** dorsal view; **c** cross-section outline

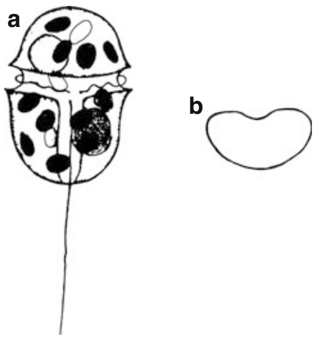

Fig. 121 *Nusuttodinium limneticum* Moestrup & Calado (after Lackey 1936). **a** ventral view showing blue chloroplasts and nucleus; **b** cross-section outline

Cells oval, epicone almost hemispherical, hypocone longer, rounded elongate. Cells dorsoventrally flattened. Cingulum circular. Sulcus does not enter the epicone. On the hypocone it extends to the antapex. Nucleus subcentral. With 8–12 blue chloroplasts (kleptochloroplasts?). Cells 25–35 µm long.
Ecology: Reelfoot Lake, Tennessee.
Geographical distribution: USA, TN (Lackey).

Note: this species is very similar to *N. amphidinioides*, mainly differing in the pronounced dorsoventral flattening.

15. ***Nusuttodinium montanum*** (J. Schiller) Moestrup & Calado *comb. nov.* (**Fig. 122**)

Basionym: *Massartia montana* Schiller 1954b, *Arch. Protistenk.* **100**, p. 116, fig. 1

Cells elliptic in ventral view, barely dorsoventrally flattened. Epicone hemispherical or elongate-hemispherical, twice the length of the hypocone. Hypocone longer

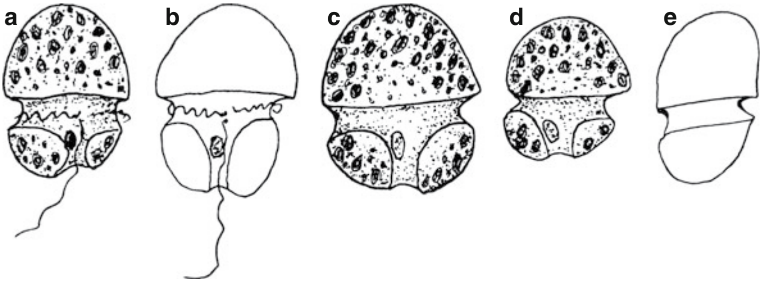

Fig. 122 *Nusuttodinium montanum* (J. Schiller) Moestrup & Calado (after Schiller 1954b). **a** ventral view with cyanelles, flagella and eyespot; **b** outline of ventral view, showing furrows, flagella and eyespot; **c**, **d** ventral views with cyanelles and eyespot; **e** lateral view, outline

Fig. 123 *Nusuttodinium oculatum* (J. Schiller) Moestrup (after Schiller 1955). **a** ventral view; **b** dorsal view

than wide, indented at the antapex. Cingulum circular. Sulcus restricted to the hypocone, extending to the antapex. Eyespot in the sulcus. Nucleus in the epicone. With numerous vacuoles containing blue bodies, sometimes interpreted as cyanelles or chloroplasts. Cells of *Chlorella* also observed inside. Cell length 16–20 µm, width 13–17 µm.
Ecology: in concrete swimming pool containing a bloom of *Chlorella pyrenoidosa*, near Hainfeld, Austria, summer.
Geographical distribution: Austria.

16. *Nusuttodinium oculatum* (J. Schiller) Moestrup *comb. nov.* (**Fig. 123**)

Basionym: *Amphidinium oculatum* J. Schiller 1955, *Wiss. Arbeiten Burgenland* **9**, p. 22, pl. I, fig. 5

Cells round-oval, dorsoventrally barely flattened. Epicone flattened, hypocone hemispherical, *ca.* 3× the length of the epicone. Cingulum circular, wide. Sulcus extends from the cingulum to the antapex. Three to five blue-green chloroplasts. Eyespot present. Cell length 8–9 µm, width *ca.* 8 µm.
Ecology: in Lake Neusiedl.
Geographical distribution: Austria.

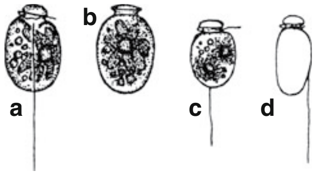

Fig. 124 *Nusuttodinium phthartum* (Skuja) Moestrup & Calado (after Skuja 1939). **a**, **b** ventral and dorsal views; **c** dorsal view of cell with two pyrenoid centers; **d** right lateral view

17. *Nusuttodinium phthartum* (Skuja) Moestrup & Calado *comb. nov.* (**Fig. 124**)

Basionym: *Amphidinium phthartum* Skuja 1939, *Acta Horti Bot. Univ. Latv.* **11/12**, p. 149, pl. X, figs 21–24

Cells more or less symmetrical, dorsoventrally somewhat compressed. Epicone very small, one sixth to one seventh of the cell length and 1/2–1/3 of the hypocone width, flattened-round. Hypocone broadly oval or inverted egg-shaped, antapex rounded. Cingulum circular. Sulcus does not reach the antapex. Longitudinal flagellum twice the cell length. One or two blue-green chloroplasts, shortly band-shaped, extending in a stellate configuration from a central pyrenoid in the hypocone. Nucleus in the middle of the hypocone, towards the ventral side. Cell length 14–17 µm, width 11–14 µm, thickness 6–8 µm.
Ecology: in brackish pools near the coast, not rare in summer.
Geographical distribution: Latvia.

Note: the taxonomic affinity of this species is uncertain. The presence of a stellate chloroplast with a central pyrenoid may indicate a permanent endosymbiosis. Alternatively, the blue-green chloroplast(s) may be kleptochloroplasts.

18. *Nusuttodinium viride* (Penard) Moestrup & Calado *comb. nov.* (**Fig. 125**)

Basionym: *Gymnodinium viride* Penard 1891, *Bull. Trav. Soc. Bot. Genève* **6**, p. 55, pl. IV, figs 11–24

Cells elongate-subcordiform, longer than wide. Epi- and hypocone of equal size, epicone rounded anteriorly, hypocone angular. Cells in transverse section ovoid, rarely circular. Cingulum slightly descending, the ends displaced about one cingulum width. Sulcus extends to half the length of the epicone, on the hypocone extends to the antapex. Chloroplasts rod-shaped, radially and slightly irregularly arranged, light green or blue-green. Eyespot present. Nucleus in the hypocone. Cell length 29–39 µm, width 22–28 µm. Resting cysts spherical.
Ecology: in plankton of ponds and lakes.
Geographical distribution: Switzerland (Penard; Christen). USA, MD (Thompson).

Note: Huber-Pestalozzi (1950, p. 124) indicates that this taxon may be identical to *Gymnodinium uberrimum* (G. J. Allman) Kofoid & Swezy.

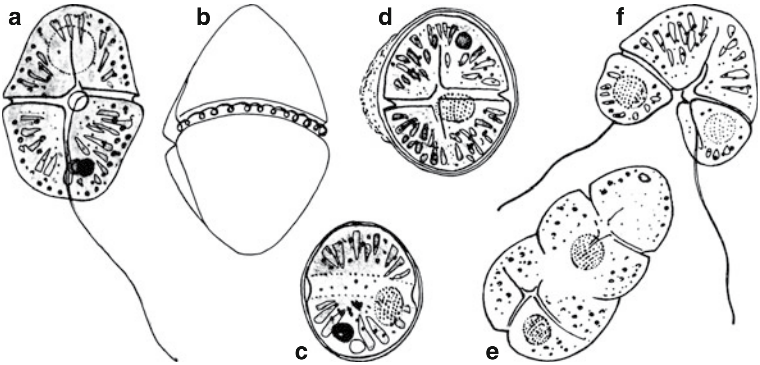

Fig. 125 *Nusuttodinium viride* (Penard) Moestrup & Calado (after Penard 1891). **a** ventral view; left lateral view, outline with transverse flagellum; **c**, **d** immobile cells, interpreted by Penard as young stages; **e** cell division in tandem; **f** cell division by longitudinal (or oblique) fission

Genus 3. "*Katodinium*"

The type species of the genus *Katodinium* Fott, *K. nieuportense* W. Conrad, was described from a brackish water shellhole in Belgium (Conrad 1926). It has rarely been reported since then and its identity is therefore somewhat uncertain. Cells were described to possess 2–4 chloroplasts, illustrated as four yellowish-brown, elongate-elliptical plates. The cells were further characterized by the epicone being much larger than the hypocone, and the generic name was subsequently used for naked marine and freshwater gymnodinioids in which the epicone is larger than the hypocone. Most of these species have now been transferred to other genera (*Gymnodinium*, *Gyrodinium* and *Opisthoaulax*), and this leaves only two species in fresh water. As the specific epithets of both these species are unavailable in *Gymnodinium* and their affinities are unclear we refrain from creating new names for them at this time.

1. "*Katodinium auratum*" Bursa 1970, p. 148, figs 9–14 (**Fig. 126**)

Cells elliptic, strongly dorsoventrally compressed. Epicone twice the length of the hypocone. Epicone hemispherical. Cingulum not displaced. Sulcus does not extend onto the epicone. On the hypocone it is at first narrow but widens towards the antapex. Nucleus centrally located in the epicone. Numerous bright golden-yellow chloroplasts dispersed in the cell periphery. Cells may discard the flagella and attach to sand grains and plants with mucus secreted from the ventral side. Cell length 24–27 µm, width 15–17 µm.
Ecology: in creek in Colorado, September 1968.
Geographical distribution: USA, CO (Bursa).

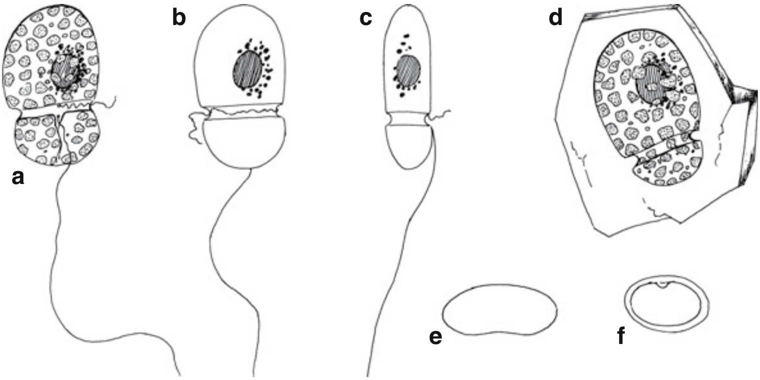

Fig. 126 "*Katodinium auratum*" Bursa (after Bursa 1970). **a**–**c** ventral, dorsal and right lateral views, respectively; **d** cell with ventral side attached to sand grain; **e** apical view (ventral surface partly concave); **f** antapical view

2. "*Katodinium viride*" Christen 1961, p. 335, fig. 19 (**Fig. 127**)

Epicone twice the length of the hypocone, barely dorsoventrally flattened. Epicone broadly rounded, hypocone slightly concave, the left side longer than the right side. Hypocone narrower than epicone, the lower edge of the epicone somewhat "hanging" over the hypocone. Several large, green parietal chloroplasts present. Eyespot present in the sulcus. Cell length 17–21 µm, width 16–18 µm. Cells swim quickly and staggeringly.
Ecology: in marshy shallow water among *Carex*, Wintherthur, Switzerland.
Geographical distribution: Switzerland.

Note: this species needs to be re-examined before its taxonomical status can be assessed. It is unlikely to belong in *Katodinium* and may be a species of *Gymnodinium* or

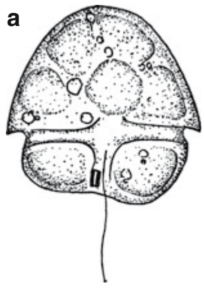

Fig. 127 "*Katodinium viride*" Christen (after Christen 1961). **a** ventral view, showing chloroplasts and eyespot

Lepidodinium. However, in both these genera species have been described with this specific epithet. To avoid unnecessary name changes we are keeping the taxon provisionally under the original name.

Family 3. Gyrodiniaceae Moestrup & Calado *fam. nov.*

Cells heterotrophic, with longitudinal striations, one of which usually extends to the tip of the cell, surrounded here by a ring-shaped or elliptic furrow-like structure. The nucleus typically with distinct capsule. The phylogenetic position of the family is somewhat uncertain.

Genus 1. *Gyrodinium* Kofoid & Swezy 1921, p. 273, *nom. cons.*

Type species: *Gyrodinium spirale* (Bergh) Kofoid & Swezy, p. 332 (marine) ≡ *Gymnodinium spirale* Bergh 1881, p. 253, figs 70, 71 (pl. XVI)
Nomenclatural synonym: *Spirodinium* F. Schütt 1896, pp 3, 5, *nom. rej.*

Species of *Gyrodinium*, as the genus is presently defined, are heterotrophic, lack chloroplasts and are longitudinally striated. *Gyrodinium* is a genus of mainly marine dinoflagellates and is represented in fresh water by very few species, of which only *G. helveticum* has been examined in detail and shown to belong in *Gyrodinium*. We include also *G. molopicum* (T. M. Harris) Moestrup & Calado *comb. nov.* in *Gyrodinium.*

Key to the species of *Gyrodinium* occurring in fresh water:
1a Epicone much shorter than hypocone .... 1. *G. helveticum*
1b Epicone much longer than hypocone .... 2. *G. molopicum*

1. *Gyrodinium helveticum* (Penard) Y. Takano & T. Horiguchi 2004, p. 115 (**Fig. 128**)

Basionym: *Gymnodinium helveticum* Penard 1891, p. 58, pl. V, figs 10–16
Taxonomic synonyms: *Glenodinium apiculatum* O. Zacharias 1901, p. 307 (illustrated in Zacharias 1903, p. 290, figs a, b), *nom. illeg.* (*non* Ehrenberg 1838) ≡ *Gymnodinium helveticum* var. *apiculatum* Utermöhl 1925, p. 404; *Gymnodinium helveticum* f. *achroum* Skuja 1948, p. 369, pl. XXXVIII, figs 38–41; *Gymnodinium coeruleum* N. L. Antipova 1955, p. 327, fig. 1-III, *nom. illeg.* (*non* Dogiel 1906, pp 35, 36, 40, pl. 2, figs 46, 47)

Cells elongated-spindle-shaped, the hypocone much longer than the epicone. Very slightly flattened dorsoventrally. Epicone rounded, helmet-shaped. Hypocone conical, usually sharply pointed. Cingulum deeply excavated, the two ends displaced 1/2–1× the width of the cingulum, sometimes not displaced. Sulcus extends to about two thirds the length of the hypocone, widening distally. On the epicone it

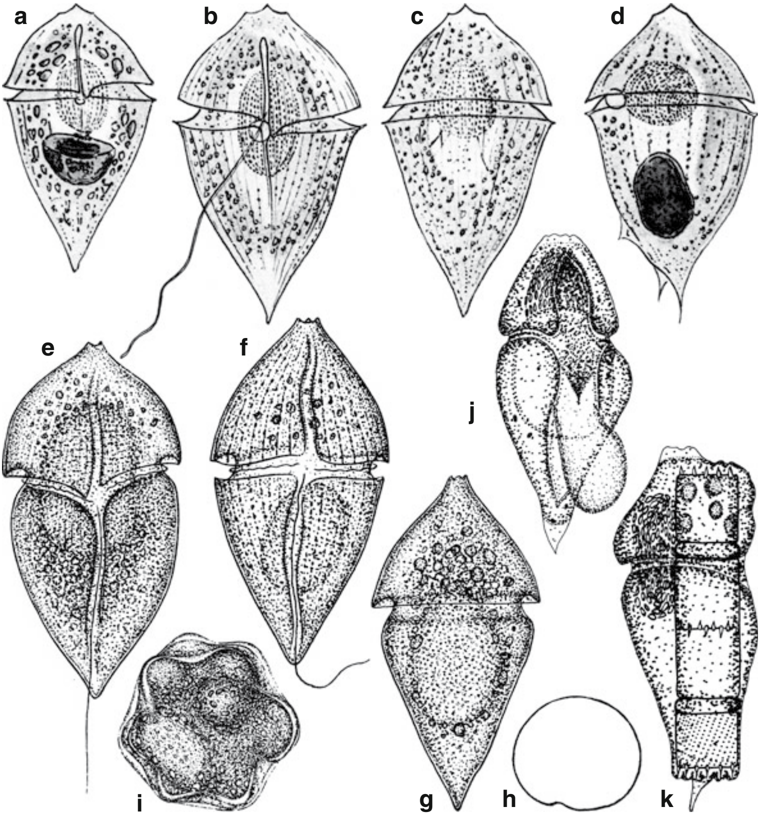

Fig. 128 *Gyrodinium helveticum* (Penard) Y. Takano & T. Horiguchi (**a**–**d** after Penard 1891; **e**–**h** after Skuja 1948; **i** after Skuja 1964; **j**, **k** after Popovský 1982). **a** ventral view with ingested cell below the nucleus; **b** ventral view showing central nucleus and longitudinal striations on the cell surface; **c**, **d** dorsal views, in **d** with and ingested green alga; **e**, **f** ventral views of different cells; **g** dorsal view; **h** outline of cross-section; **i** cyst; **j** cell with lobopode extending from sulcus; **k** cell with ingested *Aulacoseira*

extends almost to the apex. The whole cell with longitudinal striations (ridges). The anterior groove is elliptical with a central ridge formed by one of the cell striations, its longest axis being in the dorsoventral direction. Groove and ridge sometimes visible as 3 short anterior horns on the epicone. No chloroplasts or eyespot. Nucleus in the epicone. Cytoplasm colorless or pink. Cell length very variable due to ingestion of prey, 42–72 μm, width 23–55 μm. Resting cysts globose with round bulges, with thick, layered wall, 35–39 μm in diameter. Outer wall layer smooth.

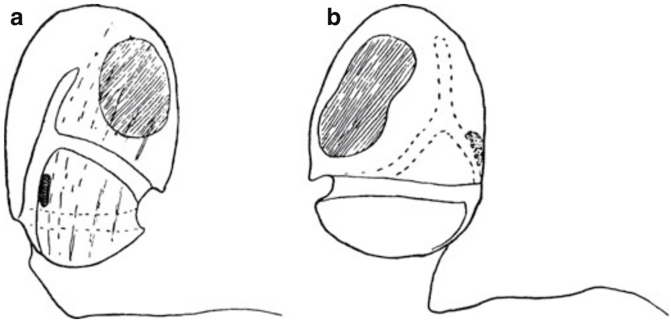

Fig. 129 *Gyrodinium molopicum* (T. M. Harris) Moestrup & Calado (after Harris 1940). **a** ventral-left view, with eyespot and longitudinal striations; **b** right lateral view (shaded bodies on the epicone in both figures represent food vacuoles). Both cells stated to be slightly shrunk with glycerine

Feeds on other plankton organisms such as diatoms (for example *Cyclotella*), unicellular cyanobacteria, the amoeba *Difflugia*, etc., using a lobopod, which extends from the sulcus (Popovský 1982).
SEM: Takano & Horiguchi (2004), Hansen & Flaim (2007).
DNA data: Takano & Horiguchi (2004).
Ecology: often considered to be a cold-water species, occurring in plankton during winter in shallow lakes and in summer in lakes with a permanently cold deep layer (Höll 1928). However, Bertilsson & Gelin (1975) found *G. helveticum* to be abundant in Swedish lakes even at temperatures of *ca.* 15 °C. They consider the occurrence of *G. helveticum* to be determined more by the amount of food present (small centric diatoms, cryptomonads), than by temperature, the largest populations forming after blooms of the food species in spring and autumn. In October 1972 *ca.* 40 % of the population in eutrophic Lake Vombsjön in Sweden contained food vacuoles with centric diatoms (Bertilsson & Gelin 1975), the population diminishing in November after termination of the diatom bloom. *Gyrodinium helveticum* occurs in oligotrophic, mesotrophic and eutrophic lakes.
Distribution: Austria (Ruttner); Czech Republic (Popovský); Denmark (*e. g.*, Kristiansen & Mathiesen); England (Irish; Lewis & Dodge); Finland (Eloranta); Germany (Höll); Italy (Hansen & Flaim); Portugal (Nauwerck); Sweden (*e. g.*, Skuja; Bertilsson & Gelin); Switzerland (Penard). Canada (Stein & Borden; Carty); USA (Munawar & Munawar; Carty). Argentina (Queimaliños *et al.*); Brazil (Cronberg). Japan (Takano & Horiguchi); Lake Baikal, Russia (Annenkova *et al.*).

Note: several morphological forms have been observed which have been explained as artifacts formed during observation (*e. g.*, var. *apiculatum* Utermöhl: the anterior horns absent). Skuja (1948) gave a separate name, forma *achroum*, to cells with colorless cytoplasm. Because of the great variation in color and cell shape, Hansen & Flaim (2007) considered these variants to be taxonomically meaningless.

2. *Gyrodinium molopicum* (T. M. Harris) Moestrup & Calado *comb. nov.* (**Fig. 129**)

Basionym: *Massartia molopica* T. M. Harris 1940, *Proc. Linn. Soc. London* **152** (1), p. 15, fig. 4, E, F
Nomenclatural synonym: *Katodinium molopicum* (T. M. Harris) A. R. Loeblich 1965, p. 16

Cells ovoid, not dorsoventrally compressed. Epicone 3× the length of the hypocone. Epicone elongate-rounded, hypocone flat-hemispherical. Cingulum spiral. Sulcus extends onto the epicone. Cells longitudinally striated. Cytoplasm colorless, eyespot near the sulcus. Longitudinal flagellum as long as the cell or slightly longer. Cell length 21 µm, width 15 µm.
Ecology: in shallow eutrophic pond.
Geographical distribution: England.

Note: the paths of the furrows are not well understood. We have included this taxon in *Gyrodinium* because of the longitudinal striations and the lack of chloroplasts.

Order 5. GONYAULACALES F. J. R. Taylor 1980, p. 102, 103

Amphiesmal vesicles with thick plates, usually visible in living cells (cells thecate). The plane of cytokinesis oblique, extending from the mid-left side of the hypocone to the mid-right part of the epicone. Cell division semiconservative, *i. e.*, each daughter cell inherits half of the mother cell amphiesmal plates and develops the missing part *de novo*. Young and old plates therefore often differently ornamented on the same cell. This mode of division, known as desmoschisis, has presently been observed in both the Ceratiaceae and the Gonyaulacaceae. Subsequent loss of the inherited half of the amphiesma was shown to occur in some species (Dürr & Netzel 1974).

Key to the families of Gonyaulacales:

1a Cells with one apical and typically 2–3 posterior, hollow horns (cytoplasm-filled processes) .... 1. Ceratiaceae
1b Cells without horns, the apex only slightly projecting ..... 2. Gonyaulacaceae

Family 1. Ceratiaceae Kofoid 1907a, p. 164

Cells with one anterior horn and typically with 2–3 posterior horns. Cells strongly flattened dorsoventrally, dorsally convex, ventrally concave. Cingulum almost equatorial, sulcus oblique, in deep cavity. Plate formula: 4′, 0a, 6″, 6c, 1–2s, 6‴, 2⁗. The anterior horn covered by 3 or all 4 apical plates, the posterior horns by plates 1‴ and 2‴ (right horn), antapical plates (middle or antapical horn), 4‴ and 5‴

(left horn). The apical horn is typically closed distally by a round apical plate with a more or less central pore surrounded by a number of smaller pores. The ventral plates are sometimes given separate names (x, y, z) since their interpretation as precingular, cingular and postcingular plates appears to be somewhat arbitrary. For simplicity, we have followed the latter convention, which appears to be gaining more general acceptance. Further, one of the antapical plates has been interpreted as an intercalary plate but, again, this appears to be somewhat arbitrary and we have in the present account identified both plates as antapical. One of the characteristic features of *Ceratium*, the large sulcal cavity (also known as the ventral chamber), through which prey is apparently ingested, was found in one species, *Ceratium cornutum*, to be covered by 7 very thin plates, in addition to two outer plates. These plates are very thin and readily destroyed, but it is to be expected that similar plates are present also in other species. Resting cysts typically with 3–4 horns, rarely without horns. The cyst walls are composed of cellulose and do not fossilize.

Genus 1. *Ceratium* Schrank 1793, p. 35

Type species: *Ceratium tetraceras* Schrank 1793 (see Dujardin 1841; Calado & Larsen 1997), herein considered synonymous with *Ceratium hirundinella* (O. F. Müller) Dujardin 1841
Taxonomic synonym: *Dimastigoaulax* Diesing 1866, p. 306, 392
For description, see the family above.

This genus is very rich in species in marine environments, but in fresh water it comprises only 7 species, one of which is restricted to the tropics. Two species, *C. furcoides* and *C. hirundinella*, vary considerably in morphology. This variation includes the length and width of the cells, the angle between the posterior horns and their direction. Also the size of the left antapical horn, which is often small or lacking in spring. The variation led Bachmann (1911), working at Vierwaldstättersee, Switzerland, to divide the two species into seven morphotypes. The number of morphotypes was raised to nine by Schröder (1920) and 10 by Huber-Pestalozzi (1950). These works should be consulted for more detailed information about the many morphotypes. The morphotypes are probably not genetically different and their relevance needs to be examined further. Are most or all types formed as a result of external factors in the environment? Bachmann merged *C. furcoides* (described at the time as a variety of *C. hirundinella*) and *C. hirundinella* under the latter name, and this convention was followed by many authors until very recently. Many data on *C. furcoides* are therefore hidden under the name *C. hirundinella*.
In the many marine species the anterior horn is apparently formed by 4 long apical plates. In the freshwater species, however, three species are unusual in having only 3 long apical plates, the fourth plate being much shorter and not reaching the tip of the horn. Surprisingly, the short plate is not the same in the three species, (plate 1′ in *C. carolinianum* and plate 4′ in *C. furcoides* and *C. rhomvoides*), in other words the shortening is the result of independent evolutionary events, of which the functional significance is unknown.

Key to the freshwater species of *Ceratium*:

1a Anterior horn directed forward, 2–3 posterior horns (rarely absent) 3
1b Anterior horn directed toward the right, 2 posterior horns only 2
2a Anterior horn short, slightly to moderately curved, with truncated end, 1′ extends to the tip of the horn .... 4. *C. cornutum*
2b Anterior horn long, elegantly curved, with pointed end, 1′ half the length of the horn .... 3. *C. carolinianum*
3a Posterior horns absent or very short, less than length of hypocone 4
3b Posterior horns longer 5
4a Short posterior horns present .... 2. *C. brachyceros*
4b Posterior horns absent .... 6. *C. monoceras*
5a Epicone conical, plate 4′ short, less than one third the length of the apical horn 6
5b Epicone bell-shaped, plate 4′ extending to the apex .... 1. *C. hirundinella*
6a Amphiesmal plates strongly reticulate .... 7. *C. rhomvoides*
6b Amphiesmal plates alveolate .... 5. *C. furcoides*

1. *Ceratium hirundinella* (O. F. Müller) Dujardin 1841, p. 377 (**Fig. 130**)

Basionym: *Bursaria hirundinella* O. F. Müller 1773, p. 63
Taxonomic synonyms: *Ceratium tetraceras* Schrank 1793, p. 36, pl. III, fig. 23; *Ceratium macroceras* Schrank 1802, p. 374, pl. II, fig. 4; *Ceratium longicorne* Perty 1849a, p. 27 (footnote) ≡ *Glenodinium longicorne* (Perty) Diesing 1866, p. 392; *Ceratium kumaonense* H. J. Carter 1871, p. 229, 230, text-fig

Cells broadly fusiform, strongly dorsoventrally compressed, with one straight anterior horn and 2–3 short posterior horns. Apical horn truncated apically with terminal crown of short thorns, closed by thin plate with large central pore surrounded by smaller pores. Posterior horns pointed, the antapical horn long, the right horn shorter, the left horn the shortest, sometimes (in spring) missing. Apical horn widens proximally, epicone bell-shaped. Posterior horns very variable, the antapical horn directed backwards or somewhat toward the left, the right horn parallel or diverging, the left horn, if present, diverging. Apical plates 1′–4′ extend the full length of the apical horn. Chloroplasts parietal, disc-shaped. Cell size range very large, length mostly between 90 μm and 450 μm (see morphotypes). Cysts triangular, reflecting the shape of the cell, with a short spine at each of the three corners.
SEM: Dodge & Crawford (1970), Dottne-Lindgren & Ekbohm (1975), Bourrelly & Couté (1976), Heaney & Talling (1980), Dodge (1985), Polligher & Hickel (1991), Olrik (1997), Cavalcante *et al*. (2013).
TEM: Dodge & Crawford (1970), Chapman *et al.* (1981, 1982).
Ecology: in oligo- to eutrophic ponds and lakes. Sometimes in highly eutrophic conditions, together with blooms of cyanobacteria. The species has been reported to be mixotrophic and a variety of organisms have been seen within its cells: bacteria, dinoflagellates, diatoms, green algae, chrysophytes (Hofeneder 1930; Entz 1927a). Food vacuoles were reported in an ultrastructural study (Dodge & Crawford 1970). However, reinterpretation of these observations by Chapman *et al.* (1981, 1982) has shed doubt over previous reports of food uptake. The matter requires further study.

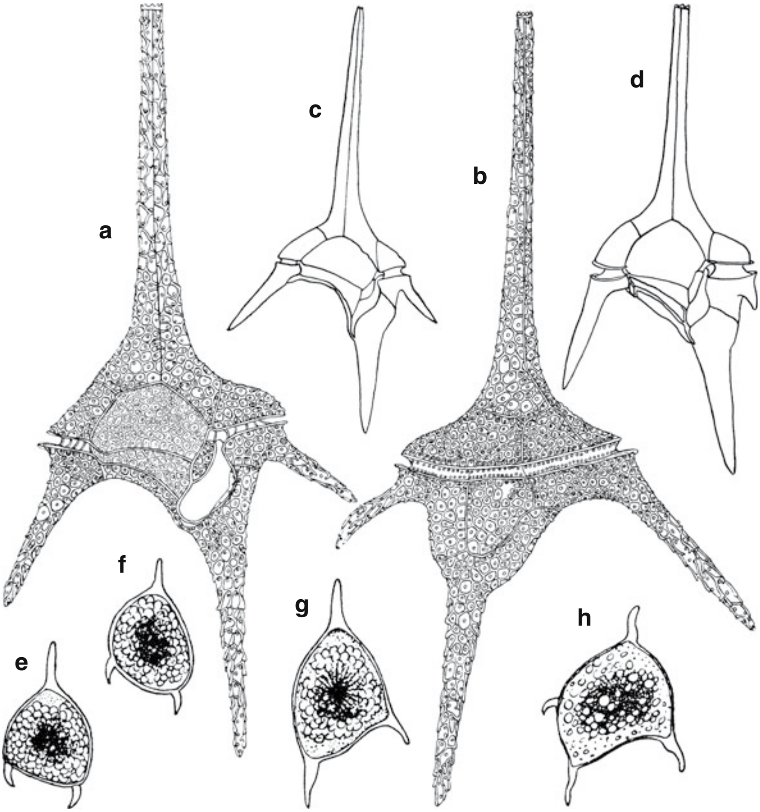

Fig. 130 *Ceratium hirundinella* (O. F. Müller) Dujardin (**a**–**d** after Entz 1927; **e**–**h** after Huber & Nipkow 1922). **a**, **b** ventral and dorsal views showing limits and ornamentation of amphiesmal plates; **c**, **d** ventral views, showing variation in length and orientation of horns in hypocone (the small left horn in **d** can be further reduced or altogether absent); **e**–**h** shape variation in cysts

Geographical distribution: reported from all over the world, although often confused or mixed with *C. furcoides*. England (Lewis & Dodge); France (Cardinal); Germany (Lemmermann); Portugal (Pandeirada *et al.* 2013); Sweden (Nauwerk). Brazil (Cavalcante *et al.*). Burma (Skuja); Israel (Pollingher & Hickel); Mongolia (Ostenfeld).

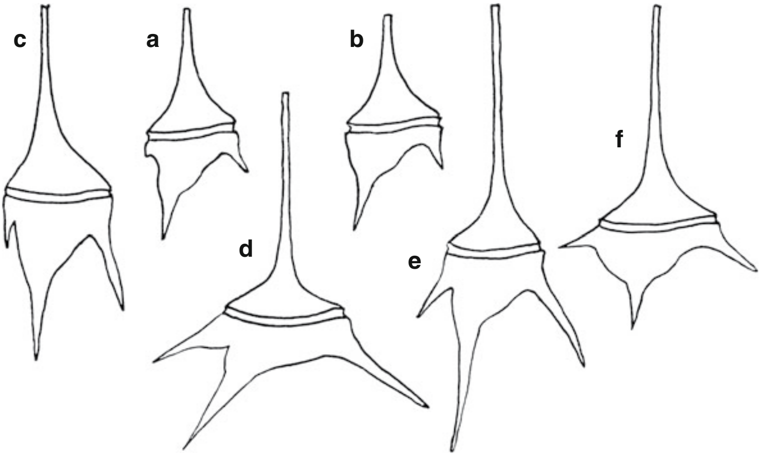

Fig. 131 Morphotypes of *Ceratium hirundinella* (O. F. Müller) Dujardin (after Huber-Pestalozzi 1950). Outlines of cells in dorsal view. **a** morphotype austriacum; **b** morphotype carinthiacum; **c** morphotype gracile; **d** morphotype piburgense; **e** morphotype robustum; **f** morphotype scotticum

Morphotypes (mostly from Huber-Pestalozzi 1950):

1. Morphotype austriacum Bachmann (**Fig. 131a**)
Small, rather plump form. Epicone broadly conical. Apical horn short. Antapical horn directed towards the left. Cells 120–234 µm long, 45–72 µm wide.
Common morphotype in Europe (Huber-Pestalozzi); Burma (Skuja).
This morphotype is more or less intermediate in morphology between *C. hirundinella* and *C. furcoides*/*C. rhomvoides* and the shape of 4′ needs to be determined before its identity can be assessed.

2. Morphotype carinthiacum Bachmann (**Fig. 131b**)
Cells short and wide, epicone triangular, with 2 posterior horns, both horns slightly diverging. Cells 115–170 µm long, 45–60 µm wide.
Austria (Bachmann).

3. Morphotype gracile Bachmann (**Fig. 131c**)
Antapical horn and left postcingular horn parallel to apical horn, right postcingular horn slightly diverging. Cell dorsally flattened. Cells 140–302 µm long, 60–75 µm wide.
The most common morphotype in Europe (Huber-Pestalozzi).

4. Morphotype piburgense Bachmann (**Fig. 131d**)
Postcingular horns very strongly diverging, more than 90°. Antapical horn directed towards the left. Cells 180–260 µm long, 50–60 µm wide.

Piburg, Tyrol (Zederbauer; Huber-Pestalozzi). USA, MN (Ngô & Pfiester). Burma (Skuja).

5. Morphotype robustum Bachmann (**Fig. 131e**)
Antapical horn directed slightly to the left, postcingular horns directed outwards but diverging less than 90°. Cells 270–310 µm long, 45–55 µm wide.
Rare type: Switzerland, Austria, France.

6. Morphotype scotticum Bachmann (**Fig. 131f**)
Postcingular horns diverge more than 90°. All the posterior horns short. Antapical horn very short, nearly in the longitudinal direction, hypocone short. Cells 160–210 µm long, 50–60 µm wide.
Scotland, Switzerland, Poland.

2. *Ceratium brachyceros* Daday 1907, p. 251, fig. A (**Fig. 132**)

Nomenclatural synonym: *Ceratium hirundinella* var. *brachyceros* (Daday) Ostenfeld 1909, p. 175 ("*brachyceras*")

Cells dorsoventrally flattened, dorsal side somewhat convex, ventral side concave. Epicone triangular, with long horn, left side curved, right side with slight sharp hump or shoulder. Apical horn blunt, closed by flat, ring-shaped plate with ca 5 small pores. Hypocone with two short, straight, pointed horns, left side of hypocone with sharp hump approximately halfway, right side straight or nearly so. Left antapical horn longer than right antapical horn. Sulcal furrow wide. Amphiesmal plates reticulate. Cell length 130–195 µm, width 52–70 µm. Cysts unknown.
SEM: Bourrelly & Couté (1976).
Ecology: planktonic in lakes, mainly in the tropics.
Geographical distribution: Lake Victoria (Daday, Ostenfeld); Sierra Leone (Gerrath & Denny). USA, OH (Carty). Cigombong (Tjigombong), Java (Bourrelly & Couté).

3. *Ceratium carolinianum* (Bailey) Jörgensen 1911, p. 14 (**Fig. 133**)

Basionym: *Peridinium carolinianum* Bailey 1851, p. 41, pl. 3, figs 4, 5
Nomenclatural synonym: *Dimastigoaulax caroliniana* (Bailey) Diesing 1866, p. 393
Taxonomic synonym: *Ceratium curvirostre* Huitfeldt-Kaas 1900, p. 6, figs 10, 11

Epicone with more or less sickle-shaped, anterior horn pointed. Below the horn the epicone is wider than long, and steeper on the left than on the right side, which has a sharp hump midway. Apical horn formed of 2′, 3′ and 4′, while 1′ is short and reaches only *ca.* halfway to the apex. Hypocone triangular, on the left side steep, on the right side less so. Antapical horn of various length and thickness, pointed, right posterior horn short, triangular or longer, pointed. Cingulum horizontal. Amphiesmal plates strongly areolated. The right cingular corner of 2″ with distinct pore which continues into the cell as a 8–9 µm long closed tube. Chloroplasts parietal,

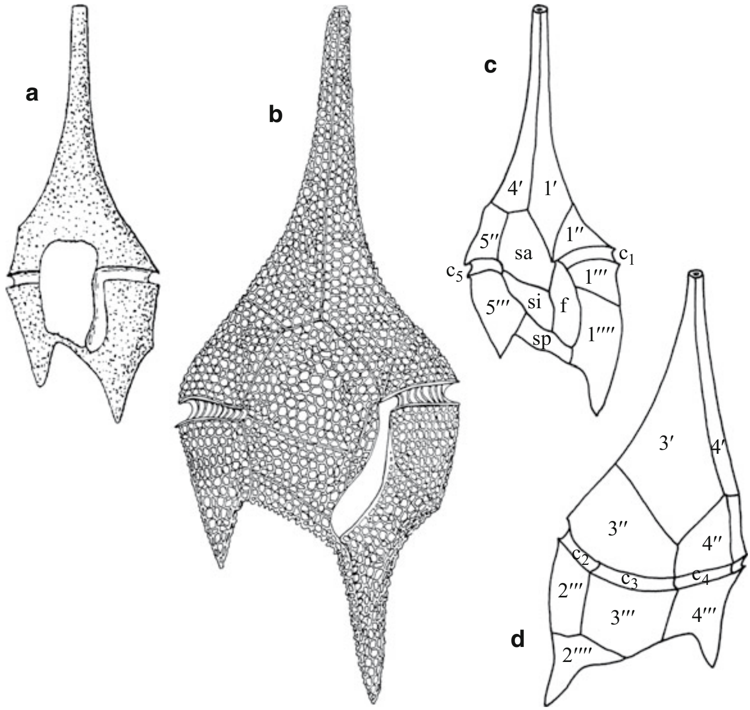

Fig. 132 *Ceratium brachyceros* Daday (**a** after Daday 1907; **b** after Entz 1927; **c**, **d** after Bourrelly & Couté 1976). **a** ventral view showing general shape of the cell; **b** ventral view, with plate limits and ornamentation; **c**, **d** ventral and dorsal views with tabulation (ventral plates marked sa, si and sp; f sulcal aperture)

disc-shaped. Cell length 100–210 µm, width 60–135 µm, with a maximum in summer. Cysts irregularly quadrangular with very short spines (Skuja 1964).
SEM: Wall & Evitt (1975), Bourrelly & Couté (1976), Morling (1980).
Ecology: according to Morling (1980, Swedish material), *C. carolinianum* tolerates relatively large variation in environmental parameters but prefers deep oligotrophic lakes (pH 5.0–7.3, conductivity 9–20 µS), which can be oligohumic or polyhumic. Maximum concentration 150 cells per liter (Aug.–Oct., rare in winter, cysts hatching at 10°C in May). The unusual pore on 2″ and its finger-like internal projection may indicate that the cell can attach, as in *C. cornutum*.
Geographical distribution: England (Lewis & Dodge); Estonia (Mölder); Finland (Järnefelt); France (Virieux); Germany (Zacharias); Holland (Redeke); Norway (Huitfeldt-Kaas); Scotland (West); Sweden (*e. g.* Almestrand, Morling); Switzerland (Schilling). Newfoundland, Canada and Miquelon Island (Huber-Pestalozzi);

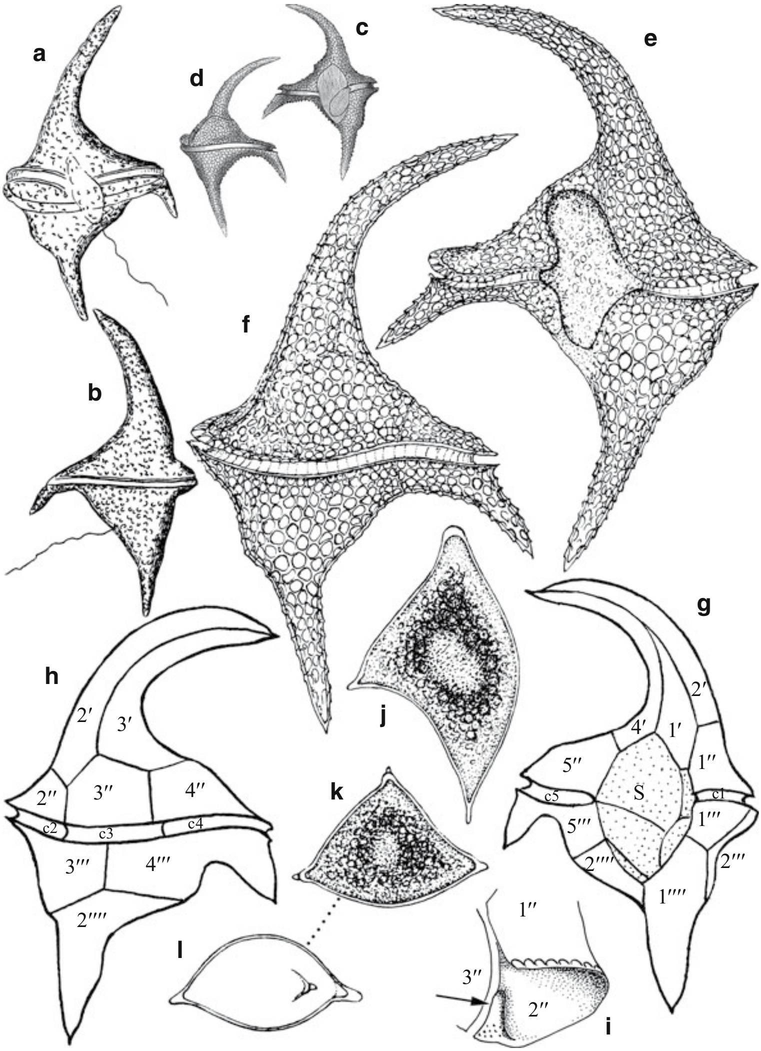

Fig. 133 *Ceratium carolinianum* (Bailey) Jörgensen (**a**, **b** after Bailey 1851; **c**, **d** after Huitfeldt-Kaas 1900; **e**, **f**, **j**–**l** after Skuja 1964; **g**–**i** after Bourelly & Couté 1976). **a**, **b** ventral and dorsal views (apparently reversed); **c**–**f** ventral and dorsal views showing shape variation and plate ornamentation; **g**, **h** ventral and dorsal views with tabulation (the ventral plates are stippled and marked with an S in **g**); **i** the finger-like, internal extension of plate 2″ (arrow); **j**–**l** cysts (**k** and **l** are different views of the same cyst)

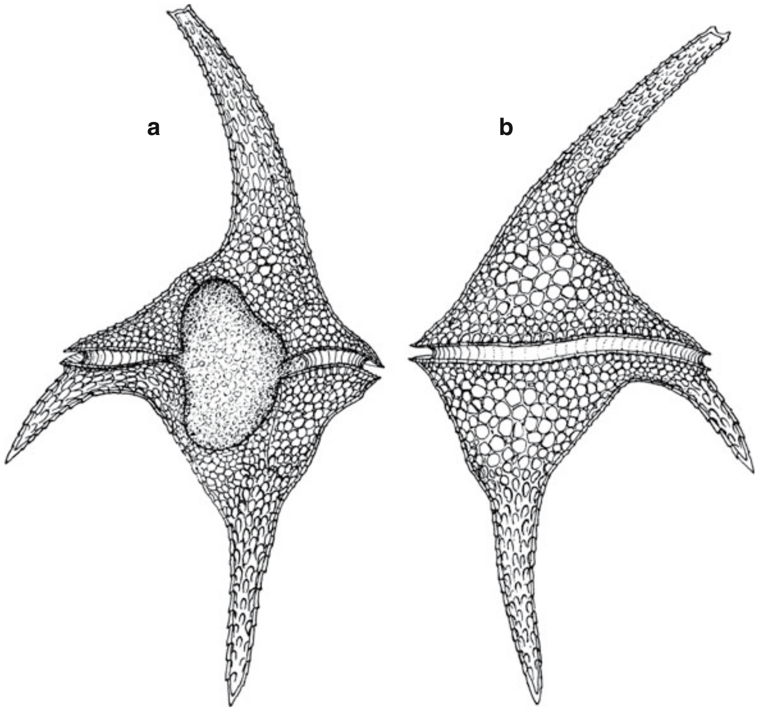

Fig. 134 *Ceratium carolinianum* var. *elongatum* Skuja (after Skuja 1964). **a** ventral view; **b** dorsal view

USA, MA (Prescott & Croasdale; Wall & Evitt), NC, (Bourrelly & Couté), SC (Bailey). Ural Mountains, Russia (Woronichin).

Note: the species is exceptional among the freshwater species of *Ceratium* in having a short 1′.

var. *elongatum* Skuja 1964, p. 357, pl. LXIX, figs 1–4 (Fig. 134)
The combination "*Ceratium elongatum* (Skuja) Morling (1980, p. 966)" was proposed as a provisional name and was therefore not validly published.

Apical horn slightly curved only, somewhat more elongate than in the typical variety, with a truncated end. Cell length *ca.* 170–220 µm long, 100–110 µm wide, and 28–32 µm thick.
SEM: Morling (1980).

Ecology: found only in Lake Nissejaure, Abisko, Lapland and adjacent lakes at higher pH, higher alcalinity, and higher conductivity (pH 8, conductivity 200 µS) than the typical variety.
Geographical distribution: Lapland, Sweden (Skuja).

Note: Morling (1980) mentions that this may be considered a variety of *C. cornutum*. However, her fig. 35b, which seems to show a pointed apical horn and an apparently short 1′ speaks against this suggestion.

4. *Ceratium cornutum* (Ehrenberg) Claparède & J. Lachmann 1859, p. 394 (**Fig. 135**)

Basionym: *Peridinium cornutum* Ehrenberg 1832, p. 75
Nomenclatural synonym: *Dimastigoaulax cornuta* (Ehrenberg) Diesing 1866, p. 392

Strongly dorsoventrally flattened cells with short anterior horn and two short posterior horns. The epicone more or less conical, the anterior horn slightly curved or nearly straight and directed towards the right. Apically the horn is obtuse or truncated, with small spines and closed with a plate, containing one large and many smaller pores. The horn is formed by all four apical plates reaching the apex. The length of the horn equals the length of the epicone. Hypocone rounded triangular, wider than long. Antapical horn short, thick, straight, rounded to pointed, sometimes slightly bent ventrally, formed by the two antapical plates. Right, postcingular horn very short (occasionally missing), thick conical, formed by 1‴ and 2‴. Amphiesmal plates strongly reticulate, each polyedric area with one or more trichocyst pores. Intercalary bands striated at right angles to the plate edges. Chloroplasts parietal, disc-shaped, nucleus central. Cell length 97–180 µm, width 48–85 µm, with a maximum during summer. Cysts thick-walled, tri- or quadrangular, with rounded ends, a short, narrow spine at each of the 3 ends. Cyst length 80–90 µm, hatches at 8–10°C (Morling 1980).
SEM: Bourrelly & Couté (1976), Morling (1980), Vyverman & Compère (1991); in more detail by Happach-Kasan (1982).
Ecology: in shallow lakes or near the margins of deeper lakes; pH 5.5–7.6, conductivity 65–270 µS (Morling); acid lakes? (Bourrelly & Couté). In culture, Happach-Kasan observed that cells tend to attach by a flat ribbon extending from the dorsal side, perhaps from the right cingular corner of 2″, indicating that this species is partially benthic or epiphytic. In England considered as a summer species (West), in Switzerland more common at lower temperatures (Huber-Pestalozzi), in the Jura Mountains (France) present throughout the year but more common in summer (Virieux). Generation time in culture at 21°C, 4 days (Happach-Kasan).
Geographic distribution: appears to be distributed over most of Europe, from Lapland in the North (Skuja) to Italy in the South (Imhof), and in the West from the British Isles (Lewis & Dodge) and Portugal (Calado & Craveiro) towards the East, reaching into Northern Asia (Skvortsov) and New Guinea (Vyverman & Compère). Also in North America (Eddy).

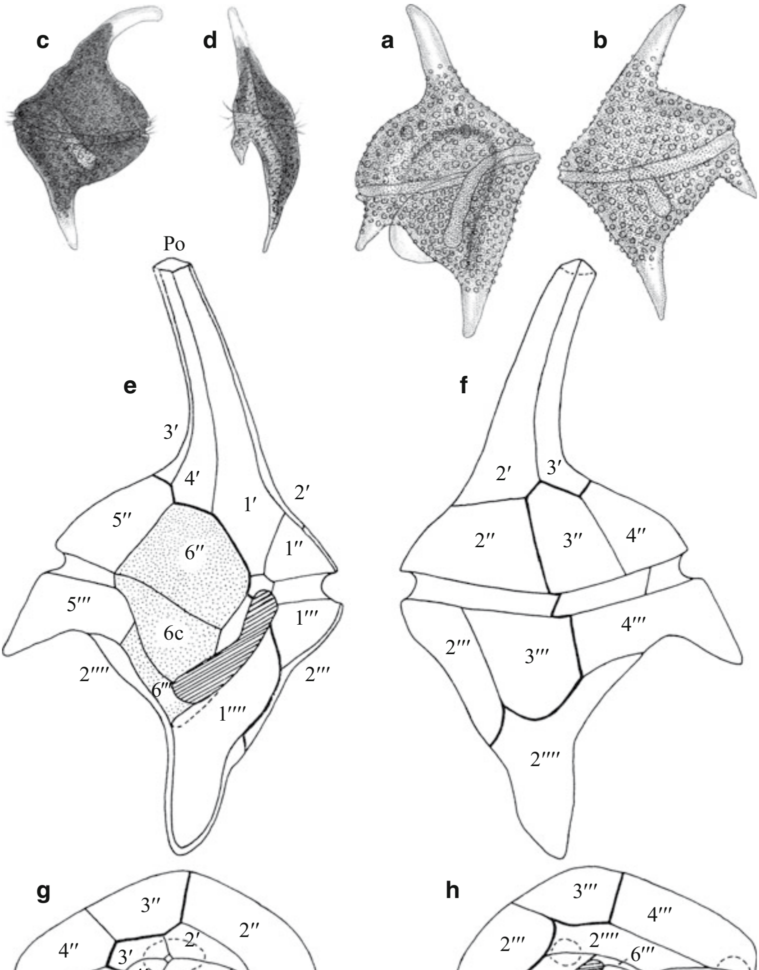

Fig. 135 *Ceratium cornutum* (Ehrenberg) Claparède & J. Lachmann (**a**–**d** after Ehrenberg 1838; **e**–**h** after Happach-Kasan 1982). **a** ventral view; **b** dorsal view; **c** dorsal view of a cell with only one horn in the hypocone; **d** cell viewed from the left side (**c** and **d** show the "crown" of cilia thought at the time to be present in the cingulum); **e**–**h** ventral, dorsal, apical and antapical views, respectively, showing the arrangement of amphiesmal plates (ventral plates marked with a dotted pattern in **e** sulcal aperture dashed; the thicker lines mark where plates separate during cell division)

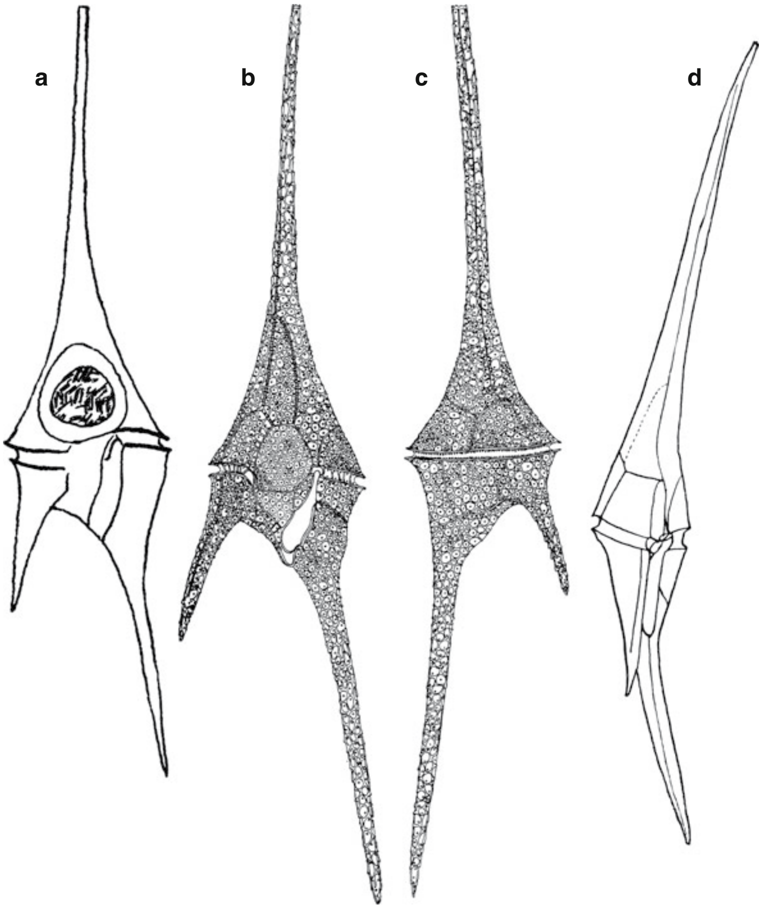

Fig. 136 *Ceratium furcoides* (Levander) Langhans (**a** after Levander 1894; **b**–**d** after Entz 1927). **a** outline of cell in ventral view showing the position of the nucleus; **b**, **c** ventral and dorsal views with plate limits and ornamentation; **d** cell viewed from the right

5. *Ceratium furcoides* (Levander) Langhans 1925, p. 602 (Fig. 136)

Basionym: *Ceratium hirundinella* var. *furcoides* Levander 1894, p. 53, pl. II, fig. 24
Taxonomic synonyms: *Ceratium furca* var. *lacustre* L. Maggi 1880, p. 128 ("*lacustris*"); *Ceratium handelii* Skuja in Handel-Mazzetti 1937, p. 48, pl. III, figs 9–12

Cells narrowly elongate, dorsoventrally compressed. Epicone conical, extending into long straight anterior horn, formed by apical plates 1′, 2′ and 3′. Apical plate 4′

short, reaching less than one third of the length of the apical horn. Apical end of the horn truncated, with crown of small spines. Hypocone wider than epicone, with 2–3 posterior horns. Antapical horn long and narrow, right horn shorter, parallel to the antapical horn or diverging. Left horn, if present (apparently mainly at colder temperatures), short, diverging. Amphiesmal plates areolate. Nucleus typically in the epicone. Chloroplasts parietal, disc-shaped. Cells 130–364 µm long and 32–63 µm wide.
Sexual reproduction examined in detail in Plußsee in Germany (Hickel). Gametes form in July–August. They are anisogamic, the smaller male gamete fusing with and becoming incorporated into the female gamete which opens up ventrally to engulf the male. The planozygote may remain in the water column for several weeks before developing into a resting cyst (hypnozygote). The hypnozygote slender with 3 relatively long, pointed, hyaline spines and a smooth cell wall. The length is 119–173 µm with spines, 61–79 µm without spines, the width 40–47 µm. The cyst overwinters in the bottom sediment and is resuspended into the plankton in March. It germinates into a planomeiocyte with two longitudinal flagella. Meiosis probably takes place in this cell. The first motile cells in spring are somewhat similar in shape to cysts.
SEM: Hickel (1988a, 1988b), Senzaki & Horiguchi (1994, as *C. hirundinella*), Olrik (1997), Hansen & Flaim (2007), Cavalcante *et al.* (2013).
TEM: Roberts (1989).
Ecology: plankton in oligotrophic, mesotrophic and eutrophic lakes, sometimes forming blooms (*e. g.*, 67 × 10^4 cells per liter in early August and 10.3 × 10^4 cells per litre in May in Plußsee, Germany; Hickel 1988a).
Geographical distribution: temperate-tropical regions. In Europe from Sweden and Finland in the north (Lemmermann, Levander) to Italy in the south (Zacharias) and from Portugal in the west (Craveiro & Santos) to Turkey in the east (Imhof). USA, LA (Roberts). Argentina (Meichtry de Zaburlin *et al.*); Brazil (Cavalcante *et al.*); Chile (Almanza *et al.*); Rio Chico, Columbia (Bustamante Gil *et al.*). Burma (Skuja, Entz); China (Brehm, Skuja); Java (Wołoszyńska); Philippines (Rott *et al.*).

Note: this species and the closely related *C. rhomvoides* stand out among freshwater species of *Ceratium* in having a short 4′.

Morphotypes of *C. furcoides* (see also under *C. hirundinella*):

1. Morphotype **brachyceroides** Schröder (**Fig. 137a**)
All horns more or less parallel but the antapical horn is directed slightly inwards. Cells 130–145 µm long, 30–45 µm wide.
Lake Schlawasee, Poland, rare elsewhere (Huber-Pestalozzi). Burma (Skuja).

2. Morphotype **furcoides** Schröder (**Fig. 137b**)
Antapical horn parallel to the apical horn, the right posterior horn almost parallel or slightly diverging. Cells elongate and narrow, 130–300 µm long, 30–45 µm wide.
Denmark (Wesenberg-Lund).

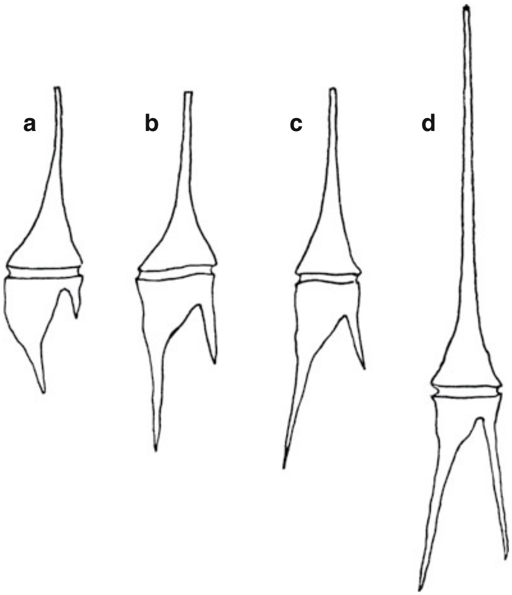

Fig. 137 Morphotypes of *Ceratium furcoides* (Levander) Langhans (after Huber-Pestalozzi 1950). Outlines of cells in dorsal view. **a** morphotype brachyceroides; **b** morphotype furcoides; **c** morphotype silesiacum; **d** morphotype yuennanense

3. Morphotype **silesiacum** Schröder (**Fig. 137c**)
Posterior horns slightly diverging from each other. Cells rather long and narrow, 148–280 µm long, width only 28–34 µm.
Denmark (Wesenberg-Lund); Finland (Levander); Poland (Huber-Pestalozzi).

4. Morphotype **yuennanense** Huber-Pestalozzi (**Fig. 137d**)
Cells long and narrow, 375–443 µm long, 44–55 µm wide. The anterior horn exceptionally long, the posterior horns diverging less than 45°.
China (Huber-Pestalozzi, Skuja).

6. *Ceratium monoceras* Temponeras *in* Temponeras *et al.* 2000, p. 101, text-figs 1, 2, pls 1–2, figs 1–14 (**Fig. 138**)

Epicone conical with reniform base, slightly asymmetrical with an inflexion on the right hand side. All apical plates reach the apex. Hypocone short, without horns, asymmetrical, longest on the left side. Cells dorsoventrally compressed. Cell length 90–110 µm, width 40–53 µm. Cysts oblong, 40–50 µm long and 30–40 µm wide, with one short, anterior spine.
SEM: Temponeras *et al.* (2000).

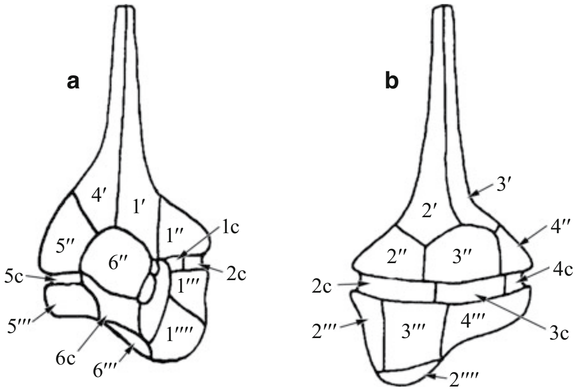

Fig. 138 *Ceratium monoceras* Temponeras (after Temponeras *et al.* 2000). **a** ventral view; **b** dorsal view

Ecology: apparently a warm-water species. Formed blooms in Lake Doïrani, Greece, in June–August 1996 at temperatures of 25–32 °C. Cell numbers up to 3.3×10^6 per liter. Co-occurred with blooms of blue-green algae. Cysts were found in June only. Lake Doïrani is a shallow, eutrophic lake with weak summer stratification. The species was not refound the following year, when temperatures were lower. Other lakes in the area contained *Ceratium hirundinella*, but this species was not recorded from Lake Doïrani, which had not been found to contain any *Ceratium* species prior to the sampling in 1996.
Geographical distribution: known only from Lake Doïrani, Greece (Temponeras *et al.*).

Note: apart from the missing posterior horns, the cell is similar to *C. hirundinella*.

7. *Ceratium rhomvoides* B. Hickel 1988b, p. 49, figs 1–18 (**Fig. 139**)

Cells rhombic in ventral and dorsal view, compressed dorsoventrally. Epicone with long straight anterior horn formed by three apical plates (1′, 2′, 3′), while 4′ is short and does not reach the tip. Hypocone with long, straight antapical horn and shorter right horn, the two horns diverging or parallel. A short left horn rarely present. Amphiesmal plates strongly reticulate. Chloroplasts red- or dark-brown. Cell length 123–203 µm, width 32–56 µm. Cysts rounded triangular, ovoid, smooth, with rather short spines, 72–101 µm in total length, 47–65 µm without spines, cyst diameter 36–47 µm. Sexual reproduction anisogamic, the smaller male gamete is incorporated into the larger female gamete.
SEM: Hickel (1988b).
Ecology: found in Lake Plußsee in Northern Germany, a medium-deep sheltered, eutrophic lake which is stratified in summer. *Ceratium rhomvoides* occurred July–November in numbers up to 100,000 per liter, less numerous than *C. furcoides* and *C. hirundinella*.

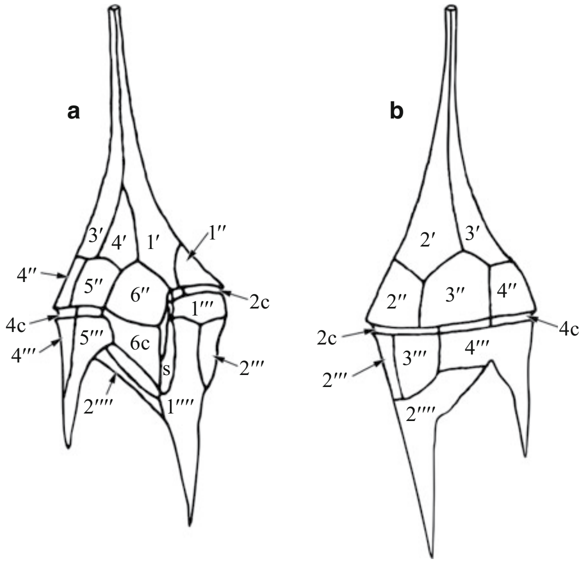

Fig. 139 *Ceratium rhomvoides* B. Hickel (after Hickel 1988b). **a** ventral view; **b** dorsal view

Geographical distribution: Germany (Hickel).

Note: *Ceratium rhomvoides* is very similar to *C. furcoides*, but was described to differ in having shorter, more compact cells, wider 6″ and 6c, the amphiesmal plates more coarsely reticulate and the resting spores ovoid. The chloroplasts of *C. rhomvoides* were said to be red-brown to dark-brown, while those of *C. furcoides* are yellow-brown. The two species are obviously closely related and need to be compared from other localities and studied also by molecular methods.

Family 2. Gonyaulacaceae Er. Lindemann 1928b, p. 34, 80, 84

Without horns. With apical pore. Two unequal antapical plates or one antapical plate and a small, posterior intercalary plate.

Genus 1. *Gonyaulax* Diesing 1866, p. 305, 382

Type species: *Gonyaulax spinifera* (Claparède & J. Lachmann) Diesing 1866, p. 382 (marine).

Plate formula: 3–4′, 0–2a, 5–6″, 6c, 3–8s, 5–6‴, 1p, 1″″. Very few species known from fresh water.

1. *Gonyaulax clevei* Ostenfeld 1901, p. 133, fig. 2 (**Fig. 140**)

Nomenclatural synonym: *Gonyaulax apiculata* var. *clevei* (Ostenfeld) Ostenfeld 1908, p. 164
Taxonomic synonyms: *Gonyaulax apiculata* Entz 1904, p. 11 [proposed as a combination based on *Peridinium apiculatum* Penard (1891, p. 51, pl. III, figs 3–13), *nom. illeg.* (non *P. apiculatum* (Ehrenberg) Claparède & J. Lachmann 1859)]; *Gonyaulax polonica* Wołoszyńska 1916, p. 265, pl. 10, figs 1–9; *Gonyaulax limnetica* Er. Lindemann 1919, p. 220, text-fig. 10, pl. 17, figs 2–4; *Gonyaulax austriaca* J. Schiller 1926, p. 34, fig. 30

Cells somewhat elongated, epi- and hypocone of nearly the same length. Epicone cone-shaped, often with slight hump midway on each side. Apex extended into a short apical horn terminating in a pore surrounded by a short tubular structure. Hypocone rounded. Cingulum strongly descending, the ends of the cingulum displaced 2–3 cingulum widths. Sulcus extends as a thin canal (the anterior sulcal plate) halfway to the apex. On the hypocone the anterior sulcal plate (as) continues halfway or a little less to the antapex. Posterior intercalary plate very small. Antapical plate (1″″), sulcal posterior (sp) and the rim between 1‴ and 2‴ with small spines. Amphiesmal plates areolated, with trichocyst pores. The cell breaks along the suture between the cingulum and the hypocone. Plate formula: 4′, 0a, 5″, 6c, 3s, 6‴, 1p, 1″″. With many yellow-green chloroplasts. Nucleus in the mid-region. Cell length 30–64 μm, width 29–58 μm. Cysts with an apical protuberance and short spines on the surface, 45–60 μm in diameter. Chloroplasts contracted to the center of the cell and surrounded by refractile orange oil droplets. Cyst found in the plankton of Selenter See, Germany, July–November, in low numbers (Hickel & Pollingher 1986), and in the sediments of Lake Zürich (Evitt *et al.* 1985).
SEM: Bourrelly & Couté (1980), Hickel & Pollingher (1986).
Ecology: plankton in smaller or larger, slightly alkaline lakes (pH *ca.* 7.5–8.4), oligotrophic to slightly mesotrophic; said to tolerate eutrophication poorly (Höll 1928). Also in brackish water (Ostenfeld 1908). Vertical migration observed in Selenter See, North Germany (Hickel & Pollingher 1986), at night the cells distributed evenly to 7 m, at dawn migrating upwards, the maximum accumulation of cells found within the top 3 m (max. 48,000 cells per liter). Cytokinesis occurred at night, up to 9% of the population dividing.
Distribution: Caspian Sea, Aral Sea, Russia (Ostenfeld); Finland (Lindholm, pers. comm.); Germany (Huber-Pestalozzi; Höll; Hickel & Pollingher); Hungary (Entz); Poland (Wołoszyńska; Bourrelly); Switzerland (Penard; Huber-Pestalozzi). USA, IA (Prescott), IL (Eddy).

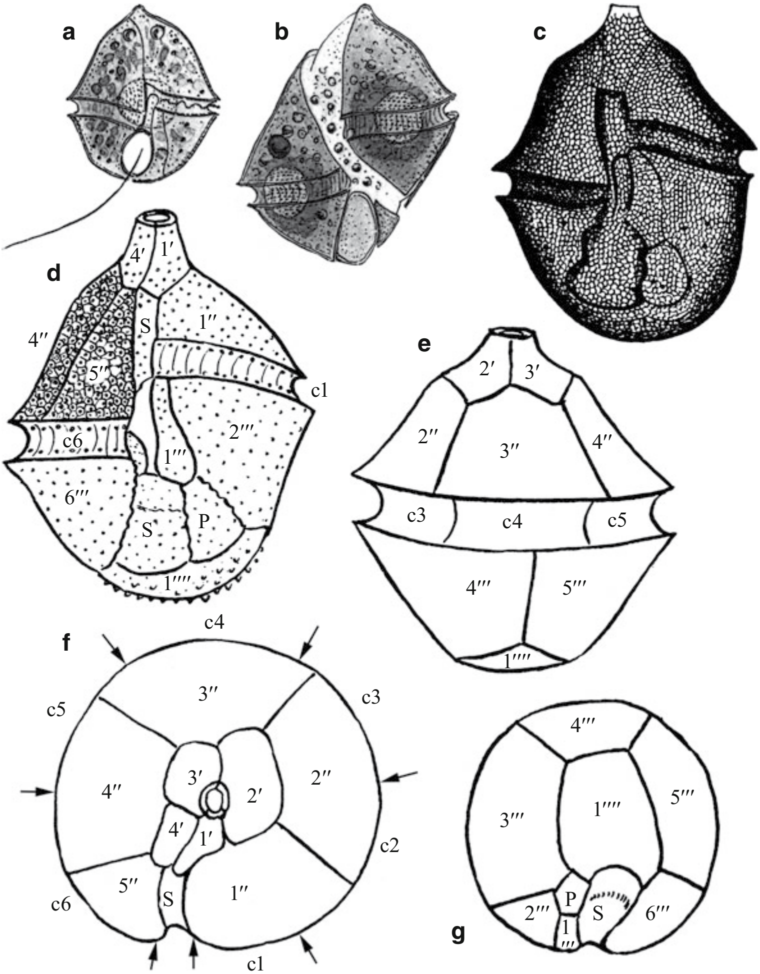

Fig. 140 *Gonyaulax clevei* Ostenfeld (**a**, **b** after Penard 1891; **c** after Wołoszyńska 1916; **d**–**g** after Bourrelly 1970). **a** live cell, ventral view; **b** cell division, ventral view; **c** ventral view with plate ornamentation; **d**–**g** ventral, dorsal, apical and antapical views, respectively, showing arrangement of amphiesmal plates (plate ornamentation indicated on left side of **d**; the arrows in **f** mark the edges of the cingular plates)

Order 6. PERIDINIALES Haeckel 1894, p. 127 ("Peridinea")

Cell lined by amphiesmal plates that can usually be seen with the light microscope, and which conform with the Kofoidian system for description of plates, i. e. the plates are arranged in series of apical, intercalary, precingular, cingular, sulcal, postcingular and antapical plates. Posterior intercalary plates are absent. Eyespot, if present, of type A. The order Peridiniales is sometimes merged with Gonyaulacales, but in molecular trees Gonyaulacales always come out separate. The Peridiniales, as presented here, may be polyphyletic, but further information is required before the affinities of the different families can be assessed. Typically, the hypocone of Peridiniales is composed of 7 plates, 5 postcingular and 2 antapical, exceptions being: the single species of Dinosphaeraceae and Thecadiniaceae; three genera of the Protoperidiniaceae (*Kansodinium*, *Kolkwitziella* and *Matvienkoella*), which lack one of the antapical plates ($5'''$, $1''''$), thus resembling the Gonyaulacales; and the two species of the Glenodiniopsidaceae, which have two additional postcingular plates ($7'''$, $2''''$). Desmoschisis, observed in the Gonyaulacales, is atypical in the Peridiniales. However, a kind of apparent desmoschisis has been reported in *Peridiniopsis cunningtonii* (Lefèvre 1932, p. 23, 24). In *Palatinus apiculatus* cells may leave the parent amphiesma and complete division in a motile, naked stage (Craveiro *et al.* 2009). In *Peridinium bipes*, Lefèvre (1932, p. 21) described cells to stop swimming prior to cell division and two daughter cells forming within the old theca, which was subsequently discarded. This type of cell division is widespread in the Peridiniales. Further observations are needed to clarify the division modes in the Peridiniales.

Key to the families of Peridiniales:

1a One antapical plate 2
1b Two antapical plates 4
2a Epi- and hypocone of approximately the same size 3
2b Epicone much smaller than hypocone .... 6. Thecadiniaceae
3a Apical pore absent .... 1. Dinosphaeraceae
3b Apical pore present .... 5. Protoperidiniaceae *p.p.*
4a Apical pore absent 5
4b Apical pore present 6
5a Amphiesmal plates very thin, usually visible only after staining, 7 postcingular plates .... 2. Glenodiniopsidaceae
5b Amphiesmal plates relatively thick, usually visible without staining, 5 postcingular plates .... 4. Peridiniaceae *p.p.* (*Palatinus*, *Peridinium* subg. *Cleistoperidinium*)
6a Epicone much smaller than hypocone, chloroplasts absent .... 5. Protoperidiniaceae *p.p.* (*Amphidiniopsis*)
6b Epi- and hypocone of approximately the same size 7
7a Chloroplasts absent .... 5. Protoperidiniaceae *p.p.* (*Protoperidinium*)
7b Chloroplasts present (often absent in *Glochidinium*) 8
8a Chloroplasts of diatom origin, containing fucoxanthin .... 3. Kryptoperidiniaceae
8b Chloroplasts lacking fucoxanthin .... 4. Peridiniaceae *p.p.*

Note: species of Kryptoperidiniaceae were formerly, as indicated by the name, included in Peridiniaceae. However, they have been found to form a separate, monophyletic, group, characterized in particular by the fucoxanthin-containing chloroplast. To distinguish the family as such from the Peridiniaceae it is probably necessary to examine the chloroplast or the chloroplast pigments. However, a second, less conspicuous nucleus (not a dinokaryon) is often made visible in cells of Kryptoperidiniaceae by applying a nuclear stain, such as acetocarmine.

Family 1. Dinosphaeraceae Er. Lindemann 1928b, pp 34, 80, 84

Apical pore lacking. With one large antapical plate. Tabulation on the hypocone 5‴, 0p, 1⁗.

Genus 1. *Dinosphaera* Kofoid & J. R. Michener 1912, p. 23

Type species: *Dinosphaera palustris* (Lemmermann) Kofoid & J. R. Michener 1912

With the characters of the family. The only described species has numerous chloroplasts.

1. *Dinosphaera palustris* (Lemmermann) Kofoid & J. R. Michener 1912, p. 23 (**Fig. 141**)

Basionym: *Gonyaulax palustris* Lemmermann 1907a, p. 296, figs 1–5
Nomenclatural synonym: *Glenodinium palustre* (Lemmermann) J. Schiller 1935a, p. 99

Cells spherical, epi- and hypocone of same size or epicone somewhat larger. Cells not dorsoventrally compressed. Sulcus wide, extending very slightly onto the epicone. On the hypocone it narrows posteriorly but does not reach the antapex. Cingulum slightly descending. Plate formula 3′, 1a, 6″, 6c, 6s(?), 5‴, 1⁗. Numerous parietal chloroplasts. Yellow oil globules also seen. Cell length 27–34 µm, width 25–31 µm.
Ecology: pool in a heath, Mark Brandenburg (Lemmermann 1907a); soft water lakes and acid bogs (Prescott 1962); peat bog in Auvergne (Bourrelly 1970); ultra-oligotrophic, altitude lake in Tasmania (Ling *et al.* 1989).
Geographical distribution: France (Bourrelly); Germany (Lemmermann); Poland (Wołoszyńska); Ukraine (Wołoszyńska; Krakhmalny *et al.*). USA, IA, WI (Prescott), IL (Eddy), MA (Prescott & Croasdale). Tasmania, Australia (Ling *et al.*).

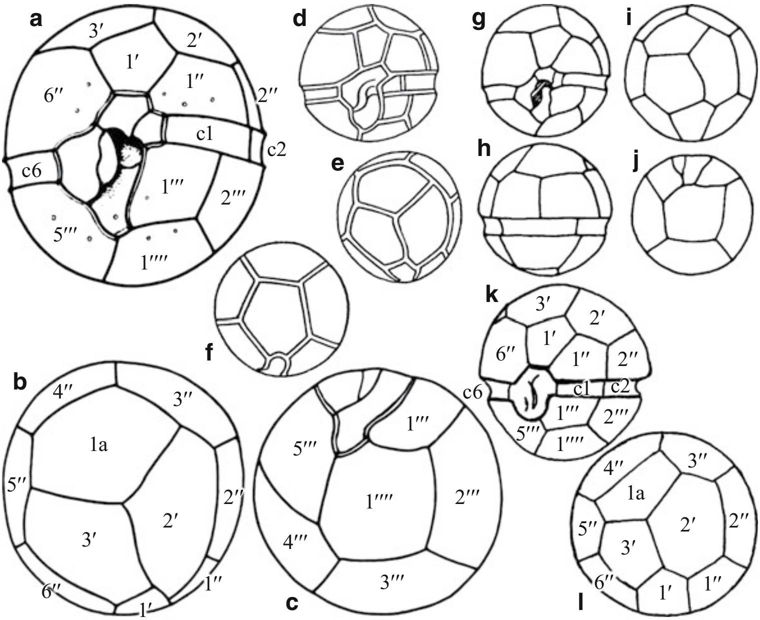

Fig. 141 *Dinosphaera palustris* (Lemmermann) Kofoid & J. R. Michener (**a**–**c** after Kofoid & Michener 1912, from examination of Lemmermann's original material; **d**–**f** after Lemmermann 1907a; **g**–**j** after Ling *et al.* 1989; **k**, **l** after Bourrelly 1970). **a**–**c** ventral, apical and antapical views, with main plates labelled (sulcal area delimited by double lines); **d**–**f** ventral, apical and antapical views; **g**–**j** ventral, dorsal, apical and antapical views; **k**, **l** left-ventral and apical views with main plates labelled

Family 2. Glenodiniopsidaceae J. Schiller 1935a, p. 80

A family comprising a single genus of somewhat uncertain phylogeny. Apical pore absent. Cell periplast of thin, relatively large, amphiesmal plates, usually visible only after staining or in the SEM. The absence of an apical pore makes plate homologies somewhat uncertain and the plate pattern has been interpreted in different ways. The plate pattern is asymmetric. The epicone is covered by 15–16 amphiesmal plates, one of which has been identified as an anterior sulcal plate, the hypocone by 10 amphiesmal plates. Plate formula interpreted from SEM as 2–3′, 4a, 8″, ?c, ?s, 7‴, 2⁗.

Genus 1. *Glenodiniopsis* Wołoszyńska 1916, p. 278

Type species: *Glenodiniopsis steinii* Wołoszyńska, herein considered synonymous with *Glenodiniopsis uliginosa* (A. J. Schilling) Wołoszyńska

Cells oval or nearly spherical, slightly compressed dorsoventrally. Epicone larger than hypocone. Cingulum descending but cingular displacement very small. Chloroplasts present, eyespot unknown. Reproduction observed in *G. uliginosa*. Vegetative division takes place within the theca and the daughter cells exit through a slit formed between the precingular and cingular plates on the cell's left side. Sexual reproduction induced by nitrogen starvation. Gametes similar to vegetative cells, but smaller (Highfill & Pfiester 1992a). One gamete fuses head-on with the cingulum-sulcus region of the other gamete. Resting cysts spherical, warty, the warts apparently reflecting the plates of one of the gametes. Germination not observed but empty resting cysts observed in cultures (Highfill & Pfiester 1992a).
Two species, which appear to be similar in the plate pattern, and may turn out to represent a single species.

Key to species of *Glenodiniopsis*:

1a Cells oval, epicone considerably longer than hypocone, widely distributed ... . 1. *G. uliginosa*

1b Cells almost spherical, epicone only slightly longer than hypocone, tropical . ... 2. *G. pretiosa*

1. *Glenodiniopsis uliginosa* (A. J. Schilling) Wołoszyńska *in* Lindemann 1928b, p. 82 (**Fig. 142**)

Basionym: *Glenodinium uliginosum* A. J. Schilling 1891a, p. 283, pl. X, fig. 16
Nomenclatural synonym: *Peridinium uliginosum* (A. J. Schilling) Wołoszyńska 1917, p. 116
Taxonomic synonyms: *Glenodinium steinii* Lemmermann 1900b, p. (117) (validated by reference to Stein 1883, pl. III, figs 18–21, as *Glenodinium cinctum*) ≡ *Glenodiniopsis steinii* (Lemmermann) Wołoszyńska 1917, p. 116, *nom. illeg.*; *Glenodiniopsis steinii* Wołoszyńska 1916, p. 278, pl. 11, figs 30–36; (?) *Glenodinium australicum* Playfair 1920, p. 799, text-fig. 4

Cells ovoid with rounded epi- and hypocone, slightly dorsoventrally compressed, more so on the hypocone than on the epicone. Epicone elongate hemispherical, longer and slightly wider than the hypocone. Cingulum descending, the ends displaced *ca.* one cingulum width. Nucleus elongate, slightly curved, located centrally and extending slightly into the hypocone (Highfill and Pfiester 1992b) or in the right hand side of the epicone (Stein 1883; Wołoszyńska 1916; Hansen & Flaim 2007). Chloroplasts greenish-brown, numerous, forming a network with radial and parietal branches, often interpreted as many, separate plate-like chloroplasts. Trichocysts present. Cells 26–50 μm long, 26–40 μm wide, *ca.* 28 μm thick. Plate formula interpreted as 2–3′, 4a, 8″, 7‴, 2″″, but the identity of individual plates of apical and intercalary series varies with authors (*cf.* Highfill & Pfiester 1992a *vs.* Bourrelly 1970). Ventral plate adjacent to anterior sulcal and first precingular, la-

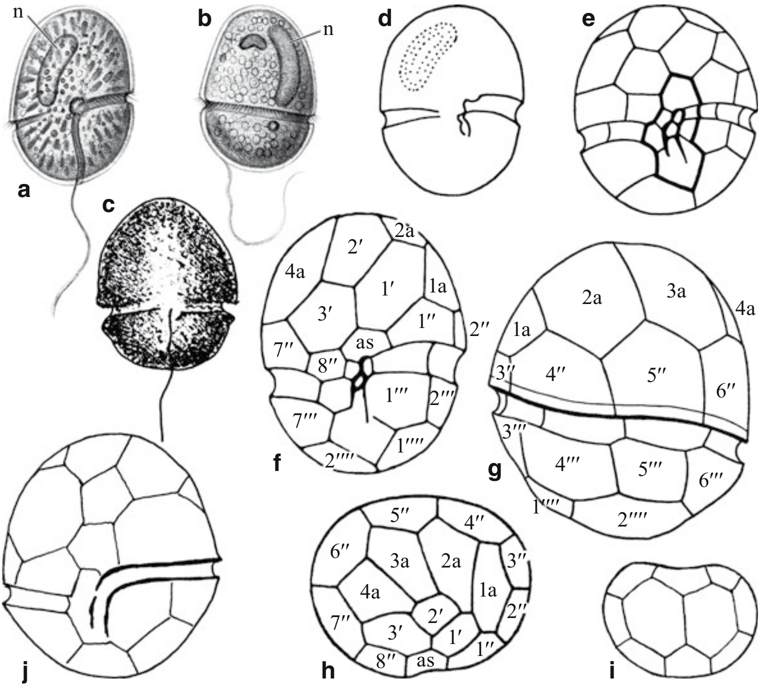

Fig. 142 *Glenodiniopsis uliginosa* (A. J. Schilling) Wołoszyńska (**a**, **b** after Stein 1883; **c** after Schilling 1891a; **d**, **f** after Wołoszyńska 1916; **e**, **g** after Wołoszyńska 1917; **h**, **i** after Lindemann 1925c; **j** after Bourrelly 1970). **a**, **b** ventral and dorsal views with cell contents, showing elongate nucleus (n) on the right side of the epicone; **c** ventral view; **d** outline of cell in ventral view, nucleus indicated; **e** ventral view with main plates, edge of sulcus marked with thick line; **f**–**h** ventral, dorsal and apical views, respectively, with main plates labelled after Bourrelly (slightly modified); **i** antapical view; **j** ventral view showing plate variation on the epicone

belled 1a in Hansen & Flaim (2007), sometimes divided into two plates (Hansen & Flaim 2007). That plate is here interpreted as 1′ or, if divided, as 1′ and 2′. Cysts globular, warty (Highfill & Pfiester 1992a).
SEM: Highfill & Pfiester (1992a, b), Hansen & Flaim (2007), Cavalcante *et al.* (2017).
TEM: Highfill & Pfiester (1992b).
DNA data: Moestrup & Daugbjerg (2007), Logares *et al.* (2007b).
Ecology: a species of peaty ponds and bogs with low calcium content, mostly at pH 4.0–6.5 (Höll 1928), sometimes bloom-forming (Schilling 1891a). Maximum occurrence in summer, prefers temperatures of 12–17 ˚C, overwinters as non-motile stage (Lewis & Dodge 2011).

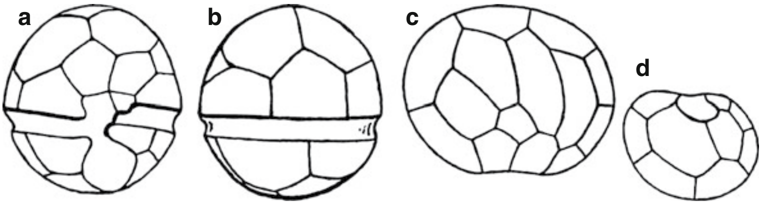

Fig. 143 *Glenodiniopsis pretiosa* Er. Lindemann (after Lindemann 1931). **a**, **b** ventral and dorsal views; **c**, **d** apical and antapical views (schematic)

Geographical distribution: Czech Republic (Popovský); England (Lewis & Dodge); France (Lefèvre; Bourrelly); Germany (Schilling; Höll; Popovský); Italy (Hansen & Flaim); Tatra Mountains, Poland (Wołoszyńska); Sweden (Skuja; Gert Hansen, pers. comm.). British Columbia, Canada (Carty); USA, MN (Highfill & Pfiester). Brazil (Cavalcante *et al.*). Japan (NIES Culture Collection). Australia (Playfair). New Zealand (Thompson).

Note: this species was first described by Schilling (1891a) who did not provide any details of plate pattern. Wołoszyńska (1916, 1917) was the first to describe the plate pattern, in *G. steinii,* subsequently considered to be identical to Schilling's *Glenodinium uliginosum*. Wołoszyńska described 15 plates in the epicone, of which one was interpreted as the anterior sulcal (Wołoszyńska 1916). Highfill & Pfiester (1992b) confirmed her studies, interpreting one of the plates as an anterior sulcal plate, and the remaining 14 plates as mentioned above, although they labelled as apical two plates here considered as 2a and 3a.

2. *Glenodiniopsis pretiosa* Er. Lindemann 1931, p. 696, figs 1–4 (**Fig. 143**)

Cells rounded ovoid, slightly compressed dorsoventrally. Epicone slightly larger than hypocone. Cingulum descending, the ends displaced *ca.* half a cingulum width. Plate formula interpreted as 2′, 4a, 8″, 7‴, 2″″ or 3′, 3a, 8″, 7‴, 2″″, but material from Poland and Sumatra differ. Small extra plates present but homology not understood, and additional studies needed. Plates smooth, but papillae may be present on the anterior ventral plates. With numerous chloroplasts. Eyespot absent. Cells 35–40 µm long.
Ecology: found at pH below 7.
Geographical distribution: Poland (Popovský). Sumatra, Indonesia (Lindemann).

Family 3. Kryptoperidiniaceae Er. Lindemann 1925c, p. 152—the "dinotoms"

Cells naked or with amphiesmal plates. Chloroplasts contain fucoxanthin as major light-harvesting carotenoid.
Monophyletic group whose photosynthetic ancestor ingested a diatom, which was subsequently retained as a separate compartment in the cytoplasm of the dinofla-

gellate (Takano *et al.* 2008). The diatom endosymbiont retained many of its cell organelles, while all traces of a silica frustule are absent. Species of this family possess both the dinoflagellate nucleus (with condensed chromosomes) and, in the separate compartment, the diatom nucleus (without condensed chromosomes), together with the diatom chloroplasts, mitochondria, etc. The eyespot, located in the dinoflagellate cytoplasm, is surrounded by 3 membranes, indicating a previous endosymbiosis, while the diatom endosymbiont is surrounded by a single membrane, probably the cell membrane of the diatom. Cells also contain a unique lamellate body of unknown function.

The dinokaryon of *Durinskia* was observed to divide in synchrony with the apparent amitosis of the symbiont diatom nucleus (Tippit & Pickett-Heaps 1976). Ultrastructural aspects of sexual reproduction in *Durinskia*, including synchronous fusion of host and symbiont of both gametes, have been reported (Chesnick & Cox 1987, 1989).

Members of this group were formerly included in *Peridinium* and *Peridiniopsis*. However, molecular studies have shown that they form a monophyletic group separate from the type species of either of these genera.

Cell division by oblique division of the cytoplasm into two gymnodinioid cells within the mother amphiesma was described in *Unruhdinium durandii* by Javornický (1972, as *Peridinium penardii* f. *californicum*) and in *Unruhdinium kevei* by Leitão *et al.* (2001, as *Peridiniopsis corillionii*).

Cases of “red tides” in fresh water have been reported for species of the genus *Unruhdinium*.

Key to the genera of Kryptoperidiniaceae occurring in fresh water:

1a Epicone with two intercalary plates .... 1. *Durinskia*
1b Epicone with 0–1 intercalary plates .... 2. *Unruhdinium*

Genus 1. ***Durinskia*** Carty & El.R. Cox 1986, p. 200

Type species: *Durinskia baltica* (Levander) Carty & El.R. Cox 1986

Cells rounded or ovoid with plate formula po, x, 4′, 2a, 6″, 5c, 4s, 5‴, 0p, 2⁗. Amphiesmal plates thin. Plate arrangement on the epicone very asymmetric when seen from above. Plate 1′ rather large, rhombic, 2′ pentagonal, 3′ four-sided and small, 4′ pentagonal. Intercalary plate 1a small, pentagonal, 2a large, hexagonal.

Note: the three species reported from fresh water can be difficult to separate, *D. baltica* and *D. oculata* in particular. However, *D. baltica* typically occurs in brackish water, with few reports from fresh water. In addition, some variation in plate arrangement has been reported in both *D. baltica* and *D. oculata*. The three taxa need to be examined further.

Key to species of *Durinskia* occurring in fresh water:

1a Cells dorsoventrally compressed 2
1b Cells very slightly or not dorsoventrally compressed .... 3. *D. oculata*
2a Amphiesmal plates with transverse rows of pores .... 2. *D. dybowskii*
2b Amphiesmal plates smooth .... 1. *D. baltica*

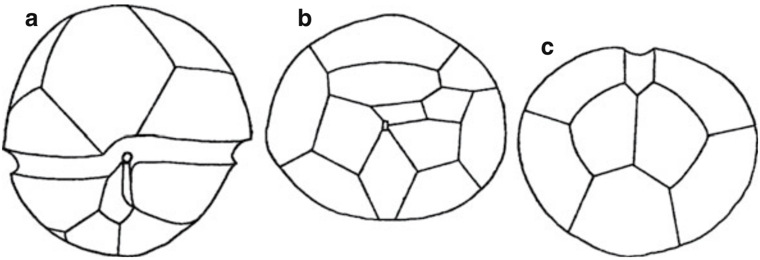

Fig. 144 *Durinskia baltica* (Levander) Carty & El.R. Cox (after Levander 1892). **a** ventral view (somewhat imprecise, but faithful to the original); **b**, **c** apical and antapical views

1. *Durinskia baltica* (Levander) Carty & El.R. Cox 1986, p. 200 (**Fig. 144**)

Basionym: *Glenodinium balticum* Levander 1894, p. 52
Nomenclatural synonym: *Peridinium balticum* (Levander) Lemmermann 1900b, p. (120)

Cells rounded, somewhat dorsoventrally compressed. Epicone and hypocone equal in size or epicone slightly larger (and sometimes wider) than hypocone. Cingulum descending, the ends displaced *ca.* half the width of the cingulum. Amphiesmal plates smooth, without ornamentation. With numerous yellowish-brown, discoid, parietal chloroplasts. Rectangular, distinct eyespot in the sulcus. Nucleus (dinokaryon) in the central part of the cell. Cell length 20–33 μm, width 18–28 μm.
SEM: Tippit & Pickett-Heaps (1976), Chesnick & Cox (1985), Carty & Cox (1986), Couté *et al.* (2012), Pandeirada *et al.* (2013).
TEM: Tomas & Cox (1973), Tomas *et al.* (1973), Tippit & Pickett-Heaps (1976), Chesnick & Cox (1987, 1989).
DNA data: Zhang *et al.* (2011b).
Ecology: this species was first described during summer from brackish water in Lövö, inner Baltic Sea (Levander 1892, 1894). It has been reported repeatedly from brackish water but also on a few occasions from freshwater ponds and pools (usually humus-rich) from July to October.
Geographical distribution (reports from fresh water): Portugal (Pandeirada *et al.*; isolate maintained in freshwater growth medium). USA, drainage ditch in College Station, TX (Carty & Cox). China (Guangdong, Hubei, Shandong; Zhang *et al.*).

2. *Durinskia dybowskii* (Wołoszyńska) Carty 2014, pp 105, 222 ("*dybowski*") (**Fig. 145**)

Basionym: *Peridinium dybowskii* Wołoszyńska 1916, p. 273, pl. 13, figs 9–14
Nomenclatural synonym: *Glenodinium dybowskii* (Wołoszyńska) Er. Lindemann 1925c, pp 162, 166

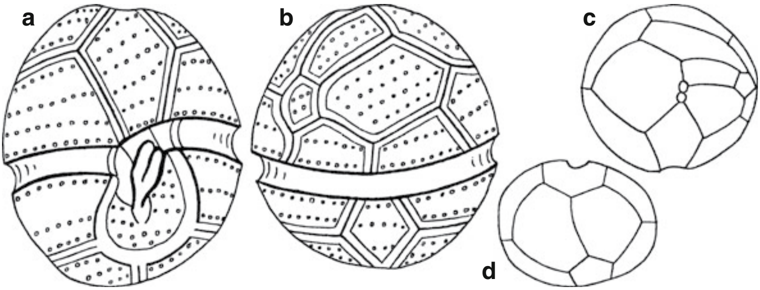

Fig. 145 *Durinskia dybowskii* (Wołoszyńska) Carty (after Wołoszyńska 1916). **a**, **b** ventral and dorsal views showing major amphiesmal plates with transverse rows of pores; **c**, **d** apical and antapical views with outline of plates (ornamentation not shown)

Cells round to ovoid, somewhat dorsoventrally compressed. The epi- and hypocone of similar size. Cingulum descending, the two ends displaced *ca.* half the width of the cingulum. Amphiesmal plates smooth but ornamented with transverse rows of pores. With numerous golden chloroplasts. Cell length 25–35(–40) μm, width 35 μm.
Ecology: plankton in pond (Wołoszyńska 1916), acid peat bogs (Höll 1928).
Geographical distribution: Poland (Wołoszyńska). Brazil (Cardoso *et al.*)?

3. *Durinskia oculata* (F. Stein) Gert Hansen & Flaim 2007, p. 134, 136 ("*occulata*") (**Fig. 146**)

Basionym: *Glenodinium oculatum* F. Stein 1883, pl. III, figs 5–7
Nomenclatural synonym: *Peridinium oculatum* (F. Stein) Wołoszyńska 1917, p. 116, *nom. illeg.* (non *Peridinium oculatum* Dujardin 1841, p. 374) ≡ *Peridiniopsis oculata* (F. Stein) Bourrelly 1968, p. 9 ("*oculatum*")

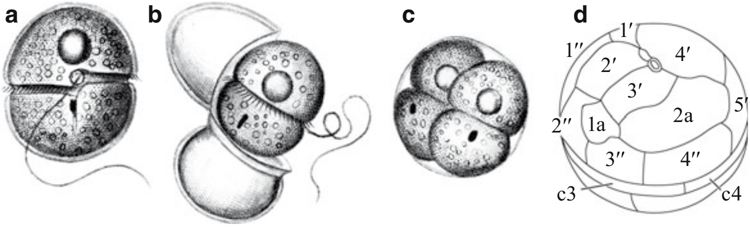

Fig. 146 *Durinskia oculata* (F. Stein) Gert Hansen & Flaim (**a**–**c** after Stein 1883; **d** original). **a** ventral view, with small eyespot near upper end of narrow sulcus; **b** ecdysis, the firm amphiesma opening along the edge of the cingulum; **c** division stage; **d** apical-dorsal view, based on SEM illustration in Hansen & Flaim (2007)

Cell globular to widely ovate, very slightly dorsoventrally compressed. Cingulum median, slightly descending. Amphiesmal plates thin, smooth, penetrated by scattered, minute pores, which tend to be more numerous along plate margins and along the cingulum. Numerous small yellowish-brown chloroplasts present in the cell periphery. Minute eyespot present near the sulcus. Cell length 19–36 µm, width 18–35 µm.
SEM: Hansen & Flaim (2007).
Ecology: in River Vltava in Prag (Stein 1883); plankton in meso-eutrophic lake in Italy (Hansen & Flaim 2007).
Geographical distribution: Czech Republic (Stein); Germany (Lindemann); Italy (Hansen & Flaim); Poland (Wołoszyńska)?

Genus 2. ***Unruhdinium*** Gottschling *in* Gottschling *et al.* 2017, p. 297

Type species: *Unruhdinium jiulongense* (H. Gu) Gottschling
Solitary dinoflagellates with chloroplasts of diatom origin. Cells covered by amphiesmal plates which are sometimes visible in the light microscope. Plate formula po, x, 4′, 0a, 6″, 5c, 5s, 5‴, 0p, 2″″ or po, x, 3′, 1a, 6″, 5c, 5s, 5‴, 0p, 2″″. Eyespot, if present, of type A.

Key to species of *Unruhdinium*:

1a Cells with single, central, antapical spine or spines absent 2
1b Cells with 2 or more antapical spines 4
2a Cells with single, central, antapical spine .... 4. *U. kevei*
2b Spines absent 3
3a Plate pattern symmetrical in apical view .... 6. *U. penardii*
3b Plate pattern very asymmetrical in apical view .... 1. *U. jiulongense*
4a Epicone larger than hypocone, one robust spine on each antapical plate .... 5. *U. niei*
4b Epi- and hypocone of almost same size, with two or more small antapical spines 5
5a Cells asymmetrical in apical view, plate 4′ larger than 2′, tropical species .... 2. *U. armebeense*
5b Cells symmetrical when seen from above, plates 2′ and 4′ equal in size; temperate species 6
6a Amphiesmal plates smooth (SEM!), with 2-more very short antapical spines .... 6. *U. penardii* var. *robustum*
6b Amphiesmal plates reticulate (SEM!), with several short antapical spines .... 3. *U. durandii*

1. *Unruhdinium jiulongense* (H. Gu) Gottschling *in* Gottschling *et al.* 2017, p. 297 (**Fig. 147**)

Basionym: *Peridiniopsis jiulongensis* H. Gu *in* You *et al.* 2015, p. 316, figs 1–4

Cells subspherical. Epi- and hypocone of almost equal length. Cingulum descending, the ends displaced *ca.* half its own width. Amphiesmal plates smooth apart from trichocyst pores. Several band-shaped chloroplasts in the cell periphery, with

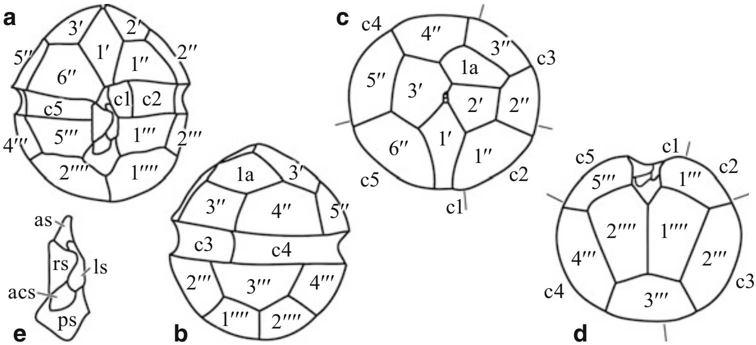

Fig. 147 *Unruhdinium jiulongense* (H. Gu) Gottschling (after You *et al.* 2015). **a**–**d** ventral, dorsal, apical and antapical views, respectively, showing main amphiesmal plates; **e** plate composition of the sulcus showing anterior (as), right (rs), left (ls), posterior (ps) and middle or accessory (acs) sulcal plates

lens-shaped internal pyrenoids. Distinct elongate eyespot in the sulcal area, formed by two rows of eyespot globules. Plate pattern strongly asymmetrical in apical view: the single intercalary plate is located on the left side of the cell, closely appressed to 2′, while the equivalent space on the cell's right is occupied by 3′. Cell length 18–32 µm, width 14–28 µm. Cysts oval or elliptical, 25–30 µm long, without ornamentation.
SEM: You *et al.* (2015).
TEM: You *et al.* (2015).
DNA data: You *et al.* (2015).
Ecology: established in culture from germination of cysts collected from the sediments of the Xipi reservoir of the Jiulong River, China.
Geographical distribution: Fujian, China.

Note: this species is very similar to *U. penardii*, but differs in the asymmetrical arrangement of the plates in the apical end of the cell, the only species in *Unruhdinium* with this type of asymmetry.

2. *Unruhdinium armebeense* (Ten-Hage, K. P. Da & Couté) Moestrup & Calado *comb. nov.* (**Fig. 148**)

Basionym: *Peridiniopsis armebeensis* Ten-Hage, K. P. Da & Couté *in* Ten-Hage *et al.* 2007, *Nova Hedwigia* **85**, p. 261, figs 2–17

Cells pentagonal to rhombic in ventral view, not dorsoventrally compressed. Epi- and hypocone of equal size. Epicone rounded conical, hypocone more rounded. Cingulum descending, the ends displaced half to one cingulum width. Sulcus narrow. Hypoconal cingular list and sulcal lists denticulated. Amphiesmal plates reticulate. Cells somewhat asymmetrical when seen from above, 4′ being of approximately the same size as 2′ and 3′ combined. Plate 2′ pentagonal, 3′ and 4′

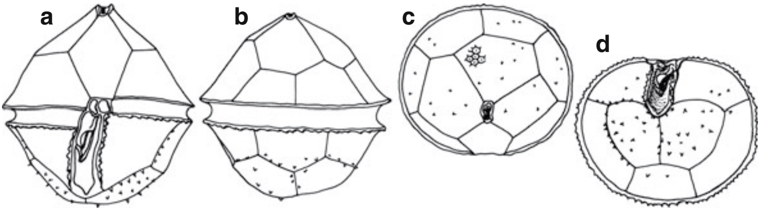

Fig. 148 *Unruhdinium armebeense* (Ten-Hage, K. P. Da & Couté) Moestrup & Calado (after Ten-Hage *et al.* 2007). **a**–**d** ventral, dorsal, apical and antapical views, respectively

hexagonal. Small spines present on antapical plates, on the suture between the antapical plates, and on the sutures between postcingular plates. Many small, golden-brown chloroplasts. Nucleus central. Cell length 44–49 µm, width 37–45 µm.
Ecology: found in river plankton and also in brackish water in Ebrié Lagoon, Ivory Coast.
Geographical distribution: Ivory Coast (Ten-Hage *et al.*).

3. *Unruhdinium durandii* (S. Rodriguez, Couté, Ten-Hage & Mascarell) Moestrup & Calado *comb. nov.* (**Fig. 149**)

Basionym: *Peridiniopsis durandii* S. Rodriguez, Couté, Ten-Hage & Mascarell 1999, *Algol. Stud.* **95** (*Arch. Hydrobiol., Suppl.* **130**), p. 27, figs 3–25 ("*durandi*")
Taxonomic synonym: *Peridinium penardii* f. *californicum* Javornický 1972, p. 304. An intended new combination "*Peridinium californicum*" was not validly published by Rodriguez *et al.* (1999) for lack of full and direct reference to place of publication of basionym (no page indication).

Cells more or less rhombic, epicone and hypocone equal in size. Epicone conical with convex sides, hypocone more or less trapezoid. The ventral side of the cell is flattened or concave. Cingulum descending, displaced *ca.* half the cingulum width, bordered both anteriorly and posteriorly by small teeth. Sulcus widens towards the antapex, with short spines on the sutures between the posterior sulcal and the antapical plates, and on the suture between antapical plates. Spines close to the antapex slightly longer. Apical pore plate with low rim except on the ventral side. Plate 3′ hexagonal. Plates appear smooth in the light microscope but a reticulation is visible in the SEM. With a variable number of rounded or elongate discoid, brown, parietal chloroplasts. Both parts of the cell with brown or reddish-brown bodies. Cell length 23–33 µm, width 21–31 µm.
SEM: Rodriguez *et al.* (1999).
Ecology: planktonic, on calcareous soil, forming blooms in reservoirs of the Ain River system in the Jura mountains of eastern France, 1995–1997, resulting in wine-red water (Rodriguez *et al.* 1999); in Clear Lake, California, in April 1970 (Javornický 1972).
Geographical distribution: France (Rodriguez *et al.*). USA, CA (Javornický).

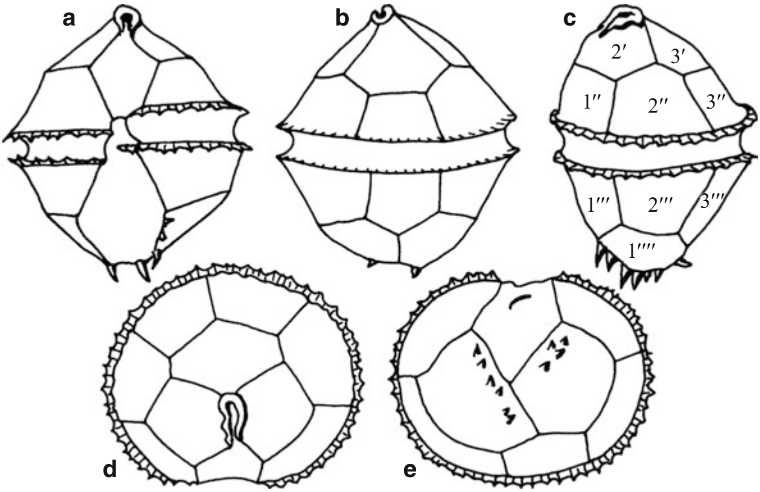

Fig. 149 *Unruhdinium durandii* (S. Rodriguez, Couté, Ten-Hage & Mascarell) Moestrup & Calado (after Rodriguez *et al.* 1999). **a**–**c** ventral, dorsal and left lateral views; **d**, **e** apical and antapical views

Note: this species appears to differ from *U. penardii* mainly in the ornamentation of the amphiesmal plates, especially when viewed in the SEM.

4. ***Unruhdinium kevei*** (Grigorszky & F. Vasas) Gottschling *in* Gottschling *et al.* 2017, p. 298 (**Fig. 150**)

Basionym: *Peridiniopsis kevei* Grigorszky & F. Vasas *in* Grigorszky 1999, pp 31, 122
Taxonomic synonyms: *Peridiniopsis corillionii* M. Leitão, Ten-Hage, Mascarell & Couté 2001, p. 13, figs 1 (type), 2–22; *Peridiniopsis rhomboides* Krakhmalny 2001, p. 469

Cells almost rhomboidal in ventral view. Epicone and hypocone both conical, epicone slightly longer than hypocone. Cells more or less dorsoventrally compressed, dorsal side of the cell convex in transverse view, ventral side flat or very slightly concave. Cingulum descending, the ends displaced 1/2–1× its own width. With short, conical spine on 1⁗. Very small spines may be present elsewhere, for example on the cingulum rim and in the antapical region. Amphiesmal plates smooth (Japanese material) or reticulate (material from Europe and Ukraine). Numerous yellowish-brown chloroplasts located in the cell periphery. Each chloroplast with internal lenticular pyrenoid, sometimes traversed or penetrated by single thylakoids. A thin membrane may be present around the pyrenoid. Eyespot conspicuous, located near the sulcus. It consists of two parts, a curved anterior part and an

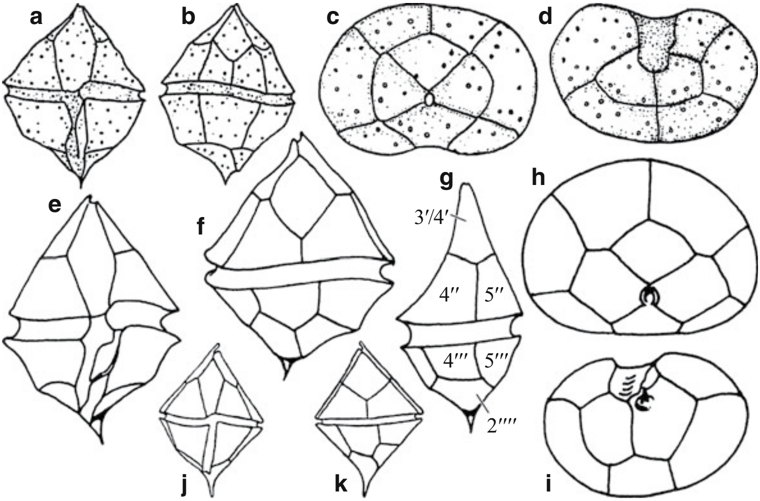

Fig. 150 *Unruhdinium kevei* (Grigorszky) Gottschling (**a**, **b** after Grigorszky 1999; **c**, **d** after Grigorszky *et al.* 2001; **e**–**i** after Leitão *et al.* 2001; **j**, **k** after Krakhmalny 2001). **a**–**d** ventral, dorsal, apical and antapical views, respectively; **e**, **f** ventral and dorsal views; **g** right lateral view; **h**, **i** apical and antapical views; **j**, **k** ventral and dorsal views

ovoid antapical part, connected by a narrow strand. Cell length 26–47 µm, width 23–37 µm, thickness 18–25 µm.

Note: the third apical plate is often separated from the apical pore complex, thus formally becoming an intercalary plate. If so considered, the plate formula of the epicone is po, x, 3′, 1a, 6″.
SEM: Grigorszky (1999), Grigorszky *et al.* (2001), Krakhmalny (2001, 2002), Leitão *et al.* (2001), Hansen & Flaim (2007), Takano *et al.* (2008, as *P.* cf. *kevei*).
TEM: Takano *et al.* (2008, as *P.* cf. *kevei*).
DNA data: Takano *et al.* (2008, as *P.* cf. *kevei*).
Ecology: plankton in lakes and ponds (Ukraine: May–September) and in running water, in the Loire region of France forming extensive red tides in August 1994 (12×10^3 cells per liter, temperature 24 ˚C), and five years later in August, September 1999, during which cell concentrations reached 18.8×10^6 cells per liter and chlorophyll concentrations of 1300 µg/l.
Geographical distribution: France (Leitão *et al.*, as *Peridiniopsis corillionii*); Hungary (Grigorszky); Italy (Hansen & Flaim); Ukraine (Krakhmalny, as *Peridiniopsis rhomboides*). Japan (Takano *et al.*).

Note: in view of the difference in ornamentation of the European and the Japanese material, molecular data are needed to determine whether they belong to the same taxon.

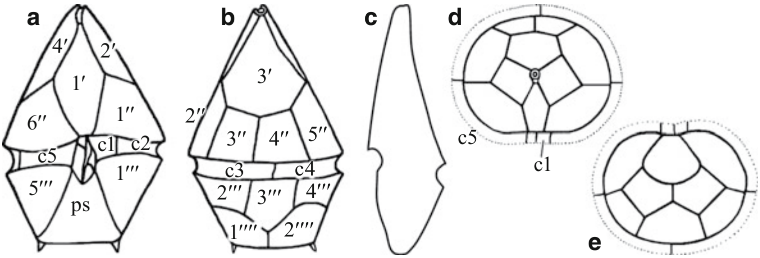

Fig. 151 *Unruhdinium niei* (G. X. Liu & Z. Y. Hu) Gottschling (**a**, **b**, **d**, **e** after Liu *et al.* 2008b; **c** original, based on light micrograph in Lui *et al.* 2008b). **a**, **b** ventral and dorsal views showing plate arrangement; **c** outline of left lateral view; **d**, **e** apical and antapical views (schematic)

5. *Unruhdinium niei* (G. X. Liu & Z. Y. Hu) Gottschling *in* Gottschling *et al.* 2017, p. 298 (**Fig. 151**)

Basionym: *Peridiniopsis niei* G. X. Liu & Z. Y. Hu *in* Liu *et al.* 2008b, p. 490, figs 3–6

Cells pentagonal in ventral view, the epicone triangular, the hypocone trapeziform, truncated. Cells compressed dorsoventrally. Cingulum descending, displacement less than one cingular width. Sulcal area only slightly excavated, reaching the antapex. The two antapical plates both with a robust 2-μm long spine. Amphiesmal plates ornamented with papillae. Cells contain numerous small chloroplasts. Cells 26–46 μm long and 16–26 μm wide, thickness 7–12 μm. Cyst shaped like the vegetative cells, but without the posterior spines. Cyst length 25–40 μm, width 18–26 μm.
Ecology: plankton in lakes and rivers. Formed red or brown blooms in the area of Lake Donghu and the Three-Gorge Reservoir (2004–2008), the largest irrigation works on the Changjiang River. Cell numbers reached 15×10^6 cells per liter. In one case, the bloom was apparently terminated by ciliates ingesting the dinoflagellates.
Geographical distribution: China.

6. *Unruhdinium penardii* (Lemmermann) Gottschling *in* Gottschling *et al.* 2017, p. 298 (**Fig. 152**)

Basionym: *Glenodinium penardii* Lemmermann 1900b, p. (117), without description or figure (validated by reference to *Glenodinium cinctum* sensu Penard 1891, p. 52, pl. III, figs 14–21)
Nomenclatural synonyms: *Peridinium penardii* (Lemmermann) Lemmermann 1910, p. 670 ≡ *Peridiniopsis penardii* (Lemmermann) Bourrelly 1968, p. 9

Cells ovoid to more or less rhomboidal in ventral view, ventral side flat-concave, dorsal side convex. Epi- and hypocone of almost equal length. Epicone conical, hy-

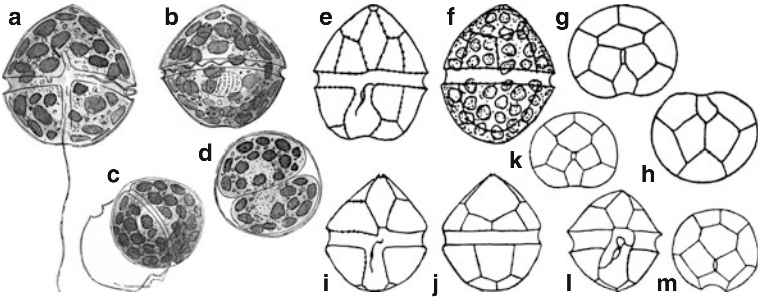

Fig. 152 *Unruhdinium penardii* (Lemmermann) Gottschling (**a**–**d** after Penard 1891; **e**–**h** after Lemmermann 1910; **i**–**k** after Lindemann 1919; **l**, **m** after Wołoszyńska 1921). **a** ventral view showing both flagella and part of cell contents; **b** dorsal view, with chloroplast profiles and the position of the dinokaryon; **c** ecdysing cell; **d** division stage; **e** ventral view, outline of major plates; **f** outline of plates and cell contents in dorsal view; **g**, **h** apical and antapical views; **i**–**k** ventral, dorsal and apical views, respectively; **l**, **m** ventral and apical views

pocone rounded. Cingulum descending, the ends displaced *ca.* half its own width. Amphiesmal plates typically smooth, occasionally with slight reticulation. With two or more small antapical spines. Cells with numerous disc-shaped yellowish chloroplasts. Each chloroplast with internal pyrenoid penetrated by single thylakoid. Eyespot in the sulcus. Eyespot consists of one or two parts, connected by a narrow strand (Japanese material), or the antapical part is missing, but the strand retained (material from Italy). Cell length 23–38 µm, width 23–36 µm. Sexual reproduction described by Sako *et al.* (1987), cysts *ca.* 28 µm in diameter.
SEM: Hansen & Flaim (2007), Takano *et al.* (2008).
TEM: Takano *et al.* (2008).
DNA data: Takano *et al.* (2008).
Ecology: plankton in ponds and lakes, sometimes forming blooms. According to Höll (1928) mostly at pH 7.5–7.8.
Geographical distribution: Italy (Hansen & Flaim; Takano *et al.*); Switzerland (Penard; Lemmermann). Japan (Takano *et al.*).

Note 1: *Peridinium andrzejowskii* Wołoszyńska (1921, p. 132, figs 1–4), from the plankton of the River Dnieper, differs only by being smaller (12–23 µm long and wide).

Note 2: another species, related to *U. penardii*, has been described recently from China. It is named *Unruhdinium minimum* (Qi Zhang, G. X. Liu & Z. Y. Hu) Gottschling *in* Gottschling *et al.* 2017, p. 298 (basionym: *Peridiniopsis minima* Qi Zhang, G. X. Liu & Z. Y. Hu 2014, p. 122, figs 1–3). It differs from *U. penardii* by having smaller cells (8–15 µm long) and in having a small, rhomboid anterior intercalary plate on the dorsal side (Fig. 154b). In the latter respect it resembles *Peridiniopsis kulczynskii*, which is larger. *Unruhdinium minimum* was found in River Jiulongjian, Fujian Province, China.

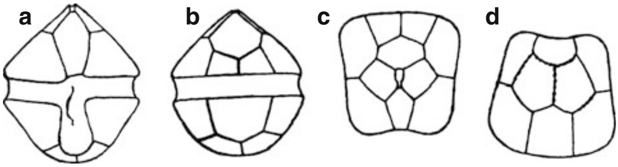

Fig. 153 *Unruhdinium penardii* var. *maius* (Er. Lindemann) Moestrup & Calado (after Lindemann 1919). **a**–**d** ventral, dorsal, apical and antapical views, respectively

var. *maius* (Er. Lindemann) Moestrup & Calado *comb. nov.* (**Fig. 153**)
Basionym: *Peridinium penardii* f. *maius* Er. Lindemann 1919, *Arch. Protistenk.* **39**, p. 248, text-figs 101–104 ("*maior*")

Cells quadrangular in transverse section. Cells 36–38 µm long, 32–34 µm wide.
Ecology: in Lake Kummerower, Mecklenburg, Germany, July 1917 (Lindemann 1919).
Geographical distribution: Germany.

var. *robustum* (Qi Zhang, G. X. Liu & Z. Y. Hu) Gottschling *in* Gottschling *et al.* 2017, p. 298 (**Fig. 154a**)
Basionym: *Peridiniopsis penardii* var. *robusta* Qi Zhang, G. X. Liu & Z. Y. Hu 2011a, p. 151, figs 2, 3, 4C

Cells with several robust antapical spines and a conspicuous apical spine. Cells 32–43 µm long, 27–38 µm wide, 17–28 µm thick.
SEM: Zhang *et al.* (2011a).
Ecology: planktonic in freshwater lakes and rivers.
Geographical distribution: River Luodi at Manwan, Yunnan, and River Daning at Dachang, Hubei, China.

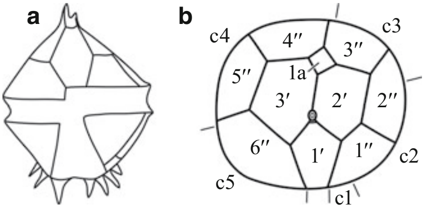

Fig. 154 **a** *Unruhdinium penardii* var. *robustum* (Qi Zhang, G. X. Liu & Z. Y. Hu) Gottschling (original), ventral view, outline of cell with apical and antapical spines, and major plates (based on LM and SEM illustrations in Zhang *et al.* 2011a). **b** *Unruhdinium minimum* (Qi Zhang, G. X. Liu & Z. Y. Hu) Gottschling (original), diagram of amphiesmal plates in apical view (limits of cingular plates marked by lines around the outline)

Family 4. Peridiniaceae Ehrenberg 1831, p. [32] (“Peridinaea”)

A diverse group of genera with a cover of relatively robust amphiesmal plates and the cingulum positioned near the middle of the cell. Apical pore complex present in most species, but absent in *Palatinus* and in *Peridinium* subg. *Cleistoperidinium*. Tabulation on the hypocone typically 5‴, 2⁗. Epicone with widely variable numbers of plates on the main series, in general: 3–5′, 0–3a, 6–7″. Plates in the cingulum varying from 3 in *Glochidinium* to 5 in some species of *Peridinium* and 6 in most other members of the family. Most have chloroplasts with the accessory pigment peridinin. Some have been reported as colorless, raising doubt about their photosynthetic nature (see *Glochidinium*, *Staszicella*).

Division into monophyletic genera is not presently possible. Lemmermann (1904a) described *Peridiniopsis* as a separate genus, but subsequently changed his mind and discarded *Peridiniopsis* (Lemmermann 1910). The independent status of *Peridiniopsis* as a different genus was taken up again half a century later by Bourrelly (1968). The two genera were defined by the number of anterior intercalary plates, 0–1 in *Peridiniopsis* and 2–3 in *Peridinium*. However, the number of intercalary plates may vary, and modern studies, combining ultrastructure and molecular sequencing, have shown this system to be misleading. *Peridiniopsis* will eventually be divided into several genera, but whether the new genera will correspond, in part or entirely, to the present groups recognized in *Peridiniopsis* must await additional information on ultrastructure, combined with molecular studies. *Peridinium*, as originally circumscribed by Ehrenberg 180 years ago, is also very diverse, and the different species have been divided into two sections (Lemmermann 1910) or subgenera (Lefèvre 1932), which were further subdivided into groups (Lefèvre 1932). Some of these groups will probably turn out to represent monophyletic genera, whilst the fate of other groups must likewise await studies on ultrastructure and molecular sequencing before a system reflecting phylogeny can be made with any degree of confidence. The 14 genera or groups of peridinioids included in the present treatment are mainly separated on the basis of plate formula. They all share the possession of five postcingular plates and two antapical plates, while in the epicone the number of plates differs between groups and genera. Two genera stand out in the key below by possessing only 3 plates in the cingulum (or 3 + 1 transional plate in *Protoperidinium*, of the Protoperidiniaceae) while all other genera or groups, as far as known, possess 5 or 6 plates in the cingulum.

Due to occasional variation in the position of plates and thus the plate designation, not all cells in a sample can be named using the following key. Variation should be noted and typical specimens selected for identification.

Key to genera and groups within genera of Peridiniaceae (excluding groups in *Peridinium* subg. *Cleistoperidinium*):

1a Cells with 3 cingular plates (or 3 + 1 transitional plate), no sutures visible in the cingulum in dorsal view 2
1b Cells with 5–6 cingular plates, two sutures typically visible in dorsal view 3
2a Epicone with 6 precingular plates, fresh water .... 1. *Glochidinium*

2b Epicone with 7 precingular plates, brackish water (and marine) .... *Protoperidinium* (Protoperidiniaceae)
3a Epicone with 6 precingular plates 4
3b Epicone with 7 precingular plates 8
4a Epicone with 3 intercalary plates .... 7. *Thompsodinium*
4b Epicone with 0–2 intercalary plates 5
5a Epicone with 5 apical plates, 1′ usually very narrow, 4–5 times longer than wide, cells free-swimming or attached with the apex to *Dinobryon* .... 6. *Staszicella*
5b Epicone with 3–4 apical plates 6
6a Sulcus extends well onto the epicone 7
6b Sulcus barely extends onto the epicone .... 4. *Peridiniopsis*, the *P. borgei* group
7a With 4–6 distinct spines on the hypocone .... 4. *Peridiniopsis*, the *P. cunningtonii* group
7b Hypocone lacks large spines, but many tiny crenulations or small spines may be present .... 5. *Peridinium*, the *P. crenulatum* group
8a With 3 apical plates .... 4. *Peridiniopsis*, the *P. lindemannii* group
8b With more than 3 apical plates 9
9a With 4 apical plates 10
9b With 5 apical plates .... 4. *Peridiniopsis*, the *P. thompsonii* group
10a Epicone lacks intercalary plates ... 4. *Peridiniopsis*, the *P. elpatiewskyi* group
10b Epicone with 1–3 intercalary plates 11
11a Epicone with 1 intercalary plate .... 4. *Peridiniopsis*, the *P. viguieri* group
11b Epicone with 2–3 intercalary plates 12
12a Epicone with 2 intercalary plates 13
12b Epicone with 3 intercalary plates 14
13a Epicone lacks apical pore .... 2. *Palatinus*
13b Apical pore present on the epicone .... 3. *Parvodinium*
14a Epicone lacks apical pore .... 5. *Peridinium* subg. *Cleistoperidinium*
14b Epicone with apical pore 15
15a Plate pattern on the epicone symmetrical, 2a much larger than 1a and 3a, 2a the only intercalary plate that touches 4″ ... 5. *Peridinium*, the *P. bipes* group
15b Plate pattern on the epicone not completely symmetrical, 2a not notably larger than the other intercalary plates, 4″ touches two intercalary plates 16
16a Plate 1a small, much smaller than 2a and 3a, 4-sided .... 5. *Peridinium*, the *P. allorgei* group
16b Plate 1a similar in size to 2a and 3a, 6-sided .... 5. *Peridinium*, the *P. gutwinskii* group

Genus 1. *Glochidinium* Boltovskoy 1999, p. 98

Type species: *Glochidinium penardiforme* (Er. Lindemann) Boltovskoy 1999

Tabulation po, x, 3′, 1a, 6″, **3c**, 4s, 5‴, 2⁗, also interpretable as po, x, 4′, 0a, 6″, **3c**, 4s, 5‴, 2⁗. Cells often without distinct chloroplasts, sometimes entirely colorless. However, populations of chloroplast-bearing cells matching the morphology and plate arrangement of *G. penardiforme* have been reported (Lefèvre 1932; Pandeirada *et al.* 2013). Both species described are strongly compressed dorsoventrally.

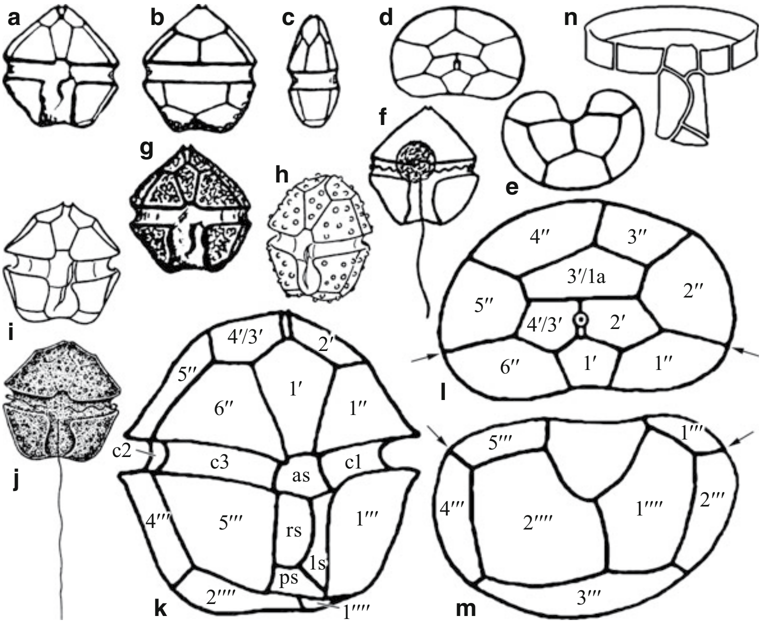

Fig. 155 *Glochidinium penardiforme* (Er. Lindemann) Boltovskoy (**a**, **b**, **d** after Lindemann *in* Schröder 1919; **c**, **e**–**g** after Lindemann 1920; **h**–**j** after Thompson 1951; **k**–**n** after Boltovskoy 1999). **a**–**e** ventral, dorsal, lateral, apical and antapical views, with main plates; **f** outline of cell with both flagella and nucleus; **g** ventral view with plate ornamentation; **h** left-ventral view of specimen ornamented with verrucae; **i**, **j** main plates and live cell appearance in ventral view; **k**–**m** outline and tabulation in ventral, apical and antapical views, respectively (alternative interpretations of apical plates indicated; arrows in **l** and **m** point to the limits of the large, dorsal cingular plate, c2); **n** plates of the cingulum and sulcus

Key to species of *Glochidinium*:

1a Cells ovoid with concave antapex, spines lacking on the two posterior lobes .... 1. *G. penardiforme*

1b Cells subpentagonal with concave antapex, blunt antapical spines present on the two posterior lobes .... 2. *G. platygaster*

1. *Glochidinium penardiforme* (Er. Lindemann) Boltovskoy 1999, p. 99 (Fig. 155)

Basionym: *Peridinium penardiforme* Er. Lindemann *in* Schröder 1919, p. 654, fig. 1; again in Lindemann 1920, p. 126, figs 10–15
Nomenclatural synonyms: *Glenodinium penardiforme* (Er. Lindemann) J. Schiller 1935a, p. 113 ≡ *Peridiniopsis penardiformis* (Er. Lindemann) Bourrelly 1968, p. 8 (“*penardiforme*”)

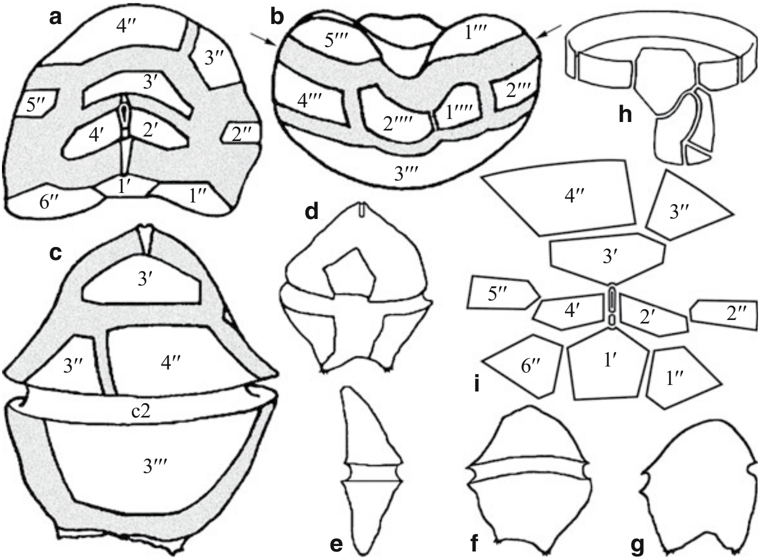

Fig. 156 *Glochidinium platygaster* Boltovskoy (after Boltovskoy 1999). **a**–**c** apical, antapical and dorsal views, respectively (the arrows in **b** mark the limits of the large, dorsal cingular plate, c2; shaded areas represent the wide sutures between plates); **d**–**g** ventral, lateral and dorsal outlines of different cells; **h** plates of the cingulum and sulcus; **i** projection of epiconal plates in apical view. Plates labelled as in Boltovskoy (1999); in alternative interpretation (3 apical and 1 intercalary plate) 3′ = 1a and 4′ = 3′

Cells ovoid, dorsoventrally strongly compressed. Epicone rounded cone-shaped, hypocone rounded, indented posteriorly. Epi- and hypocone of similar size. Cingulum practically circular. Sulcus wide, barely or not extending onto the epicone. Cingular plates c1 and c3 aligned with adjacent plates on the epicone (1″ and 6″) and on the hypocone (1‴ and 5‴). Plate sculpturing variable, with sparse round nodules connected by low rims. Growth bands usually narrow. Nucleus central. Chloroplasts usually apparently absent although some populations reported with chloroplast-bearing cells. Cell length 17–42 µm, width 17–30 µm (average of Argentinian material 27 × 21 µm; Boltovskoy 1999). Cells open at ecdysis by discarding the 3 dorsal plates on the epicone: 3′, 3″ and 4″.
SEM: Pollingher & Hickel (1991), Toriumi & Dodge (1993; cell apex), Boltovskoy (1999), Hansen & Flaim (2007), Cavalcante *et al.* (2017).
Ecology: streams, ponds and lakes, mainly in warm waters; also in subtropical reservoirs (Cardoso *et al.* 2010).
Geographical distribution: Denmark (Calado, unpublished); France (Lefèvre); Germany (Lindemann); Italy (Hansen & Flaim); Poland (Lindemann); Portugal (Pandeirada *et al.*). USA, KS (Thompson). Argentina, Uruguay (Boltovskoy). Brazil

(Uherkovich; Cardoso *et al.*; Cavalcante *et al.*). Israel (Pollingher & Hickel); Japan (Imamura & Fukuyo; Senzaki & Horiguchi).

2. *Glochidinium platygaster* Boltovskoy 1999, p. 101, figs 8–13, 24–33 (**Fig. 156**)

Cell subpentagonal, longer than wide. Epicone bell-shaped. Hypocone slightly wider, bilobed antapically. Each posterior lobe ornamented with a group of small spines. Cells strongly dorsoventrally compressed, the ventral side slightly concave, the dorsal side convex, cells bean-shaped in apical and in antapical view. Plate formula on the epicone po, x, 4′, 6″. Cingulum circular. Plates ornamented with small nodules, interconnected by low rims. Cells typically with very wide growth bands. Nucleus central. Cell length 45–55 µm, width 30–36 µm.
SEM: Boltovskoy (1999).
Ecology: plankton in reservoirs during summer at pH 7 or higher, temperature up to 28 ˚C.
Geographical distribution: subtropical Argentina (Boltovskoy).

Genus 2. *Palatinus* Craveiro, Calado, Daugbjerg & Moestrup 2009, p. 1177

Type species: *Palatinus apiculatus* (Ehrenberg) Craveiro, Calado, Daugbjerg & Moestrup

Apical pore absent. Amphiesmal plates smooth or finely granulate. With two intercalary plates on the epitheca. Six cingular plates. Plate formula 4′, 2a, 7″, 6c, 5s, 5‴, 2⁗. Chloroplast lobes radiating from central pyrenoid. Eyespot of type A. Cell release at ecdysis involving the antapical and sometimes also postcingular plates.

Key to species of *Palatinus*:

1a Epicone asymmetrical, many short antapical spines often present .... 1. *P. apiculatus*
1b Epicone symmetrical or nearly so 2
2a Antapical spines absent, plate sutures distinctly striated .... 2. *P. pseudolaevis*
2b Antapical spines present, plate sutures faintly striated .... 1. *P. apiculatus* var. *laevis*

1. *Palatinus apiculatus* (Ehrenberg) Craveiro, Calado, Daugbjerg & Moestrup 2009, p. 1178 (**Fig. 157**)

Basionym: *Glenodinium apiculatum* Ehrenberg 1838, p. 258, pl. XXII, fig. XXIV
Nomenclatural synonyms: *Peridinium apiculatum* (Ehrenberg) Claparède & J. Lachmann 1859, p. 404 ≡ *Properidinium apiculatum* (Ehrenberg) Meunier 1919, p. 60 ≡ "*Peridinium apiculatum* (Ehrenberg) Er. Lindemann 1928, p. 260", isonym
Taxonomic synonyms: *Peridinium palatinum* Lauterborn 1896, p. 17; *Peridinium marssonii* Lemmermann 1900a, p. 28 ≡ *Peridinium laeve* subsp. *marssonii* (Lemmermann) Er. Lindemann 1919, p. 256; *Peridinium anglicum* G. S. West 1909b, pp 187–190, fig. 23 ≡ *Peridinium laeve* subsp. *anglicum* (G. S. West) Er. Lindemann 1919, p. 259 ≡ *Peridinium apiculatum* f. *anglicum* (G. S. West) Er. Linde-

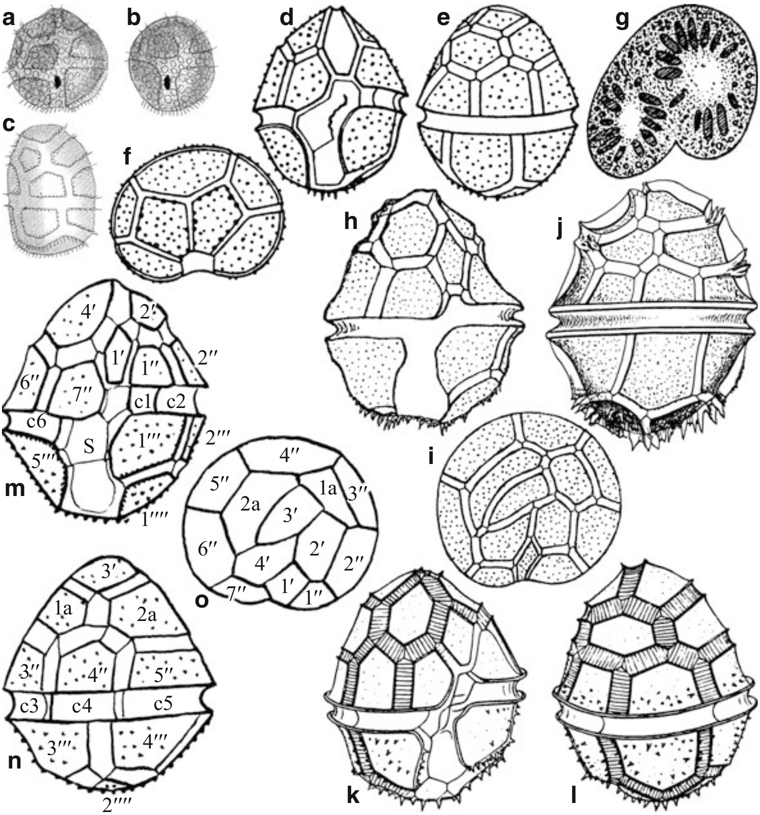

Fig. 157 *Palatinus apiculatus* (Ehrenberg) Craveiro, Calado, Daugbjerg & Moestrup (**a**–**c** after Ehrenberg 1838; **d**–**g** after West 1909b; **h**, **i** after Lindemann 1925c; **j** after Lindemann 1919; **k**, **l** after Skuja 1930; **m**–**o** after Bourrelly 1968). **a**, **b** ventral views of living cells showing the eyespot; **c** dorsal view; **d**–**f** ventral, dorsal and antapical views; **g** division stage of ecdysed cell; **h**, **i** ventral and apical views; **j** dorsal view of heavily ornamented cell, with flanges along several sutures; **k**, **l** ventral and dorsal views showing the seldom depicted fine striae on the sutures; **m**–**o** ventral, dorsal and apical views with main plates labelled

mann 1928a, p. 260 ≡ *Peridinium palatinum* f. *anglicum* (G. S. West) M. Lefèvre 1932, p. 107; *Peridinium laeve* var. *paradoxum* Er. Lindemann 1919, p. 255, text-fig. 128; *Peridinium laeve* var. *stylatum* Er. Lindemann 1919, p. 255, text-fig. 127; *Peridinium laeve* subsp. *marssonii* f. *cristatum* Er. Lindemann 1919, p. 257, pl. 17, figs 20–22 ≡ *Peridinium apiculatum* var. *cristatum* (Er. Lindemann) Er. Lindemann 1928a, p. 260 ≡ *Peridinium palatinum* f. *cristatum* (Er. Lindemann) M. Lefèvre

1932, p. 107; *Peridinium laeve* subsp. *marssonii* var. *contactum* Er. Lindemann 1919, p. 259, text-figs 142, 143; several tabulation variants of the *travectum* and *collineatum* types described as varieties of *Peridinium laeve* subsp. *marssonii in* Lindemann (1919, 1920)

Cells ovoid, the epicone rounded conical, the hypocone rounded. Ventral side flat. Cingulum descending, the ends displaced about one cingulum width. Sulcus extends to the antapex. It barely extends onto the epicone. Epicone somewhat twisted to the left, leaving 7″ longitudinally aligned with the right sulcal plate, and 1′ aligned with the right side of 1‴. Four apical plates and two intercalary plates very asymmetrically arranged, centered around the elongate 3′, which is oriented dorsal-left to ventral-right and pointed on the ventral side. Five uppermost amphiesmal plates often with raised edges. Edges of the sulcus also often with ridges. Edges of remaining plates with numerous spines, larger on the hypocone and largest in the antapical area. Small spines also present on the surface of some plates, especially on the hypocone. Cell length mostly 32–48 μm, width 28–42 μm, thickness 23–28 μm. Cysts thin-walled, smooth, spherical (West 1909; Dangeard 1939, p. 271). Cell division in a naked, motile stage observed in rapidly growing populations.
SEM: Cambra *et al.* (1989), Senzaki & Horiguchi (1994), Hansen & Flaim (2007), Liu *et al.* (2008a), Craveiro *et al.* (2009).
TEM: Craveiro *et al.* (2009).
DNA data: Craveiro *et al.* (2009).
Ecology: in lakes and ponds, predominantly in winter and early spring in temperate zones. Also present in tropical areas.
Geographical distribution: widely distributed. Denmark (Nygaard); England (West; Harris); France (Lefèvre; Bourrelly); Germany (Ehrenberg; Lauterborn; Lemmermann; Lindemann); Italy (Hansen & Flaim); Latvia (Skuja); Poland (Wołoszyńska); Portugal (Pandeirada *et al.*); Slovakia (Popovský); Spain (Cambra *et al.*); Switzerland (Höll). China (Hubei, Shandong; Liu *et al.*); Japan (Senzaki & Horiguchi); Sabah, Malaysia (Moestrup, unpubl.).

var. *laevis* (Huitfeldt-Kaas) Craveiro, Calado, Daugbjerg & Moestrup 2009, p. 1178 (**Fig. 158**)
Basionym: *Peridinium laeve* Huitfeldt-Kaas 1900, p. 4, figs 1–5
Nomenclatural synonyms: *Peridinium palatinum* f. *laeve* (Huitfeldt-Kaas) Er. Lindemann 1925b, pp 478, 481, *Peridinium apiculatum* f. *laeve* (Huitfeldt-Kaas) Er. Lindemann 1928, p. 260
Taxonomic synonym: *Peridinium laeve* var. *bitravectum* Er. Lindemann 1919, p. 256, text-fig. 129

This variety differs in having a more symmetrical arrangement of the plates on the epicone. Plate 3′ is almost square and rather small, occasionally slightly elongate. The four plates surrounding 3′ are almost equal in size. The hypocone often carries distinct spines.
SEM: Craveiro *et al.* (2009).
Ecology: in cold water ponds, mainly during late autumn, winter and spring (seldom up to June; Thompson 1951).

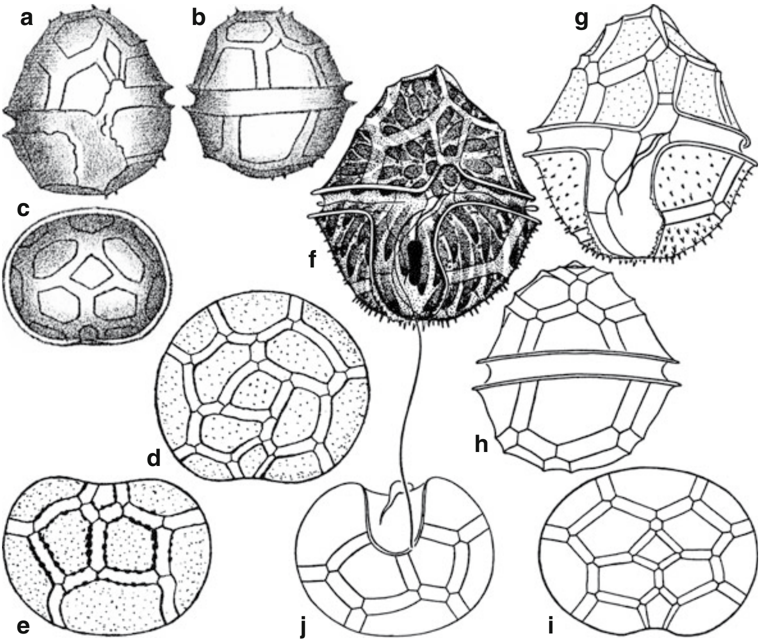

Fig. 158 *Palatinus apiculatus* var. *laevis* (Huitfeldt-Kaas) Craveiro, Calado, Daugbjerg & Moestrup (**a**–**c** after Huitfeldt-Kaas 1900; **d**, **e** after Lindemann 1919; **f**–**j** after Thompson 1951). **a**–**c** ventral, dorsal and apical views; **d**, **e** apical and antapical views; **f** aspect of a living cell; **g**–**j** ventral, dorsal, apical and antapical views

Geographical distribution: England (Harris); France (Lefèvre); Germany (Lindemann); Norway (Huitfeldt-Kaas). USA, KS (Thompson).

2. *Palatinus pseudolaevis* (M. Lefèvre) Craveiro, Calado, Daugbjerg & Moestrup 2009, p. 1178 (**Fig. 159**)

Basionym: *Peridinium pseudolaeve* M. Lefèvre 1926a, p. 341, pl. XI, figs 6–9 ("*pseudo-laeve*")

Cells oval, not or only very slightly dorsoventrally flattened. Epicone larger or of the same size as the hypocone. Cingulum displaced about one cingulum width. Sulcus extends slightly onto the epicone. Epicone with a twist to the left similar to *P. apiculatus*. Plates on the epicone symmetrically arranged around the relatively small, nearly square plate 3′. Plates often convex, without bordering flanges, finely punctuate or with small warts. Ornamentation on epi- and hypocone sometimes different. Sutures distinctly striated transversely. Cells 28–45 µm long, 25–42 µm wide.

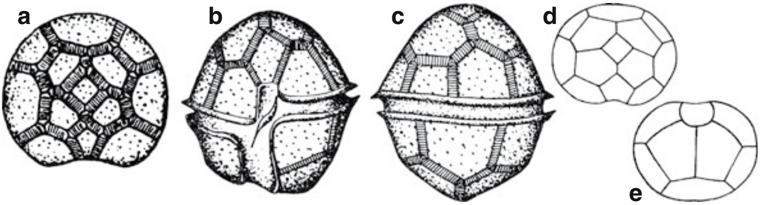

Fig. 159 *Palatinus pseudolaevis* (M. Lefèvre) Craveiro, Calado, Daugbjerg & Moestrup (**a** after Lindemann 1920; **b**–**e** after Lefèvre 1926a). **a** apical view of a cell without dorsoventral compression, with distinctly striated sutures; **b**, **c** ventral and dorsal views showing main plates; **d**, **e** outlines of apical and antapical plates

SEM: Craveiro *et al.* (2009).
Ecology: pools, ponds and lakes in nutrient-poor water in the spring; in alpine peat bogs in summer.
Geographical distribution: Denmark (Craveiro *et al.*); England (Lewis & Dodge); France (Lefèvre); Germany (Lindemann); Poland (Wołoszyńska).

Genus 3. ***Parvodinium*** Carty 2008, p. 106

Type species: *Parvodinium umbonatum* (F. Stein) Carty 2008

Ovoid to pentagonal cells with a wide cingulum, plate formula po, x, 4′, **2a**, 7″, 6c, 5s, 5‴, 2″″. Where this is known, the amphiesma opens posteriorly. Resting spore with posterior archeopyle (Tardio *et al.* 2009).
There are few genera of thecate dinoflagellates in which species identification is as difficult and unsatisfactory as in *Parvodinium*. Many species of the genus are very similar and numerous variations in plate pattern have been described. Apparently the species concept has widened over the years with an increasing tendency to refer variant forms within the group to the two main species, *P. umbonatum* and *P. inconspicuum*, and this has resulted in diffuse borders between species. Thus *P. inconspicuum* and *P. africanum* as circumscribed by Lefèvre, and followed by Huber-Pestalozzi, can no longer be separated by morphological characters. To try a new approach we have therefore gone back and defined the two species solely by the original descriptions. Hopefully the two morphotypes can be refound (in Hawaii or the Chathams and in Africa, respectively) and defined by using molecular fingerprints, to provide a more reliable concept of the species. Morphological deviants can then be compared and the morphological variation within each species evaluated. The same applies also to other species of *Parvodinium*.
Elbrächter & Meyer (2001) found that the three common variations in plate tabulation of peridinioids known as “conjunctum”, “contactum” and “remotum” (**Fig. 160**) may all be produced in a single clonal culture, although one formula was dominant in their studies. In field populations, one tabulation was also dominant. This information is considered less relevant and is therefore not included in the descriptions of the individual species.

The key below only includes the nominal species, not the many forms described, but the varieties and forms are illustrated. The illustrations should be consulted for more reliable identification.

Before using the key, it may be useful to recapitulate what Růžička (1977) wrote in his book about desmids when providing a key to identification of species in the genus *Closterium*: "When using the key, the user must realize that the differences between many species are still unclear and that such species cannot be reliably identified from the key". And later: "The key must only be considered a guide to identification, the final determination must be based on the written description and the illustrations". And finally: "When using the key, several specimens of a population must always be studied. Identification based on a single cell is not reliable" (translated from the German).

Key to species of *Parvodinium*:

1a Cells globose or almost so .... 4. *P. centenniale*
1b Cells oval, ovoid or pentagonal 2
2a Epicone hemispherical or bell-shaped 3
2b Epicone conical or angular 4
3a Sutures often sinuous .... 10. *P. morzinense*
3b Sutures straight, not sinuous .... 1. *P. umbonatum*
4a With 1 or 2 prominent antapical spines 5
4b With several short posterior spines or without spines 6
5a With single, curved, antapical spine in or near the cell axis . 7. *P. goslaviense*
5b With two long antapical spines measuring 1/4 of the cell length .... 5. *P. deflandrei*
6a Cells with short posterior spines, typically 3 or several in a row 7
6b Cells without posterior spines 9
7a Cells with row of very short spines on 2″″, which is much larger than 1″″ .... 3. *P. belizense*
7b Cells with short spines, spines single or in groups of a few spines 8
8a Cells 12–15 µm wide, epicone distinctly longer than hypocone, typically with 3, sometimes more (rarely absent), short antapical spines .... 8. *P. inconspicuum*
8b Cells 23–27 µm wide, epicone barely longer than hypocone, with single or groups of a few antapical spines .... 2. *P. africanum*
9a Hypocone almost hemispherical .... 11. *P. pusillum*
9b Hypocone more or less angular or with concave plates 10
10a Hypocone with concave plates, the two antapical plates very different in size, both without papillae .... 6. *P. dzieduszyckii*
10b Hypocone convex or concave, the antapical plates of nearly the same size, both with papillae .... 9. *P. lubieniense*

1. *Parvodinium umbonatum* (F. Stein) Carty 2008, p. 106 (**Fig. 160**)

Basionym: *Peridinium umbonatum* F. Stein 1883, pl. XII, figs 1–8
Taxonomic synonyms: (?) *Peridinium minimum* A. J. Schilling 1891a, p. 293, pl. X, fig. 25; *Peridinium umbonatum* var. *inaequale* Lemmermann 1910, p. 669, fig. on p. 670 ≡ *Properidinium inaequale* (Lemmermann) Meunier 1919, p. 62;

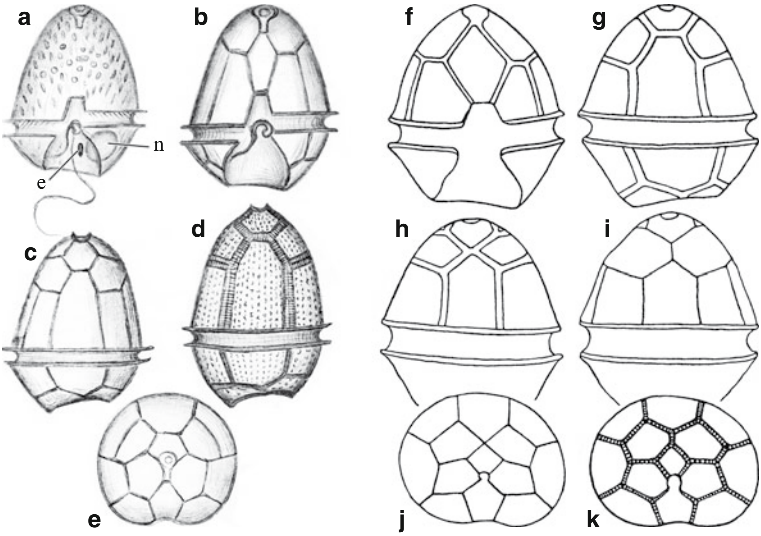

Fig. 160 *Parvodinium umbonatum* (F. Stein) Carty (**a**–**e** after Stein 1883; **f**–**k** after Lefèvre 1932). **a** ventral view showing the position of the nucleus (n) and eyespot (e); **b** ventral view; **c**, **d** dorsal views, cell with wider sutures and stronger ornamentation in **d**; **e** apical view (tabulation conjunctum); **f** ventral view; **g**–**i** dorsal views, tabulations respectively conjunctum, contactum and remotum; **j**, **k** apical views, tabulations contactum and remotum, respectively

Peridinium caudatum var. *guildfordense* Playfair 1920, p. 800, text-fig. 5 ≡ *Glenodinium guildfordense* (Playfair) Er. Lindemann 1931, p. 700; *Peridinium caudatum* var. *planktonicum* Playfair 1920, p. 801, text-figs 6, 7; *Peridinium geminum* Playfair 1920, p. 803, text-fig. 9 ≡ *Glenodinium geminum* (Playfair) Er. Lindemann 1931, p. 697; *Glenodinium kamptneri* J. Schiller 1955, p. 51, pl. X, fig. 52 (?; plates not described)

Cells elongate ovoid, epicone considerably longer than hypocone, rounded bell-shaped. Cells slightly flattened dorsoventrally. Cingulum circular or slightly descending. Sulcus extends slightly onto the epicone, on the hypocone widening towards the antapex. Amphiesmal plates areolated, the areolae in longitudinal rows. Sutures often wide, transversely striated. Chloroplasts stellate with central pyrenoid (Geitler 1926). Cells 25–40 µm long, 21–32 µm wide. Resting cysts spherical or elongate (Tardio *et al.* 2008).
In material from Oklahoma, USA, referred to *P. inconspicuum* but identifiable as *P. umbonatum*, sexual reproduction was reported to take place by isogamy between gametes smaller than vegetative cells, the planozygote remaining motile for a short period. The zygote formed its own new wall and shed the old. The zygote eventu-

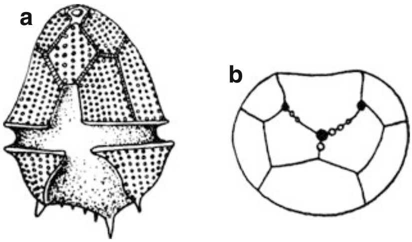

Fig. 161 *Parvodinium umbonatum* var. *armatum* (M. Lefèvre) Moestrup (after Lefèvre 1932). **a** ventral view; **b** antapical view

ally stopped swimming and formed a resting cyst, which underwent meiosis, resulting in four new haploid cells (Pfiester *et al.* 1984).
Ecology: eurytrophic in both small and large waterbodies.
Geographical distribution: Austria (Geitler); England (Lewis & Dodge); Germany (Lemmermann; Elbrächter & Meyer). Ivory Coast (Bourrelly). USA, FL, NC, OH, TX, WA (Carty). Brazil (Cardoso *et al.*). Hubei, China (Liu *et al.*). New Zealand (Thompson).

var. *armatum* (M. Lefèvre) Moestrup *comb. nov.* (**Fig. 161**)
Basionym: *Peridinium umbonatum* var. *armatum* M. Lefèvre 1927, *Bull. Mus. Natl. Hist. Nat.* **33**, p. 120
Nomenclatural synonym: *Peridinium umbonatum* f. *armatum* (M. Lefèvre) M. Lefèvre 1932, p. 125

Differs in having 3 large posterior spines, at the corners where the sulcus adjoins the antapical plates.
Geographical distribution: Spain (Lefèvre).

var. *papilliferum* (Lemmermann) Moestrup *comb. nov.* (**Fig. 162**)
Basionym: *Peridinium umbonatum* var. *papilliferum* Lemmermann 1908b, *Arch. Hydrobiol. Planktonk.* **4**, p. 180, pl. V, figs 17–20
Nomenclatural synonym: *Peridinium umbonatum* f. *papilliferum* (Lemmermann) M. Lefèvre 1932, p. 123

Differs in having very small knobs along the sutures of the antapical plates and the edges of the sulcus.
Geographical distribution: France (Lefèvre); Italy (Lemmermann); Poland (Lindemann, Wołoszyńska); Spain (Lefèvre). Java, Sumatra, Indonesia (Wołoszyńska).

var. *spiniferum* (M. Lefèvre) Moestrup *comb. nov.* (**Fig. 163**)
Basionym: *Peridinium umbonatum* var. *spiniferum* M. Lefèvre 1927, *Bull. Mus. Natl. Hist. Nat.* **33**, p. 120

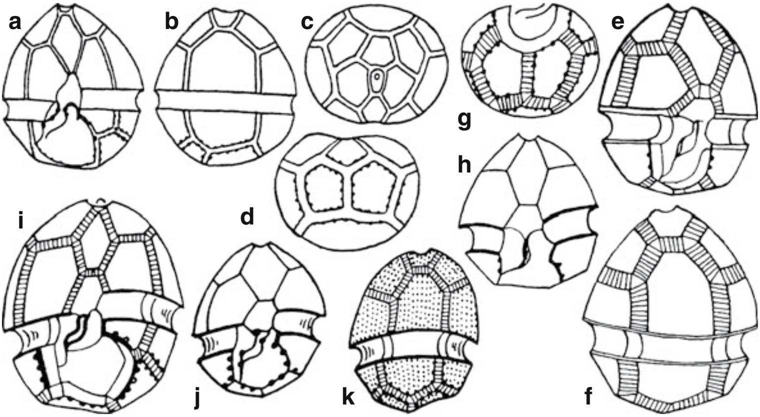

Fig. 162 *Parvodinium umbonatum* var. *papilliferum* (Lemmermann) Moestrup (**a**–**d** after Lemmermann 1908b; **e**–**h** after Wołoszyńska 1930b; **i**–**k** after Wołoszyńska 1952). **a**–**d** ventral, dorsal, apical and antapical views, respectively; **e**–**g** ventral, dorsal and antapical views; **h** ventral view of small cell; **i** ventral view of very large cell; **j**, **k** ventral and dorsal views

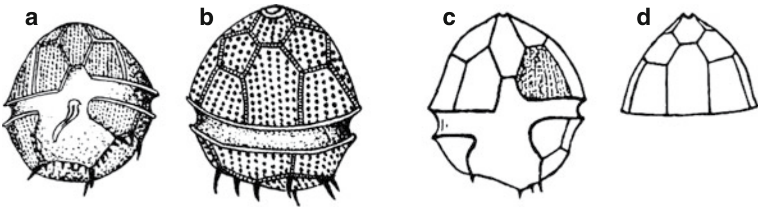

Fig. 163 *Parvodinium umbonatum* var. *spiniferum* (M. Lefèvre) Moestrup (**a**, **b** after Lefèvre 1932; **c**, **d** after Lindemann 1931). **a**, **b** ventral and dorsal views; **c**, **d** ventral view and outline of plates on the epicone in dorsal view (as *Peridinium ambiguum*)

Taxonomic synonyms: *Peridinium linzium* Er. Lindemann 1920, p. 137, figs 40–43; *Peridinium ambiguum* Er. Lindemann 1931, p. 707, figs 23, 24

Differs in possessing several small spines on the sutures of the hypocone and along the sulcal edges.
Geographical distribution: France (Lefèvre); Poland (Lindemann); Spain (Lefèvre). Bali, Indonesia (Lindemann).

2. ***Parvodinium africanum*** (Lemmermann) Carty 2008, p. 106 (**Fig. 164**)

Basionym: *Peridinium africanum* Lemmermann *in* West 1907, p. 188, pl. 9, fig 1

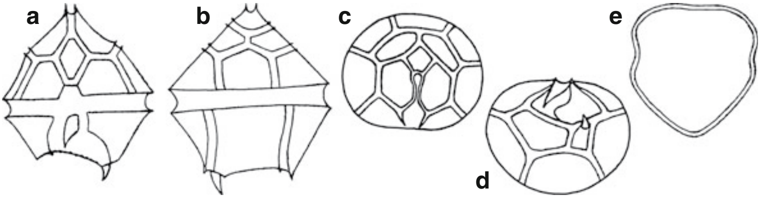

Fig. 164 *Parvodinium africanum* Lemmermann (after Lemmermann *in* West 1907). **a**–**d** ventral, dorsal, apical and antapical views; **e** cyst (with the same orientation as original)

Nomenclatural synonym: *Peridinium tabulatum* var. *africanum* (Lemmermann) Playfair 1913, p. 544
Taxonomic synonyms: *Peridinium tabulatum* var. *intermedium* Playfair 1913, p. 544, pl. lv, figs 15, 16 ≡ *Peridinium intermedium* (Playfair) Playfair 1920, p. 808 ≡ *Peridinium africanum* var. *intermedium* (Playfair) M. Lefèvre 1932, p. 145; *Peridinium africanum* var. *contactum* Er. Lindemann 1919, p. 244, text-figs 87, 88; *Peridinium intermedium* var. *conicum* Playfair 1920, p. 809, text-fig. 16f

The following description is based on Lemmermann *in* West (1907) and Lemmermann (1910): cells pentagonal, 24–30 μm long, 23–27 μm wide. Cingulum nearly circular. Sulcus extends slightly onto the epicone, on the hypocone widens strongly towards the antapex, reaching the antapical end. Epicone larger than hypocone, conical. Hypocone a half cone, the antapical side concave, the right antapical plate larger than the left antapical plate. The ventral edge of the left antapical plate with a curved hyaline spine. Amphiesmal plates smooth. Resting cysts cordiform, 20.5 μm long, 22 μm wide, with thick smooth wall.
Ecology: in ponds and lakes, both nutrient-rich and nutrient-poor. In England in late winter, early spring (Lewis & Dodge 2002, 2011).
Geographical distribution: England (Harris; Lewis & Dodge); France (Huber-Pestalozzi); Germany (Lindemann 1919, text-fig. 82). African lakes Tanganyika, Victoria, Malawi (Lemmermann; Lindemann; Wołoszyńska). USA, TX (Carty). Brazil (Cardoso *et al.*). Australia (Ling *et al.*; Playfair).

Note: material from France illustrated by Lefèvre (1932, figs 593–598) needs to be examined further before its taxonomic relationship can be determined.

var. *javanicum* (Wołoszyńska) K. P. Cavalcante, Craveiro, Calado & L. S. Cardoso *in* Cavalcante *et al.* 2017, p. 250 (**Fig. 165**)
Basionym: *Peridinium marchicum* var. *javanicum* Wołoszyńska 1912, p. 703, text-fig. 25 ("*javanica*")
Nomenclatural synonym: *Peridinium africanum* var. *javanicum* (Wołoszyńska) M. Lefèvre 1932, p. 145
Taxonomic synonyms: *Gonyaulax jensenii* Nygaard 1926, p. 206, pl. IV, fig. 34 ≡ *Peridinium jensenii* (Nygaard) Nygaard 1932, p. 128; *Peridinium ornamentosum* Er. Lindemann 1931, p. 708, figs 25–28

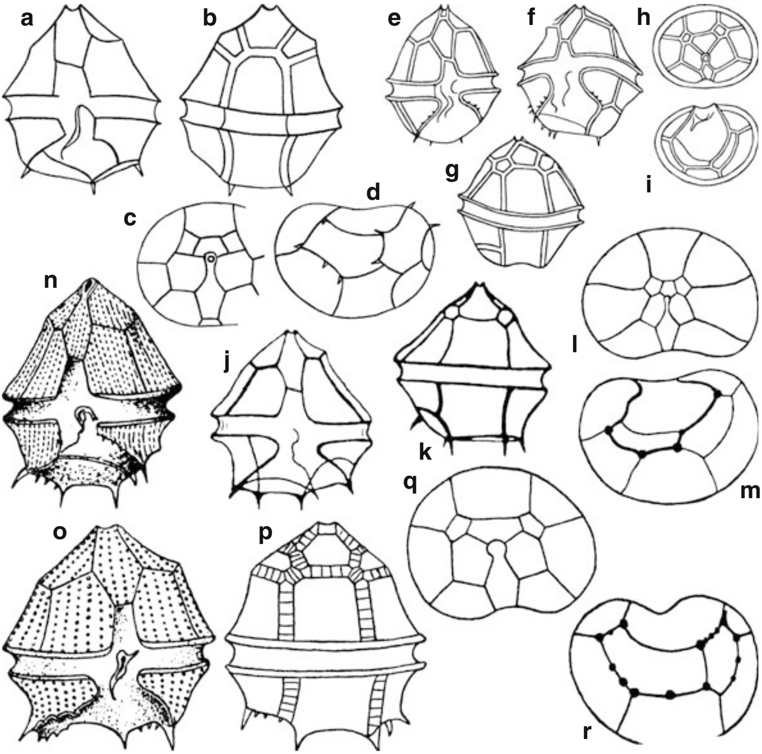

Fig. 165 *Parvodinium africanum* var. *javanicum* (Wołoszyńska) K. P. Cavalcante, Craveiro, Calado & L. S. Cardoso (**a**–**d** after Wołoszyńska 1912; **e**–**i** after Nygaard 1926; **j**–**m** after Lindemann 1931; **n**–*r*, after Lefèvre 1932). **a**, **b** ventral and dorsal views; **c** incomplete apical view; **d** antapical view; **e** ventral view; **f** ventral-posterior view; **g** dorsal view; **h**, **i** apical and antapical views; **j**–**m** ventral, dorsal, apical and antapical views; **n**, **o** two ventral views showing plate ornamentation; **p**, dorsal view of cell with wide, striated sutures; **q**, **r**, apical and antapical views

The sulcus extends onto the epicone for about 1/3 the length of the epicone. Plates 1a and 2a are very small.

Ecology: in lakes of very different sizes, with temperature intervals in the (mainly) volcanic crater lakes in the Pacific given as 19.5–36°C, pH as 6–9.8 and conductivity as 3–88 $\mu S \cdot cm^{-1}$ (Schabetsberger *et al.* 2009).

Geographical distribution: Madagascar (Lefèvre). Brazil (Cavalcante *et al.*). Indonesia (Wołoszyńska; Nygaard; Lindemann). Several islands in the Pacific: Fiji; French Polynesia; Samoa; Tonga; Vanuatu (Schabetsberger *et al.*).

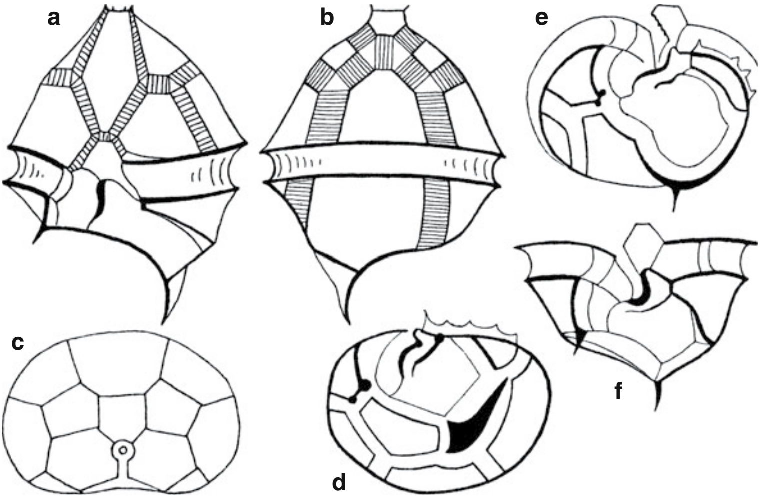

Fig. 166 *Parvodinium africanum* var. *spinulosum* (Wołoszyńska) Moestrup (after Wołoszyńska 1916). **a**–**d** ventral, dorsal, apical and antapical views; **e**, **f** tilted-antapical and ventral views of posterior half of the cell cover

var. *spinulosum* (Wołoszyńska) Moestrup *comb. nov.* (**Fig. 166**)
Basionym: *Peridinium tatricum* var. *spinulosum* Wołoszyńska 1916, *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math., Sér. B, Sci. Nat.* **1915**, p. 270, pl. 11, figs 19–25 ("*spinulosa*")
Nomenclatural synonyms: *Peridinium spinulosum* (Wołoszyńska) Er. Lindemann 1925c, p. 176, *nom. illeg.* (non *Peridinium spinulosum* G. Murray & Whitting 1899, p. 328, pl. 29, fig. 8) ≡ *Peridinium africanum* f. *spinulosum* (Wołoszyńska) M. Lefèvre 1932, p. 146

Differs in having a very strong spine on the left antapical side, and a shorter one on the right antapical side.
Geographical distribution: Poland (Wołoszyńska).

var. *tatricum* (Wołoszyńska) Moestrup *comb. nov.* (**Fig. 167**)
Basionym: *Peridinium tatricum* Wołoszyńska 1916, *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math., Sér. B, Sci. Nat.* **1915**, p. 269, pl. 11, figs 10–18
Nomenclatural synonyms: *Peridinium africanum* f. *tatricum* (Wołoszyńska) M. Lefèvre 1932, p. 147 ≡ *Peridinium africanum* var. *tatricum* (Wołoszyńska) Kisselev 1960, p. 45
Taxonomic synonym: *Peridinium africanum* var. *tatricum* f. *mezeniense* Kisselev 1960, p. 45, fig. 2

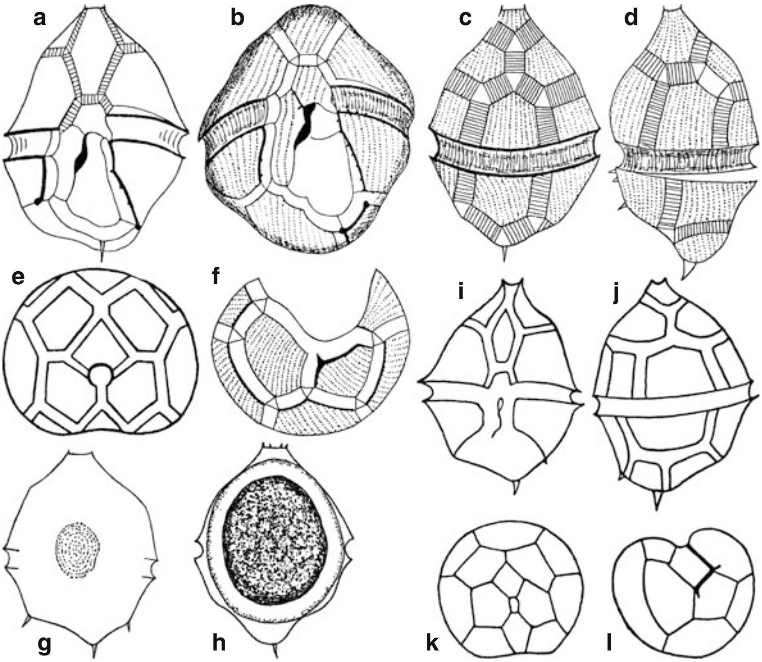

Fig. 167 *Parvodinium africanum* var. *tatricum* (Wołoszyńska) Moestrup (**a**–**h** after Wołoszyńska 1916; **i**–**l** after Kisselev 1960). **a** ventral view; **b** ventral-posterior view; **c** dorsal view with plate ornamentation and wide, striated sutures; **d** left lateral view of open cell cover; **e**, **f** apical and antapical views; **g** outline of cell with position of nucleus; **h** resting cyst; **i**–**l** ventral, dorsal, apical and antapical views (as *Peridinium africanum* f. *mezeniense* Kisselev)

Differs from the type in being elongate-ovoid and narrower. Hypocone with three corners, each of which carries a short spine, but the spines may sometimes be absent. Cells 34–43 µm long, *ca.* 30 µm wide. Resting cysts oval, smooth.
Ecology: in plankton of lakes, apparently a summer form. Form *mezeniense* described from brackish water (4.5–26.2‰; Kisselev 1960).
Geographical distribution: Poland, Tatra (Wołoszyńska); Russia (Kisselev).

3. ***Parvodinium belizense*** (Carty) Carty 2008, p. 106 ("*belizensis*") (**Fig. 168**)

Basionym: *Peridinium belizense* Carty *in* Carty & Wujek 2003, p. 137, figs 14–16 ("*belizensis*")

Epicone slightly larger than hypocone, more or less cone-shaped with convex sides. Hypocone angular, left side longer than right side. Antapical margin with a row

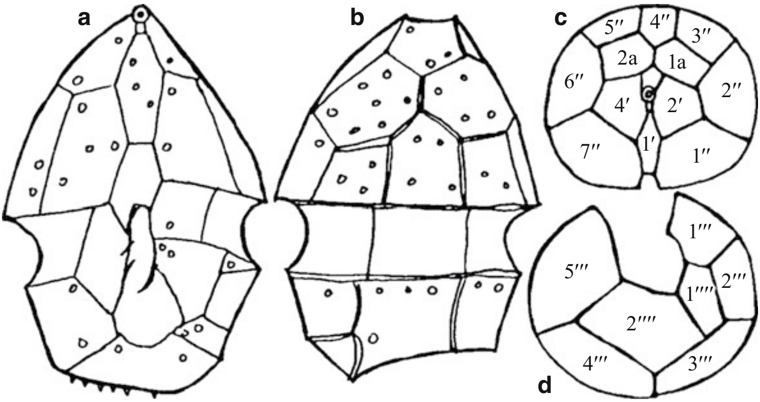

Fig. 168 *Parvodinium belizense* (Carty) Carty (after Carty & Wujek 2003). **a**–**d** ventral, dorsal, apical and antapical views, respectively

of small spines. Sulcus extends onto the epicone but does not reach the antapical end. In the hypocone, 1⁗ is much smaller than 2⁗. Cell length 12–16 µm, width 10–13 µm.
SEM: Carty & Wujek (2003).
Ecology: tropical pond.
Geographical distribution: Belize.

4. *Parvodinium centenniale* (Playfair) Carty 2008, p. 106 (**Fig. 169**)

Basionym: *Peridinium umbonatum* var. *centenniale* Playfair 1920, p. 806, text-fig. 14
Nomenclatural synonym: *Peridinium centenniale* (Playfair) Er. Lindemann 1931, p. 709
Taxonomic synonyms: *Peridinium umbonatum* var. *globosum* M. Lefèvre 1927, p. 120; *Peridinium centenniale* var. *fistulatum* Er. Lindemann 1931, p. 711, fig. 32 ≡ *Peridinium centenniale* f. *fistulatum* (Er. Lindemann) Wołoszyńska 1952, p. 314

Cells almost globose, very slightly flattened dorsoventrally. Epicone twice as long as hypocone. Epicone rounded and bowl-shaped, hypocone very shallow. Cingulum descending, displaced about one cingulum width. Sulcus forms a distinct extension on the epicone. On the hypocone it usually first widens, but then narrows towards the antapex. Cells are slightly asymmetric, the apex is shifted slightly towards the left side. The two antapical plates of equal or different size. Plates have numerous scattered pores with elevated rim, and also tiny knobs, the latter generally arranged in a single row along the plate margins. Nucleus posterior. Cell length and width 21–44 µm, thickness 27–32 µm.
SEM: Ling *et al.* (1989), Hansen & Flaim (2007), Cavalcante *et al.* (2017).
Ecology: in the plankton of ponds.

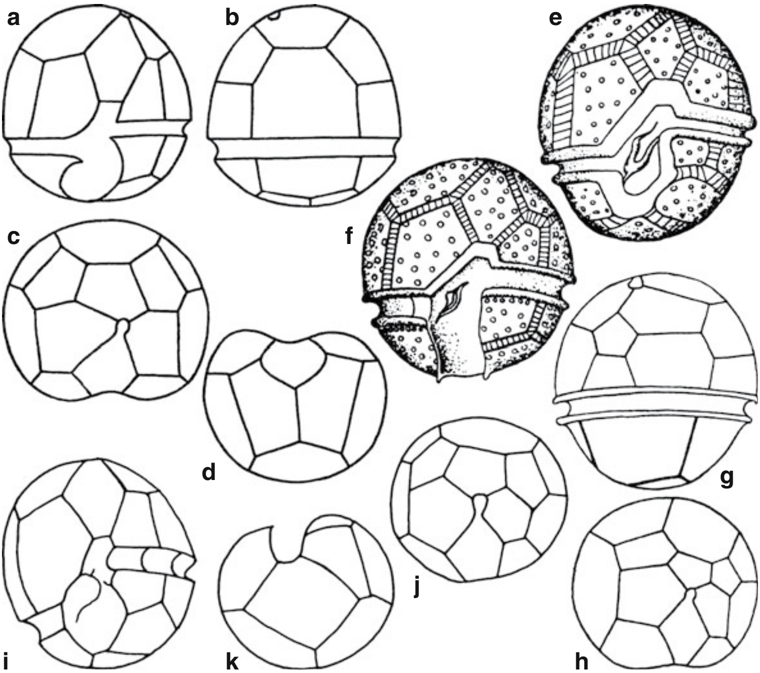

Fig. 169 *Parvodinium centenniale* (Playfair) Carty (**a**–**d** after Playfair 1920; **e**–**h** after Lefèvre 1932; **i**–**k** after Ling *et al.* 1989). **a**–**d** ventral, dorsal, apical and antapical views; **e**, **f** ventral views, with plate ornamentation and striated sutures; **g** dorsal view; **h** apical view; **i**–**k** ventral, apical and antapical views, respectively

Geographical distribution: France (Lefèvre); Italy (Hansen & Flaim); Tatra, Poland (Wołoszyńska); Spain (Lefèvre). Ivory Coast (Bourrelly); Madagascar (Lefèvre). Belize (Carty); Brazil (Borics *et al.*; Cavalcante *et al.*). Sumatra, Indonesia (Lindemann). New South Wales, Tasmania, Australia (Playfair; Ling *et al.*).

Note: the description above covers the original material from Centennial Park, Sydney, and at Lismore, both Australia. This species has subsequently been reported from many parts of the world. Considerable morphological variation has been described. Variations include sulcus with straight sides and the presence of 9 instead of 7 postcingular plates (by doubling of plates 2‴ and 4‴, Lefèvre 1932). Sutures have been reported to be difficult to see and very faintly striated, and plates have been reported with scattered papillae (Lindemann 1931). Whether this variation can be contained within a single species needs to be examined.

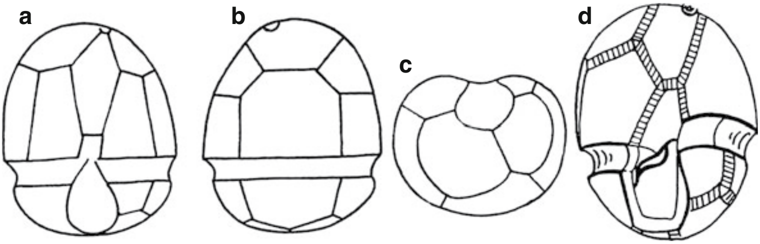

Fig. 170 *Parvodinium centenniale* var. *ovale* (Playfair) Moestrup (**a**–**c** after Playfair 1920; **d** after Wołoszyńska 1952). **a**–**c** ventral, dorsal and antapical views, respectively; **d** ventral view

var. *ovale* (Playfair) Moestrup *comb. nov.* (**Fig. 170**)
Basionym: *Peridinium umbonatum* var. *ovale* Playfair 1920, *Proc. Linn. Soc. New South Wales* **44**, p. 807, text-fig. 15
Nomenclatural synonym: *Peridinium centenniale* var. *ovale* (Playfair) Wołoszyńska 1952, p. 314

Differs in oval rather than globose cells. Cell length 28.5–32 µm, width 21–28 µm, epivalve 18–22 µm long.
Geographical distribution: Tatra, Poland (Wołoszyńska). Lismore, Guildford, Australia (Playfair).

5. *Parvodinium deflandrei* (M. Lefèvre) Carty 2008, p. 106 (**Fig. 171**)

Basionym: *Peridinium deflandrei* M. Lefèvre 1927, p. 121
Nomenclatural synonym: *Peridinium umbonatum* var. *deflandrei* (M. Lefèvre) Popovský & Pfiester 1986, p. 75

Cells ovoid, slightly dorsoventrally flattened. Epicone considerably larger than hypocone, pyramidal, bounded by slightly concave amphiesmal plates. Hypocone with two extensions, each carrying a long spine, which measures up to 1/4 the cell length. Left side of the hypocone distinctly longer than right side. Cingulum very slightly descending, the two ends displaced by *ca.* half the cingulum width. Sulcus extension on the epicone short and nearly square. On the hypocone it reaches the antapex, widening very strongly. Antapical plates of different size. The amphiesmal plates with longitudinal rows of fine points. Intercalary striae often wide, transversely striated. Nucleus in the lower part of the cell. Eyespot present. Cell length 28–35 µm, width (22–)26–32 µm. Resting cysts ovoid, surrounded by thick brown wall.
Ecology: two Bavarian bogs at pH 5 and 5.3 (Baumeister 1963); ditch with *Sphagnum* (Popovský 1968); mountain peat bog (Popovský 1971b). Dominant dinoflagellate (up to 2.75×10^5 cells per liter) during summer temperature stratification in artificial lake with pH 5.5–6.5 (Canion & Ochs 2005).
Geographical distribution: Czech Republic (Popovský); Germany (Baumeister); Spain (Lefèvre). USA, MN (Ngô & Pfiester), MS (Canion & Ochs).

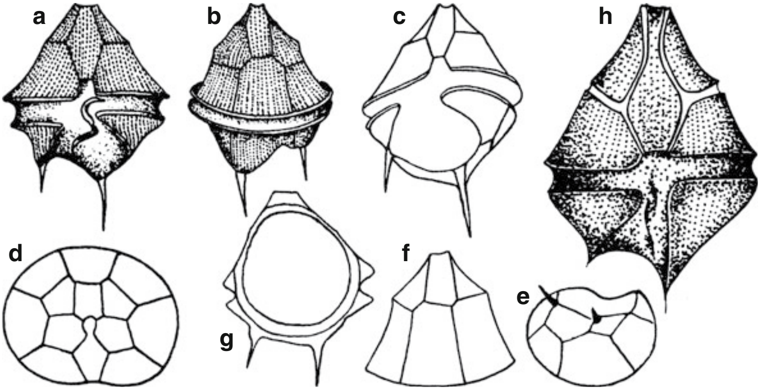

Fig. 171 *Parvodinium deflandrei* (M. Lefèvre) Carty (**a**–**g** after Lefèvre 1932; **h** after Popovský 1971b). **a**, **b** ventral and dorsal views; **c** ventral view somewhat tilted to show antapex; **d**, **e** apical and antapical views; **f** dorsal view with tabulation variant on the epicone (δ travectum); **g** oval resting cyst inside amphiesma of parent cell; **h** ventral view

6. *Parvodinium dzieduszyckii* (Wołoszyńska) Moestrup *comb. nov.* (**Fig. 172**)

Basionym: *Peridinium dzieduszyckii* Wołoszyńska 1916, *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math., Sér. B, Sci. Nat.* **1915**, p. 271, pl. 12, figs 16–20
Nomenclatural synonym: *Peridinium lubieniense* f. *dzieduszyckii* (Wołoszyńska) M. Lefevre 1932, p. 140

Cells oval, dorsoventrally compressed. Epicone larger than hypocone, the latter with concave plates. Cingulum descending, displaced *ca.* half a cingulum width. Sulcus extends for a short distance onto the epicone. On the hypocone it widens slightly towards the antapex. Sutures of the antapical plates thickened in older cells. Right antapical plate larger than left antapical plate, the suture between the two plates located on the left side of the cell. Amphiesma on the epicone areolated, on the hypocone smooth. Chloroplasts disc-shaped. Nucleus oval, central. Amphiesma opens on the hypocone, discharging the antapical plates. Cell length 34–40 µm, width 30–32 µm. Resting cysts oval.
Ecology: in the plankton of ponds.
Geographical distribution: Ukraine (Wołoszyńska).

7. *Parvodinium goslaviense* (Wołoszyńska) Carty 2008, p. 106 (**Fig. 173**)

Basionym: *Peridinium goslaviense* Wołoszyńska 1916, p. 267, pl. 10, figs 18–24
Nomenclatural synonym: *Peridinium umbonatum* var. *goslaviense* (Wołoszyńska) Popovský & Pfiester 1986, p. 76

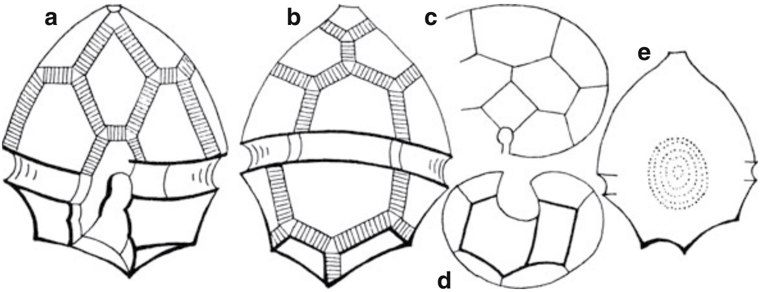

Fig. 172 *Parvodinium dzieduszyckii* (Wołoszyńska) Moestrup (after Wołoszyńska 1916). **a**, **b** ventral and dorsal views; **c** partial apical view; **d** antapical view; **e** outline of cell showing position of the nucleus

Cells ovoid pear-shaped, dorsoventrally slightly compressed. Epicone conical, pointed apically, larger than the hemispherical hypocone. In plate 1′ the two posterior lateral margins are usually longer than the two anterior ones and the adjacent 1″ and 7″ are therefore rather long. Plate 4″ also rather long. The 3 adjacent plates 1a, 2a and 3′ very similar in size. A low rim encircles the pore plate and the canal plate. Another low rim encircles the pore area of the pore plate (SEM). The right antapical plate often larger than the left. A relatively long curved spine is present posteriorly, attached to the margin between the two antapical plates, and often located in the cell axis. A second, smaller spine may also be present. Cingulum wide, descending, barely or not displaced. Sulcus extends a short distance onto the epicone. On the hypocone it widens towards the antapex. Amphiesmal plates convex, with scattered pores, particularly near plate borders, but they may be difficult to see without oil immersion. Numerous chloroplasts present. Nucleus central. Amphiesma opens on the hypocone, discarding the antapical plates. Cell length 20–30 μm, width 16–25 μm. Cysts unknown.
SEM: Hansen & Flaim (2007).
Ecology: plankton in acid brown-water lakes (Huber-Pestalozzi 1950); found in both oligotrophic-mesotrophic and mesotrophic-eutrophic small lakes in the Italian Alps (Hansen & Flaim 2007).
Geographical distribution: France (Lefèvre); Germany (Lindemann); Hungary (Grigorszky *et al.*); Italy (Hansen & Flaim 2007); Poland (Wołoszyńska; Lindemann); Switzerland (Lindemann; Huber-Pestalozzi). USA, OH (Carty); reported, but not documented, from northeastern Quebec (Janus & Duthie).

8. *Parvodinium inconspicuum* (Lemmermann) Carty 2008, p. 106 (**Fig. 174**)

Basionym: *Peridinium inconspicuum* Lemmermann 1899, p. 350
Nomenclatural synonym: *Peridinium tabulatum* var. *inconspicuum* (Lemmermann) Playfair 1913, p. 545
Taxonomic synonyms: (?) *Peridinium javanicum* C. Bernard 1908, p. 210, figs 575, 576; (?) *Peridinium javanicum* var. *tjibodense* C. Bernard 1908, p. 210, figs 577,

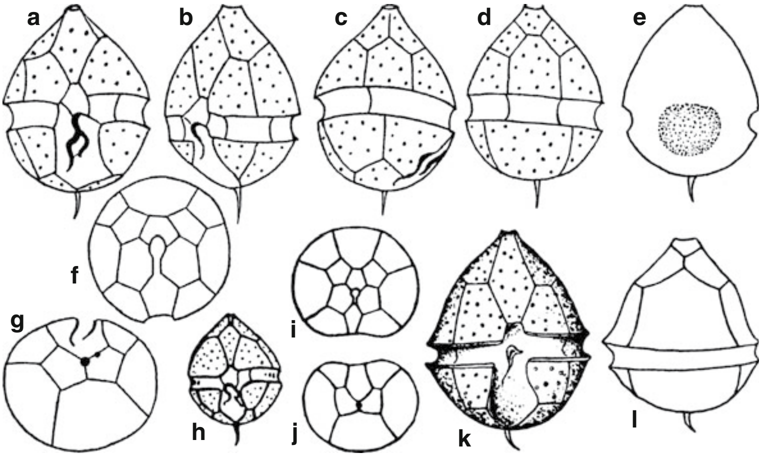

Fig. 173 *Parvodinium goslaviense* (Wołoszyńska) Carty (**a**–**g** after Wołoszyńska 1916; **h**–**j** after Lindemann 1920; **k**, **l** after Lefèvre 1932). **a** ventral view; **b** ventral-left view; **c** right side of cell cover; **d** dorsal view with tabulation conjunctum; **e** outline of cell with position of nucleus; **f**, **g** apical and antapical plate patterns; **h** ventral view; **i**, **j** apical and antapical views; **k** ventral view; **l** dorsal view with tabulation remotum

578; *Peridinium marchicum* Lemmermann 1910, p. 666, figs 16–19 ≡ *Peridinium inconspicuum* f. *marchicum* (Lemmermann) Er. Lindemann 1920, p. 142; (?) *Peridinium tabulatum* var. *caudatum* Playfair 1913, p. 544, pl. lv, fig. 18 ≡ *Peridinium caudatum* (Playfair) Playfair 1920, p. 799; (?) *Peridinium tabulatum* var. *pusillum* f. *morsum* Playfair 1913, p. 544, pl. lv, figs 19–21 ("*morsa*") ≡ *Peridinium caudatum* var. *morsum* (Playfair) Playfair 1920, p. 802; *Peridinium munusculum* Er. Lindemann 1919, p. 239, text-figs 66–74; *Peridinium munusculum* var. *contactum* Er. Lindemann 1919, p. 241, text-figs 75–77; *Peridinium munusculum* f. *spiniferum* Er. Lindemann 1920, p. 143, figs 71–74 and its homonym *Peridinium munusculum* var. *contactum* f. *spiniferum* Er. Lindemann 1920, p. 144 – both homonyms were cited by Lefèvre, each as the basionym of *Peridinium inconspicuum* f. *spiniferum* (Er. Lindemann) M. Lefèvre 1932, pp 131, 132, described under different tabulation variants; "*Peridinium inconspicuum* var. *contactum* Er. Lindemann" 1920, p. 144 (cited in synonymy); *Peridinium geminum* var. *excavatum* Playfair 1920, p. 805, text-fig. 11 ≡ *Peridinium inconspicuum* var. *excavatum* (Playfair) M. Lefèvre 1932, p. 130; *Peridinium geminum* var. *angulosum* Playfair 1920, p. 805, text-fig. 12; *Peridinium marchicum* var. *keyense* Nygaard 1926, p. 209, pl. III, fig. 29; (?) *Peridinium inconspicuum* var. *balatonicum* Entz 1927b, p. 341 (text on p. 298, but variety named only in figs legend), figs 17–19; *Peridinium steinmannii* Wołoszyńska 1930b, p. 165, fig. 4; *Peridinium parvulum* Wołoszyńska *in* Steinmann 1935, p. 238, fig. 10; *Glenodinium spiculiferum* J. Schiller 1955, p. 52, pl. X, fig. 55

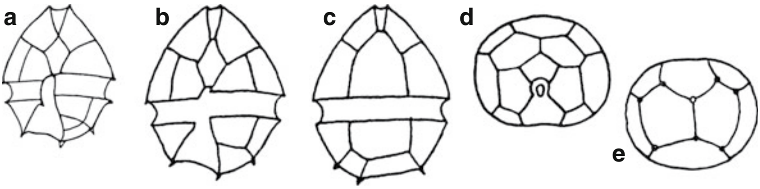

Fig. 174 *Parvodinium inconspicuum* (Lemmermann) Carty (**a** after Lemmermann 1905a; **b**, **c** after Lemmermann 1910; **d**, **e** after Lefèvre 1932). **a** ventral view, inverted relative to original (first published figure); **b**–**e** ventral, dorsal, apical and antapical views

Description based on Lemmermann (1910): cells ovoid, dorsoventrally slightly flattened, 15–18 µm long, 12–15 µm wide. Cingulum slightly descending. Sulcus extends little onto the epicone, but on the hypocone it widens strongly and reaches the antapex. Epicone conical, much larger than hypocone. Hypocone nearly hemispherical, posterior obliquely concave, with two antapical plates of which the right plate is the largest. At the end of the sulcus with two spines, and another spine further to the left. Amphiesmal plates smooth. Sutures barely visible. Resting cysts spherical, with thick wall.
The chloroplasts of cells identified as belonging to this species showed a radiate arrangement and diel migration to and from the cell center (Seo & Fritz 2002). Cysts pyriform to ovoid without ornaments (Chu *et al.* 2008).
SEM: Hansen & Flaim (2007)?
Ecology: common in plant-rich ponds and bogs (Lemmermann 1910). Also reported from plankton in both highly alkaline and in low-conductivity lakes, temperature interval in the many localities in (mainly) volcanic freshwater lakes in the Pacific given as 21–31 ˚C, pH as 6–9.8 and conductivity as 5–600 $\mu S \cdot cm^{-1}$ (Schabetsberger *et al.* 2009). Whether these data all refer to *P. inconspicuum* needs to be confirmed.
Geographical distribution (Lemmermann): Germany. Hawaii. Chatham Islands.
Subsequent findings that appear to agree with the original description, but extend the size range: Germany, Poland, Lake Victoria (Lindemann: cells 18–26 µm long and 14–22 µm wide). New South Wales, Australia (Playfair: cells 21–25 µm long, 15–17 µm wide).
Other reports of the species: Ivory Coast (Bourrelly). USA, MI, OH, OK, TX, WA, WI, WY (Pfiester *et al.*; Carty). Burma (Skuja); Java (Lemmermann). New Zealand (Thompson); many localities in the Pacific: Tahiti, Cook Isl., Fiji, Wallis, Samoa, Vanuatu (Schabetsberger *et al.*).

Note 1: *Peridinium marchicum* differs in having a conical epicone of the same size as the hypocone, stronger spines (2 small additional spines reported), the sides of the epicone straight or slightly angular rather than slightly rounded, and it is here considered to fall within the range of variation of *P. inconspicuum*.

Note 2: Material from the Italian alps referred to this species by Hansen & Flaim (2007) differs from Lemmermann's original description in some cells lacking anterior spines

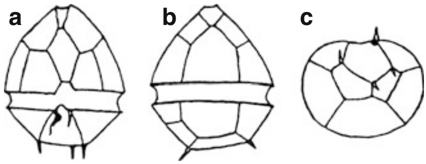

Fig. 175 *Parvodinium inconspicuum* var. *armatum* (Lemmermann) Moestrup (after Lemmermann 1910). **a**–**c** ventral, dorsal and antapical views, respectively

while others had 2 spines. Cells with 3 spines were not reported. The cell surface of the Italian material was almost smooth in some cells, highly reticulated in others.

var. *armatum* (Lemmermann) Moestrup *comb. nov.* (**Fig. 175**)
Basionym: *Peridinium inconspicuum* var. *armatum* Lemmermann 1910, *Kryptogamenflora der Mark Brandenburg: Algen I*, p. 668, figs 33–35
Nomenclatural synonym: *Peridinium inconspicuum* f. *armatum* (Lemmermann) M. Lefèvre 1932, p. 131

Differs in the presence of two additional short, thick spines on the left part of the cingulum near the sulcus, one in the longitudinal direction of the cell, the other at right angles. Cells 18–21 µm long, 15 µm wide.
Ecology: between other algae in brackish water at Saaler Bodden, Germany (Lemmermann 1910); in Ruster Canal, Lake Neusiedl, from May to September (Schiller 1955).
Geographical distribution: Austria (Schiller); Germany (Lemmermann).

Note: materials referred to this variety from France, Spain, Austria and Java lack the 2 diagnostic spines (Lefèvre 1932) and more likely represent the nominal species.

9. *Parvodinium lubieniense* (Wołoszyńska) Carty 2008, p. 106 (**Fig. 176**)

Basionym: *Peridinium lubieniense* Wołoszyńska 1916, p. 272, pl. 12, figs 21–24
Taxonomic synonym: *Peridinium lubieniense* var. *contactum* Er. Lindemann 1920, p. 137, figs 48–50 ≡ "*Peridinium linzium* var. *contactum* Er. Lindemann" 1920, p. 137 (cited in synonymy)

Cells oval, dorsoventrally compressed. Epicone larger than hypocone. Epicone pyramidal with slightly convex sides. Hypocone angular. Cingulum descending, displaced half a cingulum width or less. Sulcus extends for a short distance onto the epicone. On the hypocone it does not widen towards the antapex. The two antapical plates similar in size. Amphiesma with fine areolae, the antapical plates with papillae. Sutures wide. Chloroplasts disc-shaped. Nucleus oval, central. Cells open on the hypocone, discharging the antapical plates. Cell length 35–45 µm, width 30–32 µm.
Ecology: plankton in ponds.
Geographical distribution: France (Lefèvre); Germany (Lindemann); Holland (Beijerinck); Poland (Lindemann); Ukraine (Wołoszyńska).

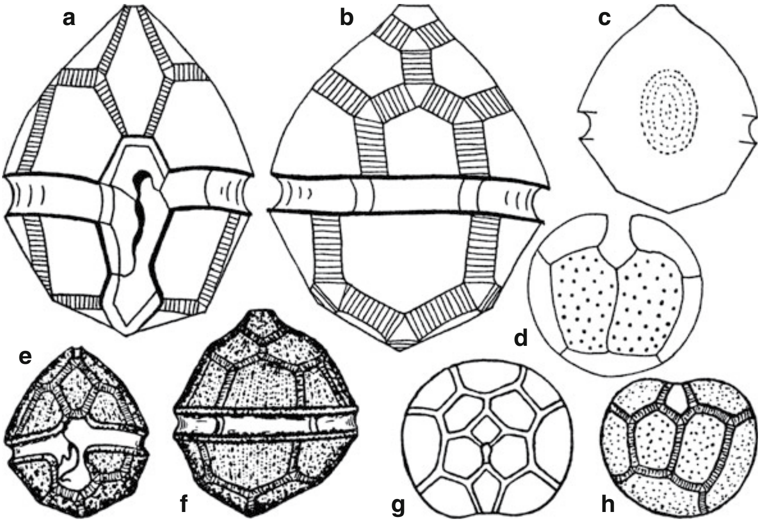

Fig. 176 *Parvodinium lubieniense* (Wołoszyńska) Carty (**a**–**d** after Wołoszyńska 1916; **e**–**h** after Lindemann 1920). **a**, **b** ventral and dorsal views; **c** cell outline showing position of the nucleus; **d** antapical view; **e**–**h** ventral, dorsal, apical and antapical views

Note: the invalidly published "*Peridinium mixtum* Wołoszyńska" (1952, p. 315; *nomen nudum*), from the Tatra Mountains, Poland, differs in the sulcus widening strongly toward the antapex.

10. *Parvodinium morzinense* (M. Lefèvre) Carty 2008, p. 106 (**Fig. 177**)

Basionym: *Peridinium morzinense* M. Lefèvre 1928b, p. 137, a replacement name for *Peridinium elegans* M. Lefèvre 1926a, 332, text-figs 1–6, *nom. illeg.* (*non* Cleve 1900, p. 16, pl. VII, figs 15, 16)
Nomenclatural synonym: *Peridinium lubieniense* f. *elegans* Er. Lindemann 1928, p. 260 (replacement name under Art. 58)

Cells ovoid, not dorsoventrally compressed. Epicone larger than hypocone, bell-shaped. Cingulum descending, the ends slightly displaced. Sulcus extension on the epicone short, square. On the hypocone it widens slightly towards the antapex. Antapical plates of different size. The characteristic feature of the species is the presence of sinuous sutures between the amphiesmal plates. Amphiesmal plates smooth. Sutures not striated, sometimes thick. Chloroplasts not reported. Cyst not reported. Cell length 30–41 μm, width 26–35 μm.
Ecology: peat bogs.
Geographical distribution: France (Lefèvre), Poland (Wołoszyńska).

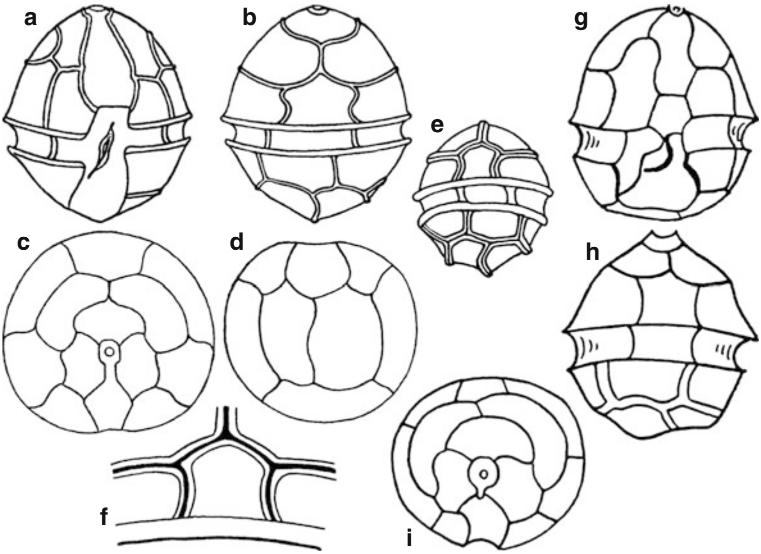

Fig. 177 *Parvodinium morzinense* (M. Lefèvre) Carty (**a**–**f** after Lefèvre 1926a; **g**–**i** after Wołoszyńska 1952). **a**–**d** ventral, dorsal, apical and antapical views; **e** dorsal view of old cell; **f** detail of wide sutures; **g**–**i** ventral, dorsal and apical views

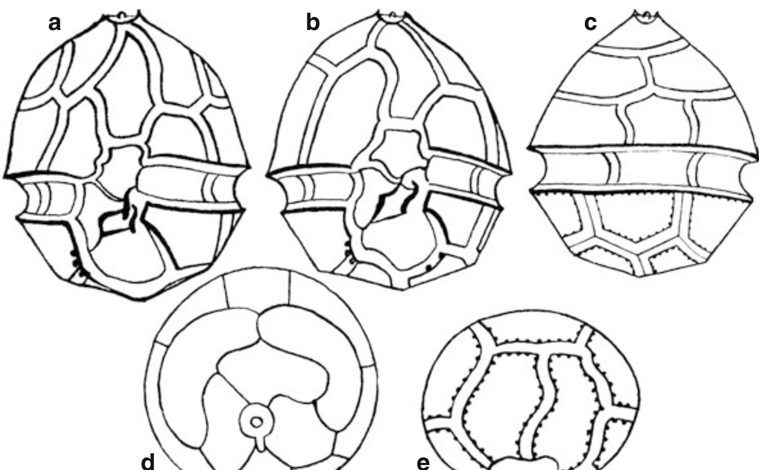

Fig. 178 *Parvodinium morzinense* var. *papilliferum* (Wołoszyńska) Moestrup & Calado (after Wołoszyńska 1930a). **a**, **b** two ventral views; **c**–**e** dorsal, apical and antapical views

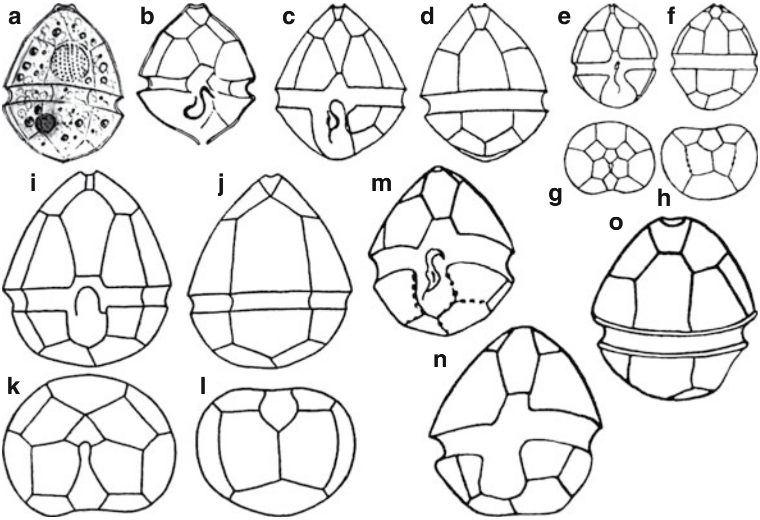

Fig. 179 *Parvodinium pusillum* (Penard) Carty (**a**, **b** after Penard 1891; **c**, **d** after Lemmermann 1910; **e**–**h** after Lindemann 1919; **i**–**l** after Playfair 1920; **m**–**o** after Lefèvre 1932). **a** dorsal view with cell contents; **b** ventral view; **c**, **d** ventral and dorsal views; **e**–**h** ventral, dorsal, apical and antapical views; **i**–**l** ventral, dorsal, apical and antapical views; **m** ventral view, cell slightly tilted away from observer; **n**, **o** ventral and dorsal views

var. *papilliferum* (Wołoszyńska) Moestrup & Calado *comb. nov.* (**Fig. 178**)
Basionym: *Peridinium elegans* f. *papilliferum* Wołoszyńska 1930a, *Acta Soc. Bot. Poloniae* **7**, p. 500, 504, pl. XXVIII, figs 1–5

Differs in the amphiesmal plates on the hypocone carrying numerous papillae along the edges.
Ecology: in *Sphagnum* bogs.
Geographical distribution: Ukraine.

11. *Parvodinium pusillum* (Penard) Carty 2008, p. 106 (**Fig. 179**)

Basionym: *Glenodinium pusillum* Penard 1891, p. 52, pl. IV, figs 1–4
Nomenclatural synonym: *Peridinium pusillum* (Penard) Lemmermann 1901, p. 65
Taxonomic synonyms: *Peridinium orrei* Huitfeldt-Kaas 1906, p. 59, pl. I, figs 25–29; *Peridinium geminum* var. *elegans* Playfair 1920, p. 804, text-fig. 10; *Peridinium pusillum* f. *gracile* M. Lefèvre 1932, p. 134

Cells ovoid. Epicone conical with convex sides, hypocone almost hemispherical. Cingulum slightly descending. Sulcus extends for a short distance onto the epicone,

on the hypocone it barely increases in width and does not reach the antapex. Cell length 18–25 µm, width 13–20 µm. Cysts spherical.
Ecology: in the plankton of lakes, ponds and swamps. Reported to form red blooms in ponds in southwest Germany (Klotter 1951).
Geographical distribution: Denmark (Nygaard); France (Lefèvre); Germany (Lemmermann; Lindemann); Holland (Beijerinck); Hungary (Entz); Latvia (Skuja); Norway (Huitfeldt-Kaas); Portugal (Nauwerck); Scotland (West & West); Spain (Lefèvre); Sweden (Lemmermann); Switzerland (Penard). Cameroon (Lefèvre). Greenland (Nygaard). Java, Indonesia (Lemmermann); Singapore (Lemmermann). Australia (Playfair).

Genus 4. *Peridiniopsis* Lemmermann 1904a, p. 134

Type species: *Peridiniopsis borgei* Lemmermann 1904a

Distinguished from other peridinioids with 5–6 cingular plates by having 0–1 anterior intercalary plates. General range of plate formulae: po, x, 3–5′, 0–1a, 6–7″, 6c, 4–6s, 5‴, 2⁗.
A polyphyletic genus, which contains species of very different plate formulas, and most of which are in need of additional studies. The species are presently assembled in 7 groups, each characterized by its plate formula. Probably only species of group 1, which includes the type species, will remain in the genus.

Artificial key to groups presently included in *Peridiniopsis*:
1a Epicone with 3 apical plates 2
1b Epicone with 4 or 5 apical plates 3
2a Epicone with 6 precingular plates .... Group 1, the *P. borgei* group
2b Epicone with 7 precingular plates .... Group 4, the *P. lindemannii* group
3a Epicone with 4 apical plates 4
3b Epicone with 5 apical plates 6
4a Epicone with 7 precingular plates 5
4b Epicone with 6 precingular plates and one intercalary plate ....
.... Group 2, the *P. cunningtonii* group
5a Epicone lacks intercalary plate .... Group 3, the *P. elpatiewskyi* group
5b Epicone with 1 intercalary plate .... Group 7, the *P. viguieri* group
6a Intercalary plates absent .... Group 6, the *P. thompsonii* group
6b One intercalary plate present .... Group 5, the *P. quadridens* group

Group 1, the *P. borgei* group

Plate formula: po, x, **3′**, **1a**, **6″**, 6c, 5s, 5‴, 2⁗ (also interpretable as po, x, **4′**, **0a**, **6″**, 6c, 5s, 5‴, 2⁗). Plates usually arranged symmetrically.

Key to species of group 1, the *P. borgei* group:
1a Cells with two prominent antapical spines or wings 2
1b Antapical spines and wings absent 3
2a Cells rhomboid, with two prominent antapical spines. No wings around apex
.... 2. *P. amazonica*

2b Cells ovoid with two antapical wings. Small wing around apex 3. *P. cristata*
3a Epicone conical, plate 1a 5-sided .... 1. *P. borgei*
3b Epicone hemispherical, plate 1a 4-sided 4
4a Cell outline somewhat angular; cells more than 25 µm long; chloroplasts usually present .... 4. *P. kulczynskii*
4b Cell outline smoothly round; cells less than 25 µm long; chloroplasts absent .... 5. *P. sphaeroidea*

1. *Peridiniopsis borgei* Lemmermann 1904a, p. 134, pl. I, figs 1–5 (**Fig. 180**)

Nomenclatural synonyms: *Peridinium borgei* (Lemmermann) Lemmermann 1910, p. 671 ≡ *Glenodinium borgei* (Lemmermann) J. Schiller 1935a, p. 112

Cells egg-shaped to globular, the epicone somewhat pyramidal with distinct apical pore. Cells almost circular in transverse view (*i. e.*, barely compressed dorsoventrally). Epicone slightly larger than hypocone. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus almost entirely restricted to the hypocone, widening towards the antapex, with curved list between the right and the left sulcal plate. Plate arrangement symmetrical. Intercalary plate 1a five-sided (rarely six-sided), the side touching 2′ and 3′ usually straight. Amphiesmal plates ornamented with network of ridges and perforated by trichocyst pores. Nucleus large, occupying major part of the hypocone. With numerous chloroplast profiles in the cell periphery, and a single multi-stalked pyrenoid in the lower dorsal part of the epicone. Large lipid globules often present in the epicone, especially near the apex. Cells commonly surrounded by well-defined layer of mucilage. Large eyespot present near the sulcus but not conspicuous in the light microscope. Large centrally located sac pusule. A flat peduncle arises near the flagellar bases, indicating mixotrophy, but source of food not identified. Cells usually 28–45 µm long, 25–50 µm wide and 25–38 µm thick. Cysts spherical, 18–48 µm in diameter, with a 0.5-µm-thick wall. The cyst is sometimes surrounded by a layer of mucilage (Entz 1926).
SEM: Dodge (1985), Ling *et al.* (1989), Pollingher & Hickel (1991).
TEM: Calado & Moestrup (2002).
DNA data: Calado *et al.* (2009).
Ecology: in lakes and ponds. Generally rare but sometimes in dense blooms proportions (Sweden, Hungary). In Tasmania mainly in dystrophic waters. Also known to form dense blooms at very low salinity in meromictic lakes (Finland).
Geographical distribution: Austria, Hungary (Entz); Finland and Åland archipelago, Baltic Sea (Lindholm & Öhman); Italy (Schiller); Sweden (Lemmermann; Calado & Moestrup). USA, WI (Prescott). Israel (Pollingher & Hickel); Turkestan (Schiller); Qinghai, China (Zhang *et al.*). Australia, Tasmania (Ling *et al.*).

2. *Peridiniopsis amazonica* Barbara Meyer *in* Meyer *et al.* 1997, p. 366, figs 1–24 (**Fig. 181**)

Cells rhomboid, slightly dorsoventrally compressed, epicone larger than hypocone. Epicone triangular, hypocone more or less trapezoidal with two distinct triangular antapical spines. Dorsal side of cell convex, ventral side almost flat with slight central indentation. Cingulum descending, the ends displaced *ca.* 1–1.5 cingulum

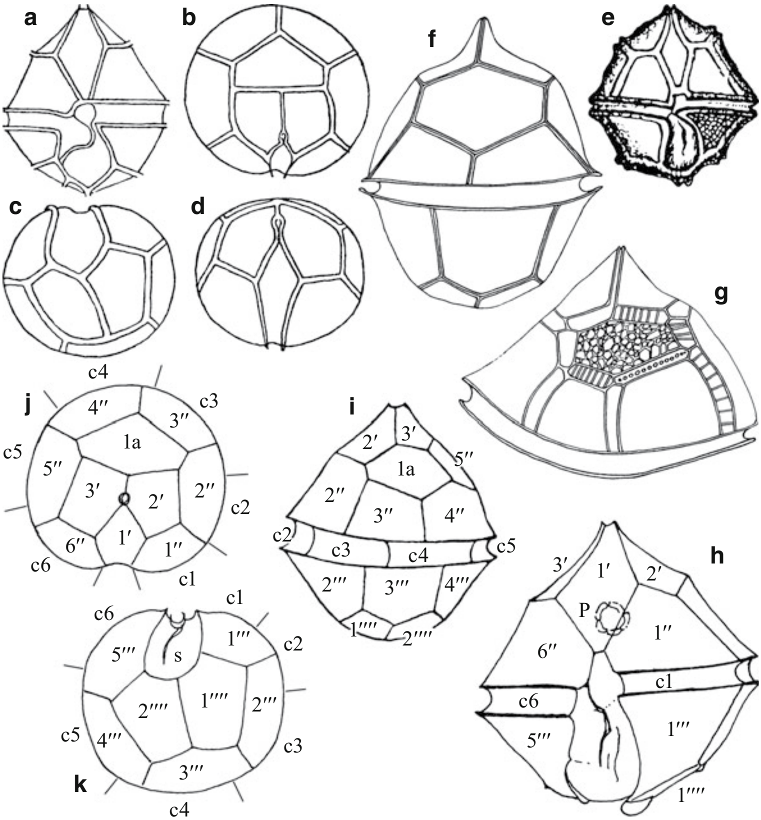

Fig. 180 *Peridiniopsis borgei* Lemmermann (**a**–**d** after Lemmermann 1904a; **e** after Lindemann 1923b; **f**, **g** after Entz 1926; **h**, **j**, **k** after Bourrelly 1970; **i** after Bourrelly 1969). **a**–**d** ventral, apical, antapical and ventral-anterior views, respectively; **e** ventral view, with ornamentation shown on plate 1‴; **f** dorsal view; **g** detail of plate and suture ornamentation; **h** ventral view with pyrenoid (p) indicated in the center of the epicone; **i** dorsal view; **j**, **k** apical and antapical views, with the limits of cingular plates indicated by straight lines outside the periphery (s, sulcus)

widths. Sutures of cingular plates collinear with those on the hypocone, except c1 which is very short. Sulcus broad, on each side lined by a list. Sutures of very different width. Spines 5–12 µm long, extending from the ventral rims of 1⁗ and 2⁗. All 3 apical plates elongate. Plates on the right and left side not symmetrical, those on the right side generally larger than those on the left side. Intercalary plate 1a six-sided. Amphiesmal plates thick, with fine reticulation. Many small chloroplasts.

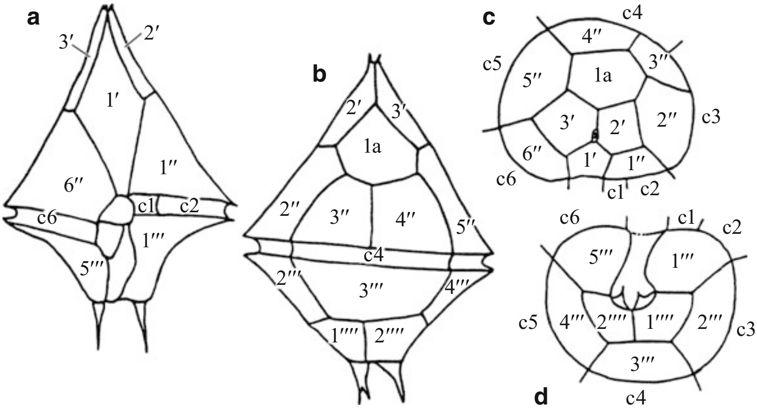

Fig. 181 *Peridiniopsis amazonica* Barbara Meyer (after Meyer *et al.* 1997). **a**, **b** ventral and dorsal views with major plates labelled; **c**, **d** apical and antapical views with limits of cingular plates indicated by bars extending from the cell outline

Cells break in the cingulum, cingular plates remain attached to epicone or hypocone. Cell length 65–98 µm, width 50–74 µm. Cyst reflects the shape of the vegetative cell, rounded with anterior spine and two short posterior projections, smooth, 55–65 µm long, 45–55 µm wide. Plate formula: po, x, 3′, 1a, 6″, 6c, 4s, 5‴, 2⁗.
SEM: Meyer *et al.* (1997).
Ecology: plankton in acidic or neutral lakes (pH 4.8–7.1), sometimes dominant. Warm-water species, found at 26–29°C.
Geographical distribution: central Amazonian floodplain lakes, Brazil.

3. *Peridiniopsis cristata* (Balech) Bourrelly 1968, p. 9 ("*cristatum*") (**Fig. 182**)

Basionym: *Glenodinium cristatum* Balech 1961, p. 47, fig. 1

Cells asymmetrically ovoid. Epicone and hypocone of equal size. Epicone conical-triangular with two small wing-like processes around the apical pore. The hypocone rounded. Cingulum descending, the two ends only slightly displaced. Sulcus extends for a short distance onto the epicone. Margins of sulcus flanged. A double-winged projection is present at the cell's antapex. Cells in apical view bilaterally symmetrical. Intercalary plate 1a six-sided. Amphiesmal plates papillate, often with reticulate ridges. With chloroplasts, in the epicone with a pyrenoid. Cell length 40–50 µm (without wings), width 29–36 µm, thickness 29–32 µm.
SEM: Ricard & Bourrelly (1982), Couté *et al.* (2012).
Ecology: brackish and marine water.
Geographical distribution: Clipperton Island lagoon, Eastern Pacific Ocean (Balech; Bourrelly; Couté *et al.*).

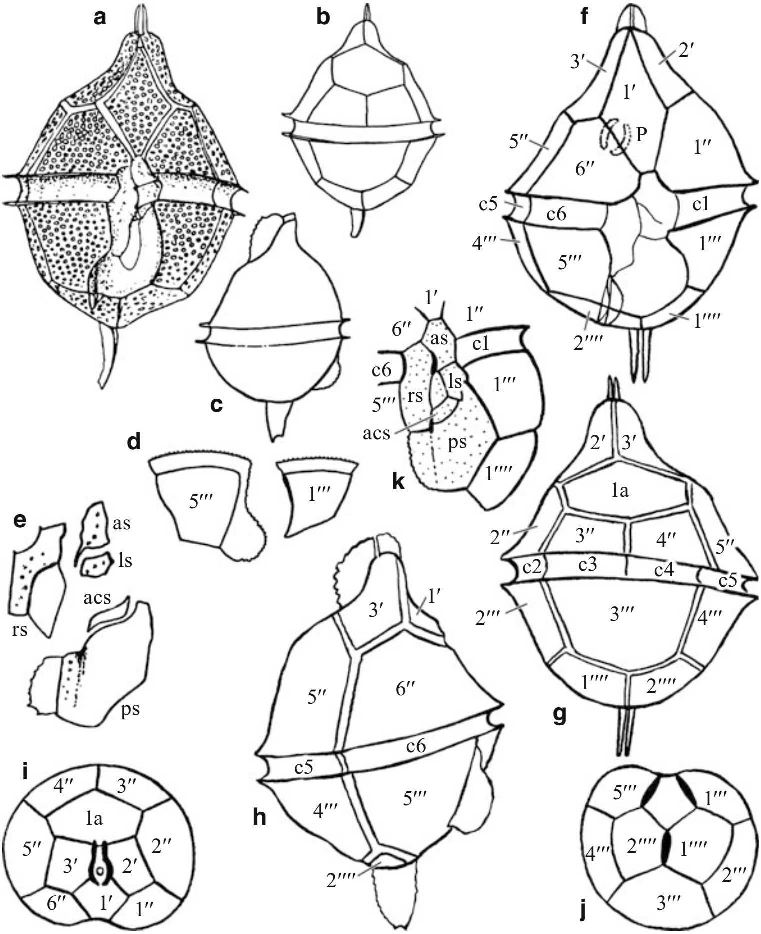

Fig. 182 *Peridiniopsis cristata* (Balech) Bourrelly (**a**–**e** after Balech 1961; **f**–**k** after Bourrelly 1970). **a** ventral view showing plate ornamentation; **b** dorsal view; **c** outline of cell in right lateral view; **d** detail of postcingular plates on the ventral side with position of flange; **e** sulcal plates; **f**–**h** ventral, dorsal and right lateral views, respectively, with major plates labelled (P, starch-enveloped pyrenoid); **i**, **j** apical and antapical views, with position of flanges indicated by thick lines; **k** detail of the sulcal area

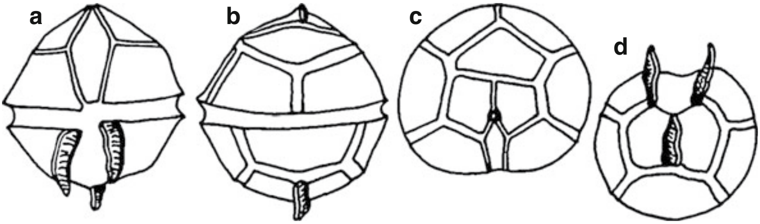

Fig. 183 *Peridiniopsis cristata* var. *boliviensis* A. Iltis & Couté (after Iltis & Couté 1984). **a**–**d** ventral, dorsal, apical and antapical views

var. *boliviensis* A. Iltis & Couté 1984, p. 283, pl. II, figs 6–8, pl. III, figs 1–7, pl. V, figs 14–17 ("*boliviense*") (**Fig. 183**)
Differs by a more rounded epicone and the absence, or small development, of the apical wing-like projection.
SEM: Iltis & Couté (1984).
Ecology: in the plankton of Lake Poopó (altitude 3686 m), abundant in November together with *Nodularia harveyana* var. *sphaerica*, at a salinity of 7.5‰. Also, in smaller numbers, in the Bolivian part of Lake Titicaca.
Geographical distribution: Bolivia.

var. *tubulifera* Couté, Perrette & Chomérat 2012, p. 63, figs 4, 18–24, 27, 30, 31, 46–51 (**Fig. 184**)
Differs by the absence of plate ornamentation and by the lack of wing-like projections, both on the apex and on the hypocone. Shows tubular rim on apex.
SEM: Couté *et al.* (2012).
Ecology: planktonic in brackish water, co-occurring with *P. cristata* var. *cristata*.
Geographical distribution: Clipperton Island lagoon, Eastern Pacific Ocean.

4. *Peridiniopsis kulczynskii* (Wołoszyńska) Bourrelly 1968, p. 8 (**Fig. 185**)

Basionym: *Peridinium kulczynskii* Wołoszyńska 1916, p. 272, pl. 12, figs 25–31
Nomenclatural synonym: *Glenodinium kulczynskii* (Wołoszyńska) Er. Lindemann 1928a, p. 260

Cells oval, dorsoventrally compressed. Epi- and hypocone of the same size and both rounded, in the material from Kansas the epicone slightly angular. Cingulum descending, the two ends displaced *ca.* half the width of the cingulum. Sulcus extends very slightly onto the epicone. Plates on the right and left side symmetrical. The intercalary plate 1a is four-sided. Amphiesmal plates smooth. Sutures usually thin. The cell opens along the cingulum. Chloroplasts plate-like, arranged radially. With small obovoid to rod-shaped stigma. Nucleus round or oval, central. Cell length 28–48 µm, width 23–36 µm. Cyst unknown.
Ecology: plankton in lakes and ponds, mainly in summer.
Geographical distribution: Denmark (Calado); Poland (Wołoszyńska). USA, KS (Thompson).

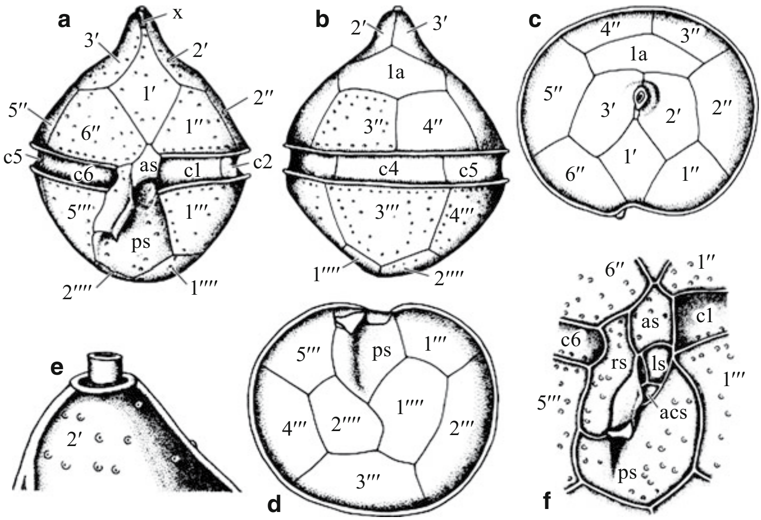

Fig. 184 *Peridiniopsis cristata* var. *tubulifera* Couté, Perrette & Chomérat (after Couté *et al.* 2012). **a**–**d** ventral, dorsal, apical and antapical views; **e** lateral view of the apex with tubular rim; **f** detail of the sulcal area

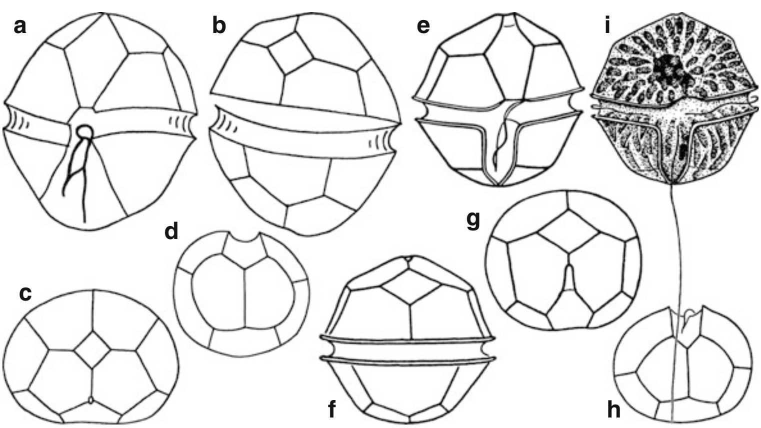

Fig. 185 *Peridiniopsis kulczynskii* (Wołoszyńska) Bourrelly (**a**–**d** after Wołoszyńska 1916; **e**–**i** after Thompson 1951). **a** ventral view; **b** dorsal view of open cell cover; **c**, **d** apical and antapical views; **e**–**h** ventral, dorsal, apical and antapical views; **i** ventral view showing flagella and cell contents

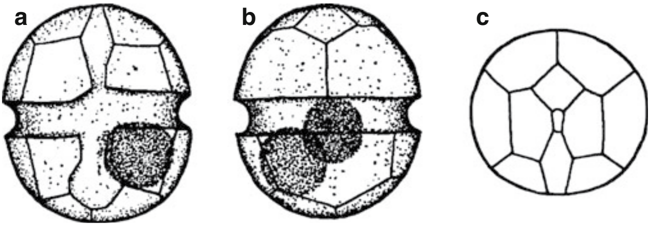

Fig. 186 *Peridiniopsis sphaeroidea* Bourrelly (after Christen 1958b). **a**, **b** ventral and dorsal views with one and two food vacuoles, respectively; **c** apical view

Note: colorless cells with other features identical to *P. kulczynskii* were found to co-occur with a *P. kulczynskii* plastid-bearing population in Denmark (Calado 2011).

5. *Peridiniopsis sphaeroidea* Bourrelly 1968, p. 9 ("*sphaeroideum*") (**Fig. 186**)

Replacement name (under Art. 58, McNeill *et al.* 2012) for *Peridinium sphaeroideum* Christen 1958b, p. 71, fig. 4, *nom. illeg.* (non *Peridinium sphaeroideum* L. Mangin 1922, p. 81, fig. 24-II)

Cells elongate-spherical, barely dorsoventrally compressed. Epi- and hypocone both hemispherical, of equal size or the epicone marginally larger. Periplast very thin and readily discarded, the cells then becoming *Gymnodinium*-like. Epicone symmetrical when seen from above. Apical plates 2 and 4 elongated in the dorsoventral direction. Plates smooth. Chloroplasts absent. Cytoplasm colorless, with 1–3 food vacuoles, which initially are red, but later turn olive-green. Cells divide by transverse division. Cell length 20–22 µm, width 18–20 µm.
Ecology: cold-water species found in Lake Hausersee, Switzerland, feeding on small green algae.
Geographical distribution: Switzerland.

Group 2, the *P. cunningtonii* group

Plate formula po, x, **4′**, **1a**, **6″**, 6c, ?s, 5‴, 2⁗, interpretable as **5′**, **0a** when the intercalary plate contacts the apical pore. Cells somewhat asymmetrical, the single intercalary plate located on the left side. With two species.

6. *Peridiniopsis cunningtonii* Lemmermann *in* West 1907, p. 189, pl. 9, fig. 2 (**Fig. 187**)

Nomenclatural synonym: *Peridinium cunningtonii* (Lemmermann) Lemmermann 1910, p. 671
Taxonomic synonyms: *Peridinium cunningtonii* var. *pseudoquadridens* Er. Lindemann 1919, p. 235, text-figs 55–62, pl. 17, figs 14–17; *Peridinium suttonii* B. M. Griffiths 1922, p. 8, pl. 1, figs 1–6 ("*Suttoni*"); *Peridinium wildemanii* Wołoszyńska 1923, p. 265, pl. IV, figs 13–16 ("*Wildemani*") ≡ *Peridinium cunningtonii* var.

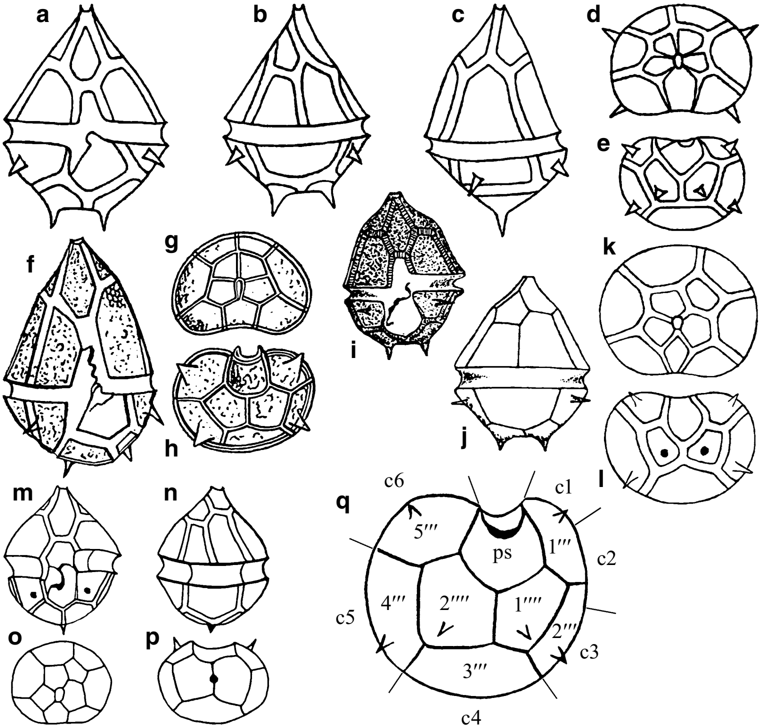

Fig. 187 *Peridiniopsis cunningtonii* Lemmermann (**a**–**e** after Lemmermann *in* West 1907; **f**–**h** after Virieux 1916; **i**–**l** after Lindemann 1919; **m**–**p** after Wołoszyńska 1923; **q** after Bourrelly 1970). **a**–**e** ventral, dorsal, lateral, apical and antapical views, respectively; **f**–**h** ventral, apical and antapical views; **i**–**l** ventral, dorsal, apical and antapical views; **m**–**p** ventral, dorsal, apical and antapical views of cell with only 3 spines (one in the suture between the antapical plates); **q** antapical view, with lines perpendicular to the cell surface indicating the limits of the cingular plates

wildemanii (Wołoszyńska) M. Lefèvre 1928a, p. 124 ≡ *Glenodinium quadridens* var. *wildemanii* (Wołoszyńska) J. Schiller 1935a, pp 117 (legend figs 115i, j), 118; *Glenodinium sedens* Er. Lindemann 1928c, p. 295, figs 15–18; *Peridinium cunningtonii* f. *quadrispinum* Wołoszyńska *in* Steinmann 1935, p. 237

Cells more or less ovoid, slightly dorsoventrally compressed. Epicone conical, longer than the broadly rounded hypocone. Cingulum circular. Sulcus extends for several µm onto the epicone. Chloroplasts brown, arranged radially. Eyespot present. Nucleus in the hypocone. Amphiesmal plates reticulated, with small spines. In

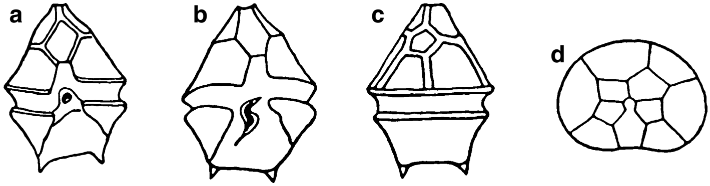

Fig. 188 *Peridiniopsis cunningtonii* var. *excavata* (M. Lefèvre) Moestrup (after Lefèvre 1928a). **a** ventral view; **b** ventral-posterior view; **c** dorsal view; **d** apical view

addition, 3–6 prominent spines are present on the hypocone. Cell length 25–36 µm, width 22–30 µm. Cyst round, relatively smooth (Sako *et al.* 1984).
SEM: Sako *et al.* (1984), Couté & Iltis (1984), Pollingher & Hickel (1991), Toriumi & Dodge (1993), Hansen & Flaim (2007).
Ecology: plankton of meso- and eutrophic ponds and lakes, sometimes forming blooms.
Geographical distribution: England (Griffiths; Lewis & Dodge); France (Virieux; Lefèvre); Germany (Lemmermann; Lindemann); Hungary (Lemmermann); Poland, Switzerland, Ukraine (Lindemann); Portugal (Pandeirada *et al.*). Ivory Coast (Couté & Iltis); Lake Tanganyika (Lemmermann). Brazil (Menezes & Fernandes; Borics *et al.*). China (Zhang *et al.*); Israel (Pollingher & Hickel); Java, Indonesia (Wołoszyńska; Lindemann); Japan (Sako *et al.*).

var. *excavata* (M. Lefèvre) Moestrup *comb. nov.* (**Fig. 188**)
Basionym: *Peridinium cunningtonii* var. *excavatum* M. Lefèvre 1928a, *Ann. Protistol*. **1**, p. 124, figs 47–50
Nomenclatural synonym: *Glenodinium quadridens* var. *excavatum* (M. Lefèvre) J. Schiller 1935a, pp 117 (legend fig. 115 f), 118

Cells slightly smaller than type. Hypocone angular, sulcus very strongly widened towards the antapex. Only the two spines on the antapical plates present, those on the postcingular plates missing. Plates very thin and barely areolated. Cell length 19–30 µm, width 18–25 µm.
Geographical distribution: Spain (Lefèvre).

var. *treubii* (Wołoszyńska) Moestrup *comb. nov.* (**Fig. 189**)
Basionym: *Peridinium treubii* Wołoszyńska 1912, *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math., Sér. B, Sci. Nat.* **1912**, p. 702, text-fig. 24 ("*Treubi*")
Nomenclatural synonyms: *Peridinium cunningtonii* f. *treubii* (Wołoszyńska) M. Lefèvre 1928a, p. 124 ≡ *Glenodinium quadridens* var. *treubii* (Wołoszyńska) J. Schiller 1935a, pp 117 (legend fig. 115k), 118
Taxonomic synonym: *Peridinium treubii* var. *minus* Wołoszyńska 1912, p. 703 ("*minor*")

Differs by having only the two antapical spines.
Geographical distribution: Java, Indonesia (Wołoszyńska).

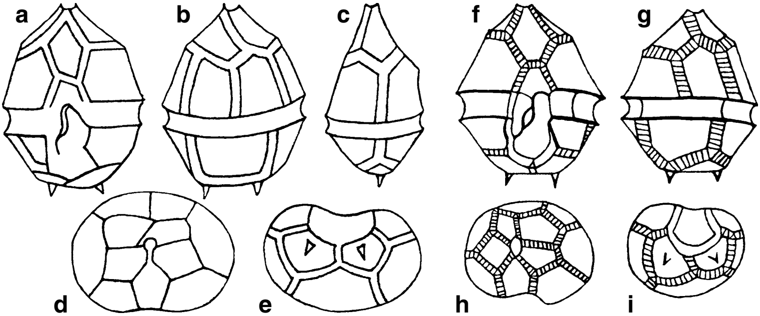

Fig. 189 *Peridiniopsis cunningtonii* var. *treubii* (Wołoszyńska) Moestrup (**a**–**e** after Wołoszyńska 1912; **f**–**i** after Wołoszyńska 1923). **a**–**e** ventral, dorsal, right lateral, apical and antapical views, respectively; **f**–**i** ventral, dorsal, apical and antapical views

7. *Peridiniopsis quinquecuspidata* (Nygaard) Gert Hansen & Flaim 2007, p. 131, 132 (**Fig. 190**)

Basionym: *Peridinium cunningtonii* var. *quinquecuspidatum* Nygaard 1926, p. 208, pl. III, fig. 28 ("*quinquecuspidata*")

Cells triangular, somewhat dorsoventrally flattened. Epicone conical, terminating in a short, thick apical horn. Hypocone smaller than the epicone, broadly angular with 5 spines, one at each of the postcingular plates 1‴, 2‴, 4‴ and 5‴, and one on the suture between the two antapical plates. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus extends for several µm onto the epicone. Cell length 16–26 µm, width 21–30 µm.
SEM: Hansen & Flaim (2007).

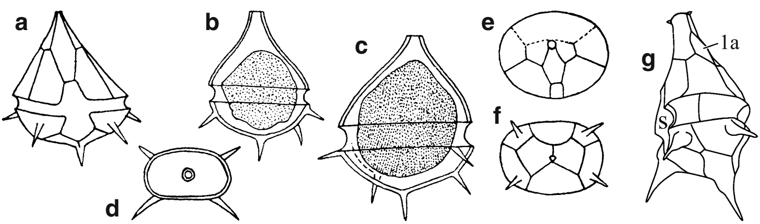

Fig. 190 *Peridiniopsis quinquecuspidata* (Nygaard) Gert Hansen & Flaim (**a**–**f** after Nygaard 1926; **g** original). **a** ventral view with main plates; **b**, **c** outline of two cells with contracted cell contents; **d** outline of cell in apical view; **e** apical view, with area marked with dotted line not resolved; **f** antapical view; **g** left-ventral view somewhat tilted away from the observer, based on SEM illustration in Hansen & Flaim (2007)

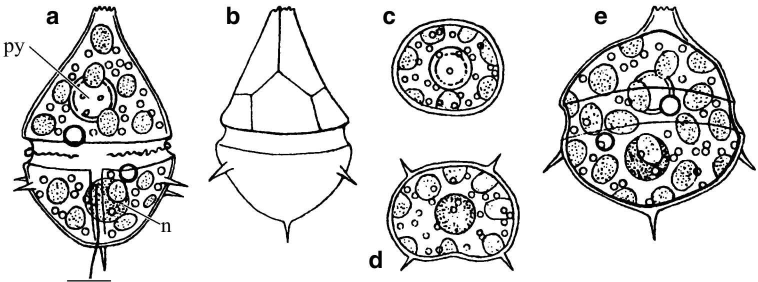

Fig. 191 *Heterocapsa quinquecuspidata* Massart (after Massart 1920). **a** ventral view, showing pyrenoid (py) in the middle of the epicone and round nucleus (n) in the hypocone; **b** dorsal view, with probably unreliable plate limits; **c**, **d** cross-sections of epicone and hypocone, respectively; **e** cyst

Ecology: in brown-water Lake Ohoitiel, in the Key Islands, Indonesia (Nygaard 1926); in Lake Serraia (altitude 974 m), Trentino, Italy (July, August) (Hansen & Flaim 2007).
Geographical distribution: Italy (Hansen & Flaim). Indonesia (Nygaard).

Note 1: Nygaard (1926) reported the amphiesmal plates as very thin and his drawings are imprecise concerning tabulation. The plate formula here considered is the one reported by Hansen & Flaim (2007).

Note 2: *Heterocapsa quinquecuspidata* Massart (1920, p. 123, fig. 9) differs in shape and in having a large pyrenoid. The cells illustrated by Massart (**Fig. 191**) seem to represent a separate species of *Peridiniopsis*, but the lack of information on the tabulation precludes assignment to a particular group.

Group 3, the *P. elpatiewskyi* group

Plate formula po, x, **4′**, **0a**, **7″**, 6c, 5s, 5‴, 2⁗.

Key to species of group 3, the *P. elpatiewskyi* group:

1a Hypocone borders lack spines 2
1b Hypocone with spines 3
2a Amphiesmal plates with scattered papillae, cells 18–33 µm long .... 9. *P. charkowiensis*
2b Amphiesmal plates without visible ornamentation, cells 40–48 µm long .... 10. *P. hiemalis*
3a Cells 22–25 µm long .... 11. *P. pygmaea*
3b Cells 33–45 µm long .... 8. *P. elpatiewskyi*

8. *Peridiniopsis elpatiewskyi* (Ostenfeld) Bourrelly 1968, p. 9 (**Fig. 192**)

Basionym: *Peridinium umbonatum* var. *elpatiewskyi* Ostenfeld 1907, p. 391, pl. IX, figs 9–12

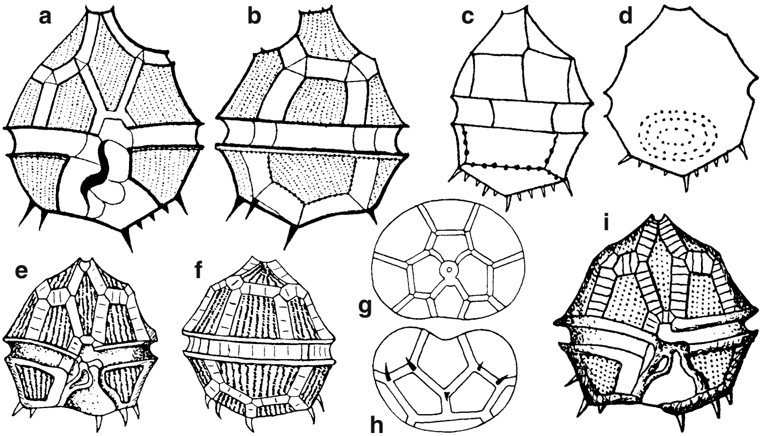

Fig. 192 *Peridiniopsis elpatiewskyi* (Ostenfeld) Bourrelly (**a**–**d** after Wołoszyńska 1916; **e**–**h** after Lefèvre 1926a; **i** after Lefèvre 1932). **a**, **b** ventral and dorsal views; **c** left lateral view; **d** outline of cell with position of the nucleus; **e**–**h** ventral, dorsal, apical and antapical views; **i** ventral view

Nomenclatural synonym: *Peridinium elpatiewskyi* (Ostenfeld) Lemmermann 1910, p. 670 ≡ *Glenodinium elpatiewskyi* (Ostenfeld) J. Schiller 1935a, p. 115
Taxonomic synonyms: *Peridinium marchicum* var. *simplex* Wołoszyńska 1916, p. 266, pl. 10, figs 10–17; *Peridinium elpatiewskyi* var. *collineatum* Er. Lindemann 1919, p. 232, text-figs 37, 38 ≡ *Peridinium marchicum* var. *simplex* f. *collineatum* (Er. Lindemann) M. Lefèvre 1926a, p. 331; *Peridinium elpatiewskyi* var. *bicollineatum* Er. Lindemann 1919, p. 233, text-fig. 39; *Peridinium elpatiewskyi* var. *cruciferum* Er. Lindemann 1919, p. 233, text-fig. 40; *Peridinium elpatiewskyi* var. *pseudopenardii* Er. Lindemann 1919, p. 233, text-figs 41–44 ("*pseudopenardi*") ≡ *Peridinium marchicum* var. *simplex* f. *pseudopenardii* (Er. Lindemann) M. Lefèvre 1926a, p. 331 ("*pseudo-Penardi*"); *Peridinium elpatiewskyi* var. *biradiatum* Er. Lindemann 1919, p. 234, text-figs 45, 46; *Peridinium elpatiewskyi* var. *contortum* Er. Lindemann 1919, p. 234, text-figs 48, 49; *Peridinium elpatiewskyi* var. *pseudocunningtonii* Er. Lindemann 1919, p. 235, text-fig. 50 ("*pseudocunningtoni*"); *Peridinium elpatiewskyi* f. *brigantinum* Er. Lindemann 1920, p. 128, fig. 17; *Peridinium elpatiewskyi* var. *beta-delta-bitravectum* Er. Lindemann 1920, p. 178, fig. 183
The name "*Peridinium elpatiewskyi* Lemmermann" has been conserved with a conserved type to preserve usage in the most common sense (as in *e. g.*, Lefèvre 1932, p. 148). In the same list of *nomina specifica conservanda* are mentioned the names *Glenodinium elpatiewskyi* (Lemmerm.) J. Schiller and *Peridiniopsis elpatiewskyi* (Lemmerm.) Bourrelly with a connection with the conserved name, which apparently stands as their basionym (McNeill *et al.* 2006). In the proposal for conservation was expressed the intention that this would extend to the basionym (Meyer & Elbrächter 1996), which is now possible under the new edition of the nomencla-

tural code (McNeill *et al.* 2012). The names used here follow the rules and anticipate correction of the list of conserved names.

Cells ovoid, somewhat angular, dorsoventrally compressed. Epicone rounded conical, larger than hypocone which is slightly excavated on the left side of the antapex. Cingulum almost circular. Sulcus extends to the antapex, becoming very wide. It extends slightly onto the epicone. A relatively large eyespot may be present (Pandeirada *et al.* 2013). Plate borders on the hypocone with numerous spines. Amphiesmal plates reticulated, sometimes forming longitudinal striae. Nucleus in the epicone. Cell length 33–45 µm, width 28–35 µm. Cysts elongate-spherical, smooth, 28 × 36 µm (Ostenfeld 1907).
SEM: Pollingher & Hickel (1991), Senzaki & Horiguchi (1994), Hansen & Flaim (2007), Krakhmalny (2008), Pandeirada *et al.* (2013), Ascencio *et al.* (2015).
Ecology: plankton in lakes and rivers, according to Höll (1928) at relatively high pH. In the Italian Alps found in neutral or alkaline lakes in summer, and in shallow lakes in Portugal during spring, early summer and autumn, indicating that it may be a warm-water species (Hansen & Flaim 2007; Pandeirada *et al.* 2013).
Geographical distribution: France (Lefèvre); Germany (Lindemann); Italy (Hansen & Flaim); Poland (Wołoszyńska; Lindemann); Portugal (Pandeirada *et al.*); Ukraine (Lindemann; Krakhmalny). Chad (Compère). USA, MD (Thompson). Brazil (Cronberg); Chile (Ascencio *et al.*). Burma (Skuja); Jilin, China (Zhang *et al.*); Israel (Pollingher & Hickel); Java, Sumatra, Indonesia (Lindemann); Japan (Imamura & Fukuyo; Senzaki & Horiguchi); Mongolia (Ostenfeld). New Zealand (Thompson).

Note: cells showing minor variations in plate morphology were described by Lindemann (1919) as varieties. We agree with Lefèvre (1932, p. 151) that these are teratological cell types and do not include them here.

9. ***Peridiniopsis charkowiensis*** (Matvienko) Bourrelly 1968, p. 9 (**Fig. 193**)

Basionym: *Peridinium charkowiense* Matvienko 1938, p. 62, 70, pl. IV, figs 39–42 ("*charkowiensis*")

Cells broadly egg-shaped. Epi- and hypocone hemispherical, of equal size or epicone slightly larger. Cingulum descending, the ends displaced *ca.* half a cingulum

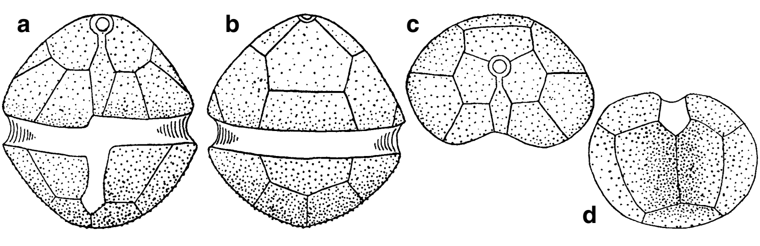

Fig. 193 *Peridiniopsis charkowiensis* (Matvienko) Bourrelly (after Matvienko 1938). **a**–**d** ventral, dorsal, apical and antapical views, respectively

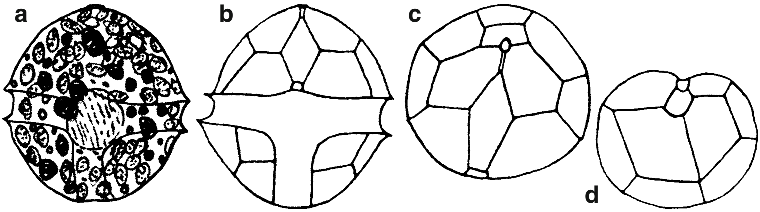

Fig. 194 *Peridiniopsis hiemalis* (J. Schiller) Moestrup & Calado (after Schiller 1955). **a** ventral view showing chloroplasts and central nucleus; **b** ventral view; **c** somewhat tilted apical view; **d** antapical view, apparently with abnormal number of postcingular plates

width. Amphiesmal plates with small warts, especially on the hypocone. Chloroplasts yellow, peripheral, discoid. Nucleus in the hypocone. Cell length 18–33 µm, width 15–30 µm.
Ecology: in the plankton of swamps.
Geographical distribution: Ukraine (Matvienko).

10. *Peridiniopsis hiemalis* (J. Schiller) Moestrup & Calado *comb. nov.* (**Fig. 194**)

Basionym: *Peridinium hiemale* J. Schiller 1955, *Wiss. Arbeiten Burgenland* **9**, p. 54, pl. XI, fig. 57
Mentioned by Popovský & Pfiester (1990, p. 239) as "*Peridiniopsis hiemale*", but ascribed to Schiller and without full and direct reference to place of publication.

Cells spherical or oval, not compressed dorsoventrally. Epi- and hypocone of the same size or the epicone slightly larger. Cingulum almost circular, sulcus does not extend onto the epicone but continues with parallel sides to the antapex. Amphiesmal plates without visible ornamentation. Numerous small chloroplasts. Cell length 40–48 µm, width 38–48 µm.
Ecology: in the Ruster Canal of Lake Neusiedl, common in winter until the end of March at temperature 1–5°C, pH 8.5.
Geographical distribution: Austria.

11. *Peridiniopsis pygmaea* (Er. Lindemann) Bourrelly 1968, p. 9 ("*pygmaeum*") (**Fig. 195**)

Basionym: *Peridinium pygmaeum* Er. Lindemann 1920, p. 145, figs 77–80

Cells ovoid, slightly flattened dorsoventrally. Epicone somewhat conical, larger than hypocone. Cingulum descending, the ends very slightly displaced. Sulcus extends for a short distance onto the epicone, and on the hypocone widens toward the antapex. Amphiesmal plates concave, reticulated. Posterior end of the cell usually with three angles, each provided with a small spine. Sutures of antapical plates with papillae or fine spines. Cell length 22–25 µm, width 20–24 µm.

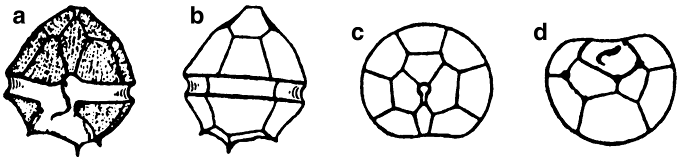

Fig. 195 *Peridiniopsis pygmaea* (Er. Lindemann) Bourrelly (after Lindemann 1920). **a**–**d** ventral, dorsal, apical and antapical views

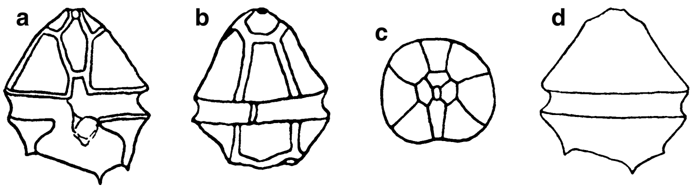

Fig. 196 *Peridiniopsis pygmaea* var. *brigantina* (Er. Lindemann) Moestrup & Calado (**a**–**c** after Lindemann 1923c; **d** after Lefèvre 1932). **a**–**c** ventral, dorsal and apical views, respectively; **d** cell outline

Ecology: plankton of lakes and rivers. In waters of medium alkalinity and a pH of 7.5–7.7 (Höll 1928).
Geographical distribution: France (Lefèvre); Germany (Lindemann); Spain (Lefèvre); Switzerland (Lindemann). Cameroon (Lindberg *et al.*, unpubl.). Sumatra, Bali, Indonesia (Lindemann).

var. *brigantina* (Er. Lindemann) Moestrup & Calado *comb. nov.* (**Fig. 196**)
Basionym: *Peridinium pygmaeum* f. *brigantinum* Er. Lindemann 1923c, *Schriften Süsswasser- Meeresk.* **1**, p. 160, figs 23, 24

Differs by plates 2′, 3′ and 4′ being very small.
Geographical distribution: France (Lefèvre); Germany (Lindemann); Switzerland (Lindemann).

var. *brigantino-armata* (M. Lefèvre) Moestrup & Calado *comb. nov.* (**Fig. 197**)
Basionym: *Peridinium pygmaeum* f. *brigantino-armatum* M. Lefèvre 1932, *Arch. Bot. Mém.* **2** (mémoire 5), p. 153, figs 694–697

Ornamented with a large number of spines along the sulcal margins and along the sutures of the antapical plates.
Geographical distribution: Spain (Lefèvre).

Group 4, the *P. lindemannii* group

Plate formula: apc, **3′**, **1a**, **7″**, ?c, ?s, 5‴, 2⁗. With a single, poorly known, species.

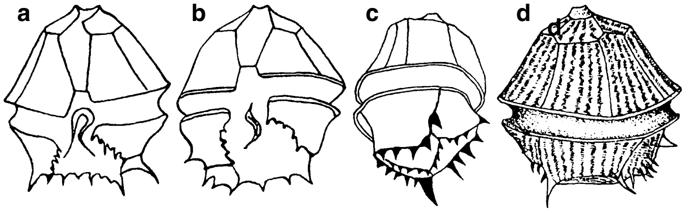

Fig. 197 *Peridiniopsis pygmaea* var. *brigantino-armata* (M. Lefèvre) Moestrup & Calado (after Lefèvre 1932). **a** ventral view; **b** slightly tilted ventral view; **c** left-posterior view; **d** dorsal view with plate ornamentation

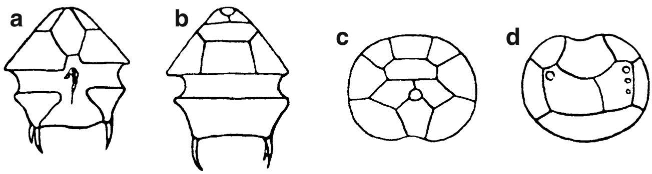

Fig. 198 *Peridiniopsis lindemannii* (M. Lefèvre) Bourrelly (after Lefèvre 1932). **a**, **b** ventral and dorsal views; **c**, **d** apical and antapical views

12. *Peridiniopsis lindemannii* (M. Lefèvre) Bourrelly 1968, p. 9 (**Fig. 198**)

Basionym: *Peridinium lindemannii* M. Lefèvre 1927, p. 121 ("*Lindemanni*")
Nomenclatural synonym: *Glenodinium lindemannii* (M. Lefèvre) J. Schiller 1935a, p. 114

Cells pentagonal. Epicone rounded cone-shaped, larger than the truncated cone-shaped hypocone. Rims of the antapical plates with (usually) 3–4 long, curved spines. Sutures narrow. Amphiesmal plates not areolated. Cells symmetrical in apical view, 1a 6-sided. Cells slightly dorsoventrally compressed. Cingulum very slightly descending. Sulcus extends for a short distance onto the epicone, on the hypocone it widens considerably towards the antapical end. Cells 10–12 µm long, 9–11 µm wide (excluding the spines).
Ecology: ponds (?) near Antananarivo, Madagascar and in Galicia, Spain.
Geographical distribution: Spain (Lefèvre). Madagascar (Lefèvre).

Group 5, the *P. quadridens* group

Plate formula: apc, **5′**, **1a**, **7″**, 6c?, 5s, 5‴, 2⁗. With a single species.

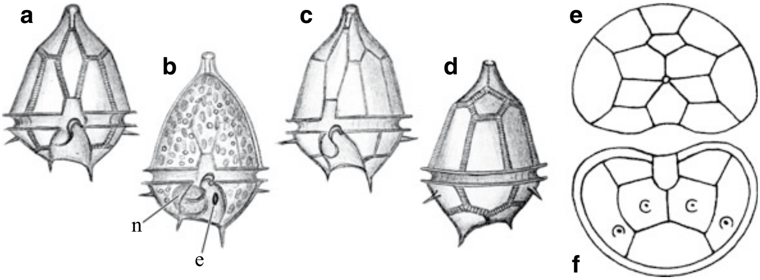

Fig. 199 *Peridiniopsis quadridens* (F. Stein) Bourrelly (**a**–**d** after Stein 1883; **e**, **f** after Schilling 1891a). **a** ventral view showing main plates; **b** ventral view, with nucleus (n) in the hypocone and eyespot (e) in the sulcus; **c** ventral-left view; **d** dorsal view; **e**, **f** apical and antapical views, respectively

13. *Peridiniopsis quadridens* (F. Stein) Bourrelly 1968, p. 9 (**Fig. 199**)

Basionym: *Peridinium quadridens* F. Stein 1883, p. XI, figs 3–6
Nomenclatural synonym: *Glenodinium quadridens* (F. Stein) J. Schiller 1935a, p. 117

Cells pointed ovoid, epicone larger than hypocone, conical. Hypocone rounded with thick spine on each of the plates 2‴, 4‴, 1⁗ and 2⁗. Cells slightly dorso-ventrally compressed, bilaterally symmetrical in apical view. The single anterior intercalary plate symmetrically placed on the dorsal surface. Cingulum descending, barely displaced. Sulcus extends onto the epicone for a distance of *ca.* one cingular width. Plates finely reticulate. Dark-brown chloroplasts. An eyespot in the sulcal area. Cell length 30–39 µm, width 20–33 µm. Cyst spherical.
SEM: Carty (1989).
Ecology: in the plankton of alkaline lakes, pH *ca.* 7.5–7.7. Apparently a predominantly cold-water species.
Geographical distribution: Czech Republic (Stein); Germany (Lemmermann, Höll); Hungary (Entz); Italy (Huber); Latvia (Conrad); Poland (Siemińska); Sweden (Lemmermann). USA, OH, TX (Carty). Turkey (Daday). New Zealand (Thompson).

var. *adens* (Entz) Moestrup & Calado *comb. nov.* (**Fig. 200**)
Basionym: *Peridinium quadridens* var. *adens* Entz 1927b, *Arch. Balaton.* **1**, p. 297, figs 30–34
Nomenclatural synonym: *Peridinium quadridens* f. *adens* (Entz) M. Lefèvre 1932, p. 160

Without the spines.
Geographical distribution: Lake Balaton, Hungary (Entz).

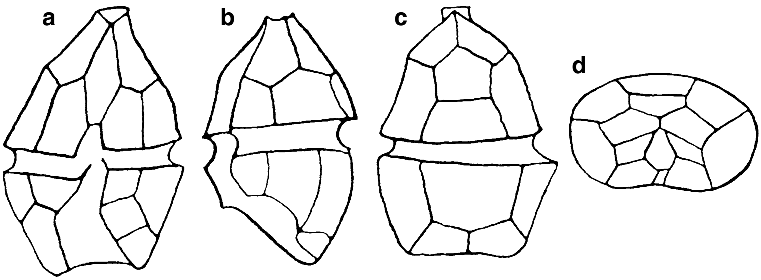

Fig. 200 *Peridiniopsis quadridens* var. *adens* (Entz) Moestrup & Calado (after Entz 1927b). **a** ventral view; **b** ventral-left view; **c** dorsal view; **d** apical view

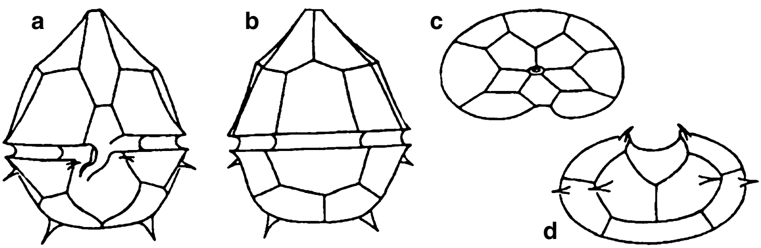

Fig. 201 *Peridiniopsis thompsonii* Bourrelly *ex* Moestrup & Calado (after Thompson 1947). **a**–**d** ventral, dorsal, apical and antapical views

Group 6, the *P. thompsonii* group

Plate formula: apc, **5′**, **0a, 7″**, 5‴, 2″″. With a single species.

14. *Peridiniopsis thompsonii* Bourrelly *ex* Carty 2014, p. 221 (**Fig. 201**)

The designation "*Peridiniopsis thompsonii* Bourrelly" (Bourrelly 1968, p. 9), originally based on *Glenodinium quadridens* sensu Thompson (1947, p. 14, pl. II, figs 12–15) was not validly published for lack of a Latin diagnosis.
Cells ovoid and somewhat flattened dorsoventrally. Epicone conical, slightly apiculate, larger than the hypocone. Hypocone rounded. Cingulum descending very slightly. Sulcus very broad, extending to the antapex. It extends onto the epicone as a truncate triangle, the length of which is approximately equal to its proximal width. The two antapical plates and postcingular plates 2 and 4 each with a spine. Sometimes postcingular plates 1 and 5 each with an inwardly curved spine. Chloroplasts brown. Eyespot absent. Cell length 25–38 µm, width 22–32 µm, thickness 19 µm.
Ecology: reservoir, lakes, canal in USA.
Geographical distribution: USA, IL (Eddy, as *P. cunningtonii*), MD (Thompson).

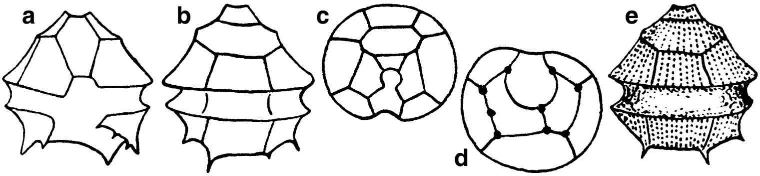

Fig. 202 *Peridiniopsis viguieri* (M. Lefèvre) Bourrelly (after Lefèvre 1932). **a**–**d** ventral, dorsal, apical and antapical views, respectively; **e** dorsal view with plate ornamentation

Group 7, the *P. viguieri* group

Plate formula: apc, **4′**, **1a, 7″**, 5‴, 2⁗. With a single species.

15. *Peridiniopsis viguieri* (M. Lefèvre) Bourrelly 1968, p. 9 (**Fig. 202**)

Basionym: *Peridinium viguieri* M. Lefèvre 1932, p. 186, figs 905–909
Nomenclatural synonym: *Glenodinium viguieri* (M. Lefèvre) J. Schiller 1935a, p. 116

Cells angular or pentagonal, epicone angular conical, the smaller hypocone wide and very short. Cingulum very slightly descending. Sulcus extends very shortly onto the epicone, on the hypocone widens very strongly and reaches the antapex. Both the antapical plate sutures and the sides of sulcus with strong spines. Amphiesmal plates concave, finely papillated longitudinally. Cell length 18–25 µm, width 15–28 µm.
Geographical distribution: Madagascar.

Genus 5. *Peridinium* Ehrenberg 1830, p. 38

Type species: *Peridinium cinctum* (O. F. Müller) Ehrenberg 1830 (see Fromentel 1874)

Cells more or less ellipsoidal or spherical, with distinct, often thick amphiesmal plates. Brown chloroplasts. Plate formula: apc (po, x) present or absent, 4′, 2–3a, 6–7″, 5–6c, 4–5s, 5‴, 2⁗.
The genus as treated here is not monophyletic (see above).

Key to the subgenera of *Peridinium*:
1a Cells without apical pore .... *Peridinium* subg. *Cleistoperidinium*
1b Cells with apical pore .... *Peridinium* subg. *Poroperidinium*

Species lacking an apical pore (*Peridinium* subg. *Cleistoperidinium*) constitute the true *Peridinium*. Most or all species with an apical pore will probably eventually be separated into new genera. However, since many species presently included in *Peridinium* and *Peridiniopsis* remain to be investigated in detail we retained, for the time being, many of the traditionally used group names, pending examination of material using electron microscopy and molecular sequencing.

subg. ***Cleistoperidinium*** (Lemmermann) M. Lefèvre 1932, p. 66, 70 ("true *Peridinium*")

Basionym: *Peridinium* sect. *Cleistoperidinium* Lemmermann 1910, p. 661, 675
Cells lacking an apical pore. Plate formula: 4′, 3a, 7″, 5c, 4–5s, 5‴, 2⁗.
This small group comprises only 8 species, 5 of which are widely distributed and sometimes very numerous, with many described varieties: the eurytrophic species *P. cinctum*, *P. willei*, *P. volzii* and *P. gatunense*; and *P. raciborskii* (particularly var. *palustre*) from acid water. *Peridinium lingii* is known at the present time from Australia only. *Peridinium zonatum* is known from Australia and China and *P. striolatum* is known from Australia, China and Japan.

Key to groups of *Peridinium* subg. *Cleistoperidinium*:
1a Plate pattern very asymmetrical (apical view) Group 1, the *P. cinctum* group
1b Plate pattern symmetrical or nearly so 2
2a Plate 1′ not adjoining plate 3′, the latter 6-sided . Group 3, the *P. willei* group
2b Plate 1′ shares side with plate 3′, which is 5-sided Group 2, the *P. striolatum* group

Group 1, the *P. cinctum* group

Plate pattern very asymmetrical.

Key to species of the *Peridinium cinctum* group:
1a Cells with three pointed posterior horns .... 3. *P. lingii*
1b Cells without pointed horns but sometimes with short blunt posterior projections 2
2a Sulcus extends well onto the epicone .... 1. *P. cinctum*
2b Sulcus hardly extends onto the epicone 3
3a Cells barely or not dorsoventrally flattened 4
3b Cells strongly dorsoventrally flattened .... 4. *P. raciborskii*
4a Plates areolated .... 2. *P. gatunense*
4b Plates not areolated, ornamented with diversely oriented ridges . 5. *P. zonatum*

1. *Peridinium cinctum* (O. F. Müller) Ehrenberg 1830, p. 38 (**Fig. 203**)

Basionym: *Vorticella cincta* O. F. Müller 1773, p. 98
Taxonomic synonyms: *Peridinium westii* var. *areolatum* Lemmermann 1908b, p. 180, pl. V, figs 7–10 ≡ *Peridinium cinctum* f. *areolatum* (Lemmermann) M. Lefèvre 1926, p. 337; *Peridinium cinctum* var. *lemmermannii* G. S. West 1909b, p. 190, 192, figs 20J, 24 ≡ *Peridinium kincaidii* var. *lemmermannii* (G. S. West) Wailes 1935, p. 5; *Peridinium cinctum* var. *angulatum* Er. Lindemann *in* Schröder 1919, p. 655, fig. 2a ≡ *Peridinium cinctum* f. *angulatum* (Er. Lindemann) Er. Lindemann 1920, p. 163, figs 143–150; *Peridinium germanicum* Er. Lindemann 1919, p. 250, text-figs 116, 117; *Peridinium rhenanum* Er. Lindemann 1919, p. 249, text-figs 114, 115; *Peridinium cinctum* var. *(beta/epsilon)-collineatum* Er. Lindemann 1920, p. 180, figs 191–193; *Peridinium cinctum* var. *curvatum*

Er. Lindemann 1920, p. 167, figs 160–162; *Peridinium cinctum* var. *dissimile* Er. Lindemann 1920, p. 166, figs 158, 159; *Peridinium cinctum* var. *irregulatum* Er. Lindemann 1920, p. 162, figs 141, 142 ≡ *Peridinium cinctum* f. *irregulatum* (Er. Lindemann) M. Lefèvre 1932, p. 89; *Peridinium cinctum* var. *laesum* Er. Lindemann 1920, p. 165, figs 156, 157; *Peridinium cinctum* subvar. *originale* Er. Lindemann 1920, p. 170, fig. 174; *Peridinium cinctum* var. *regulatum* Er. Lindemann 1920, p. 162, fig. 140 ≡ *Peridinium cinctum* f. *regulatum* (Er. Lindemann) M. Lefèvre 1932, p. 88; *Peridinium cinctum* var. *(delta/epsilon)-travectum* Er. Lindemann 1920, p. 180, 181, figs 194–196; *Peridinium eximium* Er. Lindemann 1920, p. 167, figs 163–166; *Peridinium eximium* var. *mutatum* Er. Lindemann 1920, p. 168, fig. 167; *Peridinium scallense* Er. Lindemann 1920, p. 160, 170, figs 175–177; *Peridinium scallense* subvar. *originale* Er. Lindemann 1920, p. 170; *Peridinium semicirculatum* Er. Lindemann 1920, p. 168, figs 168–171; *Peridinium semicirculatum* var. *beta-collineatum* Er. Lindemann 1920, p. 168; (?) *Peridinium kincaidii* Wailes 1933, p. 3, figs 8–12 ("*kincaidi*"); *Peridinium cinctum* var. *ornatum* M. Szabados 1954, p. 473, text-fig. 9

Cells circular or elongate ovoid, longer than wide, dorsoventrally somewhat flattened as the ventral side is flat. Epicone larger than hypocone, sulcus (*as* plate) extends onto epicone as a rather narrow, straight slit which terminates at the relatively small first apical plate. Plate 1′ with straight or convex lateral sides. Plate 3′ four-sided triangular, the tip of the triangle directed towards the cell's right. In dorsal view the 5-sided 4″ is seen to be asymmetrical, the plates adjoining it on the left being smaller than those on the right. Plates with strong areolation. With numerous brown chloroplasts. During cell division the cell contents divide into two, old theca discarded. The cells open on the epicone by shedding the dorsal part of the epitheca. Cell length 45–60 µm, width 35–55 µm. Cyst round with smooth wall (Boltovskoy 1975; Dürr 1979b).
SEM: Boltovskoy (1975), Dürr (1979a, 1979b), Calado *et al*. (1999), Hansen & Flaim (2007).
TEM: Dürr (1979a, 1979b), Calado *et al*. (1999).
DNA data: Daugbjerg *et al.* (2000), Saldarriaga et al. (2004).
Ecology: widely distributed in the plankton of oligotrophic/eutrophic ponds, lakes and rivers. Included by Höll (1928) in his group of species with almost unlimited adaptation to external conditions, pH. 4.0–8.0.
Geographical distribution: distributed in both temperate and tropical areas. Very many reports from all over the world, only a few mentioned here: Denmark (Müller); Germany (Ehrenberg); Italy (Hansen & Flaim); Poland (Wołoszyńska; Siemińska); Switzerland, Austria (Höll). South Africa (Rich). USA, IA (Prescott), IL (Eddy). Argentina (Boltovskoy). Burma (Skuja); Jilin, China (Liu *et al.*); Mongolia (Ostenfeld). New Zealand (Thompson).

Note 1: *Peridinium cinctum* var. *minus* Woronichin (1923, p. 141, "*minor*") was described as differing in size only: 36 × 31.6–33 µm. Being close to the size range of *P. cinctum*, it seems most likely to represent small specimens of *P. cinctum*.

Note 2: below we describe forms and varieties of this species. In addition, several more morphological types have been described, which were probably based on teratological cells. Huber-Pestalozzi (1950) listed the names of these morphological variations.

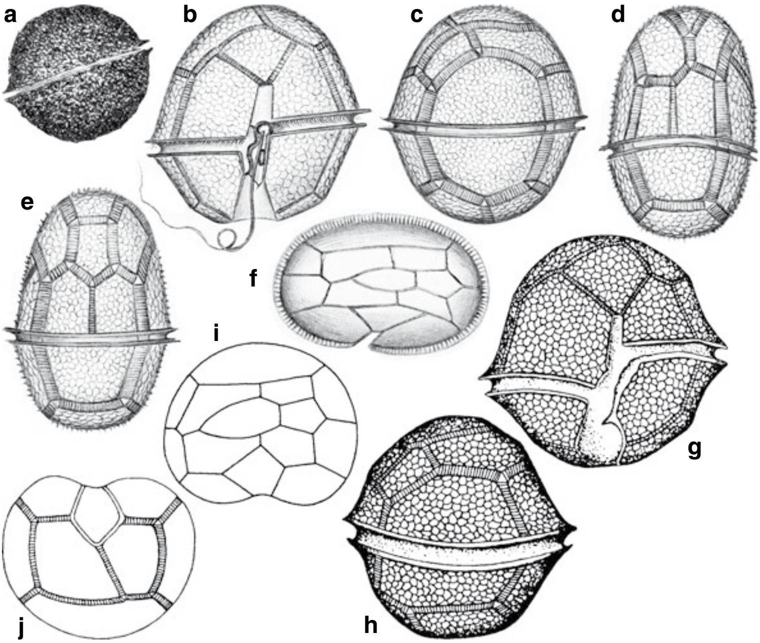

Fig. 203 *Peridinium cinctum* (O. F. Müller) Ehrenberg (*a* after Müller 1786; **b**–**f** after Stein 1883; **g**–**j** after Lefèvre 1932). **a** dorsal view; **b**, **c** ventral and dorsal views; **d** right lateral view; **e** left lateral view; **f** apical view; **g**–**j** ventral, dorsal, apical and antapical views

f. *maeandricum* M. Lefèvre 1926a, p. 334, pl. XII, figs 1–4 ("*meandricum*") (**Fig. 204**)
With vermiform ornamentation on the antapical plates or on all plates of the hypocone. Epithecal plates with areolate ornamentation.
Ecology: occurs in many different types of water (lakes, canals, puddles).
Geographical distribution: France (Lefèvre); Portugal (Pandeirada *et al.*); Spain (Lefèvre). USA, TX (Carty).

f. *ovoplanum* Er. Lindemann 1920, p. 164, figs 151–155 (**Fig. 205**)
Cells strongly dorsoventrally compressed. Ventral and dorsal surfaces nearly flat. Cysts rounded, smooth, brownish black (Pfiester 1975).
Sexual reproduction described by Pfiester (1975) and Spector *et al.* (1981a): isogamic, homothallic, the gametes thin-walled and attaching to each other laterally, with a fertilization tube.
SEM: Spector *et al.* (1981a).
TEM: Spector & Triemer (1979), Spector *et al.* (1981a, 1981b).

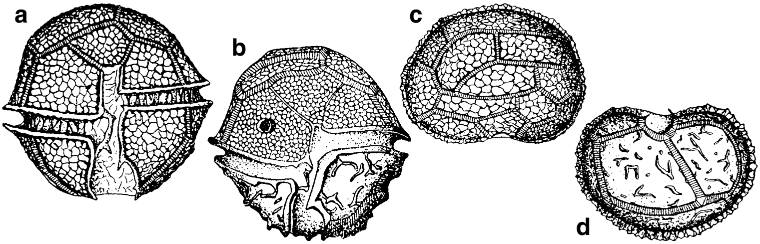

Fig. 204 *Peridinium cinctum* f. *maeandricum* M. Lefèvre (**a**, **c**, **d** after Lefèvre 1925; **b** after Lefèvre 1932). **a**, **b** ventral views with different extensions of vermiform ornamentation on hypocone; **c**, **d** apical and antapical views

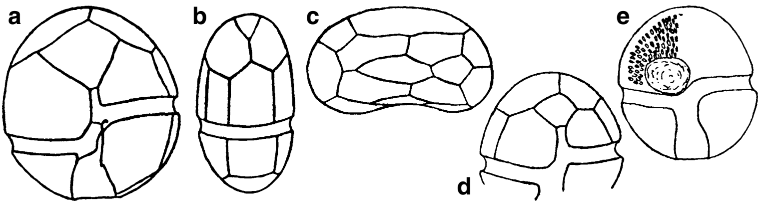

Fig. 205 *Peridinium cinctum* f. *ovoplanum* Er. Lindemann (after Lindemann 1920). **a**–**c** ventral, lateral and apical views, respectively; **d** amphiesma with smaller plate 1′; **e** ventral view showing round nucleus and chloroplast profiles on left upper quadrant of cell

Ecology: in the plankton of lakes.
Geographical distribution: Germany; Switzerland (Lefèvre). USA, MA (Pfiester).

f. ***westii*** (Lemmermann) Er. Lindemann 1925a, p. 205 (**Fig. 206**)
Basionym: *Peridinium westii* Lemmermann *in* West & West 1905, p. 495, text-fig. 2
Nomenclatural synonym: *Peridinium tabulatum* var. *westii* (Lemmermann) Playfair 1913, p. 542.
Taxonomic synonym: *Peridinium maeandricum* V. Brehm 1908, p. 112

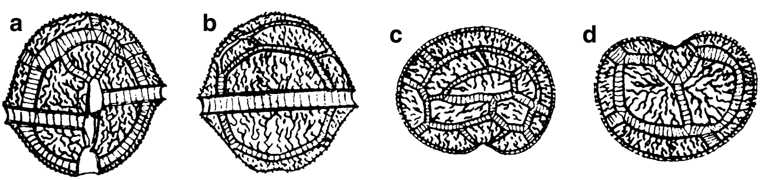

Fig. 206 *Peridinium cinctum* f. *westii* (Lemmermann) Er. Lindemann (after Lemmermann *in* West & West 1905). **a**–**d** ventral, dorsal, apical and antapical views

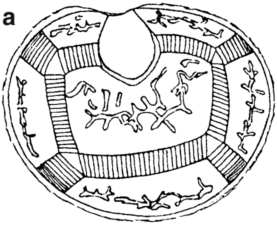

Fig. 207 *Peridinium cinctum* f. *zonatum* M. Lefèvre (after Lefèvre 1932). **a** antapical view

With vermiform ornamentation in all major plates.
Ecology: in the plankton, especially in large lakes.
Geographical distribution: Austria (Brehm); England (Lewis & Dodge); France (Virieux); Norway (Ström); Scotland (Lemmermann); Switzerland (Messikommer). Lake Victoria (Wołoszyńska); Mali (Bourrelly).

f. *zonatum* M. Lefèvre 1932, p. 88, 91, fig. 216 (**Fig. 207**)
Plates ornamented with vermiform pattern arranged parallel to the cingulum. Illustrated with a single antapical plate (tabulation 1″″ simplex).
Geographical distribution: France; Spain (Lefèvre).

var. *tuberosum* (Meunier) Er. Lindemann 1928a, p. 260 (**Fig. 208**)
Basionym: *Peridinium tuberosum* Meunier 1919, p. 52, pl. XVIII, figs 23–27
Nomenclatural synonym: *Peridinium cinctum* f. *tuberosum* (Meunier) M. Lefèvre 1932, p. 93

With three massive lobes at the posterior end, which give the hypocone the appearance of a tripod. Very little compressed dorsoventrally.
Ecology: in the plankton of ponds rich in humic compounds near Genk, Belgium; found in large numbers in August.
Geographical distribution: Belgium (Meunier).

2. *Peridinium gatunense* Nygaard *in* Ostenfeld & Nygaard 1925, p. 10, figs 5–10 (**Fig. 209**)

Nomenclatural synonym: *Peridinium cinctum* var. *gatunense* (Nygaard) Nygaard 1932, p. 128
Taxonomic synonym: *Peridinium cinctum* var. *gibbosum* M. Lefèvre 1927, p. 121

Cells more or less spherical, length slightly shorter than width. Cells not or only very slightly dorsoventrally compressed. Epi- and hypocone of equal size or epicone slightly larger. Both irregularly cone-shaped with more or less concave plates. Cingulum with wide hyaline wings, descending, the ends displaced *ca.* two cingulum widths. Sulcus extends only very slightly or not at all onto the epicone.

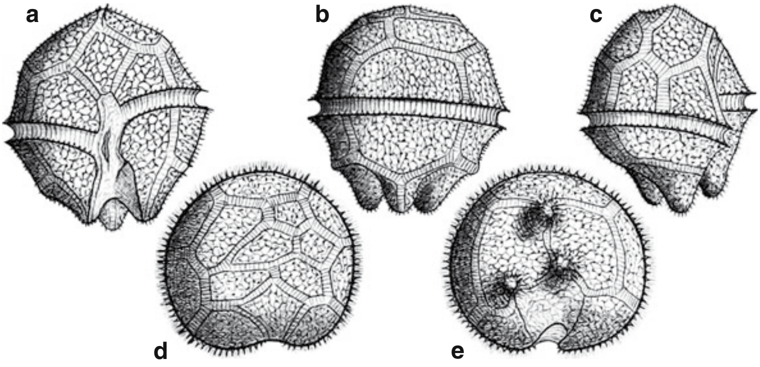

Fig. 208 *Peridinium cinctum* var. *tuberosum* (Meunier) Er. Lindemann (after Meunier 1919). **a**, **b** ventral and dorsal views; **c** right lateral view, slightly turned to the ventral side; **d**, **e** apical and antapical views

Amphiesmal plates areolated with 1–3 pores per areole. Plate 1′ small, 2′ and 4′ therefore distinctly visible in ventral view, usually both their anterior and posterior sides. Plates 1a and 2a small, pentagonal, 3a large, elongate, hexagonal, the long sides adjoining 3′ and 5″. Antapical plates large, often of unequal size. Sutures commonly wide. Cell length 38–75 µm, width 38–75 µm. Cells break open along the cingulum.

Sexual reproduction isogamous, homothallic (Pfiester 1977). Cysts spherical, smooth, 30–48 µm in diameter, with two large red bodies (Hickel & Pollingher 1988). The presence of large bubbles in the cysts has been interpreted as a sign that the cysts have died (Alster *et al.* 2006).

SEM: Boltovskoy (1974, 1983), Iltis & Couté (1984), Couté & Tell (1990), Pollingher & Hickel (1991), Hansen & Flaim (2007), Liu *et al.* (2008a), Cavalcante *et al.* (2017).

TEM: Messer & Ben-Shaul (1969).

DNA data: Logares *et al.* (2007b).

Ecology: widely distributed in plankton of lakes and ponds. Lindström (1984), in a strain from Lake Kinneret, Israel, found high biomasses above 10°C but slow growth at 5°C. The highest growth rates were at 23°C, and growth was reduced above 27ºC. Growth was slow at pH 6 and highest above pH 8, with a maximum at pH 8.3. Lindström (1991) found preference for high amounts of $NaHCO_3$ and Mo, and Se was also essential. Best growth medium used was L16. For further information on physiology and ecology, see extensive literature list compiled by Hickel & Pollingher (1988). The species formed extensive annual blooms in Lake Kinneret until 1996 after which blooms became more irregular, stopping altogether 2008–2011, conditions in the lake having changed (Zohary *et al.* 2012).

Geographical distribution: widely distributed in temperate, subtropical and tropical areas. Denmark (Attemose, unpublished); France (Lefèvre; Cardinal); Holland (Huber-Pestalozzi); Sweden (Teiling). Cameroon (Lefèvre); Ivory Coast (Bourrelly; Couté & Iltis); Madagascar (Lefèvre); Mozambique (Rino). USA, many

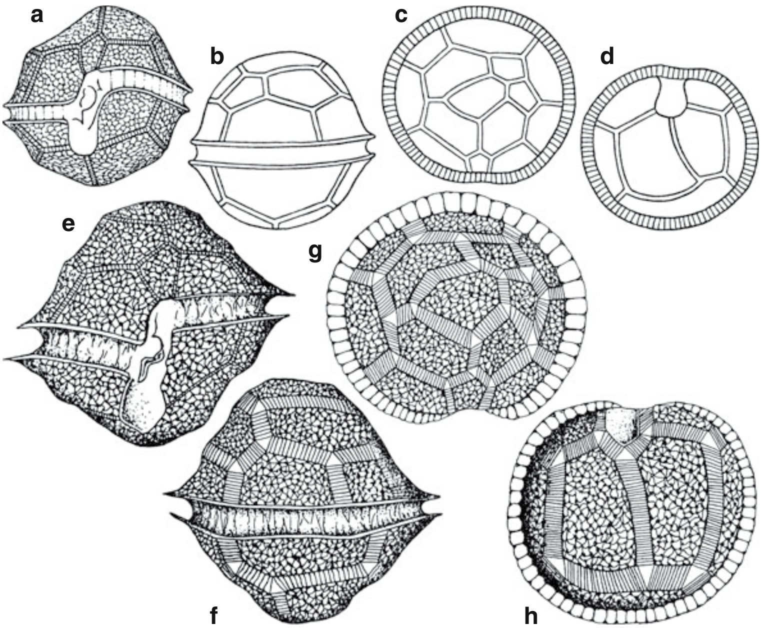

Fig. 209 *Peridinium gatunense* Nygaard (**a**–**d** after Ostenfeld & Nygaard 1925; **e**–**h** after Lefèvre 1932). **a**–**d** ventral, dorsal, apical and antapical views; **e**–**h** ventral, dorsal, apical and antapical views

places (*e. g.*, Thompson; Pfiester; Carty). Argentina (Boltovskoy; Couté & Tell); Bolivia (Iltis & Couté); Brazil (Hickel & Pollingher; Cardoso *et al.*; Cavalcante *et al.*); Cuba (Popovský); Guadeloupe (Couté & Tell); Mexico (Krakhmalny *et al.*); Panama (Nygaard). Burma (Skuja); Hubei, China (Liu *et al.*); Israel (Hickel & Pollingher); Sri Lanka (Rott *et al.*); Thailand (Rott *et al.*). Australia (Ling *et al.*).

Note: in dorsal view the species was said by Hickel & Pollingher (1988) to differ from the similar species *P. cinctum* by the width of 4″ being smaller than the width of 3‴, placing the suture between 4″ and 5″ to the left of the suture between 3‴ and 4‴. However, this feature may also be seen in *P. cinctum* (Calado *et al.* 1999, fig. 54).

f. *globosum* M. Lefèvre 1932, p. 97, fig. 278 (**Fig. 210**)
Plates convex rather than concave, the cell therefore almost regularly spherical.
Geographical distribution: France (Lefèvre).

f. *majus* M. Lefèvre 1932, p. 98, figs 279, 280 (**Fig. 211**)
Lacks hyaline wings along the cingulum. Cell length 75 µm.
Geographical distribution: Madagascar (Lefèvre).

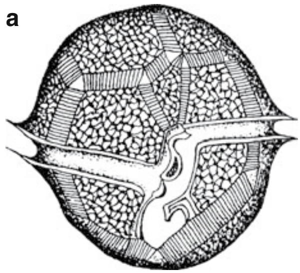

Fig. 210 *Peridinium gatunense* f. *globosum* M. Lefèvre (after Lefèvre 1932). **a** ventral view

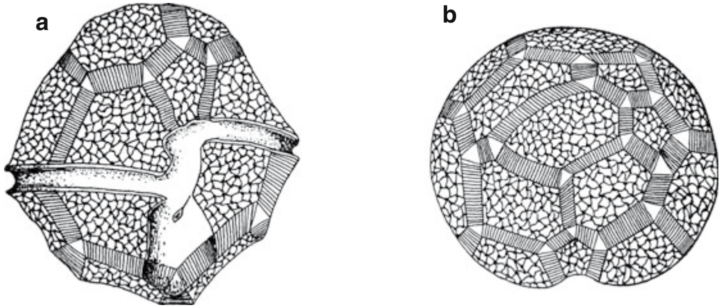

Fig. 211 *Peridinium gatunense* f. *majus* M. Lefèvre (after Lefèvre 1932). **a** ventral view; **b** apical view

f. *ornatum* M. Lefèvre 1932, p. 98, figs 283, 284 (**Fig. 212**)
Plates ornamented with ridges that extend irregularly from the sutures.
Geographical distribution: Madagascar (Lefèvre).

var. *carinatum* (Steinecke & Er. Lindemann) Moestrup & Calado *comb. nov.* (**Fig. 213**)
Basionym: *Peridinium cinctum* var. *carinatum* Steinecke & Er. Lindemann 1923, *Schriften Süsswasser-Meeresk.* **1**, p. 40, figs 1–3
Taxonomic synonym: *Peridinium cinctum* var. *tuberosum* f. *cristatum* Kisselev 1951, p. 86, pl. VIII, figs 7–12 (first described, but not named, in Kisselev 1937, pp 56, 68, fig. 1)

Cell angular-globose with hyaline flanges along the cingulum and sulcus. The posterior end with two or three distinct projections provided with comb-like flanges. Less developed flanges sometimes visible along anterior edge of cell (ventral view). Often with vermiform ornamentation on the antapical plates. Sutures often large. Length and width *ca.* 60 µm.

Fig. 212 *Peridinium gatunense* f. *ornatum* M. Lefèvre (after Lefèvre 1932). **a** apical view; **b** detail of ornamentation

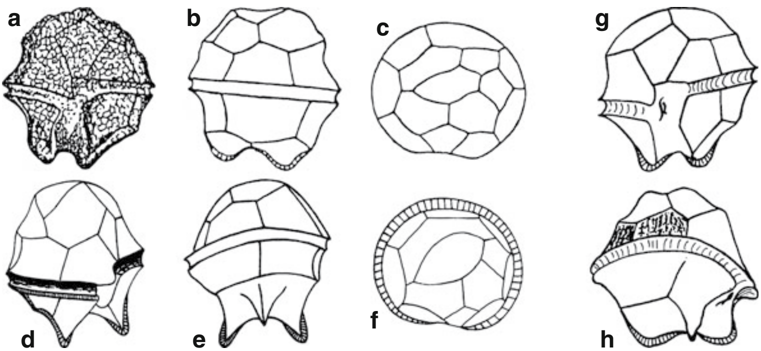

Fig. 213 *Peridinium gatunense* var. *carinatum* (Steinecke & Er. Lindemann) Moestrup & Calado (**a**–**c** after Steinecke & Lindemann 1923; **d**–**f** after Kisselev 1951; **g**, **h** after Bourrelly 1966). **a** ventral view with plate ornamentation; **b**, **c** dorsal and apical views, respectively; **d**–**f** ventral-right, dorsal and apical views; **g**, **h** ventral view and slightly tilted dorsal view (as *P. cinctum* var. *tuberosum*)

Geographical distribution: Poland (Steinecke & Lindemann); Russia (Kisselev). Canada? (Bourrelly).

Note 1: the anterior end of the sulcus, which does not penetrate the epicone, and the nearly circular apical view indicate a closer relationship with *P. gatunense* than with *P. cinctum*.

Note 2: *Peridinium cinctum* var. *tuberosum sensu* Bourrelly (1966) from Canada (Ontario, Quebec) was described with 3 posterior protuberances and with the whole hypocone predominantly ornamented by meandering ridges. In its general morphology it resembles *P. gatunense* var. *carinatum*.

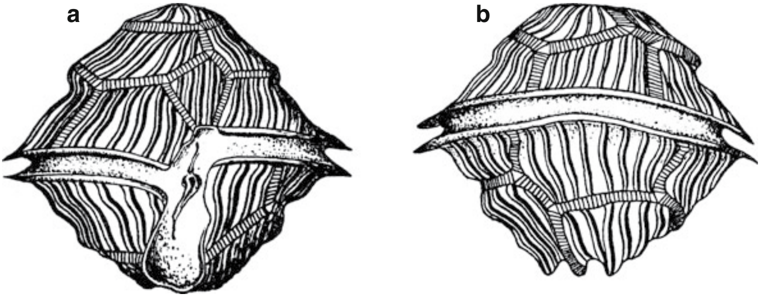

Fig. 214 *Peridinium gatunense* var. *madagascariense* (M. Lefèvre) M. Lefèvre (after Lefèvre 1932). **a** ventral view; **b** dorsal view

var. *madagascariense* (M. Lefèvre) M. Lefèvre 1932, p. 97 (**Fig. 214**)
Basionym: *Peridinium cinctum* var. *madagascariense* M. Lefèvre 1927, p. 122 ("*madagascariensis*")

Plates ornamented with ridges, mainly in the longitudinal direction of the cell.
SEM: Couté & Tell (1990).
Geographical distribution: Madagascar (Lefèvre); Mozambique (Rino; Couté & Tell).

3. *Peridinium lingii* Thomasson 1986, p. 330, pl. 4, fig. 6; pl. 5, fig. 7; pl. 13, fig. 6 (iconotype: figs 20, 21 in pl. 39 of Ling & Tyler 1980) (**Fig. 215**)

Cells ovoid with three posterior horns. Epicone rounded-angular, larger than hypocone. Cells dorsoventrally compressed. Cingulum descending, the ends displaced *ca.* one cingulum width. The sulcus barely extends onto the epicone. Plates ornamented with ridges. Cell length 116–118 µm, width 96–99 µm.
Ecology: in the plankton of ox-bow ponds.
Geographical distribution: Northern Australia.

4. *Peridinium raciborskii* Wołoszyńska 1912, p. 700, text-fig. 21 (**Fig. 216**)

Nomenclatural synonym: *Peridinium palustre* var. *raciborskii* (Wołoszyńska) M. Lefèvre 1932, p. 99

Cells almost as long as wide, strongly dorsoventrally flattened. Epicone helm-shaped, somewhat larger than hypocone. Hypocone with two posterior horn-like projections formed by the two antapical plates. Cingulum descending, the ends displaced 1.5–2 cingulum widths. Sulcus extends only very shortly onto the epicone. On the hypocone it widens strongly towards and extends to the antapex. Plates 1′ and 3′ separated by 2′ and 4′. Plate 3′ very wide. Plates 1a and 2a pentagonal, much smaller than the elongate, 5-sided 3a. Plate 4″ bordered on the anterior side by 2a and 3a. It is as wide as and located just above 3‴. Plates areolated, often with short

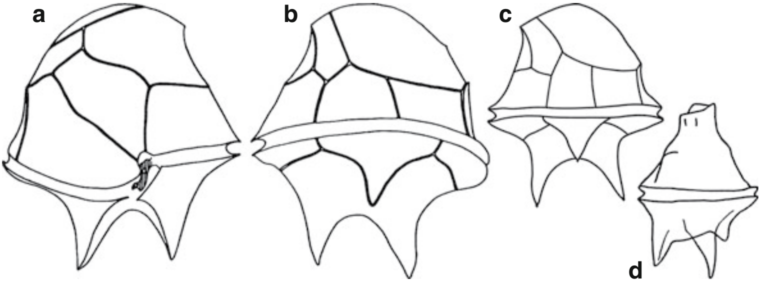

Fig. 215 *Peridinium lingii* Thomasson (**a**, **b** after Ling & Tyler 1983; **c**, **d** after Thomasson 1986). **a** ventral view; **b**, **c** dorsal views; **d** lateral view

spines along the rims. Spines also present along the sulcus and the posterior margin of the hypocone. Chloroplasts brown. Nucleus horseshoe-shaped, centrally located. Cell length 80–100 µm, width 70–90 µm. Cells break open on the epicone. Resting cysts unknown.
Ecology: ponds in tropical areas.
Geographical distribution: Madagascar (Lefèvre). Java, Indonesia (Wołoszyńska).

var. *palustre* (Er. Lindemann) Er. Lindemann 1928a, p. 260 (**Fig. 217**)
Basionym: *Peridinium cinctum* var. *palustre* Er. Lindemann 1919, p. 251, text-figs 118–123, pl. 17, fig. 18
Nomenclatural synonym: *Peridinium palustre* (Er. Lindemann) M. Lefèvre 1932, p. 98
Taxonomic synonym: *Peridinium chalubinskii* Wołoszyńska 1919a, p. 321, pl. 13, figs 1–6; 1919b, p. 199, pl. 14, figs 1–6

Cells 50–70 (90) µm long and 50–60 µm wide. Differs from the type also in the lack of distinct antapical projections and the lack of spines. Plate 1a hexangular, 2a quadrangular. Short hyaline wings are sometimes present on both the epi- and the hypocone, supported by small spines. Epi- and hypocone of nearly the same size.
Ecology: plankton in peat bogs and ponds at pH 4 or below, according to Höll (1928) not at pH above 5. However, Lindemann (1929) reported it in fishponds at pH 7.3 and 7.5. Sensitive to calcium but indifferent to humic compounds. A warm temperate form which may occur in large numbers at temperatures of 20–25 °C (Lindemann 1929). Dividing cells are non-motile and sink to the bottom. Water samples left to dry out for several weeks during summer yielded motile cells when distilled water was added to the sample (Lindemann 1929).
Geographical distribution: France (Lefèvre); Germany (Lindemann; Höll; Baumeister); Holland (Beijerinck); Poland (Wołoszyńska).

Note: although the variety is morphologically very similar to the type of *P. raciborskii*, there are morphological differences indicating that the two taxa may belong to different species, viz. shape of 1a and 2a, presence of wings and spines, cell size, ecology (water characteristics, tropical versus temperate species).

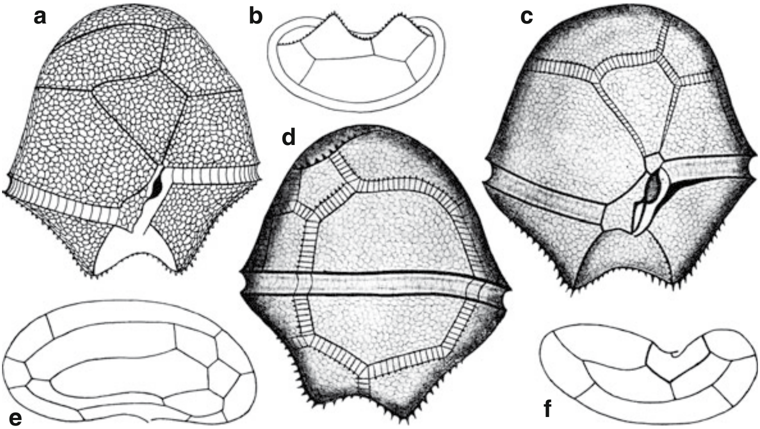

Fig. 216 *Peridinium raciborskii* Wołoszyńska (**a**, **b** after Wołoszyńska 1912; **c**–**f** after Wołoszyńska 1923). **a** ventral view with plate ornamentation; **b** dorso-antapical view; **c**–**f** ventral, dorsal, apical and antapical views

5. *Peridinium zonatum* (Playfair) Playfair 1920, p. 815 (Fig. 218)

Basionym: *Peridinium tabulatum* var. *zonatum* Playfair 1913, p. 543, pl. lv, figs 10–12
Nomenclatural synonym: *Peridinium gatunense* var. *zonatum* (Playfair) M. Lefèvre 1932, p. 96

Cells nearly spherical, epicone larger than hypocone. Sulcus does not widen on the hypocone and does not reach the antapex. Plate 1′ narrow, elongate. Plates smooth but ornamented with large rough ridges that are radiating on the antapical plates and mainly parallel to the cingulum in the other plates. Cell length 45–55 µm, width 52–60 µm.
SEM: Liu *et al.* (2008a).
Ecology: in the plankton of ponds and reservoirs.
Geographical distribution: Hubei, Guangdong, China (Liu *et al.*). Australia (Playfair, Thomasson).

Note: in its plate arrangement this species is rather similar to *Peridinium gatunense* (Lefèvre 1932). However, the peculiar plate ornamentation and the restricted geographical distribution may justify its treatment as a separate species, as recently done by Liu *et al.* (2008a).

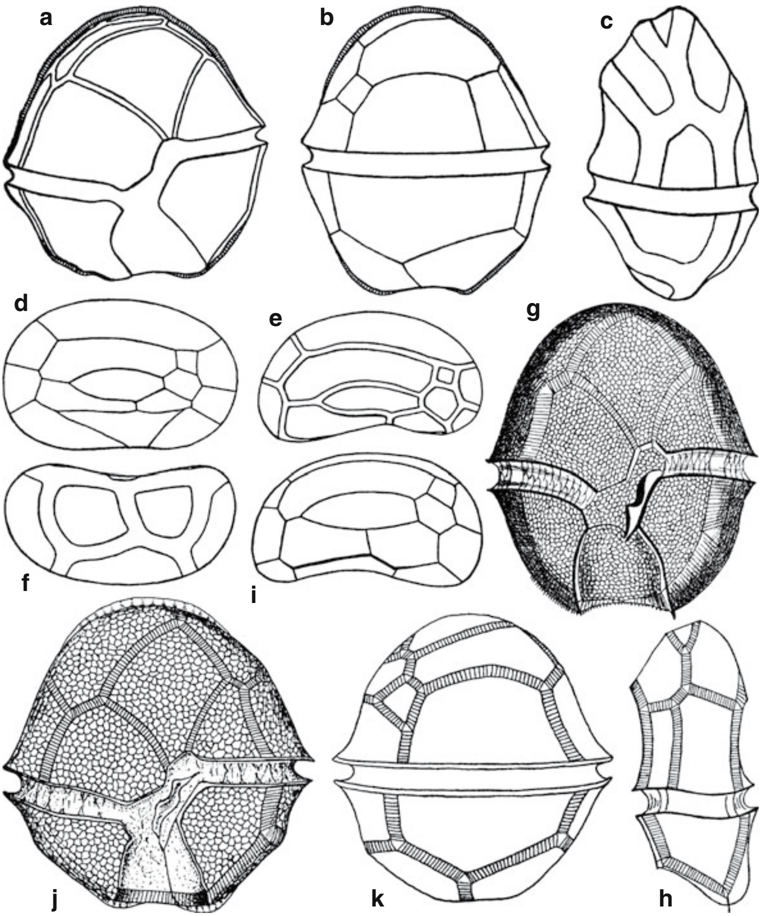

Fig. 217 *Peridinium raciborskii* var. *palustre* (Er. Lindemann) Er. Lindemann (**a**–**f** after Lindemann 1919; **g**–**i** after Wołoszyńska 1919b; **j**, **k** after Lefèvre 1932). **a**–**c** ventral, dorsal and right lateral views, respectively; **d** tabulation on the epicone; **e** natural apical view, with ventralmost plates not visible due to the dorsoventral compression of the cell; **f** antapical view; **g** ventral view with plate ornamentation; **h** right lateral view; **i** tabulation on the epicone; **j** ventral view with plate ornamentation; **k** dorsal view

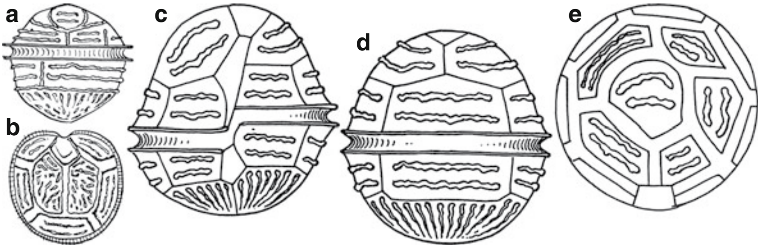

Fig. 218 *Peridinium zonatum* (Playfair) Playfair (**a**, **b** after Playfair 1913; **c**–**e** after Playfair 1920). **a** dorsal view with plate ornamentation (shape inaccurate *fide* Playfair 1920); **b** antapical view; **c**–**e** ventral, dorsal and apical views, respectively

Group 2, the *P. striolatum* group

Plate pattern symmetrical, first apical plate shares a suture with the third apical plate. In apical view the following four plates are located in a dorso-ventral line, forming a line of symmetry: 1′, 3′, 2a and 4″. A single species with 4 varieties.

6. *Peridinium striolatum* Playfair 1920, p. 810, pl. XLI, fig. 1 (**Fig. 219**)

(not *Peridinium striolatum* Wailes 1928, *nom. illeg.*)

Cells oval, dorsoventrally compressed. Epicone bell-shaped or conical, broadly rounded above, larger or of the same size as the bowl-shaped, sometimes slightly angular hypocone. Cingulum descending, the ends only very slightly displaced. Sulcus extends on the epicone *ca.* halfway to the apex. On the hypocone it is dilated posteriorly. Sometimes the dilated part gives the impression of being separated from the rest of the sulcus. Plate 1′ touches 3′. Cells ornamented with longitudinal coarse striations, the individual plates often difficult to distinguish because of the striae. The striae are interconnected by short somewhat less prominent bars or by a reticulate pattern. Cell length 37–51 µm, width 28–53 µm, thickness 18–33 µm. SEM: Ling *et al.* (1989), Liu *et al.* (2008a).

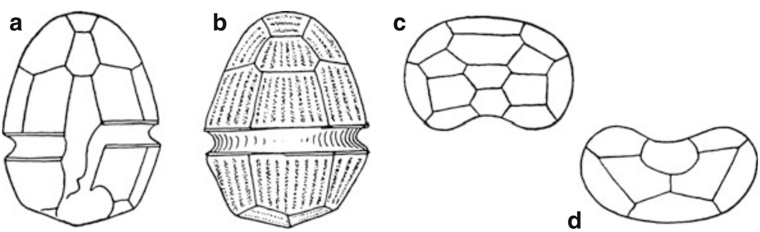

Fig. 219 *Peridinium striolatum* Playfair (after Playfair 1920). **a** ventral view; **b** dorsal view with plate ornamentation; **c**, **d** apical and antapical views, respectively

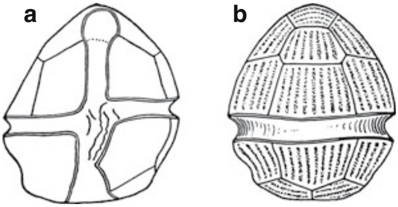

Fig. 220 *Peridinium striolatum* var. *acuminatum* Playfair (after Playfair 1920). **a** ventral view; **b** dorsal view with plate ornamentation

Ecology: found in the plankton of ponds (Playfair 1920), of alpine oligotrophic lakes (to 1120 m elevation) and dystrophic coastal lagoons (Ling *et al.* 1989), and reservoirs (Liu *et al.* 2008a).
Geographical distribution: Guangdong, China (Liu *et al.*); Japan (Takano, unpubl.). New South Wales, Tasmania, Australia (Playfair; Ling *et al.*).

var. *acuminatum* Playfair 1920, p. 811, pl. XLII, fig. 4 (**Fig. 220**)
Nomenclatural synonym: *Peridinium striolatum* f. *acuminatum* (Playfair) M. Lefèvre 1932, p. 81

Epicone somewhat angular, hypocone more irregular, with concave sides. Epicone slightly pointed. Cell length 52 µm, width 46 µm.
Geographical distribution: New South Wales, Australia (Playfair).

var. *auburnense* Playfair 1920, p. 811, pl. XLII, figs 5–7 (**Fig. 221**)
Nomenclatural synonym: *Peridinium striolatum* f. *auburnense* (Playfair) M. Lefèvre 1932, p. 81

Differs in having a slightly costate ornamentation, the costae connected by irregular reticulations. Cell length 45–57 µm, width 40–53 µm, length of epicone 24–30 µm.
Geographical distribution: New South Wales, Australia (Playfair).

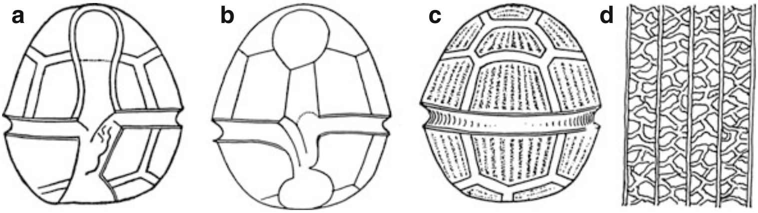

Fig. 221 *Peridinium striolatum* var. *auburnense* Playfair (after Playfair 1920). **a**, **b** two cells in ventral view; **c** dorsal view with ornamentation outlined; **d** detail of plate ornamentation

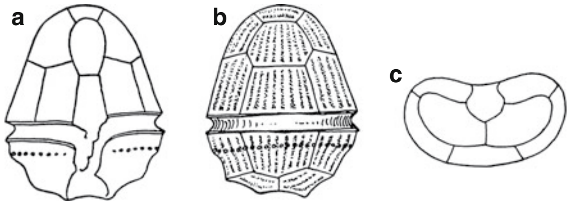

Fig. 222 *Peridinium striolatum* var. *rugosum* Playfair (after Playfair 1920). **a** ventral view; **b** dorsal view with plate ornamentation; **c** antapical view

var. *rugosum* Playfair 1920, p. 810, pl. XLI, fig. 2 (**Fig. 222**)
Nomenclatural synonym: *Peridinium striolatum* f. *rugosum* (Playfair) M. Lefèvre 1932, p. 80

Plates on the hypocone concave. Sometimes a row of granules is present below the cingulum. Cell length 44–51 µm, width 34–46 µm, epicone 23–27 µm long, cell thickness 23–27 µm.
Geographical distribution: New South Wales, Australia (Playfair).

var. *truncatum* Playfair 1920, p. 811, pl. XLII, figs 1, 2 (**Fig. 223**)
Nomenclatural synonym: *Peridinium striolatum* f. *truncatum* (Playfair) M. Lefèvre 1932, p. 80

Hypocone more or less truncate, with rounded sides. The ornamentation of the cell usually generally faint. Cell length 51–52 µm, width 42–49 µm.
Geographical distribution: New South Wales, Australia (Playfair).

Group 3, the *P. willei* group

Plate pattern in epicone symmetrically arranged or nearly so. The first apical plate is separated from the third apical plate by the second and fourth apical plates. Sulcus extends onto epicone.

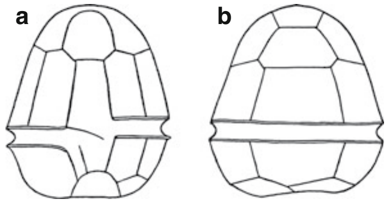

Fig. 223 *Peridinium striolatum* var. *truncatum* Playfair (after Playfair 1920). **a**, **b** ventral and dorsal views

Key to species of the *Peridinium willei* group:

1a Plate 1′ large, wedge-shaped, sulcal extension on the epicone as long as or shorter than wide, cells commonly with hyaline wings apically and antapically .... 6. *P. willei*

1b Plate 1′ small, sulcal extension on the epicone longer than wide, hyaline wings absent .... 7. *P. volzii*

7. *Peridinium willei* Huitfeldt-Kaas 1900, p. 5, figs 6–9 (**Fig. 224**)

Taxonomic synonyms: *Peridinium alatum* Garbini 1902, p. 123, figs a, b; *Peridinium willei* var. *carinthiacum* Beck [= Beck-Mannagetta] 1931, p. 229

Cells circular in ventral view or slightly longer than wide, somewhat dorsoventrally flattened. Epicone larger than hypocone, semicircular. Hypocone somewhat conical. First apical plate large, axe-shaped with slightly concave lateral sides, usually *ca.* 19–22 µm long. Plate 4′ often distinctly wider that 2′. Plates rather thick, finely reticulated, sutures wide and striated. Epicone often with three low, hyaline wings on the anterior sutures, extending from right to left, the wings supported by numerous short ribs resulting in a comb-like pattern. Right antapical plate sometimes larger than left antapical, both commonly with a low wing on the ventral sutures. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus extends for a short distance onto the epicone, narrowing anteriorly. On the hypocone it continues to the antapex, often widening slightly. The right and left sulcal borders with well-developed lists. Cell length 36–60 µm, width 30–58 µm. Cells open on the dorsal side of the epicone by the breaking away of a lid formed by plates 2′, 1a–3a, 3‴–5‴. Vegetative multiplication in immotile stage, as usual in the genus, with cell contents dividing into two, old theca discarded.

Sexual reproduction isogamous, homothallic, the gametes slightly smaller and lighter in color than vegetative cells (Pfiester 1976). Cysts (hypnozygotes) almost spherical, smooth (Pfiester 1976).

SEM: Iltis & Couté (1984), Ling *et al.* (1989), Couté & Tell (1990), Olrik (1992), Senzaki & Horiguchi (1994), Hansen & Flaim (2007).

Ecology: widely distributed in ponds and lakes, eurytrophic, also in brown water. Occurs throughout the year, most commonly in spring. Reported to occur at pH 4,0–8,0 by Höll (1928), who included it in a group of species with almost unlimited adaptation potential.

Geographical distribution: Belgium (Meunier); British Isles (Griffiths; West & West; Harris; Lewis & Dodge); Denmark (Nygaard; Olrik); Faroe Islands (Børgesen & Ostenfeld); France (Deflandre; Lefèvre; Virieux); Germany (Lemmermann; Lauterborn; Lindemann); Holland (Beijerinck); Iceland (Ostenfeld); Italy (Garbini; Lemmermann; Hansen & Flaim); Latvia (Skuja); Lithuania (Lefèvre); Norway (Huitfeld-Kaas; Ström); Poland (Lindemann; Wołoszyńska); Portugal (Pandeirada *et al.*); Sweden (Lemmermann; Ström); Switzerland (Messikommer; Lindemann; Huber-Pestalozzi: 2063 m altitude in Graubünden). British Columbia, Canada (Wailes); USA, IA (Prescott), MD (Thompson), OH (Carty), OK (Pfiester), TN (Eddy). Argentina (Boltovskoy; Couté & Tell); Bolivia (Iltis & Couté); Brazil (Cardoso *et al.*). Bali, Indonesia (Lindemann); Jilin, Huinan, China (Liu *et al.*); Japan (Senzaki & Horiguchi). Tasmania (Ling *et al.*). New Zealand (Thompson).

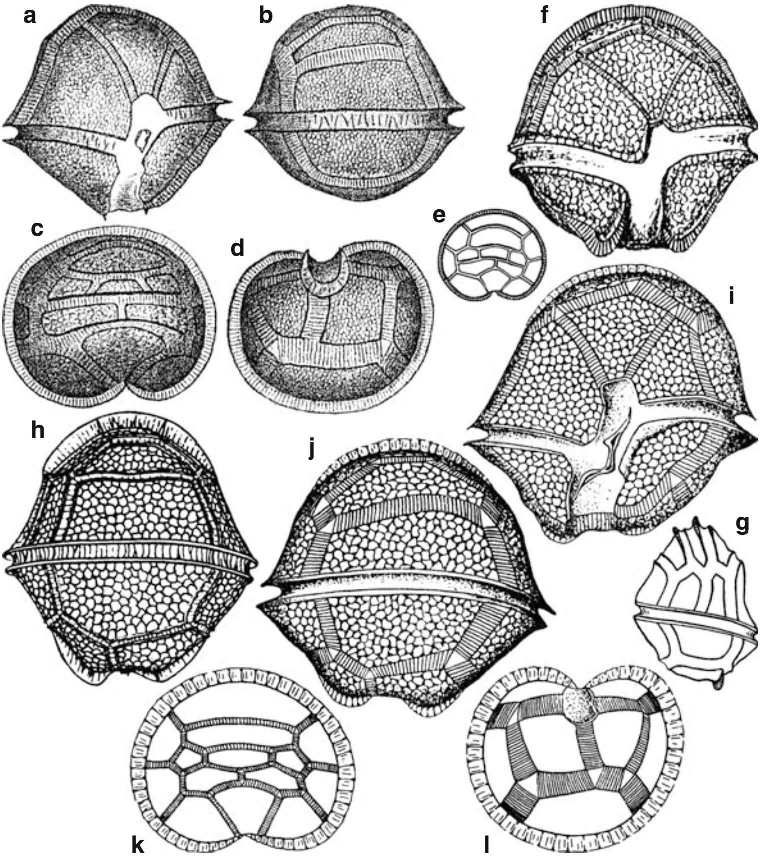

Fig. 224 *Peridinium willei* Huitfeldt-Kaas (**a**–**d** after Huitfeldt-Kaas 1900; **e** after Lemmermann 1908a; **f**, **g** after Lindemann 1920; **h** after Skuja 1930; **i**–**l** after Lefèvre 1932). **a**–**d** ventral, dorsal, apical and antapical views; **e** outline of plates in apical view; **f** ventral view; **g** right lateral view; **h** dorsal view; **i**, **j** ventral and dorsal views; **k**, **l** outline of plates in apical and antapical views

Note: a freshwater species named *P. cucumis* Wailes (1928, p. 29, pl. VI, figs 4, 5) was described from the Shaughnessy Heights, Vancouver, Canada. The description is very incomplete and the material was referred to the otherwise marine section *Oceanica* (now in *Protoperidinium*). Cells were 48–50 µm long and 42–45 µm wide. Plates were strongly ornamented (with circular punctuations) and although the plate pattern was not described in detail it was mentioned that 2a touched only 4″. This indicates that three

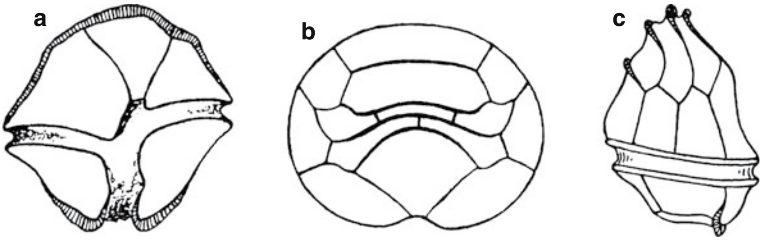

Fig. 225 *Peridinium willei* f. *lineatum* Er. Lindemann (after Lindemann 1920). **a**. ventral view; **b** apical view; **c** right lateral view of intermediate between typical form and f. *lineatum*

intercalary plates were present. From the description the material resembles *P. willei* (or perhaps *P. volzii*) but a more detailed description is required to determine its identity. It also resembles *P. gutwinskii*, but cells appear to lack an apical pore.

f. *lineatum* Er. Lindemann 1920, p. 152, figs 93, 94 (**Fig. 225**)
Plates 2′–4′, 1a and 3a very narrow, arranged in parallel bands.
Geographical distribution: France (Lefèvre); Germany (Lindemann).

f. *sphaericum* Er. Lindemann 1920, p. 151, figs 81–83 (**Fig. 226**)
Cells more regularly spherical, apical plates hardly concave in lateral view.
Geographical distribution: France (Lefèvre); Poland (Lindemann).

f. *stagnale* Er. Lindemann 1920, p. 151, figs 84, 85 (**Fig. 227**)
Cells strongly compressed dorsoventrally.
Geographical distribution: England (Lewis & Dodge); Poland (Lindemann); Istanbul, Turkey, in brackish water (Lindemann).

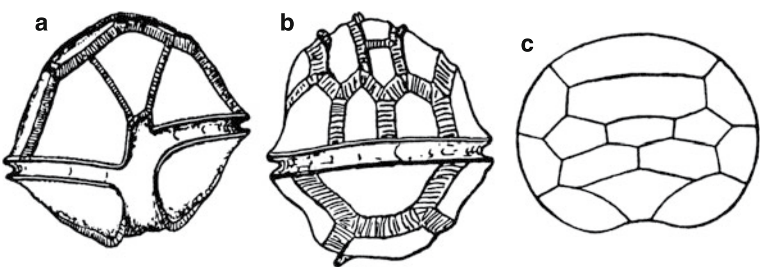

Fig. 226 *Peridinium willei* f. *sphaericum* Er. Lindemann (after Lindemann 1920). **a** ventral view; **b** left lateral view of cell with small comb-like crests; **c** apical view

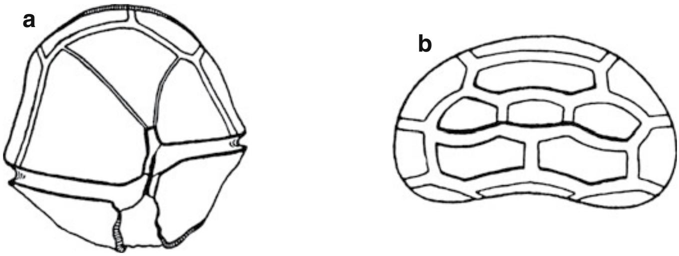

Fig. 227 *Peridinium willei* f. *stagnale* Er. Lindemann (after Lindemann 1920). **a** ventral view; **b** apical view (the thick lines mark the comb-like crests)

8. *Peridinium volzii* Lemmermann 1905b, p. 166, pl. XI, figs 15–18 (**Fig. 228**)

Taxonomic synonyms: *Peridinium volzii* var. *australe* G. S. West 1909a, p. 80, fig. 10, A–G; *Peridinium volzii* var. *maximum* C. Bernard 1909, p. 82, fig. 186; *Peridinium guestrowiense* Er. Lindemann 1916, p. 490, figs 1–12; *Peridinium guestrowiense* f. *sinuatum* Er. Lindemann 1919, p. 248, figs 107–110 ≡ *Peridinium volzii* f. *sinuatum* (Er. Lindemann) M. Lefèvre 1932, p. 78; *Peridinium guestrowiense* var. *beta-collineatum* Er. Lindemann 1920, p. 179, fig. 190; *Peridinium guestrowiense* var. *cyclicum* Er. Lindemann 1920, p. 156, figs 123, 124 ≡ *Peridinium volzii* f. *cyclicum* (Er. Lindemann) M. Lefèvre 1932, p. 78; *Peridinium guestrowiense* subvar. *originale* Er. Lindemann 1920, p. 158, fig. 133

Cells spherical or slightly elongate, somewhat dorsoventrally compressed, epi- and hypocone similar in size. Cingulum descending, displaced *ca.* one cingulum width. Sulcus extends onto the epicone by *ca.* 1.5× the cingulum width, forming a cylindrical, right-angled indentation in the epicone. On the hypocone it extends to the antapex, often with two spines along the left border. Plate 1′ small, typically *ca.* 12–14 µm long, triangular to slightly elongate with straight or slightly convex lateral sides, 2′ and 4′ usually 6-sided, 3′ 5-sided, separated from 1′ by 2′ and 4′. Plate 2a much wider than high, 1a and 3a small, almost as wide as high. Plate 4″ is bordered anteriorly only by plate 2a. Sutures sometimes very broad. Plates strongly reticulated. Numerous plate-like chloroplasts. Eyespot present in the sulcus. Cell length 38–60 µm, width 33–58 µm, thickness 29–52 µm. Cells open by the dorsal side of the amphiesma on the epicone breaking away.
Sexual reproduction isogamous, heterothallic, two mating types identified; cysts (hypnozygotes) spherical (Pfiester & Skvarla 1979; see also Kita & Fukuyo 1995).
SEM: Pfiester & Skvarla (1979), Hargraves & Víquez (1981, var. *cinctiforme*?), Ling *et al.* (1989), Couté & Tell (1990), Olrik (1992), Senzaki & Horiguchi (1994), Hansen & Flaim (2007), Liu *et al.* (2008).
DNA data: Daugbjerg *in* Hansen & Flaim (2007).
Ecology: in the plankton of calcium-rich lakes and ponds, rarer in other types of waters; prefers weakly alkaline water at pH 7.0–7.5; sensitive to humic substances; most common in late spring/summer (Höll 1928).

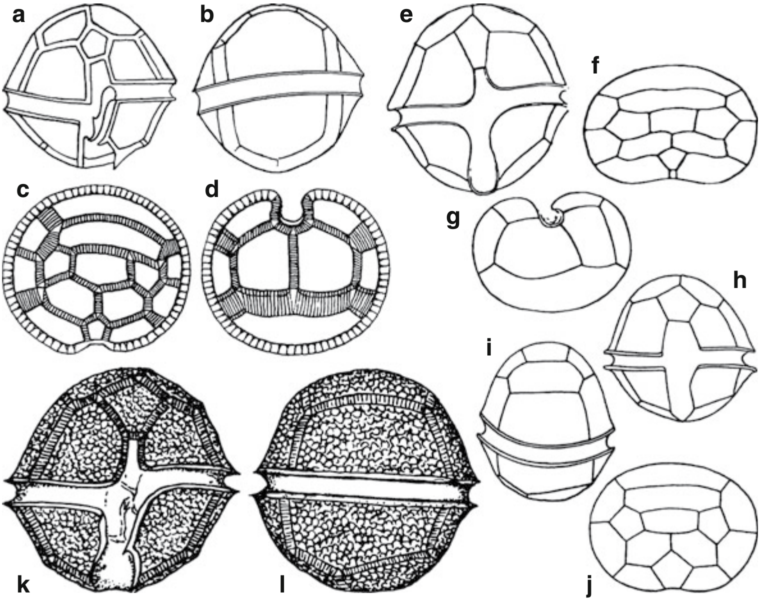

Fig. 228 *Peridinium volzii* Lemmermann (**a**–**d** after Lemmermann 1905b; **e**–**g** after Lindemann 1916; **h**–**j** after Lefèvre 1932; **k**, **l** after Huber-Pestalozzi 1950). **a**–**d** ventral, dorsal, apical and antapical views; **e**–**g** ventral, apical and antapical views; **h**–**j** ventral, slightly tilted dorsal and apical views; **k**, **l** ventral and dorsal views with plate ornamentation

Geographical distribution: Denmark (Nygaard); England (Lewis & Dodge); France (Lefèvre); Germany (Lindemann; Höll); Hungary (Entz); Italy (Hansen & Flaim); Latvia (Skuja); Poland (Lindemann; Wołoszyńska); Switzerland (Lindemann); Ukraine (Lindemann). Madagascar (Lefèvre); Victoria Nyanza (Lindemann; Wołoszyńska). USA, MA (Prescott & Croasdale), MD (Thompson), MN (Eddy), OH (Carty), OK (Pfiester & Skvarla). Argentina (Boltovskoy; Couté & Tell); Costa Rica (Hargraves & Víquez). Jilin, Guangdong, China (Liu *et al.*); Sumatra, Bali, Indonesia (Lindemann); Japan (Senzaki & Horiguchi); Singapore (Lemmermann). Tasmania (ubiquitous, Ling *et al.*), Victoria, New South Wales, Australia (West; Playfair). New Zealand (Thompson).

f. *complexum* Krakhmalny *in* Krakhmalny *et al.* 2004, p. 214, fig. 2, photo 2: figs 3–6 (**Fig. 229**)
Third apical plate divided into two plates of equal size. Epicone larger than hypocone, bell-shaped. Cells dorsoventrally compressed. Cell 35–50 µm long, 25–45 µm wide.

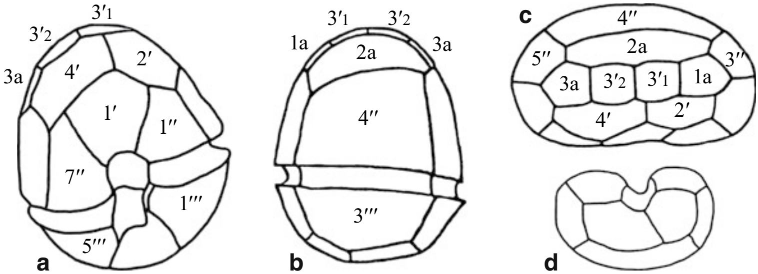

Fig. 229 *Peridinium volzii* f. *complexum* Krakhmalny (after Krakhmalny *et al.* 2004). **a**–**d** ventral, dorsal, apical and antapical views

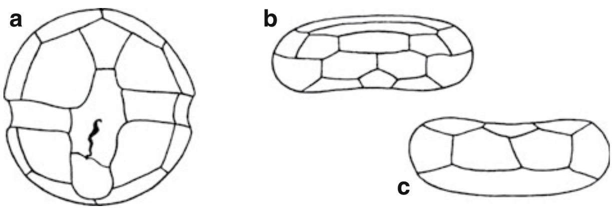

Fig. 230 *Peridinium volzii* f. *compressum* (Er. Lindemann) M. Lefèvre (after Lindemann 1919). **a**–**c** ventral, apical and antapical views, respectively

Ecology: highly mineralized freshwater fishpond (4220–5180 µS/cm), pH 7.5–7.9, in May–June (Krakhmalny *et al.* 2004).
Geographical distribution: Israel (Krakhmalny).

Note: culture studies are needed to ascertain whether the divided apical plate is a stable character.

f. *compressum* (Er. Lindemann) M. Lefèvre 1932, p. 77 (**Fig. 230**)
Basionym: *Peridinium guestrowiense* f. *compressum* Er. Lindemann 1919, p. 249, text-figs 111–113

Cells very strongly dorsoventrally compressed, 2–3× wider than thick.
Ecology: Lake near Witosław, Poznan, July 1917 (Lindemann 1919).
Geographical distribution: Poland (Lindemann).

f. *vancouverense* (Wailes) M. Lefèvre 1932, p. 78, 183 (**Fig. 231**)
Basionym: *Peridinium vancouverense* Wailes 1931, p. 110, a replacement name for *Peridinium striolatum* Wailes 1928, p. 21, pl. II, figs 4–7, *nom. illeg.* (non *Peridinium striolatum* Playfair 1920)

Amphiesmal plates with longitudinal, parallel ridges.

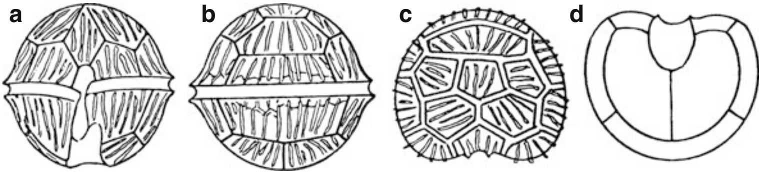

Fig. 231 *Peridinium volzii* f. *vancouverense* (Wailes) M. Lefèvre (after Wailes 1928). **a**–**c** ventral, dorsal and apical views showing plate ornamentation; **d** antapical view (outline of plates only)

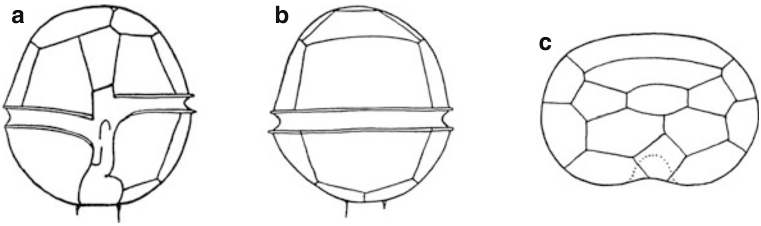

Fig. 232 *Peridinium volzii* var. *botanicum* (Playfair) Er. Lindemann (after Playfair 1920). **a**–**c** ventral, dorsal and apical views (the dotted line in **c** marks the deeply incised sulcus)

Ecology: collected from Shaughnessy Heights, Vancouver (pond?); beaver pond surrounded by forest in Algonquin Provincial Park, Ontario.
Geographical distribution: British Columbia, Ontario, Canada (Wailes; Bourrelly).

var. *botanicum* (Playfair) Er. Lindemann 1931, p. 715 (**Fig. 232**)
Basionym: *Peridinium willei* var. *botanicum* Playfair 1920, p. 813, pl. XLI, fig. 3

Differs from the species type by the presence of two spines at the posterior ends of the sulcus. Each spine is a flat triangular projection on the ventral rim of each antapical plate (Ling *et al.* 1989).
SEM: Ling *et al.* (1989, fig. 100).
Ecology: occurs together with the nominal variety.
Geographical distribution: Sumatra, Indonesia (Lindemann). Tasmania (Ling *et al.*), Fairfield, Guildford, Lismore, Sydney, Australia (Playfair).

var. *cinctiforme* M. Lefèvre 1927, p. 122 (**Fig. 233**)
Differs from the species type by 2′ and 4′ being very unequal in size, the epicone therefore in top view appearing asymmetrical.
SEM: Cavalcante *et al.* (2017).
Geographical distribution: Germany, Poland (Lindemann). Madagascar (Lefèvre). Bolivia (Thérézien); Brazil (Borics *et al.*; Cavalcante *et al.*).

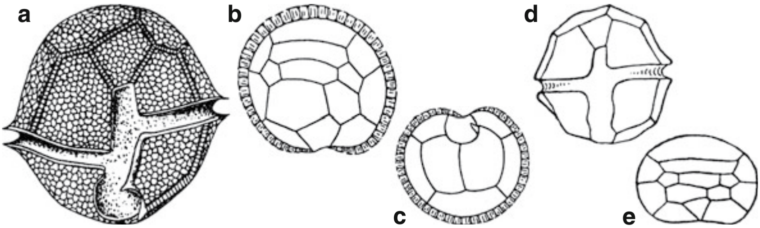

Fig. 233 *Peridinium volzii* var. *cinctiforme* M. Lefèvre (**a**–**c** after Lefèvre 1932; **d**, **e** after Lindemann 1920). **a**–**c** ventral, apical and antapical views, respectively; **d**, **e** ventral and apical views

var. *maeandricum* (Lauterborn) Moestrup & Calado *comb. nov.* (**Fig. 234**)
Basionym: *Peridinium tabulatum* var. *maeandricum* Lauterborn 1903, *Verh. Naturhist.-Med. Vereins Heidelberg, N. F.* **7**, p. 604 ("*maeandrica*")
Nomenclatural synonym: *Peridinium volzii* f. *maeandricum* (Lauterborn) Er. Lindemann 1924 f, p. 300
Taxonomic synonyms: (?) *Peridinium tabulatum* var. *westii* f. *australe* Playfair 1913, p. 542, pl. lv, figs 5–9 ("*australis*") ≡ *Peridinium australe* (Playfair) Playfair 1920, p. 814; (?) *Peridinium tabulatum* var. *hieroglyphicum* Playfair 1913, p. 543, pl. lv, fig. 13 ≡ *Peridinium hieroglyphicum* (Playfair) Playfair 1920, p. 816; *Peridinium hieroglyphicum* var. *ovatum* Playfair 1920, p. 816, pl. XLIII, figs 4, 5; *Peridinium hieroglyphicum* var. *rotundum* Playfair 1920, p. 816, pl. XLIII, fig. 6

With raised rims between the amphiesmal plates and with a meandering pattern of raised ridges on the plates.
SEM: Hansen & Flaim (2007).
DNA data: Daugbjerg *in* Hansen & Flaim (2007).

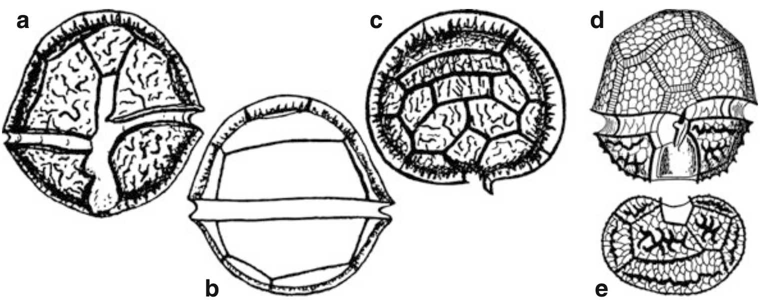

Fig. 234 *Peridinium volzii* var. *maeandricum* (Lauterborn) Moestrup & Calado (**a**–**c** after Lindemann 1924 f; **d**, **e** after Wołoszyńska 1952). **a**–**c** ventral, dorsal and apical views (**b** outline of plates only); **d**, **e** ventral and antapical view of cell with meandering ridges on the hypocone only

Ecology: in the plankton of alpine lakes; lakes and reservoirs in New South Wales, Australia (same taxon?).
Geographical distribution: Germany (Lauterborn; Lindemann); France (Hansen, unpublished); Italy (Hansen & Flaim); Tatra Mountains, Poland (Wołoszyńska); Switzerland (Lindemann). Australia (Playfair)?

Note: Wołoszyńska (1952) illustrated cells combining typical areolations on the epicone plates with meandering ridges amidst areolations on the hypocone plates.

subg. *Poroperidinium* (Lemmermann) M. Lefèvre 1932, p. 66, 110

Basionym: *Peridinium* sect. *Poroperidinium* Lemmermann 1910, p. 657, 661

Species with apical pore complex.
For identification of groups, see the general key above.

Group 1, the *P. allorgei* group

Intercalary plates asymmetrically arranged, 1a is small and four-sided. Plate formula: apo, **4′, 3a, 7″**, ?c, ?s, 5‴, 2⁗. A group of two species, both in need of further study.

9. *Peridinium allorgei* M. Lefèvre 1927, p. 120 (**Fig. 235**)

Cells spherical or slightly lens-shaped, hardly compressed dorsoventrally. Epicone rounded, almost hemispherical, larger than the hypocone. Hypocone somewhat similar but slightly shorter. Cingulum wide, descending, the ends displaced *ca.* half the cingulum width. Sulcus extends for a short distance onto the epicone, on the hypocone it extends widely towards the antapex. Amphiesmal plates convex, finely striated longitudinally, even in the cingulum and sulcus. Sutures often wide, transversly striated. Cell length 25–40 µm, width 28–43 µm.
Ecology: in the plankton of ponds.
Geographical distribution: France; Spain.

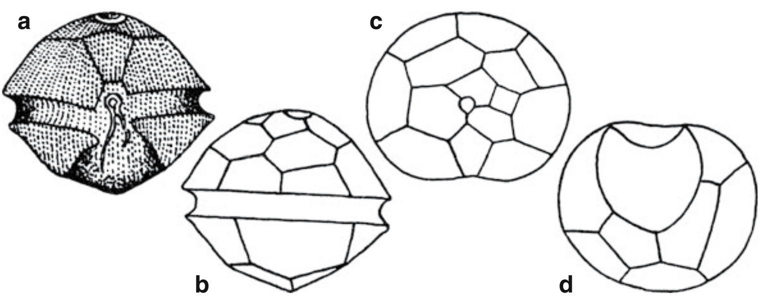

Fig. 235 *Peridinium allorgei* M. Lefèvre (after Lefèvre 1932). **a** ventral view, showing plate ornamentation; **b**–**d** dorsal, apical and antapical views, respectively

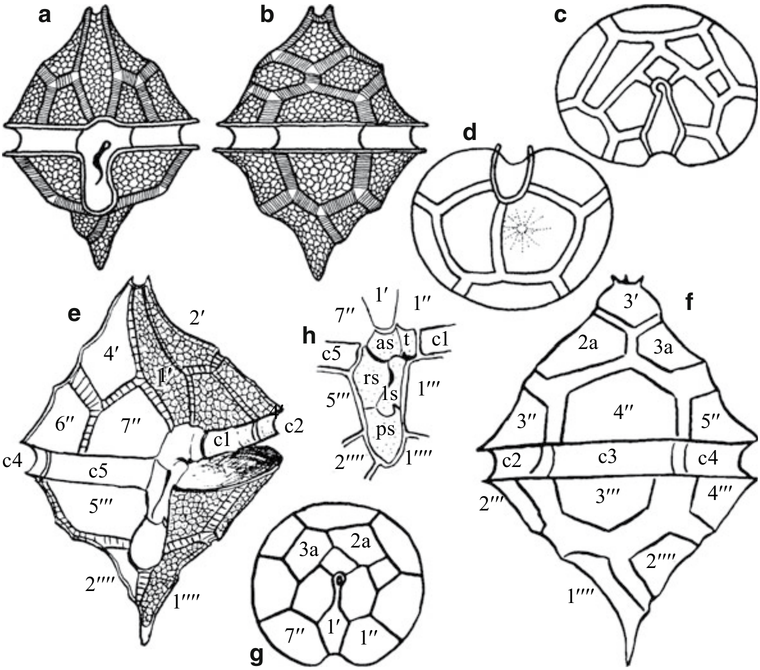

Fig. 236 *Peridinium wisconsinense* S. Eddy (**a**–**d** after Eddy 1930; **e**–**h** after Bourrelly 1970). **a**–**d** ventral, dorsal, apical and antapical views (**c** flipped relative to the original); **e**, **f** ventral and dorsal views; **g** apical view; **h** detail of sulcal area and adjacent plates (t, transitional plate, alternatively interpretable as c1)

10. *Peridinium wisconsinense* S. Eddy 1930, p. 300, fig. 51 (**Fig. 236**)

Cells biconical. Epi- and hypocone of almost the same length. Cells slightly dorsoventrally compressed. Sulcus extends for a very short distance only onto the epicone, on the hypocone it terminates before reaching the antapex. Cingulum ring-shaped in the figures published by Eddy (1930), “strongly spiral” in the description. Amphiesmal plates strongly reticulated/areolated. Sutures of older cells transversely striated, in younger cells apparently smooth. The antapical horn formed by extension of left antapical plate. Cells 55–64 µm long, 48–56 µm wide. Cysts ellipsoidal with inner round capsule. Archaeopyle formed by apical para-plates 1′–4′.
Ecology: plankton in warm lakes, mostly 20–30ºC, with pH 6–7 and oligo- to mesotrophic conditions, mainly a summer species (McCarthy *et al.* 2011).
Geographical distribution: Ontario, Canada (McCarthy *et al.*; Zippi *et al.*). USA, MA (Prescott & Croasdale; Evitt & Wall), MN, WI (Eddy), MS (Canion & Ochs), NC (Phillips & Whitford), PA (Holt *et al.*). Resting cysts recorded from sediment core, Nova Scotia (Miller *et al.*).

Note: this very unusual and poorly known *Heterocapsa*-like species occupies an isolated position among the peridinioids. Eddy (1930) drew the epicone in antapical view when describing the species, and this unusual view was apparently overlooked by both Lefèvre (1932) and Popovský & Pfiester (1990). Smith (1950, p. 529), provided a drawing of the epicone in the usual way, seen from the apical end.

Group 2, the *P. bipes* group

Plate pattern symmetric or very nearly so. Plate 4″ commonly touches only 2a, not 1a and 3a, the 2a therefore six-sided. Exceptions to this are travectum tabulations affecting the suture between 1a and 2a, such as found in *P. bipes* and sometimes ascribed to "*P. tabulatum*" types. Plate formula po, x, **4′, 3a, 7″**, 5c, 5s, 5‴, 2⁗ (s and c based on *Peridinium bipes*).
Cells very similar to *P. bipes* occur commonly in marine deposits from the Early Cretaceous, indicating the ancient origin of the genus (Norris & Hedlund 1972).

Key to species of the *Peridinium bipes* group:

1a Cells with spines or extensions 2
1b Cells without spines or extensions .... 12. *P. playfairii*
2a Cells with two short, solid, posterior spines. Anterior end straight .... 10. *P. bipes*
2b Cells with two long posterior extensions. Anterior end bent towards the left . ... 11. *P. limbatum*

11. *Peridinium bipes* F. Stein 1883, pl. XI, figs 7, 8 (Fig. 237)

Taxonomic synonyms: *Peridinium tabulatum* Ehrenberg 1832, p. 74 ≡ *Glenodinium tabulatum* (Ehrenberg) Ehrenberg 1837, p. 133; 1838, p. 257 ≡ *Peridinium bipes* f. *tabulatum* (Ehrenberg) M. Lefèvre 1932, p. 114; *Peridinium bipes* var. *excisum* Lemmermann 1900a, p. 29 ≡ *Peridinium bipes* f. *excisum* (Lemmermann) M. Lefèvre 1932, p. 113

Note: the synonymy between *P. tabulatum* and *P. bipes* has been noted by Lefèvre (1932, p. 114–116), who, however, retained the latter name. We have confirmed Lefèvre's conclusions in Ehrenberg's collection of mica preparations kept at the Museum für Naturkunde in Berlin (Lazarus & Jahn 1998). The consistent and well-defined use of the name *P. bipes* contrasts with the erratic use of the name *P. tabulatum*, which was applied to almost any freshwater peridinioid with visible plates until its redefinition by Stein (1883). We are retaining the use of *P. bipes* pending its conservation against *P. tabulatum*, to be proposed elsewhere.

Cells pear-shaped, rather strongly dorsoventrally flattened. Epicone larger than hypocone. The apical plates often with hyaline wings of different size, the antapical plates with a hyaline extension at the antapical end of each side of the sulcus. These extensions vary in shape but are often triangular. Cingulum descending, the ends displaced 1–1.5 cingulum widths. Sulcus extends onto the epicone as a short straight depression, on the hypocone it widens towards the antapical end. The plates are strongly areolated, each areole with 1–3 pores. Plates are often concave. The

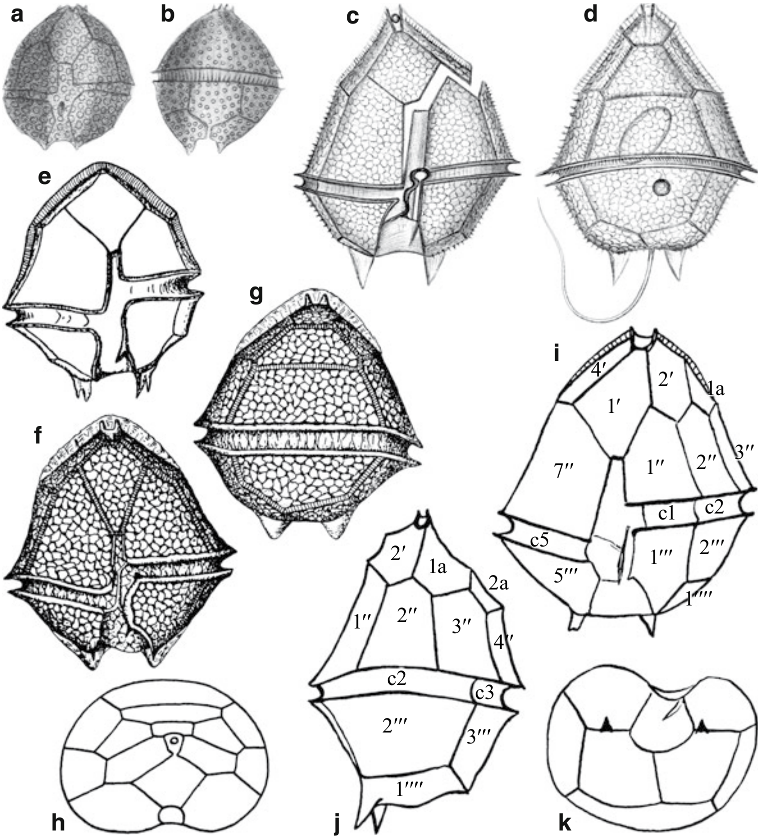

Fig. 237 *Peridinium bipes* F. Stein (**a**, **b** after Ehrenberg 1838; **c**, **d** after Stein 1883; **e** after Lindemann 1920; **f**–**h** after Lefèvre 1926a; **i**–**k** after Bourrelly 1970). **a**, **b** ventral and dorsal views (inverted relative to original); **c**, **d** ventral and dorsal views; **e** ventral view, antapical hyaline extensions divided; **f**–**h** ventral, dorsal and apical views; **i** ventral view; **j** left lateral view; **k** antapical view

two antapical plates often of different size. Sutures may be wide and transversely striated. Cells open on the epicone by shedding the dorsal half of the amphiesma. At cell division cell contents divide into two, old theca discarded. Cysts spherical with thick wall, formed within the amphiesma (Mertens *et al.* 2012).
SEM: Hickel (1975), Boltovskoy (1977), Dodge (1985), Couté & Tell (1990), Liu *et al.* (2008a).
Ecology: ponds, lakes and reservoirs.

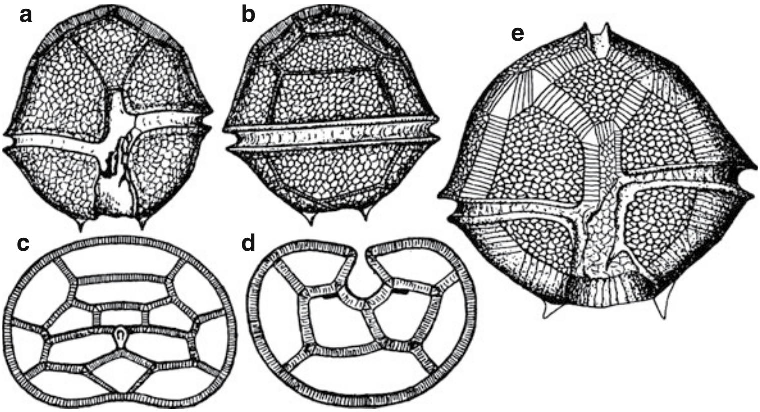

Fig. 238 *Peridinium bipes* f. *globosum* Er. Lindemann (**a**–**d** after Lindemann 1920; **e** after Lefèvre 1932). **a**–**d** ventral, dorsal, apical and antapical views; **e** ventral view of cell with wide sutures

Geographical distribution: Austria, Denmark (Moestrup, Calado, unpubl.); England (Lewis & Dodge); France, Switzerland (Lefèvre); Germany (Lemmermann, Lindemann); Poland (Wołoszyńska; Lindemann); Romania (Teodoresco); Sweden (Lemmermann). USA, OH (Carty). Hubei, China (Liu *et al.*).

f. *globosum* Er. Lindemann 1920, p. 132, figs 28–31 (**Fig. 238**)
Differs in the cells being spherical rather than pyriform (with a slight dorsoventral compression). All major plates are convex.
Geographical distribution: France (Lefèvre); Germany (Lindemann).

var. *occultatum* Er. Lindemann 1920, p. 132, fig. 35 (**Fig. 239**)
Nomenclatural synonym: *Peridinium bipes* f. *occultatum* (Er. Lindemann) M. Lefèvre 1932, p. 113

Differs in having the posterior extensions very small to entirely absent.
SEM: Boltovskoy (1977).
Geographical distribution: France (Lefèvre); Germany, Poland (Lindemann). Argentina (Boltovskoy).

Note: the designation "*P. bipes* f. *apoda* Boltovskoy" (1977, p. 149, figs 1–37), invalidly published (no type indicated), was intended for specimens without the antapical extensions that may be included in var. *occultatum*.

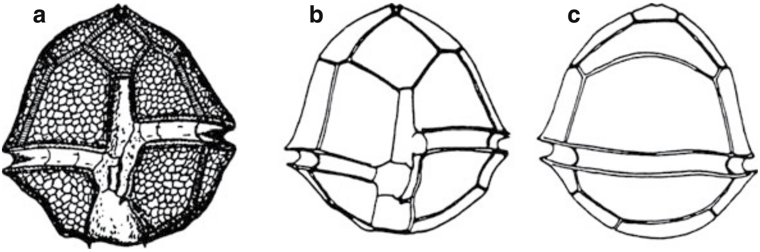

Fig. 239 *Peridinium bipes* var. *occultatum* Er. Lindemann (**a** after Lindemann 1920; **b**, **c** after Boltovskoy 1977). **a**, **b** ventral views; **c** dorsal view

12. *Peridinium limbatum* (A. Stokes) Lemmermann 1900b, p. (120) (**Fig. 240**)

Basionym: *Protoperidinium limbatum* A. Stokes 1887, p. 246, fig. 6
Taxonomic synonym: *Peridinium limbatum* subsp. *minnesotense* Eisenack *in* Eisenack & Fries 1965, p. 141

Cells pentagonal, strongly dorsoventrally compressed. Epicone triangular, longer than hypocone, which is deeply excavate at the bifurcate antapex. Apex pointed, often inclining towards the left. Cingulum descending, the ends displaced no more than one cingulum width. Sulcus extends to the antapex, and penetrates shortly onto the epicone. Amphiesmal plates reticulate. Numerous parietal chloroplasts. Cell length 76–93 µm, width 56–82 µm.
Cysts similar in shape to parent cell, with short blunt apical horn inclining to the left, moderately compressed. Paracingulum indicated by two rows of granules separated by smooth area. Posterior end with two, somewhat unequal short projections, the distal parts inclined towards the ventral surface. Surface variable, often with granules, spines or rods that define polygonal area comparable to amphiesmal plates in shape and position. With inner subcircular to subtriangular capsule, which lacks horns. It is released by the parental amphiesma splitting into a dorsal and a ventral part. The cyst germinates by splitting along a similar but not identical line. Cyst length 92–104 µm, width 64–82 µm.
SEM: Evitt & Wall (1968), Pfiester & Skvarla (1980), Kim *et al.* (2004).
DNA data: Kim *et al.* (2004).
Ecology: peaty pools; summer species.
Geographical distribution: England (Lewis & Dodge); Ireland (West & West; Lind & Pearsall). Ontario, Quebec, Canada (Bourrelly); Miquelon Island, near Newfoundland (Huber-Pestalozzi); USA, MA (Evitt & Wall), MN (Eisenack & Fries), NJ (Stokes), WI (Kim *et al.*).

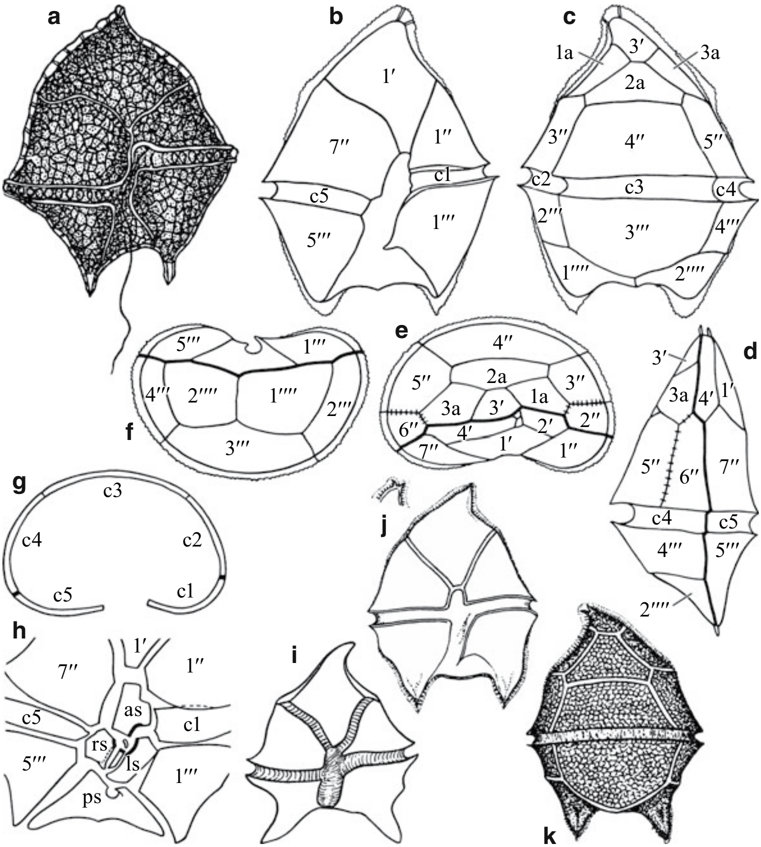

Fig. 240 *Peridinium limbatum* (A. Stokes) Lemmermann (**a** after Stokes 1887; **b**–**h** after Evitt & Wall 1968; **i** after Lind & Pearsall 1945; **j**, **k** after Huber-Pestalozzi 1950). **a** ventral view, inverted relative to the original, which depicts ventral features on a dorsal view; **b**, **c** ventral and dorsal views; **d**–**f** lateral, apical and antapical views, respectively, showing the line along which the amphiesma breaks open (thick lines) and the opening path along the cyst wall (differing only along the hachured lines); **g** cingulum in apical view; **h** sulcal plates, with the flagellar emergence area marked by thick lines and two accessory platelets unlabelled in the middle; **i**, **j** shape variation, ventral views (detail of apex on the left at **j**); **k** dorsal view with plate ornamentation

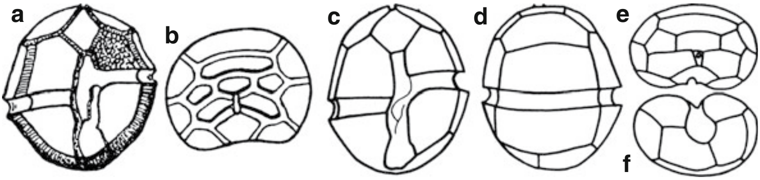

Fig. 241 *Peridinium playfairii* Er. Lindemann (**a**, **b** after Lindemann 1931; **c**–**f** after Ling *et al.* 1989). **a** ventral view, with plate ornamentation represented on plate 1″; **b** apical view, with thicker lines marking the position of comb-like lists; **c**–**f** ventral, dorsal, apical and antapical views, respectively

13. *Peridinium playfairii* Er. Lindemann 1931, p. 715, figs 43, 44 ("*Playfairi*") (Fig. 241)

Cells almost spherical, slightly compressed dorsoventrally. Epi- and hypocone of equal size or epicone slightly larger. Sulcus descending, the two ends displaced up to one cingulum width. Sulcus extends to the posterior end. Anteriorly it extends onto the epicone for about one cingulum width opposite the hypocone part of the sulcus. First apical plate rather small. Posterior rims of intercalary bands on the epicone with comb-like lists. Short list may also be present on the rims of the plates on the hypocone. Cell length 40–50 µm.
Ecology: muddy shallow waters.
Geographical distribution: Bali, Indonesia (Lindemann). Tasmania, Australia (Ling *et al.*).

Note 1: differs from *Peridinium volzii* mainly in the presence of the apical pore.

Note 2: cells of Tasmanian material ascribed to this species reported to be 39–63 µm long, 38–55 µm wide and 24–45 µm thick, therefore diverging from the original description by being distinctly compressed dorsoventrally (Ling *et al.* 1989).

Note 3: Thomasson (1974, p. 717) pointed out that two different species are represented in Playfair's original drawings of *Peridinium australe*, one without an apical pore, apparently of the *P. willei* group, and another where an apical pore is depicted. He indicated as representative of the pore-bearing species Playfair (1913, pl. lv, figs 7–9) and Playfair (1920, pl. XLII, fig. 8), and designated it "preliminarily" (and therefore not validly published) as "Peridinium sydneyense". This name has been used, and some documentation for this ornamented species has been given for localities in New Zealand (Cassie 1978; Cassie & Freeman 1980). However, its characters need to be further clarified before a useful description can be provided.

Group 3, the *P. crenulatum* group

Plate formula: po, x, **4–5′**, **1–3a**, **6″**, 5c, 4s, 5‴, 2⁗. Plates on the epicone symmetrically arranged around the apical pore.

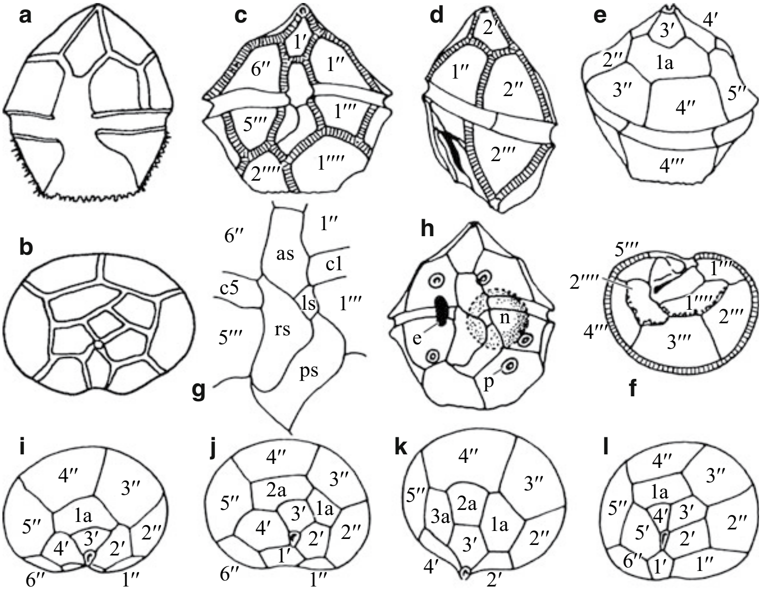

Fig. 242 *Peridinium crenulatum* Couté & A. Iltis (**a**, **b** after Couté & Iltis 1984; **c**–**l** after Da *et al.* 2004). **a** ventral view; **b** apical view with 2 intercalary plates; **c** ventral view; **d** ventral-left lateral view; **e** dorsal view; **f** antapical view; **g** sulcal plates; **h** ventral view showing eyespot (e), nucleus (n) and pyrenoids (p); **i**–**k** tabulation variants with 1, 2 and 3 intercalary plates, respectively; **l** tabulation variant with 5′ and 1a

14. *Peridinium crenulatum* Couté & A. Iltis 1984, p. 54, pl. II, figs 5, 6, pl. III, figs 1–6, pl. V, figs 7–10 (**Fig. 242**)

Nomenclatural synonym: *Bagredinium crenulatum* (Couté & A. Iltis) K. P. Da, Zongo, Mascarell & Couté 2004, p. 59

Cells ovoid, dorsoventrally compressed, epi- and hypocone of similar size. Ventral face of the cell flat. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus widens towards the antapex, becoming very wide, on the epicone extending for almost half the length of the epicone. Plate 3′ usually smaller than the other apical plates. Sutures between antapical plates, between antapical and postcingular plates and between 4‴ and 5‴ crenulated. Chloroplasts 4–6, parietal, yellowish-brown, provided with pyrenoid. An eyespot (sometimes two) reported at cingulum level or, occasionally, in the epi- or hypocone (Da *et al.* 2004). Cells 38–45 µm long, 35–52 µm wide, 29–32 µm thick.
SEM: Couté & Iltis (1984), Da *et al.* (2004).

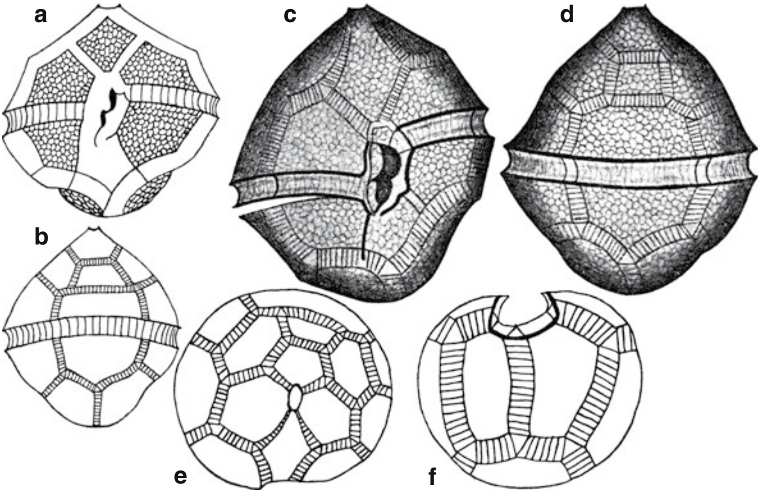

Fig. 243 *Peridinium gutwinskii* Wołoszyńska (**a**, **b** after Wołoszyńska 1912; **c**–**f** after Wołoszyńska 1923). **a** ventral view of cell with large sutures, showing plate ornamentation; **b** dorsal view; **c**, **d** ventral and dorsal views with ornamentation; **e**, **f** apical and antapical views

Ecology: in the plankton of River Bandama, Ivory Coast, near Marabadiassa and in Taabo reservoir; in Bagré reservoir, River Nakambé, Burkina Faso. Mainly in spring and summer.
Geographical distribution: Burkina Faso (Da *et al.*); Ivory Coast (Couté & Iltis; Da *et al.*).

Group 4, the *P. gutwinskii* group

Plate pattern **nearly symmetrical**, the first and second intercalary plates touching the large precingular plate 4. The second intercalary plate is four-sided. Plate formula: po, x, **4′, 3a, 7″**, 5c, 5s, 5‴, 2⁗.
A group of two species, both in need of examination.

15. ***Peridinium gutwinskii*** Wołoszyńska 1912, p. 701, text-fig. 22 (Fig. 243)

"Une espèce exotique" (Lefèvre 1932)

Cells rounded to ovoid, almost as long as wide, slightly dorsoventrally compressed. Epi- and hypocone of almost the same size or epicone slightly larger than hypocone. Epicone rounded conical, hypocone rounded. Cingulum descending, the ends displaced about 1.5× the cingulum width. Sulcus barely extends onto the epicone. On the hypocone it widens but does not reach the antapex. Plates 2′, 3′ and 4′ all

5-sided (or 6-sided when counting the suture towards the apical pore plate), 1a and 3a 6-sided, 2a 4-sided. The sutures of the cingulum generally follow the sutures of the postcingulars. The dorsal part of the cell with a symmetry line formed by 3′, the small 4-sided 2a, the large 4″, the equally wide 3c, and 3‴ on the hypocone. Sutures are often wide, and the amphiesmal plates distinctly reticulate. The amphiesma opens along the anterior rim of the cingulum. Chloroplasts brown. Nucleus centrally located, horseshoe shaped. Cell length 40–60 µm, width 35–60 µm. Resting cyst unknown.
SEM: Couté & Tell (1990), Liu *et al.* (2008a).
Ecology: tropical plankton species, presently known with certainty only from South-East Asia and West Africa.
Distribution: Ivory Coast (Couté & Iltis). Hubei, Guangdong, China (Liu *et al.*); Indonesia, in Java (one of the commonest species of *Peridinium*) and Sumatra, often bloom-forming (Wołoszyńska, Lindemann, Couté & Tell), Borneo, Bali (Lindemann); Malaysia, in Sabah, sometimes dominant (Mohammad-Noor & Moestrup, unpubl.).

Note: this species was reported from Madagascar by Lefèvre (1932). However, the material he described as *P. gutwinskii* tab. δ-travectum (Lefèvre 1932, p. 118, figs 385–388) differs in many respects, notably in the shape of the intercalary plates (5-sided rather than 4- and 6-sided) and appears to be related to the following species.

16. *Peridinium corrientes* Moestrup *sp. nov.* (**Fig. 244**)

Type: Boltovskoy 1989, *Nova Hedwigia* **49**, figs 1–5, representing the plate arrangement of a cell in different views, from a collection taken near Colonia Garani (*ca.* 28˚12′S, 55˚48′W), NW Corrientes, Argentina, in April 1975. Preserved material from this collection is not known to exist.

Cells biconical, epicone longer than hypocone, moderately flattened dorsoventrally. Width and length similar. Antapex with posteriorly directed spine. Cingulum descending, the ends displaced 2.5–3 cingulum widths. The sulcus extends for a short distance onto the epicone, forming a short, narrow tube. Plate 7″ extends as a lobe over the sulcus, which is very narrow in the area between the two ends of the cingulum. Plate 1a hexagonal, 2a and 3a both pentagonal. Plate 3a does not touch 4″. The spine is attached to the ventral-median corner of 2⁗. Plate surface areolated. Width of intercalary bands variable. Cell length 65–85 µm (without the spine), width 53–76 µm. Cyst unknown.
SEM: Boltovskoy (1989, identified as *P. gutwinskii*).
Ecology: found in a shallow swamp, pH 6.5–6.8, associated with *Lemna*, *Azolla*, *Ricciocarpus* and *Spirodela*.
Geographical distribution: Argentina (Boltovskoy). Madagascar (Lefèvre)?

Genus 6. *Staszicella* Wołoszyńska 1916, p. 277

Type species: *Staszicella dinobryonis* Wołoszyńska 1916

Cells spherical or oval. Epicone smaller than hypocone. Plate pattern on the epicone asymmetrical, plate formula: po, x, 5′, 1a, 7″, 6c, 5s?, 5‴, 2⁗.

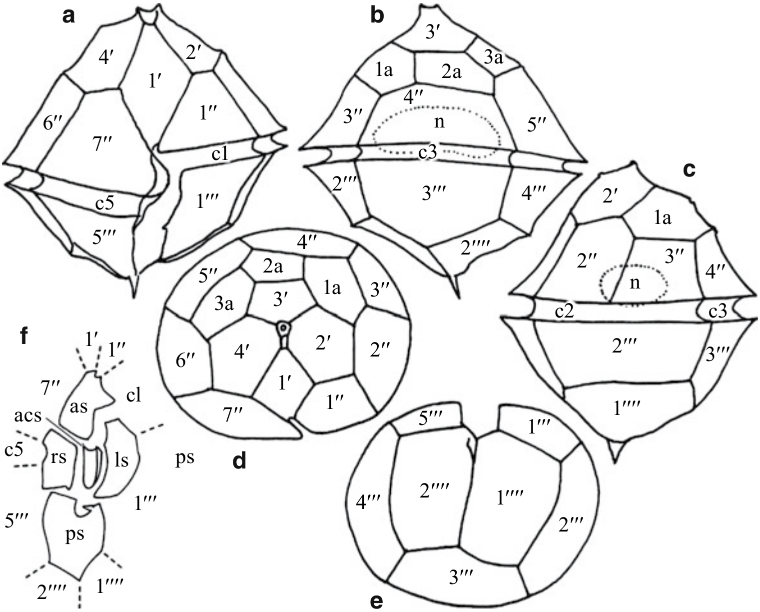

Fig. 244 *Peridinium corrientes* Moestrup (after Boltovskoy 1989). **a** ventral view; **b**, **c** dorsal and left lateral views, respectively, with the position of the nucleus (n); **d**, **e** apical and antapical views; **f** detail of sulcal and surrounding plates

1. ***Staszicella dinobryonis*** Wołoszyńska 1916, p. 278, pl. 12, figs 32–40 (**Fig. 245**)

Nomenclatural synonym: *Glenodinium dinobryonis* (Wołoszyńska) Er. Lindemann 1926a, p. 439 ≡ *Peridiniopsis dinobryonis* (Wołoszyńska) Bourrelly 1968, p. 9

Epicone smaller and slightly narrower than hypocone. Cells very slightly dorso-ventrally flattened. Cingulum descending, displaced *ca.* half a cingulum width. Sulcus continues onto the epicone lined by short flange on the right side. On the hypocone it widens and extends to the antapex. Amphiesmal plates thin, smooth, with scattered pores. Older cells sometimes with papillae along the sutures of the epicone. Plate 1′ usually very narrow, arranged as a continuation of the sulcus. Plate 1a small and rhomboid. Right sulcal plate with distinct flange on the left side, extending into the cingulum. The two antapical plates equal in size. Chloroplasts difficult to detect, perhaps absent. Eyespot not detected with certainty. Nucleus round, central. Cell cover opens along the cingulum. Cell division within the parental amphiesma. Cells 19–25 μm long, 18–23 μm wide. Resting cells unknown.
SEM: Hansen & Flaim (2007).

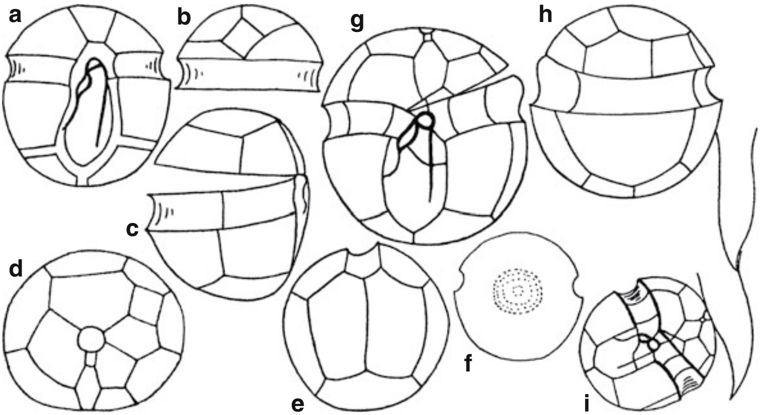

Fig. 245 *Staszicella dinobryonis* Wołoszyńska (**a**–**f** after Wołoszyńska 1916; **g**, **h** after Wołoszyńska 1917; **i** after Wołoszyńska 1952). **a** ventral view; **b** left view of anterior part of cell cover; **c** right view, opening along the upper edge of the cingulum; **d**, **e** apical and antapical views; **f** outline of cell showing the position of the nucleus; **g**, **h** ventral and dorsal views with plate arrangement; **i** cell attached by the apical end to a lorica of *Dinobryon*

Ecology: ponds and lakes, attached with the front end, apparently the apical pore, to *Dinobryon* or, if *Dinobryon* is absent, free-swimming. A transparent, sticky mass is extruded from the pore and attaches the cells to *Dinobryon* loricae.
Geographical distribution: Finland (Lindemann)?; Germany (Lindemann); Italy, March–July in several lakes in Trentino Province (Hansen & Flaim); Switzerland (Lindemann); Ukraine (Wołoszyńska).

Note: some variation in plate pattern has been noted: 4 rather than 5 apical plates, 8 rather than 7 precingular plates, 1 elongate rather than rhomboid intercalary plate (Wołoszyńska 1917, pl. 12, fig. 27). However, the more extensive variations in cell shape, arrangement of plates and size of apical pore described by Lindemann (1926a) are not considered to represent this species (Hansen & Flaim 2007, Craveiro *et al.* 2013).

Genus 7. *Thompsodinium* Bourrelly 1970, p. 81

Type species: *Thompsodinium intermedium* Bourrelly 1970

The genus was originally described as being characterized by having a posterior intercalary plate (1p). Subsequent observations have not confirmed this interpretation (Popovský 1970, Carty 1989). However the genus differs from other peridinioids in having a unique combination of plates on the epicone, and we are retaining it pending further studies. An apical pore complex (apc) is present, but was not described in detail. Plate formula: apc, 4′, 3a, 6″, 6c, 4s, 5‴, 2⁗.

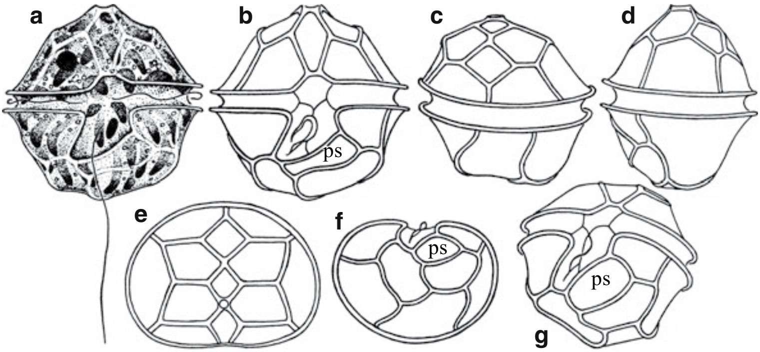

Fig. 246 *Thompsodinium intermedium* Bourrelly (after Thompson 1951). **a** live cell, ventral view; **b**–**d** ventral, dorsal and left views, respectively, showing plate arrangement; **e**, **f** apical and antapical views; **g** ventral-antapical view (the area marked "ps" on **b**, **f** and **g** is here interpreted as the posterior sulcal plate)

1. *Thompsodinium intermedium* Bourrelly 1970, p. 81 (**Fig. 246**)

Replacement name for *Peridinium intermedium* R. H. Thompson 1951, p. 298, figs 80–88, *nom. illeg.* [non *Peridinium intermedium* (Playfair) Playfair 1920, nec *P. intermedium* Candeias 1939, p. 243, fig. 5, a marine species]

Cells ovate to spherical and angular, slightly dorsoventrally compressed. Epi- and hypocone of almost equal size. Cingulum only little displaced. Sulcus not reaching the antapex, extending slightly onto the epicone. Antapical wing-like flange present, located on the sutures between the antapical plates and postcingular plates 2, 3 and 4; it was mentioned by Carty (1989) to be a useful feature for identifying this species. Sutures striated. Chloroplasts pale to deep brown. Eyespot pale to deep red. Amphiesmal plates smooth, penetrated by numerous pores, especially along the sutures and the cingulum. Cell length 30–46 µm, width 28–40 µm.
SEM: Carty (1989, 2003), Carty & Wujek (2003).
Ecology: ponds, lakes; abandoned clay pit (Thompson 1951).
Geographical distribution: USA, KS (Thompson), OH, NY, TX, (Carty). Belize (Carty & Wujek); Cuba (Popovský).

Note: *Peridinium pseudointermedium* Couté & A. Iltis (1984, p. 55, pl. II, figs 1–4, pl. VI, figs 32–34; "*pseudo-intermedium*") differs in having a slightly smaller maximum size (cell length 36–40 µm, width 30–33 µm) and in lacking the posterior intercalary plate that was originally interpreted to be present in *Thompsodinium*. It is otherwise identical.

Family 5. Protoperidiniaceae Balech 1988, p. 77, *nom. cons.*

Taxonomic synonyms: Kolkwitziellaceae Er. Lindemann 1928b, pp 34, 70, 71; Diplopsalidaceae Matsuoka 1988, p. 98

Apical pore present. One or 2 (in *Protoperidinium* and *Amphidiniopsis*) antapical plates. No posterior intercalary plates. The plate formula and the arrangement of the plates on the epicone is very different in the five genera included (from 9 epiconal plates in *Matvienkoella* to 14 in *Protoperidinium*) and freshwater species of all genera are in need of molecular analysis. Classification into Protoperidiniaceae must therefore be taken as a qualified guess and somewhat preliminary.
Most species are marine and lack chloroplasts. In fresh water 5 genera, three of which lack chloroplasts (*Protoperidinium*, *Amphidiniopsis* and *Kolkwitziella*), while *Kansodinium* and *Matvienkoella* have brown chloroplasts of unknown origin.

Key to the genera of Protoperidiniaceae occurring in fresh water:

1a	Epicone much smaller than hypocone, two antapical plates	1. *Amphidiniopsis*
1b	Epicone of the same size or slightly larger than hypocone	2
2a	Two antapical plates	5. *Protoperidinium achromaticum*
2b	One antapical plate	3
3a	Chloroplasts absent, epicone conical and hypocone rounded ..	3. *Kolkwitziella*
3b	Chloroplasts and eyespot present	4
4a	Epicone helmet-shaped, larger than hypocone, plates on the epicone symmetrically arranged (apical view), cells 17–23 µm long	4. *Matvienkoella*
4b	Epi- and hypocone of almost the same size, plates on epicone very asymmetrical in apical view, cells 31–42 µm long	2. *Kansodinium*

Genus 1. *Amphidiniopsis* Wołoszyńska 1929, p. 174, 256

Type species: *Amphidiniopsis kofoidii* Wołoszyńska 1929, p. 174, pl. VII (from Baltic Sea)

Epicone much shorter than hypocone. Cells bilaterally or dorsoventrally distinctly compressed. Cells surrounded by distinct amphiesmal plates. The plate formula given for the type species was 3′, 7″, 5‴, 2″″. However, Hoppenrath (2001), based on studies of several marine species, gave the plate formula: po, 4′, 1–3a, 6–8″, 5–8c, 3–5s, 5–6‴, 2″″. Chloroplasts absent. Type species originally described from brackish water in the Baltic, and several marine species are now known. A freshwater species was subsequently found in a lake in Canada in 1997. Molecular analysis of some marine species of *Amphidiniopsis* (SSU rDNA) has shown phylogenetic relationship between these species and *Protoperidinium* (Hoppenrath *et al.* 2012).

1. *Amphidiniopsis sibbaldii* K. H. Nicholls 1999, p. 74 (**Fig. 247**)

Description and illustrations in Nicholls (1998, p. 338, figs 1–20), where the species name was not validly published for lack of complete reference to type material

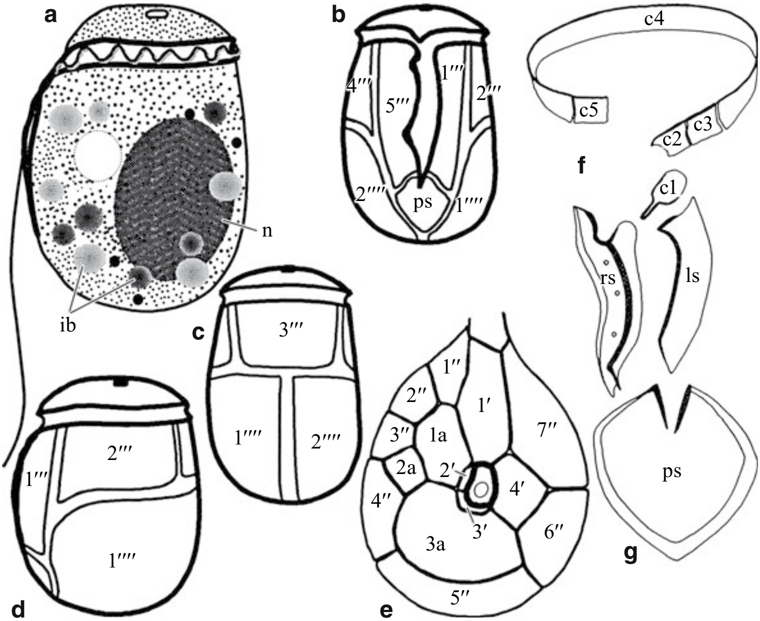

Fig. 247 *Amphidiniopsis sibbaldii* K. H. Nicholls (after Nicholls 1998). **a** left lateral view of live cell, with dorsal-posterior nucleus (n) and inclusion bodies (ib); **b**–**d** ventral, dorsal and left lateral view of cell cover, respectively, with major plates labelled; **e** apical view of cell cover, with plates interpreted according to Nicholls (1998); **f** cingular and adjacent sulcal plates right (rs) and left (ls); **g** posterior sulcal plate (ps)

Cells ovoid, bilaterally compressed. Epicone one quarter of hypocone length. Cingulum circular. Sulcus extends from the cingulum towards the antapex but terminates before reaching the antapex. Chloroplasts absent. Eyespot absent. Nucleus in the cell posterior. Cell length 33–45 µm, width 19–29 µm, thickness 24–35 µm. Cell division takes place after loss of motility, the contents of the cell dividing into two daughter cells complete with amphiesmal plates and flagella. They are released through slit in the dorsal plates of the parent cell. Plate formula: po, 4′, 3a, 7″, 5c, 4s, 5‴, 2⁗.
Ecology: in sand along the shore of mesotrophic Lake Simcoe, Canada, on 30 October 1997, in water at 9 °C. Subsequently kept for some time in the laboratory at 16–19 °C.
Geographical distribution: Canada.

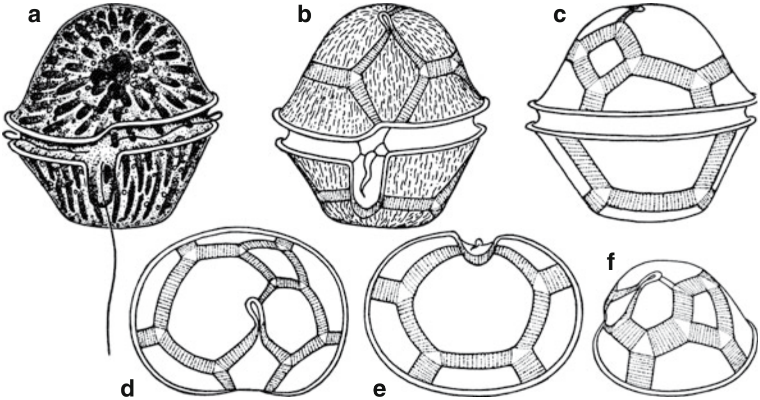

Fig. 248 *Kansodinium ambiguum* (R. H. Thompson) Carty & El.R. Cox (after Thompson 1951). **a** ventral view of living cell; **b**–**e** ventral, dorsal, apical and antapical views; **f** left lateral view of plates on tilted epicone

Genus 2. *Kansodinium* Carty & El.R. Cox 1986, p. 197

Type species: *Kansodinium ambiguum* (R. H. Thompson) Carty & El.R. Cox 1986

Plate formula: po, x, 3′, 1a, 5″, ?c, ?s, 5‴, 1⁗. Apical pore surrounded by horseshoe-shaped ridge which opens towards the ventral side of the cell. Theca thin, cingular and sulcal plates not described. Second and third apical plate of very different size. Anterior intercalary plate eccentric, rhomboidal-square.

1. *Kansodinium ambiguum* (R. H. Thompson) Carty & El.R. Cox 1986, p. 197 (**Fig. 248**)

Basionym: *Glenodinium ambiguum* R. H. Thompson 1951, p. 294, figs 73–79
Nomenclatural synonym: *Diplopsalis ambigua* (R. H. Thompson) Bourrelly 1970, p. 78 (“*ambiguum*”)

Cells ovate, elliptical to spherical, slightly dorsoventrally compressed. Theca lightly reticulate. Cingulum barely displaced. Sulcus does not enter the epicone. Antapically it does not reach the antapex. Sutures striated. Chloroplasts dark brown. With elongate eyespot. Cells 31–42 μm long, 27–40 μm wide, 27–31 μm thick.
SEM: Carty & Cox (1986).
Ecology: in creeks, oxbow and lake in Kansas and Texas, in June and July.
Geographical distribution: USA, KS (Thompson; Carty & Cox).

Genus 3. ***Kolkwitziella*** Er. Lindemann 1919, p. 219

Type species: *Kolkwitziella salebrosa* Er. Lindemann 1919, herein considered synonymous with *Kolkwitziella acuta* (Apstein) Elbrächter 1993

Amphiesmal plates relatively thick, chloroplasts absent. Plate formula 4′, 2a, 7″, 3c, ?s, 5‴, 1⁗.

1. *Kolkwitziella acuta* (Apstein) Elbrächter 1993, p. 174 (**Fig. 249**)

Basionym: *Glenodinium acutum* Apstein 1896, p. 152, fig. 54
Nomenclatural synonyms: *Diplopsalis acuta* (Apstein) Entz 1904, p. 12 ≡ *Peridinium latum* Paulsen 1908, p. 41, replacement name (non *Peridinium acutum* G. Karsten 1907, p. 417, pl. L, fig. 8) ≡ *Entzia acuta* (Apstein) M. Lebour 1922, p. 808 ≡ *Apsteinia acuta* (Apstein) T. H. Abé 1981, p. 16 (legend to fig. 1)
Taxonomic synonyms (based on observations by Sebestyén 1935): *Kolkwitziella salebrosa* Er. Lindemann 1919, text-figs 6–9, pl. 17, fig. 1; *Kolkwitziella salebrosa* var. *gibbera* Er. Lindemann 1924b, p. 439, pl. 21, figs 7–10 ≡ *Kolkwitziella gibbera* (Er. Lindemann) Er. Lindemann 1928b, p. 72

Epicone slightly larger than hypocone. Epicone conical, extended into a short apical horn; epicone slightly concave (plate 1′ concave), hypocone rounded. Plate pattern nearly symmetrical, 3′ very small, dorsal, 2′ and 4′ almost equal, to the left and right, respectively. Plate 2c very large, U-shaped, 1c and 3c small. Plates with small pointed granules, finely areolated. Chloroplasts absent. Cytoplasm pink to reddish/brown. Nucleus elongate, central. Cell length 30–39 µm, width 26–27 µm.
Nutrition heterotrophic, but food uptake not reported.
Cyst resembling the motile cell in shape, epicone rounded conical, hypocone with ventral bulge on each side. Cyst wall rough, cyst smoke gray. Distinct paracingulum and parasulcus present. Cyst 41–45 µm long, 45–50 µm wide and 36–39 µm thick.
SEM: Bourrelly & Couté (1980), Pollingher & Hickel (1991), Olrik (1997), Pandeirada *et al.* (2013).
Ecology: typical in plankton of larger eutrophic lakes, also seen in brackish water (Lemmermann 1910). In central Europe Höll (1928) found it at pH 7.5–7.8, blooms occurring in mesotrophic lakes rich in calcium. In Denmark occurring April–October, often maximum in late summer (large bloom in Lake Furesø, 1 Sept. 2007).
Geographical distribution: Denmark (Nygaard; Moestrup & Calado, unpubl.); Hungary (Entz; Sebestyén); Germany, Poland (Lemmermann; Lindemann; Höll); Portugal (Pandeirada *et al.*); Sweden (Skuja). USA, OH (Carty).

Note: Skuja (1948) observed a pusule-like contractile vacuole in the middle of the hypocone. Systole took place once every 1–2 min. When largest at diastole, the vacuole was spherical and sharply delineated, when in systole it was not readily visible. During the bloom in Furesøen, Denmark, in 2007, and on several occasions in Portuguese populations we carefully checked the cells for contractile vacuoles but could not confirm Skuja's observations.

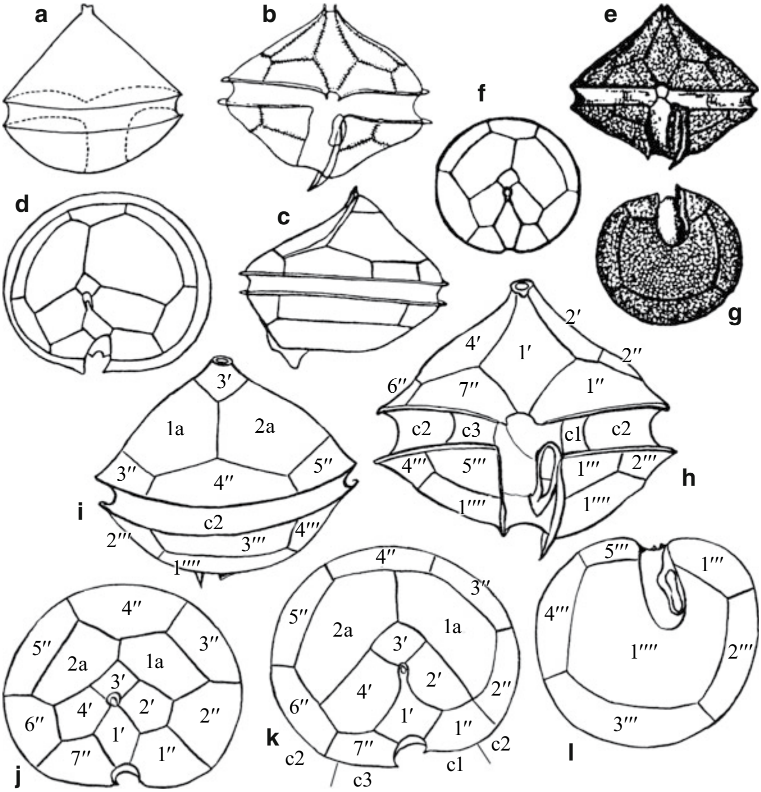

Fig. 249 *Kolkwitziella acuta* (Apstein) Elbrächter (**a** after Apstein 1896; **b**–**d** after Entz 1904; **e**–**g** after Lindemann 1920; **h**–**l** after Bourrelly 1970). **a** outline of cell in dorsal view; **b** ventral view; **c** left lateral view; **d** slightly tilted apical view; **e**–**g** ventral, apical and antapical views; **h**, **i** ventral and dorsal views; **j** apical view, relatively small intercalary plates; **k** apical view, large intercalary plates; **l** antapical view

Genus 4. ***Matvienkoella*** Moestrup & Calado *gen. nov.*

Type species: *Matvienkoella ovum* Moestrup & Calado
Etymology: the name honors Alexandra Michailovna Matvienko (1910–1996), former professor at the Kharkov University, Ukraine, who described the only known species of the genus.

Photosynthetic dinoflagellates. Amphiesmal plates well developed. Plate formula: po, x, 4′, 0a, 5″, ?c, ?s, 5‴, 0p, 1⁗.

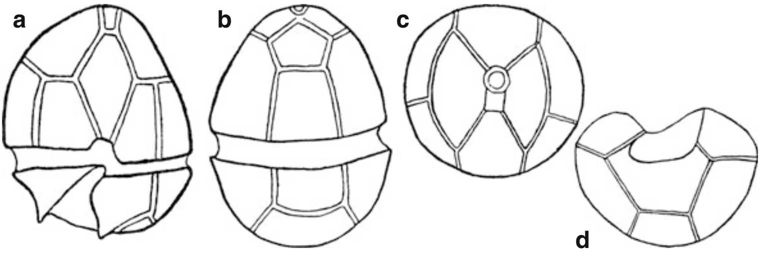

Fig. 250 *Matvienkoella ovum* (Bourrelly) Moestrup & Calado (after Matvienko 1938). **a**–**d** ventral, dorsal, apical and antapical views, respectively, showing the main plates

1. *Matvienkoella ovum* (Bourrelly) Moestrup & Calado *comb. nov.* (**Fig. 250**)

Basionym: *Diplopsalis ovum* Bourrelly 1970, *Les algues d'eau douce* **3**, p. 78, here taken as replacement name (under Art. 58, McNeill *et al.* 2012) for *Peridinium ovum* Matvienko 1938, *Trudy Nauchno-Issl. Inst. Bot.* **3**, pp 61, 70, pl. III, figs 29–38, *nom. illeg.* (non *Peridinium ovum* J. Schiller 1911, p. 332, fig. 1)

Cells oval, not dorsoventrally flattened. Epicone larger than hypocone. Epicone helmet shaped, hypocone rounded. Sulcus extends very slightly onto the epicone, on the hypocone it widens towards the antapex. Cingulum descending, the ends displaced *ca.* one cingulum width. Numerous discoid chloroplasts, sometimes radially arranged. Eyespot present, up to 3 um long. Reproduction by division into two cells in immobile stage. Cell length 17–23 µm, width 12–20 µm.
Ecology: peat bogs.
Geographical distribution: Ukraine (Matvienko).

Genus 5. *Protoperidinium* Bergh 1881, p. 234

Type species: *Protoperidinium pellucidum* Bergh 1881, p. 227, figs 46–48 (marine)

Characterized by having only 4 plates (3 + 1 transitional plate) in the cingulum. Chloroplasts absent. Plate formula: po, x, 4′, 2–3a, 7″, 4 (3 + 1)c, 6–7?s, 5‴, 2″″.

1. *Protoperidinium achromaticum* (Levander) Balech 1974, p. 56 (**Fig. 251**)

Basionym: *Peridinium achromaticum* Levander 1902, p. 49B, figs 1, 2

Cells rhombic, dorsoventrally somewhat flattened, antapex excavate. Cingulum circular, sulcus wide, not or very barely extending onto the epicone. The edges of the sulcus raised, with small spines at the antapical end. Plate 1′ four-sided, 2a six-sided. Nucleus elongate kidney-shaped, central. Cell length 28–48 µm, width 24–40 µm. Cyst globular (Ostenfeld 1908, described from an Aral Sea population with only two anterior intercalary plates).

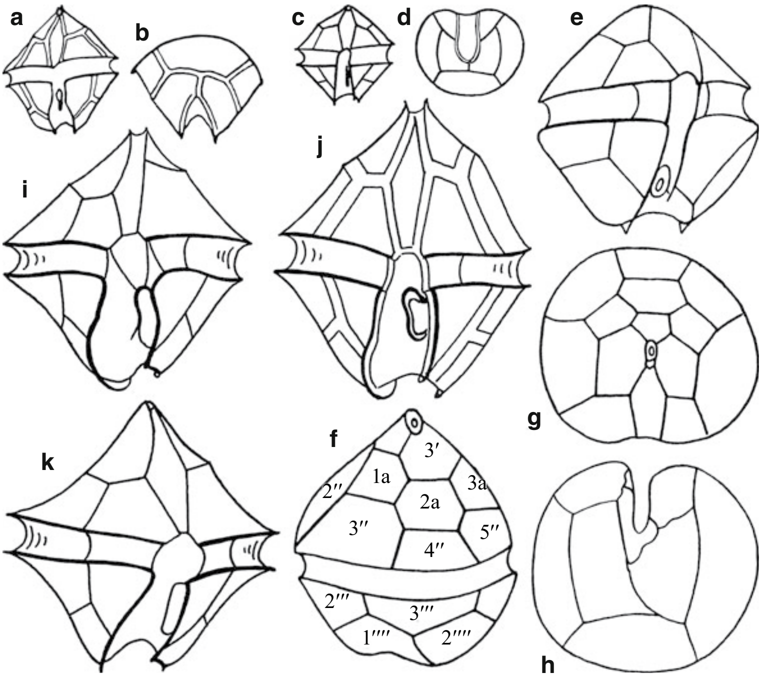

Fig. 251 *Protoperidinium achromaticum* (Levander) Balech (**a**, **b** after Levander 1902; **c**, **d** after Ostenfeld 1908; **e**–**h** after Biecheler 1952; **i**–**k** after Wołoszyńska 1929). **a** ventral view; **b** dorsal view of posterior end; **c**, **d** ventral and antapical views; **e**–**h** approximately ventral, dorsal, apical and antapical views; **i**–**k** ventral views showing shape variation

Ecology: pool in a heath, Mark Brandenburg (Lemmermann 1910); mainly marine. Geographical distribution: widely distributed in brackish and marine waters around the world. Also reported from fresh water in Germany (Lemmermann) and Poland (Wołoszyńska).

Family 6. Thecadiniaceae Balech 1956, p. 36 ("Thecadinidae")

Cells covered with thick amphiesmal plates. Epicone much smaller than hypocone. Chloroplasts present.

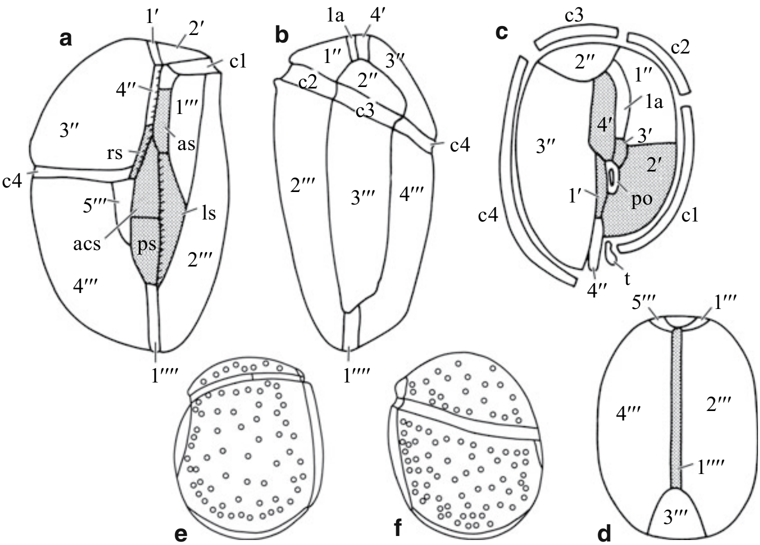

Fig. 252 *Thecadiniopsis tasmanica* Croome, Hallegraeff & P. A. Tyler (after Croome *et al.* 1988). **a** ventral view, with sulcal plates stippled and wings indicated by hatched lines; **b** dorsal view; **c** apical view, with apical plates stippled (t, transitional plate); **d** antapical view, with antapical plate stippled; **e**, **f** left lateral and right lateral views, respectively. Plate interpretation following Croome *et al.* (1988)

Genus 1. ***Thecadiniopsis*** Croome, Hallegraeff & P. A. Tyler 1988, p. 331

Type species: *Thecadiniopsis tasmanica* Croome, Hallegraeff & P. A. Tyler 1988

Photosynthetic, with thick amphiesmal plates, plate formula po, 4′, 1a, 4″, 5c, 5(?) s, 5‴, 1⁗. Amphiesma very asymmetrical. Cells strongly laterally compressed, in side view more or less ovoid. Cingulum displaced about 1/3–1/2 the cell length, the right side of the epicone therefore much longer than the left side. With pore plate and many plates on the epicone. Two lateral postcingular plates large and single antapical plate.

1. *Thecadiniopsis tasmanica* Croome, Hallegraeff & P. A. Tyler 1988, p. 331, figs 2–22 (**Fig. 252**)

Cells ovoid, bilaterally flattened. Cingulum descending strongly, the two ends displaced *ca.* 5 cingulum widths, the right side of the epicone therefore much longer than the left side. Apical plates 1′ and 4′ long and narrow, 3′ very small, 2′ large, occupying almost a quarter of the epicone. Anterior intercalary plate long

and narrow. Of the four precingular plates, 3″ occupies a very large part of the right side of the epicone, 4″ is short and very narrow. On the hypocone 2‴ and 4‴ are large and occupy most of the lateral sides, 3‴ is narrow, and the single antapical plate is very long and narrow. Plates with numerous large pores. Numerous chloroplasts scattered in the cell. Cell length 42–48 µm, width 36–41 µm, thickness 25–30 µm.
SEM: Croome *et al.* (1988), Ling *et al.* (1989).
Ecology: plankton in dystrophic fresh waters and coastal lagoons in Tasmania, at pH 3.6–5.6 and conductivity of 22–445 $\mu S \cdot cm^{-1}$, in Lake Garcia with 4×10^5 cells per liter on 5 May 1985. Also alpine dystrophic (Ling *et al.* 1989).
Geographical distribution: Tasmania, Australia.

Order 7. THORACOSPHAERALES Tangen *in* Tangen *et al.* 1982, p. 210

Cells with amphiesmal plates of very different thickness, in some species plates difficult to see in the light microscope. Plate formula po, cp, x, 4–5′, 0–3a, 6–7″, 6c, 5–?s, 5‴, 2⁗. Eyespot, if present, of type A. Peduncle, if present, supported internally by a microtubular basket, in which the microtubules are arranged in several layers. Resting cysts calcified or non-calcified.
The order comprises the families Thoracosphaeraceae and Pfiesteriaceae, and includes marine genera such as *Scrippsiella*, *Pfiesteria* and *Thoracosphaera*. Most of the freshwater species were previously included in *Peridinium* and *Peridiniopsis* but electron microscopy and molecular data have demonstrated the polyphyletic nature of these genera as previously described. The chloroplast-containing species transferred from *Peridinium* to *Chimonodinium* and *Apocalathium* below are all in need of study to determine whether they belong to these or to separate, undescribed genera.
The genus *Thoracosphaera* is characterized by coccoid cells surrounded by a calcareous cell wall and when first described *Thoracosphaera* was thought to be a coccolithophorid.

Key to the families of Thoracosphaerales occurring in fresh water:
1a Cells without chloroplasts .... 1. Pfiesteriaceae
1b Cells with chloroplasts .... 2. Thoracosphaeraceae

Family 1. Pfiesteriaceae Steidinger & J. M. Burkholder *in* Steidinger *et al.* 1996, p. 158

Phagotrophic, mostly marine species. Chloroplasts absent. Amphiesmal plates thin but visible in empty cells or in the SEM. Cells ingest food through a feeding tube supported by overlapping rows of microtubules (microtubular basket). Resting cysts non-calcified. Plate formula: po, cp, x, 4–5′, 0–2a, 5–7″, 6c, pc + 5–?s, 5‴, 0p, 2⁗. The proximal part of the longitudinal flagellum is located in a tube, formed by a flap-like plate interconnecting sulcal plates on the right and left hand side of the sulcus (peduncle cover plate, pc).

According to present knowledge the Pfiesteriaceae form a distinct group that appears nested within the Thoracosphaeraceae (Gottschling *et al.* 2012).

In fresh water only 2 (3) genera with 3 species. The marine and brackish water species *Pfiesteria shumwayae*, which is known to cause fishkills, can be adapted to and grown in fresh water in the laboratory, but there appear to be no reports of its occurrence in fresh water in nature.

Key to the genera of Pfiesteriaceae occurring in fresh water:

1a Cells spherical, ellipsoidal or rhomboidal, in ventral view round to oval 2
1b Cells fungiform, epicone longer and wider than hypocone ...... 2. *Speroidium*
2a Epicone without intercalary plates; common freshwater species .... 3. *Tyrannodinium*
2b One intercalary plate present on the epicone; marine species that may adapt to fresh water .... 1. *Pfiesteria*

Genus 1. ***Pfiesteria*** Steidinger & J. M. Burkholder *in* Steidinger *et al.* 1996, p. 158

Type species: *Pfiesteria piscicida* Steidinger & J. M. Burkholder *in* Steidinger *et al.* 1996, p. 159, figs 1–10 (marine species)

Epi- and hypocone of approximately the same size, *i. e.* the cingulum more or less equatorial. Cells covered with very thin plates arranged according to the formula po, cp, x, 4′, 1a, 5–6″, 6c, pc, 5s, 5‴, 0p, 2⁗. Phagotrophic, food uptake by means of a hollow peduncle (feeding tube).

1. *Pfiesteria shumwayae* Glasgow & J. M. Burkholder *in* Glasgow *et al.* 2001, p. 237, figs 1–6, 11–13 (**Fig. 253**)

Nomenclatural synonym: *Pseudopfiesteria shumwayae* (Glasgow & J. M. Burkholder) Litaker, Steidinger, P. Mason, Shields & P. Tester *in* Litaker *et al.* 2005, p. 647

Cells oval, epicone slightly wider than hypocone. Cingulum descending, the ends displaced *ca.* half the cingulum width. Sulcus extends to the antapex. Nucleus in the hypocone. Tabulation with 6 precingular plates. Cell length 8–24 µm, width 7–18 µm.

SEM: Glasgow *et al.* (2001), Burkholder *et al.* (2001), Mason *et al.* (2003), Parrow & Burkholder (2003; fusing gametes and planozygote), Marshall *et al.* (2006).

TEM: Marshall *et al.* (2006).

DNA data: Glasgow *et al.* (2001), Marshall *et al.* (2006).

Ecology: a marine or brackish water species that can adapt to fresh water; it has been shown to grow well in full strength seawater as well as in freshwater media (Moestrup *et al.* 2014). It may cause extensive fishkills, apparently due to production of toxin(s). See further in the chapter on toxic dinoflagellates.

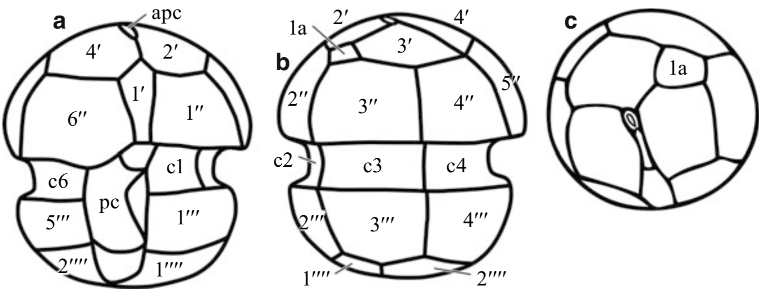

Fig. 253 *Pfiesteria shumwayae* Glasgow & J. M. Burkholder (**a**, **b** after Glasgow *et al.* 2001; **c** after Litaker *et al.* 2005). **a** ventral view with main amphiesmal plates and the peduncle cover (pc) in the sulcus; **b** dorsal view; **c** apical view

Geographical distribution: Denmark (Moestrup *et al.*); Latvia (Allen *in* Glasgow *et al.*); Norway (Jakobsen *et al.*). USA, E and SE coast (Glasgow *et al.*). New Zealand (Allen *in* Glasgow *et al.*; Rhodes *et al.*).

Genus 2. *Speroidium* Moestrup & Calado *gen. nov.*

Type species: *Speroidium fungiforme* (Anisimova) Moestrup & Calado
Etymology: the name honors Howard J. Spero for his inspiring work on the feeding mode and chemosensory capabilities of *Speroidium fungiforme*.

Cells fungiform, epicone longer and wider than hypocone. Plate formula apc, 4′, 2a, 6″, ?c, ?s, 5‴, 2⁗. Differs from the marine genus *Luciella* in the absence of a canal plate in the apical pore complex, the pentagonal rather than quadrangular 2a plate (Calado *et al.* 2009), and in SSU rDNA molecular phylogeny.
The clone known as "Bullet" (strain VDH034S) by Seaborn *et al.* (2006) agrees in shape with Anisimova's (1926) and Spero's (1982) material and can be considered to represent this species.

Key to species of *Speroidium*:
1a Cingulum descending, the ends displaced *ca.* 1 cingulum width; mainly in brackish water .... 1. *S. fungiforme*
1b Cingulum circular (ends not displaced); freshwater species ... 2. *S. austriacum*

1. *Speroidium fungiforme* (Anisimova) Moestrup & Calado *comb. nov.*
(**Fig. 254**)

Basionym: *Gymnodinium fungiforme* Anisimova 1926, *Russk. Gidrobiol. Zhurn.* **5**, pp 191, 193, figs 9, 10
Nomenclatural synonyms: *Massartia fungiformis* (Anisimova) J. Schiller 1955, p. 47 ≡ *Katodinium fungiforme* (Anisimova) A. R. Loeblich 1965, p. 16

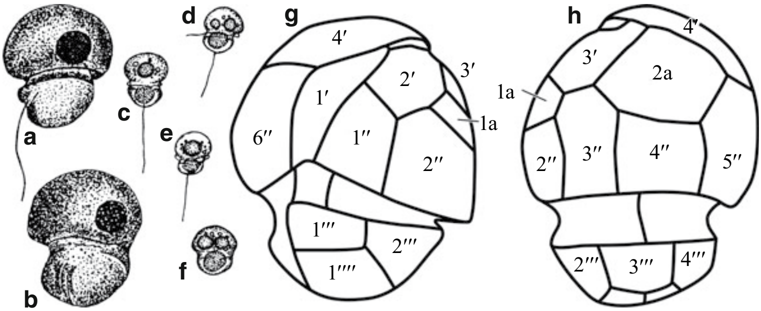

Fig. 254 *Speroidium fungiforme* (Anisimova) Moestrup & Calado (**a**, **b** after Anisimova 1926; **c**–**f** after Skuja 1939; **g**, **h** original drawings based on SEM images in Seaborn *et al.* 2006). **a** left lateral view; **b** ventral-left view; **c**–**f** respectively ventral and two dorsal views, and a cell without flagella, showing ingested bodies in the epicone and the nucleus in the hypocone; **g**, **h** ventral-left and dorsal views, respectively, with main amphiesmal plates

Cells fungiform, epicone much longer and wider than the hypocone. Epicone *ca.* 2/3 of cell length. Cingulum descending, the ends displaced 1–1.25× cingulum width. Nucleus in the hypocone, food vacuoles may be present in both epi- and hypocone. Chloroplasts absent. Eyespot not observed. Cell length 9–19 µm, width 5–17 µm.

The cells swim abruptly in circles, making stops of various duration during which they rotate around the longitudinal axis. Cell division proceeds in temporary cysts following loss of flagella and cease of swimming. The cell contents divide into two cells, which are released as zoospores. Sexual reproduction by isogametes and formation of smooth-walled spherical cysts (hypnozygotes; Spero & Morée 1981). Cells feed on prey such as the unicellular alga *Dunaliella* and injured ciliates or metazoans, to which they are attracted by a chemosensory mechanism (Spero 1985).

SEM: Seaborn *et al.* (2006), Hoppenrath *et al.* (2014).

TEM: Spero & Morée (1981), Spero (1982).

DNA data: Seaborn *et al.* (2006), Mason *et al.* (2007).

Ecology: in salt lakes, in the upper part of the bottom sediment, on *Enteromorpha* and in floating detritus on the surface. Salinity of the lakes *ca.* 1 % Cl. Also reported from fresh water.

Geographical distribution: Marine species associated with sandy sediments and presently known from many parts of Europe, Australia and East Asia (see Hoppenrath *et al.* 2014 for details). Also from Chesapeake Bay, USA (Seaborn *et al.*), and probably Texas (Spero & Morée). In salt lake in Northwestern Russia (Novgorod), and from freshwater lake in Västerbotten, Sweden (Skuja).

Note: only the study from Chesapeake Bay contains information on amphiesmal plates, and studies on material from elsewhere indicate that more than one species may be involved.

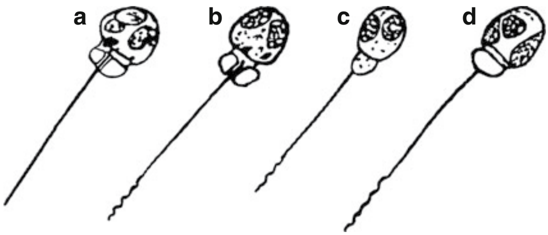

Fig. 255 *Speroidium austriacum* (J. Schiller) Moestrup & Calado (after Schiller 1955) **a**, **b** ventral views; **c**, **d** dorsal views. Bodies in the epicone were interpreted as ingested chrysomonads

2. *Speroidium austriacum* (J. Schiller) Moestrup & Calado *comb. nov.* (**Fig. 255**)

Basionym: *Massartia austriaca* J. Schiller 1955, *Wiss. Arbeiten Burgenland* **9**, p. 45, pl. VIII, fig. 42
Nomenclatural synonym: *Katodinium austriacum* (J. Schiller) A. R. Loeblich 1965, p. 15

Cells elongate ovoid, barely flattened. Epicone egg-shaped, hypocone flattened, hemispherical. Cingulum horizontal, the ends not displaced. Sulcus does not extend onto the epicone. Longitudinal flagellum very long, mostly straight, the distal part wavy. Red body present in the epicone near the cingulum. Often moves in jumps. Cell length 10–12 µm, 8–9 µm wide.
Ecology: mesosaprobic lake near Vienna, Austria.
Geographical distribution: Austria.

Note: as pointed out by Christen (1961) this species resembles *Speroidium fungiforme*. If differs mainly in the cingulum being circular rather than descending. The two species may prove to be identical.

Genus 3. *Tyrannodinium* Calado, Craveiro, Daugbjerg & Moestrup 2009, pp 1202–1203

Type species: *Tyrannodinium berolinense* (Lemmermann) Calado, Craveiro, Daugbjerg & Moestrup, herein considered synonymous with *Tyrannodinium edax* (A. J. Schilling) Calado

Heterotrophic dinoflagellates. Cells covered with thin amphiesmal plates arranged in the Kofoidian plate formula po, cp, x, 4′, 0a, 6″, 6c, pc, 5–?s, 5‴, 2⁗. The peduncle cover plate (pc) arches over the middle part of the sulcus partially hiding underlying sulcal plates. Cingulum very slightly descending, nearly circular. Sulcus extends very shortly onto the epicone. Cell division in non-motile stage.

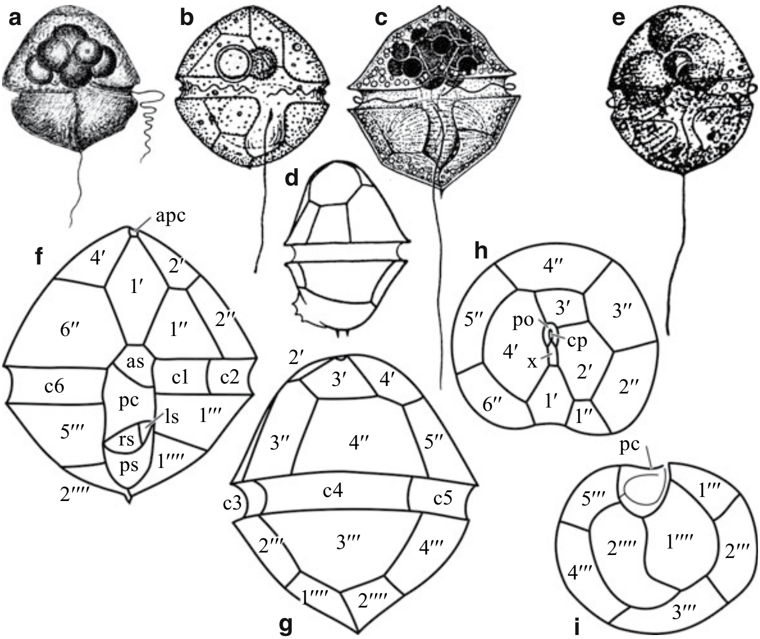

Fig. 256 *Tyrannodinium edax* (A. J. Schilling) Calado (**a** after Schilling 1891b; **b** after Nygaard 1945; **c**, **d** after Thompson 1951; **e** after Litvinenko 1965; **f**, **g** original drawings, modified from Calado *et al.* 2009; **h**, **i** original, from SEM images). **a**–**c**, **e** ventral views showing ingested material in the epicone (the large nucleus is marked in the hypocone in **b**, **c** and **e**); **d** left lateral view showing ridge on left side of sulcus; **f**–**i** ventral, dorsal, apical and antapical views showing amphiesmal plates

1. *Tyrannodinium edax* (A. J. Schilling) Calado 2011, p. 643 (**Fig. 256**)

Basionym: *Glenodinium edax* A. J. Schilling 1891b, pp 206, 207, pl. X, figs 23, 24
Nomenclatural synonym: *Peridiniopsis edax* (A. J. Schilling) Bourrelly 1968, p. 9
Taxonomic synonyms: *Peridinium berolinense* Lemmermann 1900c, p. 308 ≡ *Glenodinium berolinense* (Lemmermann) Er. Lindemann 1925c, pp 162, 164 ≡ *Peridiniopsis berolinensis* (Lemmermann) Bourrelly 1968, p. 9 ("*berolinense*") ≡ *Tyrannodinium berolinense* (Lemmermann) Calado, Craveiro, Daugbjerg & Moestrup 2009, p. 1203; *Peridinium berolinense* var. *apiculatum* Lemmermann *in* West 1907, p. 188, pl. 9, fig. 3 ≡ *Tyrannodinium berolinense* var. *apiculatum* (Lemmermann) Calado, Craveiro, Daugbjerg & Moestrup 2009, p. 1203; *Gymnodinium alatum* Litvinenko 1965, p. 92, figs 4–7

Cells spherical, ellipsoidal or rhomboidal in ventral view, slightly dorsoventrally flattened. The cingulum almost circular, very slightly descending. Plate pattern asymmetrical. Amphiesmal plates on the hypocone usually more clearly visible than on the epicone. Suture between the antapical plates S-shaped. Nucleus very conspicuous, occupying most of the hypocone. Cell size: 20–42 µm long and 20–41 µm wide. Cell division in temporary cysts, theca opening along upper edge of the cingulum.
Cells are voracious feeders which move around continuously in search of food items. They feed using a feeding tube supported by several overlapping layers of microtubules.
Sexual reproduction results in planozygotes with two longitudinal flagella but hypnospores are unknown.
SEM: Hansen & Flaim (2007), Calado *et al.* (2009).
TEM: general structure, Wedemayer & Wilcox (1984), Calado *et al.* (2009); feeding cells, Calado & Moestrup (1997).
DNA data: Calado *et al.* (2009).
Ecology: plankton in ponds rich in organic material at pH 7.2–7.6 according to Höll (1928), but almost certainly overlooked and much more widely distributed. Frequent in eutrophic, mesosaprobic ponds. Large forms, originally described as var. *apiculatum*, in the plankton of Lake Tanganyika, Africa.
Geographical distribution: Denmark (Nygaard); England (illustrated by figs 333, 335–336, 340, as "*Peridinium*", in Canter-Lund & Lund 1995); Germany (Lemmermann, Höll); Poland (Höll, Wołoszyńska); Portugal (Pandeirada *et al.*). Tanzania, Africa (Lemmermann). USA, KS (Thompson). Brazil (Cavalcante *et al.*). Japan (Senzaki & Horiguchi).

Family 2. Thoracosphaeraceae J. Schiller 1930, p. 154, 156, 171, 173

Taxonomic synonym: Calciodinellaceae Deflandre 1947, p. 1781

Family comprising four recently described genera from fresh water (one species also from brackish water), in addition to the extant marine *Thoracosphaera* and species in the *Scrippsiella* group, both recent and fossil. Chloroplasts always present. Plate formula apc, 3–4′, 1–3a, 7″, 5‴, 0p, 2⁗. Where known, furrow plates number 6c and 5s. Resting cysts calcified (*Theleodinium*) or non calcified (*Apocalathium*, *Chimonodinium, Naiadinium*).

Key to the genera of Thoracosphaeraceae occurring in fresh water:

1a Cells with 3 intercalary plates on the epicone .... 1. *Apocalathium,* 2. *Chimonodinium*
1b Cells with 1–2 intercalary plates on the epicone 2
2a Epicone conical or sometimes pointed, without projecting nipple-like apical pore .... 3. *Naiadinium*
2b Epicone rounded with projecting, nipple-like apical pore ..... 4. *Theleodinium*

Note: the characters identifying the two genera *Apocalathium* and *Chimonodinium* are not visible at the level of light microscopy. For identifying species of these genera use the combined key below.

Genus 1. *Apocalathium* Craveiro, Daugbjerg, Moestrup & Calado 2016, p. 32

Type species: *Apocalathium aciculiferum* (Lemmermann) Craveiro, Daugbjerg, Moestrup & Calado 2016

Plate formula po, cp, x, 4′, 3a, 7″, 6c, 5s, 5‴, 2⁗. Plate pattern asymmetric, usually 1a is 4 or 5-sided, 2a is five-sided, 3a is 6-sided. The three anterior intercalaries form a single group. Amphiesmal plates smooth or with fine ornamentation. Chloroplasts with internal pyrenoids. Cells lack a microtubular basket and are therefore probably not mixotrophic or, if so, they use another means of food uptake. Cysts smooth.

Species of *Apocalathium* and *Chimonodinium* previously formed group "lomnickii" of *Peridinium* (Peridiniales), a set of species characterized by the presence of an apical pore complex, three intercalary plates on the epicone and six cingular plates. The four *Apocalatium* species have been studied with modern methods, including molecular sequencing, but the generic affinity of five of the other species needs to be determined. They have been included in *Chimonodinium* until further studies prove otherwise.

Key to species of *Apocalathium* and *Chimonodinium*:

1a Hypocone with 1–6 distinct spines 2
1b Hypocone smooth or with numerous short spines 7
2a Hypocone with two antapical spines 3
2b Hypocone with 3 or more spines, rarely one spine 4
3a Cells strongly dorsoventrally compressed, with two diverging antapical spines .... 3. *A. euryceps*
3b Cells barely compressed dorsoventrally, with two short, parallel antapical spines .... 5. *C. granulosum*
4a Hypocone with 4–6 spines, plate 3a sometimes with spine ... 2. *A. baicalense*
4b Hypocone with 1 or 3–4 distinct spines, 3a without spine 5
5a Hypocone with 3 strong spines interconnected by a hyaline ridge .... 2. *C. baliense*
5b Hypocone with 3–4 thin spines, no interconnecting hyaline ridges, or with single antapical spine 6
6a Cells with 3–4 thin spines .... 1. *A. aciculiferum*
6b Cells with single, slightly curved spine .... 1. *A. aciculiferum* var. *juratense*
7a Cells distinctly longer than wide 8
7b Cells as long as wide 11
8a Cell with numerous spines at the antapical end 9
8b Antapical end without spines 10
9a Cingulum and sulcus with very thick margins, right side of hypocone longer than left side .... 1. *C. lomnickii* var. *splendidum*

9b Cingulum and sulcus margins not notably thickened, cell longest in the cell axis .... 1. *C. lomnickii*
10a First apical plate as long as wide .... 1. *A. aciculiferum* var. *inerme*
10b First apical plate longer than wide .... 4. *A. malmogiense*
11a Cells spherical to very slightly elongate, all plates convex .... 1. *C. lomnickii* var. *wierzejskii*
11b Cells more or less angular as some plates are concave 12
12a Epicone finely areolated, hypocone with numerous small spines .... 4. *C. godlewskii*
12b The same ornamentation in epi- and hypocone, spines absent 13
13a Antapical plates of the same size or nearly so .... 6. *C. keyense*
13b Antapical plates very asymmetrical, 1⁗ twice the size of 2⁗ .... 3. *C. brasiliense*

1. ***Apocalathium aciculiferum*** (Lemmermann) Craveiro, Daugbjerg, Moestrup & Calado 2016, p. 32 (**Fig. 257**)

Basionym: *Peridinium aciculiferum* Lemmermann 1900a, p. 28
Nomenclatural synonyms: *Peridinium umbonatum* var. *aciculiferum* (Lemmermann) Lemmermann 1908b, p. 181 ≡ *Glenodinium aciculiferum* (Lemmermann) Er. Lindemann 1928a, p. 260
Taxonomic synonym: *Peridinium stagnale* Meunier 1919, p. 53, pl. XVIII, figs 28–32

Cells ovoid, dorsoventrally flattened. Epi- and hypocone of almost equal size. Epicone conical, pointed, with very small apical teeth around the pore area, hypocone rounded with 3 (rarely 4) spines. One spine inserted at the antapex (on the suture between 1⁗ and 2⁗), the others a short distance from the antapex (on the sutures between 1‴ and 1⁗, and 5‴ and 2⁗, respectively). Amphiesma plates thin, smooth, with numerous scattered pores which may sometimes be difficult to see in the LM. Plate formula: po, cp, x, 4′, 3a, 7″, 6c, 5s, 5‴, 2⁗. Plate 1′ longer than wide, 3′ often very small; 1a and 2a five-sided, 3a six-sided; antapical plates of equal size. Sulcus extends for a short distance onto the epicone. Cingulum descending, very slightly displaced. Striae often wide. Chloroplasts numerous, disc-shaped, brown. Nucleus central, oval or round. Eyespot not observed. The amphiesma opens along the cingulum. Cells 35–51(–60) µm long and 28–42(–45) µm wide. Cysts ellipsoid or peanut-shaped, with red pigments, smooth, without trace of amphiesmal plates (Rengefors 1998), or ovoid-elliptical (Dangeard 1939, p. 271). Cysts from Sweden germinated at temperatures below 7 ˚C, after a maturation period of 2.5 months (Rengefors & Anderson 1998).
Also reported from Vanuatu in the Pacific at temperatures of 27–37 ˚C (Schabetsberger *et al.* 2009) but this needs to be confirmed. It may have been confused with *Chimonodinium granulosum*, which is not included in flora treatments by Huber-Pestalozzi (1950) and Popovský & Pfiester (1990).
SEM: Rengefors & Legrand (2001), Hansen & Flaim (2007), Annenkova *et al.* (2015).
TEM: Craveiro *et al.* (2016).
DNA data: Logares *et al.* (2007a).

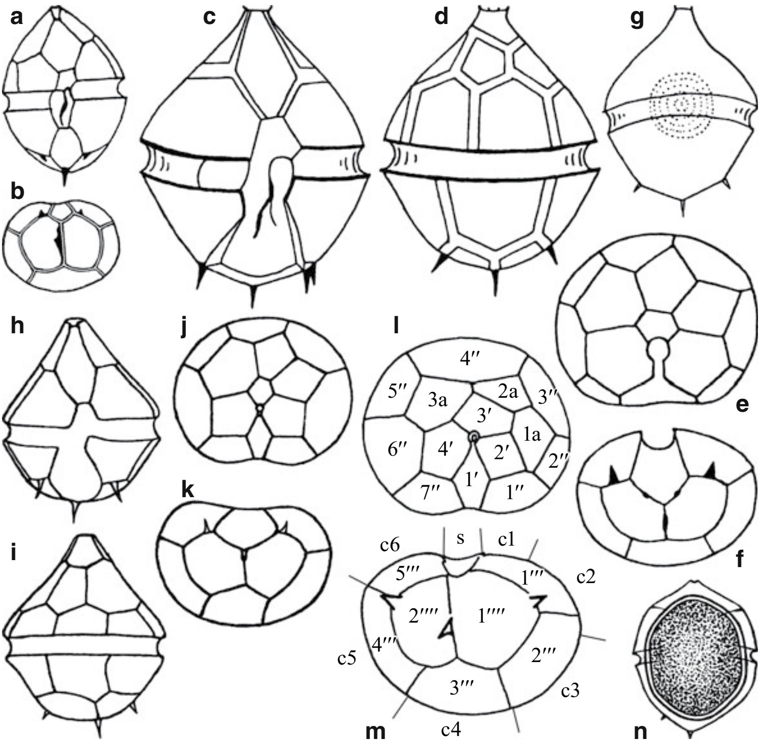

Fig. 257 *Apocalathium aciculiferum* (Lemmermann) Craveiro, Daugbjerg, Moestrup & Calado (**a**, **b** after Lemmermann 1910; **c**–**g** after Wołoszyńska 1916; **h**–**k** after Lindemann 1919; **l**, **m** after Bourrelly 1970; **n** after West 1909b). **a**, **b** ventral and antapical views, respectively, showing three posterior spines; **c**–**f** ventral, dorsal, apical and antapical views, showing posterior spines and the three anterior intercalary plates; **g** outline of cell with the nucleus indicated; **h**–**k** ventral, dorsal, apical and antapical views, showing posterior spines and the three anterior intercalary plates; **l** tabulation on the epicone; **m** tabulation on the hypocone with edges of cingular plates indicated by lines on the margin; **n** resting cyst inside the old amphiesma

Ecology: plankton in ponds and lakes. Cold-water species that may form blooms at temperatures as low as 1–2 ˚C (Iceland). In Lake Tovel, Italian Alps, seen to give the ice a brownish color. Occurs at temperatures up to 10–12 ˚C and pH 7.0–8.0 (Lemmermann 1910; Höll 1928; Nygaard 1945); Schiller & Stefan (1935) in a pond in Vienna found it in January and February at temperatures up to 5 ˚C, disappearing in March. Calcium-mesotrophic. Vertical migration was observed to take place under the ice, the cells moving away from the surface in the morning and

returning in the afternoon. The movement was ascribed to the cells avoiding strong light (Schiller & Stefan 1935).
Reported to be mixotrophic, sucking out the contents of other dinoflagellates (*e. g.* "*Woloszynskia hiemale*") through a tube (Entz & Sebestyén *in* Huber-Pestalozzi 1950). However, a peduncular system is absent (Craveiro *et al.* 2016). Toxic to cryptomonads (Rengefors & Legrand 2001, 2007).
Geographical distribution: Denmark (Nygaard); England (West; Lewis & Dodge); France (Bourrelly); Germany (Lemmermann; Lindemann); Iceland (Ostenfeld); Italy (Hansen & Flaim); Poland (Höll); Portugal (Nauwerck); Sweden (Rengefors); Ukraine (Wołoszyńska). British Columbia (Wailes).

var. *inerme* (Wołoszyńska) Moestrup & Calado *comb. nov.* (**Fig. 258**)
Basionym: *Peridinium aciculiferum* f. *inerme* Wołoszyńska 1937, *Arch. Hydrobiol. Rybactwa* **10**, p. 195, pl. IX, figs 1–4

Differs by lacking the spines on the hypocone, only small papillae are present. Plate 1′ almost as wide as long. Cell length *ca.* 40 µm, width *ca.* 30 µm.
Ecology: in winter plankton in lakes.
Geographical distribution: Poland (Wołoszyńska).

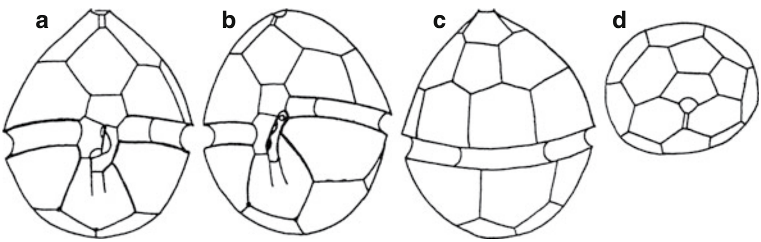

Fig. 258 *Apocalathium aciculiferum* var. *inerme* (Wołoszyńska) Moestrup & Calado (after Wołoszyńska 1937). **a** ventral view; **b** ventral view, somewhat tilted to show antapical area; **c** dorsal view; **d** apical view

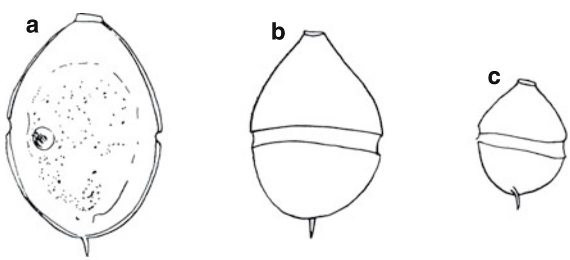

Fig. 259 *Apocalathium aciculiferum* var. *juratense* (Chodat & F. Chodat) Moestrup & Calado (after Chodat & Chodat 1925). **a** optical section, with contracted cell contents; **b**, **c** cell outlines (dorsal views?)

var. *juratense* (Chodat & F. Chodat) Moestrup & Calado *comb. nov.* (**Fig. 259**)
Basionym: *Peridinium aciculiferum* var. *juratense* Chodat & F. Chodat 1925, *Veröff. Geobot. Inst. Rübel Zürich* **3**, p. 439, figs 1, 2

Differs in being semicircular in transverse section and less dorsoventrally flattened, and in possessing a slightly curved 2.5-µm-long antapical spine. Cell length 35 µm, width 28 µm.
Ecology and geographical distribution: collected September 1924 in Lake Nantua, France (pH below 7.5).

2. *Apocalathium baicalense* (Kisselev & V. Zvetkov) Craveiro, Daugbjerg, Moestrup & Calado 2016, p. 33 (**Fig. 260**)

Basionym: *Peridinium baicalense* Kisselev & V. Zvetkov 1935, p. 518, figs 1–14

Cells elongate pear-shaped, strongly dorsoventrally flattened. Epicone helm-shaped to conical with angular edges, often about twice the length of the hypocone. Apex extended almost horn-like. A stout spine sometimes but not always extends later-

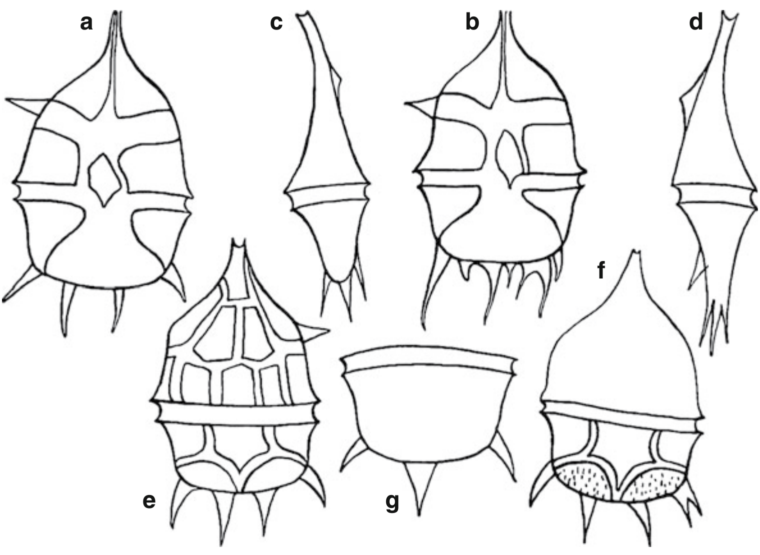

Fig. 260 *Apocalathium baicalense* (Kisselev & V. Zvetkov) Craveiro, Daugbjerg, Moestrup & Calado (after Kisselev & Zvetkov 1935). **a**, **b** ventral views showing variation in shape and antapical spines; **c**, **d** lateral views; **e**, **f** dorsal views, variation of shape and ornamentation; **g** outline of posterior part of cell in dorsal view, with only three posterior spines

ally from a low ridge on the right side of the epicone. Hypocone rounded with 4–6, occasionally more, teeth-like projections. Cingulum almost circular, sulcus extends towards the apex as a relatively long sulcal anterior plate, and widens distinctly towards the antapex. Older cells with very distinct ridges along and parallel to many sutures, thus two longitudinal ridges often extend along the sides of the epicone from the apex to the cingulum. Amphiesmal plates smooth or with scattered tiny spines. Chloroplasts present. Cell length 55–72 µm, width 42–50 µm, thickness 18–27 µm. Spine length 12–18 µm.
SEM: Annenkova *et al.* (2015).
DNA data: Annenkova *et al.* (2015).
Ecology: in deep water, stenotherm.
Geographical distribution: Lake Baikal, Russia.

3. ***Apocalathium euryceps*** (Rengefors & Barbara Meyer) Craveiro, Daugbjerg, Moestrup & Calado 2016, p. 33 (**Fig. 261**)

Basionym: *Peridinium euryceps* Rengefors & Barbara Meyer 1998, p. 285, figs 1–31

Cells slightly longer than wide, the left side slightly longer than the right side. Epicone and hypocone of almost equal size. Epicone semicircular, hypocone trapezoidal-angular with two prominent, diverging posterior spines. Cells strongly dorsoventrally compressed. Cingulum descending, the ends displaced *ca.* half its width. Sulcal area only little excavated, reaching halfway to the antapex. A conspicuous rectangular plate on the ventral side of the epicone opposite the sulcus is interpreted as an anterior sulcal plate (as). Amphiesmal plates thin and difficult to see without staining, smooth or slightly granulated. First apical plate asymmetrical,

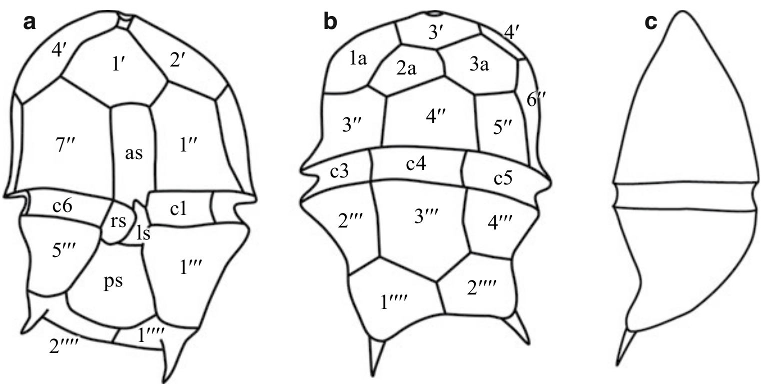

Fig. 261 *Apocalathium euryceps* (Rengefors & Barbara Meyer) Craveiro, Daugbjerg, Moestrup & Calado (original drawings, based on information from LM and SEM images published in Rengefors & Meyer 1998 and Annenkova *et al.* 2015). **a**, **b** ventral and dorsal views with main amphiesmal plates; **c** outline of left lateral view

separated from the cingulum by the anterior sulcal plate. It further abuts plates 2′, 4′, 1″ and 7″. The three anterior intercalary plates of different shape: 1a quadrangular, 2a pentagonal and 3a hexangular. On the hypocone the two antapical plates are located dorsally, are of different size and each extends into a solid spine. Spines occasionally smaller or even lacking. Nucleus in the cell center. Numerous small brownish-green chloroplasts. Cells 48–60 µm long, 36–40 µm wide and 16–18 µm thick. Resting cysts rectangular in ventral view, oval in lateral view, unornamented, 42–48 µm long and 27–30 µm wide.
SEM: Rengefors & Meyer (1998), Annenkova *et al.* (2015).
Ecology: cold-water species presently known from under the ice in the naturally eutrophic Lake Erken and Lake Mälaren in Sweden, but also present in Lake Baikal in Siberia (Annenkova *et al.* 2015).
Geographical distribution: Sweden (Rengefors & Meyer). Russia (Annenkova *et al.*).

4. *Apocalathium malmogiense* (G. Sjöstedt) Craveiro, Daugbjerg, Moestrup & Calado 2016, p. 33 (**Fig. 262**)

Basionym: *Peridinium malmogiense* G. Sjöstedt 1921, p. 184, figs 1–6
Taxonomic synonyms: *Peridinium hangoei* J. Schiller 1935a, p, 135, fig. 129 (replacement name for *Peridinium gracile* Er. Lindemann 1924c, p. 2, pl. I, figs 3–6, *nom. illeg.* – non *Peridinium gracile* Meunier 1910, p. 31, pl. III, fig. 51) ≡ *Scrippsiella hangoei* (J. Schiller) J. Larsen *in* Larsen *et al.* 1995, p. 136 ≡ *Protoperidinium hangoei* (J. Schiller) Jane Lewis, J. D. Dodge & Tett 1984, p. 28

Cells ovoid, not or barely dorsoventrally compressed. Epicone rounded conical, hypocone hemispherical. Cingulum descending, the ends displaced *ca.* half a cingulum width. Sulcus extends three quarters of the way to the antapex, forming a slight invagination in the epicone. Amphiesmal plates very delicate and smooth. Plate formula: po, cp, x, 4′, 3 (4)a, 7″, 6c, 7s, 5‴, 2″″. Many disc-shaped, brown chloroplasts, each with several small pyrenoids. Nucleus in the cingular region or in the hypocone. Cell length 23–32(–34) µm, width 18–28(–30) µm and thickness 14–22 µm. Cysts spherical to somewhat oval, 18–30 µm in the longest dimension, with an orange-red accumulation body and a smooth wall (Kremp *et al.* 2005).
SEM: Larsen *et al.* (1995), Annenkova *et al.* (2015).
DNA data: Logares *et al.* (2007a, as *Scrippsiella hangoei*).
Ecology: First described from a pond in Slottsparken, Malmö, Sweden, a year after the pond had been connected to a brackish-water channel, resulting in a salinity of 5 psu. Subsequently found to be a common cold-water form in the Northern Baltic and identified under a variety of names, most recently *Scrippsiella hangoei* (Larsen *et al.* 1995). Occurs in winter and spring, sometimes under the ice, a concentration of 26×10^6 cells per liter observed under the ice in February 1986. Will grow in culture at salinities of 0–30 psu (Logares *et al.* 2007a).
Geographical distribution: the Baltic area. Lake Baikal, Russia (Annenkova *et al.*).

Note: this species shows sequences coding for ribosomal RNA identical to those of *Apocalathium aciculiferum*, a cold-water species from fresh water.

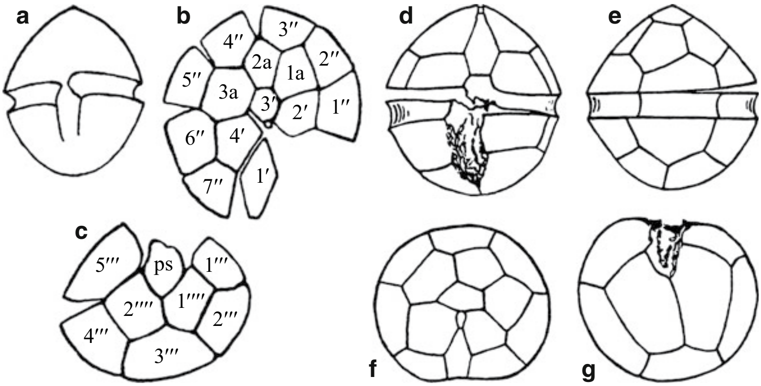

Fig. 262 *Apocalathium malmogiense* (G. Sjöstedt) Craveiro, Daugbjerg, Moestrup & Calado (**a**–**c** after Sjöstedt 1921; **d**–**g** after Lindemann 1924c). **a** ventral view, outline; **b** squashed amphiesma showing plates covering the epicone (reversed relative to the original); **c** plates on squashed hypocone; **d**–**g** ventral, dorsal, apical and antapical views, respectively

Genus 2. *Chimonodinium* Craveiro, Calado, Daugbjerg, Gert Hansen & Moestrup 2011, p. 604

Type species: *Chimonodinium lomnickii* (Wołoszyńska) Craveiro, Calado, Daugbjerg, Gert Hansen & Moestrup 2011

Plate formula po, cp, x, 4′, 3a, 7″, 6c, 5s, 5‴, 2⁗. Plate pattern asymmetric, plate 1a is 4 or 5-sided, 2a is five-sided, 3a is 6-sided, The three anterior intercalaries form a single group (cf. two groups in *Bysmatrum*, a genus of marine benthic species). The amphiesma opens along the cingulum to release the cells after division. Amphiesmal plates with ornamentation of papillae and small spines. The cells contain a microtubular basket and are therefore possibly mixotrophic. Chloroplasts lack pyrenoids. Cyst uncalcified, smooth.
Only *C. lomnickii* has been examined in detail. The phylogenetic position of the other five species needs to be confirmed, some may belong in *Apocalathium*.

1. *Chimonodinium lomnickii* (Wołoszyńska) Craveiro, Calado, Daugbjerg, Gert Hansen & Moestrup 2011, pp 605, 606 (**Fig. 263**)

Basionym: *Peridinium lomnickii* Wołoszyńska 1916, p. 267, pl. 10, figs 25–29
Nomenclatural synonym: *Glenodinium lomnickii* (Wołoszyńska) Er. Lindemann 1925c, pp 162, 168, 169
Taxonomic synonym: *Peridinium lomnickii* var. *punctulatum* Er. Lindemann 1924b, p. 436, pl. 21, figs 1–6 ("*punktulatum*")

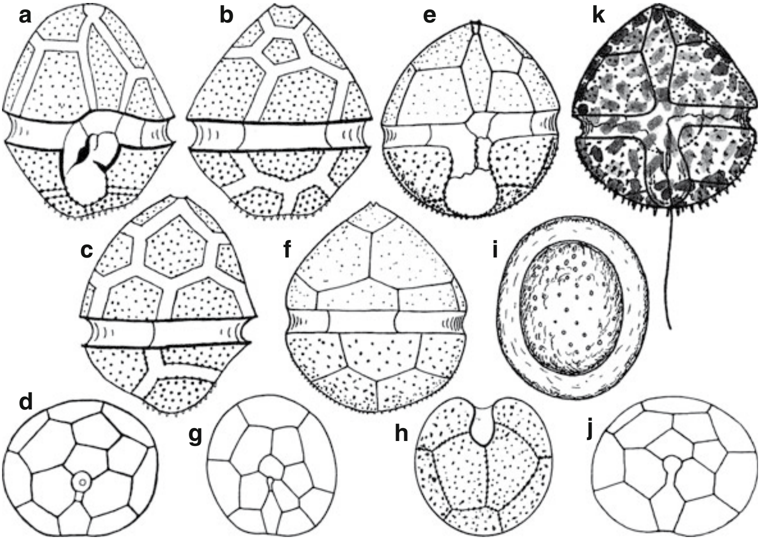

Fig. 263 *Chimonodinium lomnickii* (Wołoszyńska) Craveiro, Calado, Daugbjerg, Gert Hansen & Moestrup (**a**–**d** after Wołoszyńska 1916; **e**–**i** after Lindemann 1924b; **j** after Lefèvre 1932; **k** after Nygaard 1945). **a** ventral view; **b** dorsal view; **c** right lateral view; **d** apical view; **e**–**h** ventral, dorsal, apical and antapical views, respectively; **i** resting cyst; **j** apical view; **k** ventral view of live cell with peripheral chloroplasts and central nucleus

Cells ovoid, dorsoventrally slightly compressed. Epicone considerably larger than hypocone, bell-shaped, hypocone rounded, somewhat indented posteriorly. Cingulum descending, only very slightly displaced. Sulcus does not extend onto the epicone. On the hypocone it widens slightly towards the posterior end but does not reach the antapex. Plates thickly ornated with papillae and small spines. Sutures often visible. Numerous small chloroplasts, pyrenoid absent. Large eyespot present in the right hand side of the sulcus. Nucleus oval, located centrally. Red lipid droplets often present. Microtubular basket present in the cell, indicating mixotrophy, but mixotrophy not observed. The amphiesma opens along the anterior rim of the cingulum. Cell length 25–40 µm, width 22–35 µm. Cysts ovoid to ellipsoid, with very thick, non-calcareous wall.
SEM: Dodge (1985), Ling *et al.* (1989), Senzaki & Horiguchi (1994), Grigorszky *et al.* (2003a), Liu *et al.* (2008), Craveiro *et al.* (2011), Pandeirada *et al.* (2013).
TEM: Craveiro *et al.* (2011).
DNA data: Craveiro *et al.* (2011).
Ecology: in plankton of ponds, maximum occurrence in winter, more rare in summer.
Geographical distribution: Denmark (Nygaard), England (Lewis & Dodge); France (Lefèvre); Germany (Lindemann); Holland (Beijerinck); Hungary (Grigorszky *et al.*). Poland (Wołoszyńska; Lindemann); Portugal (Pandeirada *et al.*); Ukraine

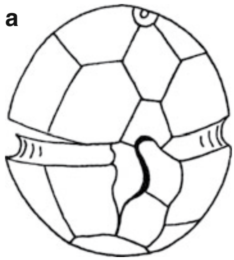

Fig. 264 *Chimonodinium lomnickii* var. *minus* (Wołoszyńska) Moestrup (after Wołoszyńska 1916). **a** ventral view showing limits of main amphiesmal plates

(Wołoszyńska). Patagonia (Thomasson). Guangdong, China (Liu *et al.*); Japan (Senzaki & Horiguchi). Tasmania, Australia (Ling *et al.*).

var. *minus* (Wołoszyńska) Moestrup *comb. nov.* (**Fig. 264**)
Basionym: *Peridinium wierzejskii* var. *minus* Wołoszyńska 1916, *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math., Sér. B, Sci. Nat.* **1915**, p. 269, pl. 11, fig. 9 ("*minor*")

Differs from the nominal form in the sulcus extending onto the epicone, the smooth amphiesmal plates and the smaller cell size: 20–25 µm long.
Ecology: in bog near Zakopane, August 1912 (Wołoszyńska 1916).
Geographical distribution: Poland (Wołoszyńska).

var. *splendidum* (Wołoszyńska) Craveiro, Calado, Daugbjerg, Gert Hansen & Moestrup 2011, p. 606 (**Fig. 265**)
Basionym: *Peridinium lomnickii* var. *splendidum* Wołoszyńska 1916, p. 268, pl. 10, figs 30–40 ("*splendida*")
Nomenclatural synonym: *Glenodinium lomnickii* var. *splendidum* (Wołoszyńska) Er. Lindemann 1928a, p. 260

Cells pentagonal in ventral view, dorsoventrally strongly compressed. Cingulum wide with exceptionally thick borders, descending. Displacement *ca.* half the cingulum width. Sulcus likewise with very thick borders, does not extend onto the epicone. Epicone conical, larger than the hypocone, which is also conical, indented antapically. The right side of the cell more strongly developed than the left side. The left side of the hypocone therefore shorter than the right side. The sutures of older cells strongly thickened, in the apex extending as two tooth-like projections. Amphiesmal plates densely covered with spines, which are particularly strong on the antapical plates. Sutures wide. Chloroplasts disc-shaped, dark brown. Nucleus large, central. The amphiesma opens along the cingulum. Cell length 30–50 µm, width 28–40 µm. Resting cysts irregularly shaped, with very thick wall.
Ecology: in plankton of forest pond in Poland, March 1913 (Wołoszyńska 1916).
Geographical distribution: Poland (Wołoszyńska).

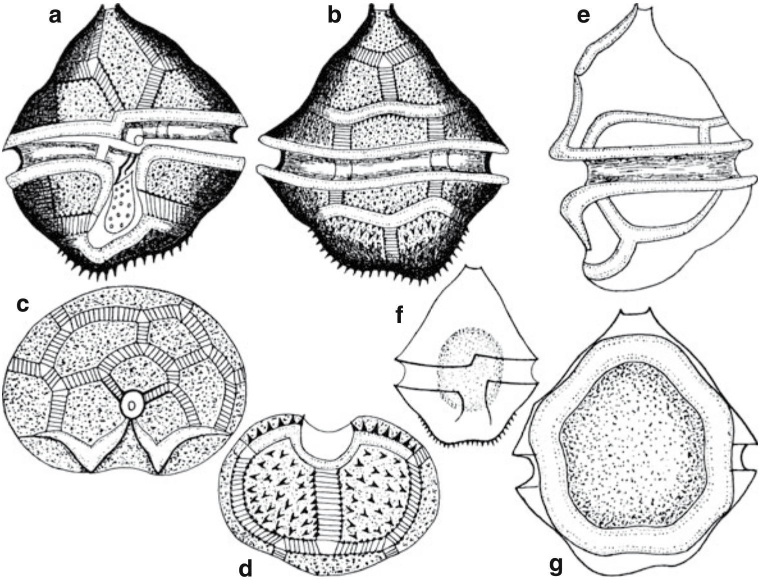

Fig. 265 *Chimonodinium lomnickii* var. *splendidum* (Wołoszyńska) Craveiro, Calado, Daugbjerg, Gert Hansen & Moestrup (after Wołoszyńska 1916;). **a**–**d** ventral, dorsal, apical and antapical views; **e** left lateral view, outline and prominent sutures; **f** outline of ventral view showing position of nucleus; **g** thick-walled resting cyst within old amphiesma

var. *wierzejskii* (Wołoszyńska) Craveiro, Calado, Daugbjerg, Gert Hansen & Moestrup 2011, p. 606 (**Fig. 266**)
Basionym: *Peridinium wierzejskii* Wołoszyńska 1916, p. 269, pl. 11, figs 1–8
Nomenclatural synonym: *Glenodinium lomnickii* var. *wierzejskii* (Wołoszyńska) Er. Lindemann 1928a, p. 260
Taxonomic synonym: "*Peridinium wierzejskii* f. *carpaticum* Wołoszyńska" (1952, p. 313; *nomen nudum*)

Cells rounded, barely longer than wide, not dorsoventrally flattened. Epi- and hypocone of similar size. Cingulum descending, displaced half the cingulum width or less. Sulcus does not extend onto the epicone. On the hypocone it widens posteriorly. Right antapical plate smaller than left antapical plate. Amphiesmal plates with numerous small papillae. Sutures often wide. Chloroplasts disc-shaped. Nucleus round, centrally located. Cell length 30–35 µm. Resting cysts unknown.
Ecology: pond in the Tatra Mountains, August 1913 (Wołoszyńska 1916).
Geographical distribution: England (Lewis & Dodge); Poland, Ukraine (Wołoszyńska). New Zealand (Thompson).

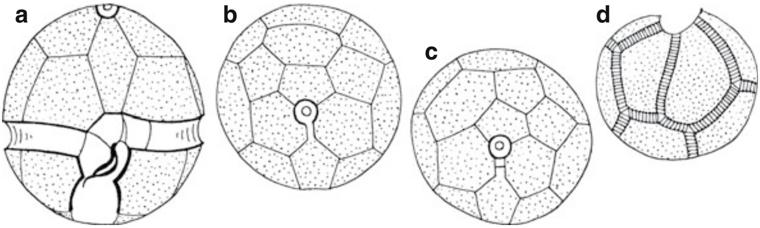

Fig. 266 *Chimonodinium lomnickii* var. *wierzejskii* (Wołoszyńska) Craveiro, Calado, Daugbjerg, Gert Hansen & Moestrup (after Wołoszyńska 1916). **a** ventral view; **b**, **c** apical views showing plate variation; **d** antapical view

2. *Chimonodinium baliense* (Er. Lindemann) Moestrup & Calado *comb. nov.* (**Fig. 267**)

Basionym: *Peridinium baliense* Er. Lindemann 1931, *Arch. Hydrobiol., Suppl.* **8**, p. 712, figs 38–41

Cells almost spherical or epicone somewhat conical. Cells not dorsoventrally compressed. Cingulum descending, displacement *ca.* half the cingulum width. Sulcus extends a short distance onto the epicone, on the hypocone widening very markedly towards the antapex. Amphiesmal plates smooth or finely structured. Three strong, solid spines present on the hypocone, directed posteriorly. All three spines are located along the antapical rims of the sulcus. In antapical view of the hypocone, the three spines may be seen to extend from the corners where the antapical plates meet the sulcus. Spines interconnected by a hyaline membrane. A fourth smaller spine sometimes present to the right of the other three. Cell length 45–61 µm, width 50–58 µm, thickness 41–50 µm. Spines 5–7 µm long.
Ecology: Danu Bratan, Caldera lake and flooded "Schwingrasen" (floating mats), dystrophic dune lake in Tasmania (Ling *et al.* 1989). Billabong in Alligator Rivers Region, northern Australia (Ling & Tyler 1983, as *P. aciculiferum* f.).
Geographical distribution: Bali, Indonesia (Lindemann). Tasmania (Ling *et al.*), tropical Australia (Ling & Tyler).

Note: *Chimonodinium baliense* was reported from Brazil by Borics *et al.* (2005). In the Brazilian material some specimens differ by having very short spines which are not connected by a membrane and by the amphiesma with linearly arranged ornamentation; they were interpreted as young cells and noted to resemble *P. keyense*, which was suggested may be a synonym (Borics *et al.* 2005). The matter needs to be further examined.

3. *Chimonodinium brasiliense* (Borics & Grigorszky) Moestrup & Calado *comb. nov.* (**Fig. 268**)

Basionym: *Peridinium brasiliense* Borics & Grigorszky *in* Borics *et al.* 2005, *Algol. Stud.* **118** [*Arch. Hydrobiol., Suppl.* **160**], pp 54, 56, figs 2e–h, 3 (fig. 3 designated as type)

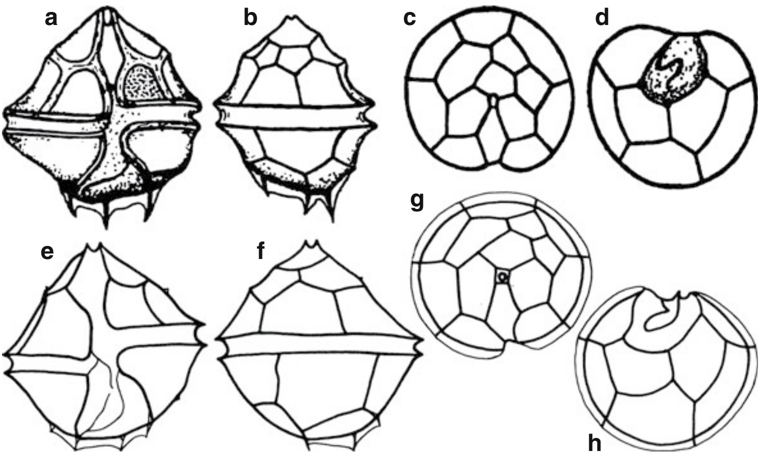

Fig. 267 *Chimonodinium baliense* (Er. Lindemann) Moestrup & Calado (**a**–**d** after Lindemann 1931; **e**–**h** after Ling *et al.* 1989). **a** ventral view with main amphiesmal plates, ornamentation indicated on first precingular plate; **b**–**d** dorsal, apical and antapical views; **e**–**h** ventral, dorsal, apical and antapical views

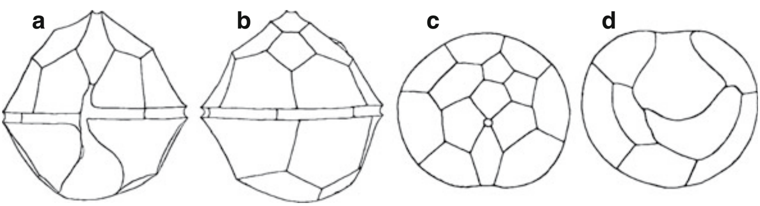

Fig. 268 *Chimonodinium brasiliense* (Borics & Grigorszky) Moestrup & Calado (after Borics *et al.* 2005). **a**–**d** ventral, dorsal, apical and antapical views, respectively

Cells oval, dorsoventrally slightly flattened. Epicone conical with prominent apical pore, hypocone hemispherical. Epi- and hypocone of the same size, cingulum therefore equatorial, very slightly descending, the ends of the cingulum displaced less than one cingular width. The sulcus extends slightly into the epicone and on the hypocone widens asymmetrically, reaching the antapex. Amphiesmal plates thin, concave, with hardly visible ornamentation. Antapical plates differ markedly in size, 1″″ almost twice the size of 2″″, the plate arrangement on the hypocone therefore very asymmetrical. With numerous yellowish-brown chloroplasts. Cell length 35–47 µm, width 31–42 µm.
Ecology: in two slightly acid, stratified tropical lakes in Brazil.
Geographical distribution: Brazil (Borics & Grigorszky).

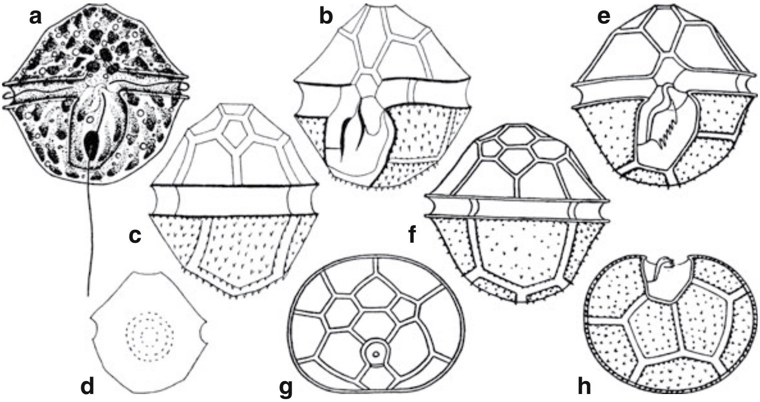

Fig. 269 *Chimonodinium godlewskii* (Wołoszyńska) Moestrup & Calado (**b**–**d** after Wołoszyńska 1916; **a**, **e**–**h** after Thompson 1951). **a** ventral view with cell contents; **b**, **c** ventral and dorsal views with main plates; **d** outline of cell with position of nucleus; **e**–**h** ventral, dorsal, apical and antapical views, respectively

4. *Chimonodinium godlewskii* (Wołoszyńska) Moestrup & Calado *comb. nov.* (**Fig. 269**)

Basionym: *Peridinium godlewskii* Wołoszyńska 1916, *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math., Sér. B, Sci. Nat.* **1915**, p. 274, pl. 13, figs 31–36

Cells ovoid, slightly dorsoventrally flattened. Epicone cone-shaped, angular, hypocone rounded angular. Epicone as large as or slightly smaller than hypocone. Apical pore area wide. Cingulum descending, displaced *ca.* half the cingulum width. Sulcus extends for a short distance onto the epicone. On the hypocone it widens posteriorly but does not reach the antapex. Antapical plates equal in size or the right plate somewhat smaller than the left plate. Sutures narrow. Amphiesmal plates finely areolated on the epicone, on the hypocone with numerous small spines, especially on the antapical plates. Many small chloroplasts. Red eyespot in the sulcus (Thompson 1951). Nucleus oval, central. Cell length 25–35 µm, width 25–32 µm. Resting cysts unknown.
Ecology: planktonic in a pond in Poland in July 1914; in a pond in Kansas, USA, in August 1950.
Geographical distribution: Poland (Wołoszyńska). USA, KS (Thompson).

5. *Chimonodinium granulosum* (Playfair) Moestrup & Calado *comb. nov.* (**Fig. 270**)

Basionym: *Peridinium tabulatum* var. *granulosum* Playfair 1913, *Proc. Linn. Soc. New South Wales* **37**, p. 542, pl. lv, figs 1–4
Nomenclatural synonym: *Peridinium granulosum* (Playfair) Playfair 1920, p. 813

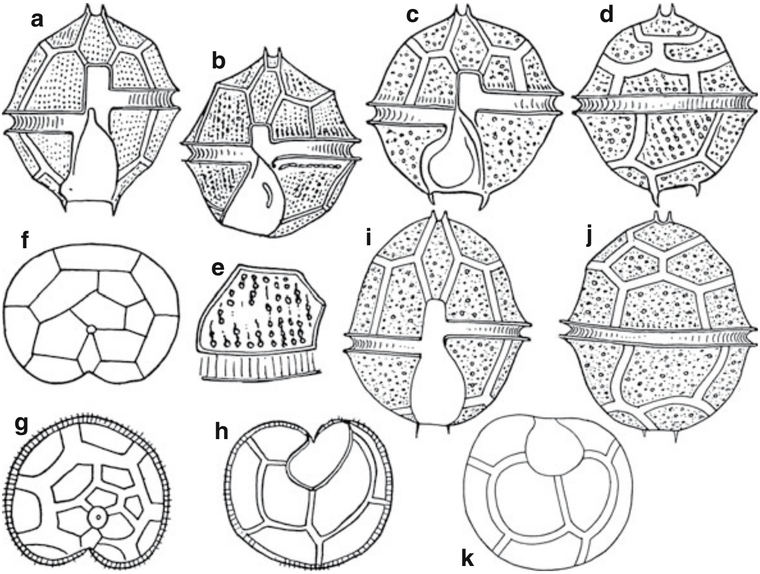

Fig. 270 *Chimonodinium granulosum* (Playfair) Moestrup & Calado (**a**–**h** after Playfair 1913; **i**–**k** after Playfair 1920). **a**–**c** ventral views; **d** dorsal view; **e** detail of ornamentation of precingular plate of cell shown in **b**; **f**, **g** apical views; **h** antapical view; **i**, **j** ventral and dorsal views; **k** antapical view

Cells more or less ovoid, epi- and hypocone of equal size. Cells as wide as long or sometimes slightly longer than wide. Epicone rounded or somewhat conical, hypocone rounded. Cingulum descending, the ends displaced *ca.* one cingulum width. Two minute spines present anteriorly and two similar spines present antapically. Sulcus extends for a short distance onto the epicone and on the hypocone reaches the antapex, widening conspicuously on the way. Amphiesmal plates finely or coarsely granulate, either in lines or scattered irregularly. An unusual feature noted by Playfair when describing the species is the somewhat twisted appearance of the postcingular plates in dorsal view. Antapical plates of different size. Cell length 49–76 µm, width 53–76 µm, thickness 63 µm.
Ecology: ponds in the Botanic Gardens, Sydney, in the Sydney Water Supply, etc.; also in Brisbane.
Geographical distribution: Australia (Playfair).

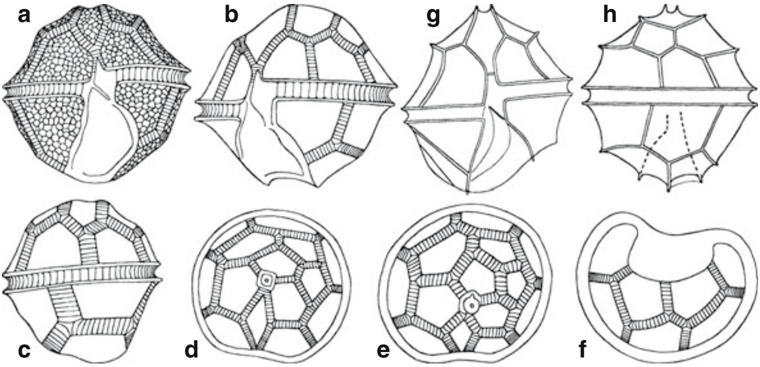

Fig. 271 *Chimonodinium keyense* (Nygaard) Moestrup & Calado (after Nygaard 1926). **a** ventral view with plate ornamentation; **b** ventral-left view; **c** right lateral view; **d**, **e** two apical views; **f** antapical view; **g**, **h** ventral and dorsal views of more angular cell (dotted lines in **h** indicate sulcus; as var. *gonyaulacoides*)

6. *Chimonodinium keyense* (Nygaard) Moestrup & Calado *comb. nov.* (**Fig. 271**)

Basionym: *Peridinium keyense* Nygaard 1926, *Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn* **82**, p. 208, pl. IV, fig. 32
Taxonomic synonym: *Peridinium keyense* var. *gonyaulacoides* Nygaard 1926, p. 208, pl. IV, fig. 33

Cells spherical, very slightly flattened dorsoventrally. Epi- and hypocone of similar size. The sulcus extends for a short distance onto the epicone, terminating acutely or with a transverse suture. On the hypocone the sulcus widens considerably towards the antapex. Cingulum descending, displacement *ca.* one cingulum width. Amphiesmal plates reticulate, many plates slightly concave, particularly on the epicone. The plates are arranged somewhat asymmetrically, 1a and 2a are located on the cell's left side, 3a – which is larger than 1a and 2a – is on the right side. Length 45–67 µm, width 47–54 µm. Plate 4′ usually larger than 2′ and 3′.
Ecology: in humic lakes.
Geographical distribution: Burma (Skuja). Lake Ohotiel, Key Islands, Indonesia (Nygaard).

Genus 3. *Naiadinium* Carty 2014, p. 120, 223

Type species: *Naiadinium polonicum* (Wołoszyńska) Carty 2014

The two known species share the plate formula po, cp, x, 4′, 1–2a, 7″, 6c (T + 5c), 5s, 5‴, 2″″ and cysts with thin spines or wart-like thickenings. Vegetative cells often with thin cover but amphiesmal plates are visible in the light microscope. One species, *N. polonicum*, is well known and widely distributed, with characteristic convex-concave cells, while the other, *N. lubieniensiforme*, has apparently not been seen since its description from Austria some 75 years ago. Its phylogenetic relationships therefore remain unresolved.

Key to species of *Naiadinium*:

1a Cells with flat or concave ventral side, less than 50 µm long .... 1. *N. polonicum*

1b Cells barely compressed dorsoventrally, 50 µm or longer .... 2. *N. lubieniensiforme*

1. *Naiadinium polonicum* (Wołoszyńska) Carty 2014, p. 120, 223 (**Fig. 272**)

Basionym: *Peridinium polonicum* Wołoszyńska 1916, p. 271, pl. 12, figs 1–10, *nom. cons. prop.*
Nomenclatural synonym: *Peridiniopsis polonica* (Wołoszyńska) Bourrelly 1968, p. 9 ("*polonicum*")
Taxonomic synonyms: ?*Glenodinium gymnodinium* Penard 1891, p. 54, pl. IV, figs 8–10, *nom. rej. prop.*; *Peridinium polonicum* var. *trilineatum* Er. Lindemann 1919, p. 223, text-fig. 21; *Glenodinium gymnodinium* var. *biscutelliforme* R. H. Thompson 1951, p. 293, figs 35–40 ≡ *Naiadinium biscutelliforme* (R. H. Thompson) Carty 2014, p. 120, 223

Cells round to oval, the ventral side flat or concave, giving the cell a distinct plano-concave or convex-concave appearance. The epi- and the hypocone of equal size or the epicone slightly larger than the hypocone. The epicone rounded conical with convex sides. Amphiesma plates finely areolated. Cingulum descending, displaced *ca.* one cingular width. Intercalary striae transversely striated. Sulcus barely extends onto the epicone, but on the hypocone widens slightly towards the antapex. Left side of the hypocone (plate 1′′′′) with wing-like extension, which sometimes extends posteriorly as a spine, often difficult to see. Sulcus composed of transitional plate adjacent to cingular plate 2c and 4 (Adachi 1965) or 5 sulcal plates (Craveiro *et al.* 2015). Sulcus with distinct oblique flange. The number of intercalary plates on the epicone can be one or two in the same population. If two are present, one is usually bigger than the other, more rarely they are of equal size. Chloroplasts discoid, mainly in the cell periphery, with up to 6 visible pyrenoids. Nucleus ovoid, excentral. Eyespot sometimes visible in the sulcal area. Microtubular basket present within the cell. Theca opens at the dorsal anterior plates. Cells 32–42 µm long, 27–36 µm wide, 18–24 µm thick. Cysts round, 38 µm in diameter, covered with numerous thin spines, each spine *ca.* 4.5 µm long.
SEM: Bourrelly & Couté (1980), Carty (1989, 2003), Craveiro *et al.* (2015).
TEM: Craveiro *et al.* (2015).
DNA data: Craveiro *et al.* (2015).
Ecology: plankton in both small and large, slightly alkaline ponds and lakes at pH around 7.5. Found in both oligotrophic to slightly mesotrophic (Höll 1928), as well as in eutrophic waters (Craveiro *et al.* 2015), sometimes bloom forming. Cause of mass fish mortality in Lake Sagami near Tokyo, Japan (Hashimoto *et al.* 1968; see further on p. 37).

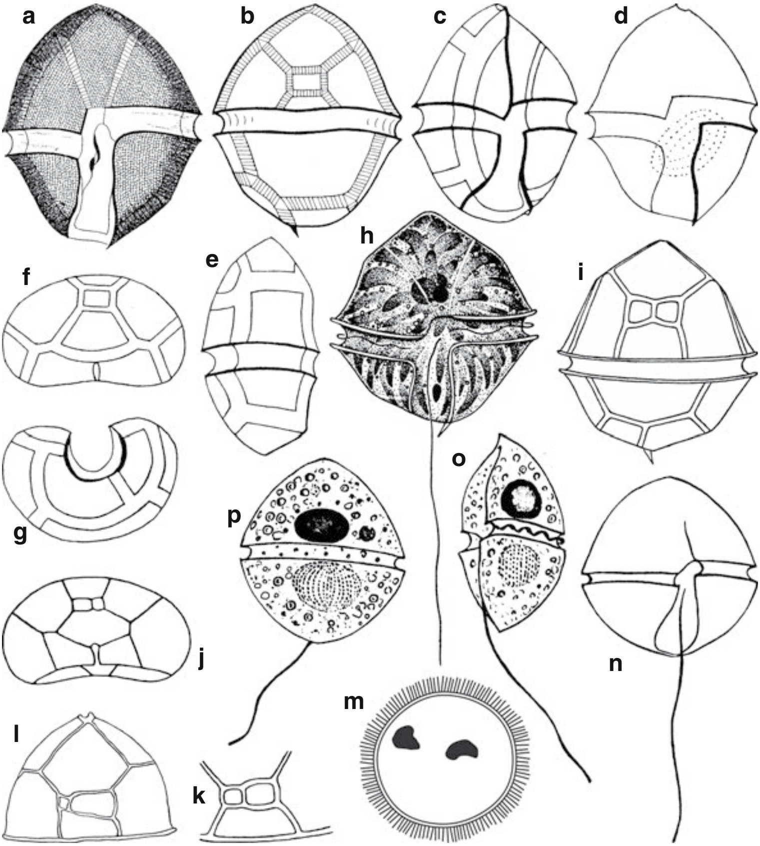

Fig. 272 *Naiadinium polonicum* (Wołoszyńska) Carty (**a**–**g** after Wołoszyńska 1916; **h**, **i** after Thompson 1951; **j**, **k** after Lefèvre 1932; **l** after Adachi 1965; **m** original, based on LM information in Craveiro *et al.* 2015; **n**–**p**, after Penard 1891). **a** ventral view with plate ornamentation; **b** dorsal view; **c** ventral-lateral view; **d** cell outline with position of nucleus; **e** right lateral view; **f**, **g** apical and antapical views; **h** ventral view of live cell, with contents; **i** dorsal view with two intercalary plates of equal size; **j** apical view; **k**, **l** dorsal views of intercalary plates of very different size; **m** resting cyst with thin spines and two red bodies; **n**–**p**, *Glenodinium gymnodinium* in ventral, left lateral and dorsal views, respectively

Geographical distribution: from Denmark in the north (Craveiro *et al.*) to Italy in the south (Hansen & Flaim), and from Portugal in the west (Pandeirada *et al.*; Craveiro *et al.*) to Ukraine in the east (Wołoszyńska; Lindemann) and Greece in the southeast (Schröder). Alaska and eastern half of USA, Cuba, Mexico (data assembled by Carty 2014). China (Hu e*t al.*), Japan (Adachi).

Note 1: *Glenodinium fungiforme* J. Schiller (1955, p. 50, pl. X, fig. 50) differs mainly in the slightly indented front end and smaller size (30–32 versus 40 µm long and 24–26 versus 35 µm wide). It was found in winter and spring in small eutrophic lakes in Austria, and may represent the same species.

Note 2: Several authors have discussed that *Glenodinium gymnodinium* Penard from Lake Geneva (Penard 1891) may be identical to *N. polonicum*. A proposal to conserve the name *Peridinium polonicum* against *Glenodinium gymnodinium* is under way (Calado *et al.*) to allow continuation of use of the specific epithet *polonicum*.

2. *Naiadinium lubieniensiforme* (Diwald) Moestrup & Calado *comb. nov.*
(**Fig. 273**)

Basionym: *Glenodinium lubieniensiforme* Diwald 1938, p. 176, figs 1–4 ("*lubiniensiforme*")
Nomenclatural synonyms: *Peridinium lubieniensiforme* (Diwald) Huber-Pestalozzi 1950, p. 234 ("*lubiniensiforme*") ≡ *Peridiniopsis lubieniensiformis* (Diwald) Bourrelly 1968, p. 9 ("*lubiniensiforme*")

Cells ovoid, dorsoventrally slightly compressed. Epi- and hypocone of the same size. Epicone shortly pointed, hypocone 5-sided. Plates with 3–6 short longitudinal striations. Cingulum wide, descending, the two ends very slightly displaced. Sulcus also wide, distally widening. Anteriorly it often extends very slightly onto the epicone. Chloroplasts lens-shaped, yellow, nucleus central. Cell division: two types of vegetative division observed: (1) approximately transverse, semiconservative division of the cell in which each daughter cell takes over half the amphiesma of the mother cell and forms the missing part; (2) formation of two small naked zoospores which are released when the cingulum breaks open. Cells grow to final size and form new amphiesmal plates during the following 30 h. The mother cell ceases swimming during cell division, often attaching to algal filaments, or other substrates. Cell length 50–76 µm, width 40–60 µm.
Sexual reproduction: Cells form 4 isogametes within the amphiesma. These are released when the cell breaks open at the cingulum. The gametes fuse to form a hypnocyst. Cysts ellipsoid, brown, with large wart-like thickenings.
Ecology: in rainwater ponds and puddles, sometimes forming blooms, coloring the water yellowish green.
Geographical distribution: Austria.

Genus 4. *Theleodinium* Craveiro, Pandeirada, Daugbjerg, Moestrup & Calado 2013, p. 490

Type species: *Theleodinium calcisporum* Craveiro, Pandeirada, Daugbjerg, Moestrup & Calado 2013

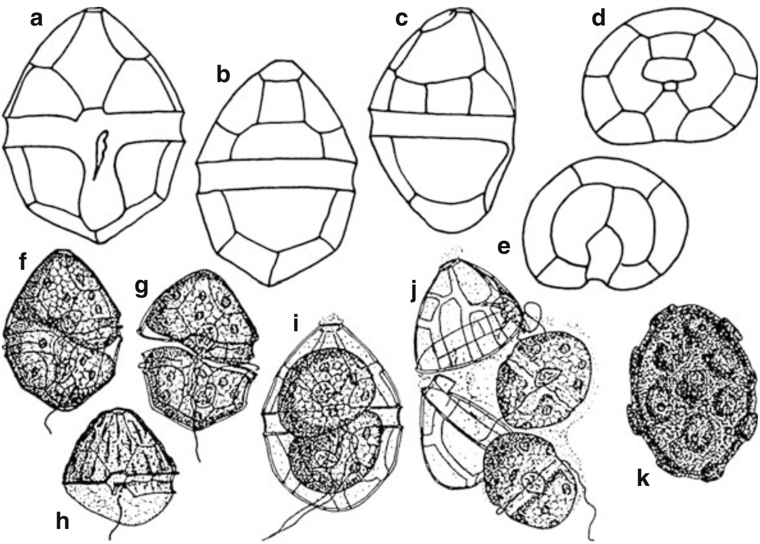

Fig. 273 *Naiadinium lubieniensiforme* (Diwald) Moestrup & Calado (after Diwald 1938). **a**, **b** ventral and dorsal views; **c** right lateral view; **d**, **e** apical and antapical views; **f**–**h** cell division with conservation of the divided parent amphiesma (desmoschisis); **i**, **j** cell division in which the daughter cells abandon the parent amphiesma (eleutheroschisis); **k** resting cyst

Plate formula po, cp, x, 3′ (4′), 2a, 7″, 6c, 5–6s, 5‴, 2⁗. Cells with projecting, nipple-like apical pore. Peduncle and microtubular basket present, and therefore possibly mixotrophic. With pyrenoid-containing chloroplasts. The single species described produces calcified cysts.

1. *Theleodinium calcisporum* Craveiro, Pandeirada, Daugbjerg, Moestrup & Calado 2013, p. 490, figs 1–26 (**Fig. 274**)

Cells rounded, barely or not dorsoventrally flattened. Epi- and hypocone of equal size. Amphiesmal plates smooth, with scattered trichocyst pores. Apical plate 2′ very large, curving around the apex, occasionally divided into two plates. Chloroplasts yellowish-brown with lobes arranged mainly along the cell periphery. Three or four pyrenoids present, surrounded by starch sheaths. Eyespot absent. Nucleus located dorsally at cingulum level. Small protruding peduncle present. Cell length 16–25 μm, width 13–23 μm.
Resting cysts round to slightly elongate, 17–30 μm in diameter, with calcified outer layer of variable crystalline elements, sometimes up to 25 μm thick (cysts then up to 60 μm in diameter), but more commonly 1–2 μm thick. Cysts usually colorless except for the presence of 1–2 large red or orange bodies. No paratabulation observed on the resting spore.

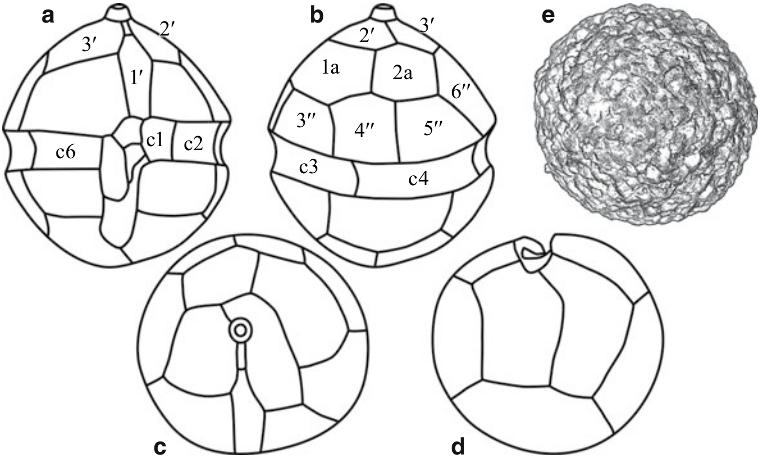

Fig. 274 *Theleodinium calcisporum* Craveiro, Pandeirada, Daugbjerg, Moestrup & Calado (original drawings, based on information from LM and SEM images). **a**–**d** ventral, dorsal, apical and antapical views, with typical arrangement of amphiesmal plates; **e** calcified cyst surface

SEM: Craveiro *et al.* (2013).
TEM: Craveiro *et al.* (2013).
DNA data: Craveiro *et al.* (2013).
Ecology: found in shallow freshwater lake near Ílhavo, Portugal, in March 2011 and established in culture. Conductivity, pH and water temperature at the time of collection 323 μS · cm^{-1}, 8.3 and 13.3 °C, respectively. Subsequently identified from a polluted Danish lake near Copenhagen (G. Hansen & Daugbjerg, unpublished).
Geographical distribution: Denmark; Portugal (Craveiro *et al.*).

Order 8. SUESSIALES Fensome, F. J. R. Taylor, G. Norris, Sarjeant, Wharton & G. L. Williams 1993, p. 56

Cells covered with amphiesmal vesicles containing very thin plates or plate-like structures. In the Linear Apical Complex, which is absent in a few genera, the row of pores all extend from a single, linear, amphiesmal vesicle, which in *Hemidinium nasutum* is *ca.* 20 μm long. The eyespot, when present, belongs to type B, E or F, in other words brick-like material is always associated with the eyespot. An order of both marine and freshwater species. With five families. The families Borghielaceae, Sphaerodiniaceae and Suessiaceae are each characterized by a type of eyespot. Eyespot type is unknown for the other two families.

Key to the families of Suessiales found in fresh water:

1a Cingulum incomplete, lacking on the right ventral side ...... 2. Hemidiniaceae
1b Cingulum complete, but in small species sometimes difficult to see 2
2a Cells with anterior carina (apical ridge) on the epicone .... 3. Lophodiniaceae
2b Carina absent 3
3a Eyespot of type F, cells with small number of relatively large amphiesmal plates usually visible in LM .... 4. Sphaerodiniaceae
3b Eyespot of type B or E, cells with numerous small amphiesmal plates which are usually not visible in LM 4
4a Eyespot of type B .... 1. Borghiellaceae
4b Eyespot of type E .... 5. Suessiaceae

Key to the genera of Suessiales found in fresh water:

1a Ectoparasitic on fish .... *Piscinoodinium*
1b Free swimming in the water, not parasitic 2
2a Epicone much smaller than hypocone (usually less than one third) .... *Prosoaulax*
2b Epi- and hypocone less different in size 3
3a Cingulum complete 4
3b Cingulum lacking on the right ventral side .... *Hemidinium*
4a Cells with paired longitudinal ridges .... *Lophodinium*
4b Cells lack paired longitudinal ridges 5
5a Cells spherical, amphiesmal plates relatively few, often visible in LM .... *Sphaerodinium*
5b Cells ovoid (rarely spherical), pentagonal or hexagonal in ventral view, amphiesmal plates few or many, not visible in LM 6
6a Cells pentagonal or hexagonal .... *Leiocephalium*
6b Cells ovoid or spherical, the hypocone may be trapezoidal 7
7a Sulcus not visible in LM .... *Protodinium*
7b Sulcus visible in LM 8
8a Chloroplasts extend from central pyrenoid .... *Baldinia*
8b Chloroplasts disc-shaped, forming network or parietal 9
9a Resting cysts with spines[1] .... *Biecheleria*
9b Resting cysts smooth[1] 10
10a Apical furrow present (not visible in LM); never a single, large central pyrenoid in the hypocone .... *Borghiella*
10b Apical furrow absent (not visible in LM); a single, large pyrenoid centrally located in the hypocone .... *Asulcocephalium*

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[1] *Borghiella* and *Biecheleria*, although very different in resting cyst morphology and in cell structure, most notably the ultrastructure of the eyespot, cannot be distinguished to generic level using light microscopy. If resting cysts are not available, we suggest trying keys of both *Biecheleria* and *Borghiella* species below to identify to species level.

Family 1. Borghiellaceae Moestrup, K. Lindberg & Daugbjerg 2009a, p. 218

Eyespot of type B *sensu* Moestrup & Daugbjerg (2007), *i. e.*, carotenoid globules intraplastidic and accompanied on the chloroplast surface by brick-like material located in cisternae. Apical furrow apparatus comprising two parallel, elongate vesicles (*Borghiella*) or furrow system absent (*Baldinia*). Cysts smooth with a clear wall, spherical to oval in *Borghiella*, more irregularly elongate and with an axial indentation in *Baldinia*.

Key to the genera of Borghiellaceae:

1a Apical furrow present (SEM); chloroplasts not radially arranged .... 2. *Borghiella*

1b Apical furrow absent; chloroplast lobes radiating from central pyrenoid .... 1. *Baldinia*

Genus 1. *Baldinia* Gert Hansen & Daugbjerg *in* Hansen *et al.* 2007, p. 91

Type species: *Baldinia anauniensis* Gert Hansen & Daugbjerg 2007

Naked flagellates. Chloroplasts with peridinin. Amphiesmal plates absent. Apical furrow absent. Cysts polygonal.

Key to species of *Baldinia*:

1a Nucleus central, chloroplasts greenish-yellow .... 1. *B. anauniensis*

1b Nucleus excentric, chloroplasts pale brown .... 2. *B. bernardinensis*

1. *Baldinia anauniensis* Gert Hansen & Daugbjerg *in* Hansen *et al.* 2007, p. 91, figs 1–55 (**Fig. 275**)

Cells ovoid with hemispherical epi- and hypocone. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus narrow, does not reach the antapex. Chloroplasts yellowish-green, radiating from central pyrenoid. Eyespot present. Nucleus in the central part of the cell. Red inclusion bodies often present, perhaps food vacuoles. The cells lack amphiesmal plates altogether and an apical furrow is also absent. Amphiesmal vesicles are, however, visible in SEM. Cell length 23–28 µm, width 18–24 µm. Cysts with two layers, an outer smooth, inflated wall, including a truncated apical and an indented antapical part. Inner wall thin, appressed to the rounded cytoplasmic part. Cyst length *ca.* 35 µm, width *ca.* 28 µm.
SEM: Hansen *et al.* (2007).
TEM: Hansen *et al.* (2007).
DNA data: Hansen *et al.* (2007).
Ecology: very common in Lake Tovel, an oligotrophic lake in the Italian Dolomites. Seems to prefer temperatures above 10 ˚C, and occurs very commonly in the

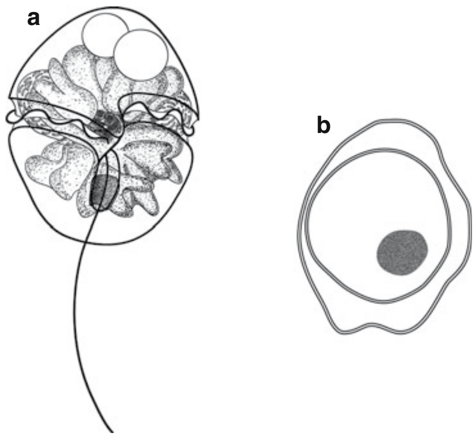

Fig. 275 *Baldinia anauniensis* Gert Hansen & Daugbjerg (**a** after Hansen *et al.* 2007; **b** original, based on light micrograph in Hansen *et al.* 2007). **a** ventral view showing radiating chloroplast lobes, an eyespot in the sulcal area, accumulation bodies in the cell middle (usually orange to red) and the elongated nucleus appearing on both sides from behind the chloroplast; **b** resting cyst with two walls and a dark accumulation body

lake in June–October. It is mixotrophic, and food vacuoles containing cryptomonad remains have been observed with the TEM.
Geographical distribution: Italy.

2. *Baldinia bernardinensis* (Chodat & Zender) Moestrup, K. Lindberg & Daugbjerg 2009a, p. 218 (**Fig. 276**)

Basionym: *Glenodinium bernardinense* Chodat & Zender *in* Chodat 1924, p. 37, figs II–VI

Cells ovoid, epi- and hypocone both semicircular in ventral view. Epicone larger than hypocone. Cells strongly dorsoventrally compressed. Cingulum descending, the ends displaced about one cingulum width. Chloroplasts pale brown, radiating, eyespot present. Nucleus excentric. Cell length 24–26 µm, width 22–24 µm. Cyst polyedric, length 26–34 µm, width 21–29 µm.
Ecology: in small alpine lake near the Grand-Saint-Bernard pass.
Geographical distribution: Switzerland.

Genus 2. ***Borghiella*** Moestrup, Gert Hansen & Daugbjerg 2008, p. 56

Type species: *Borghiella dodgei* Moestrup, Gert Hansen & Daugbjerg 2008

Cells surrounded by periplast of many, thin, often hexagonal vesicles. A narrow pair of elongate, parallel amphiesmal vesicles extends over the cell apex from the

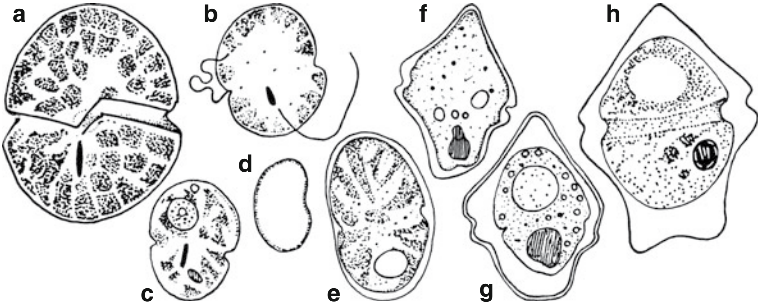

Fig. 276 *Baldinia bernardinensis* (Chodat & Zender) Moestrup, K. Lindberg & Daugbjerg (after Chodat 1924). **a** ventral view showing course of the cingulum, eyespot and chloroplast lobes in surface focus; **b**, **c** different views of cells; **d** cross section outline; **e** beginning of encystment; **f** young cyst, already with pale contents; **g** mature, pale cyst; **h** mature cyst approaching excystment

left-dorsal to the right-ventral side, lined on each side by a row of four- or five-sided vesicles. It is usually not visible in the light microscope. With many golden-green chloroplasts. Eyespot intraplastidial, with external covering of vesicles containing brick-like material (type B). Resting cysts smooth, spherical or ovoid. Cell division by fission in the motile stage or in so-called division cysts.
Species of *Borghiella* are generally in need of study. Many of the original descriptions are very incomplete, and future studies may show that some of the taxa below are conspecific. All species for which temperature preferences have been described are cold-water forms. Only one, *B. silvatica*, was not mentioned to be occurring at any particular temperature. Only *Borghiella tenuissima* is morphologically very distinct.

Key to species of *Borghiella*:

1a	Cells very flat, disc-shaped, over 50 µm wide, cingulum incomplete	6. *B. tenuissima*
1b	Cells globose or little compressed dorsoventrally, hypocone sometimes flat ventrally, cells less than 50 µm wide, cingulum complete	2
2a	Cells over 40 µm long	5. *B. silvatica*
2b	Cells less than 35 µm long	3
3a	Cells with carmine-red central material	4. *B. pascheri*
3b	Cells without carmine-red central material	4
4a	With numerous chloroplasts	5
4b	With 4–6 chloroplasts	3. *B. marylandica*
5a	With ridge-like structure along the left side of the sulcus	7. *B. woloszynskae*
5b	No ridge along the left edge of the sulcus	6
6a	Epicone cone-shaped	1. *B. dodgei*
6b	Epicone hemispherical	2. *B. andersenii*

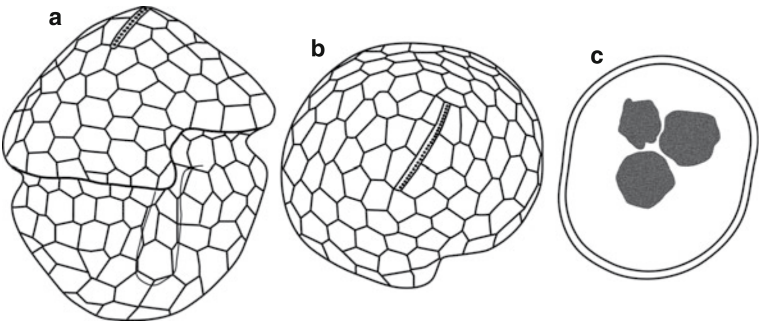

Fig. 277 *Borghiella dodgei* Moestrup, Gert Hansen & Daugbjerg (**a**, **b** original drawings, based on SEM images in Moestrup *et al.* 2008; **c** original drawing, based on LM in Flaim *et al.* 2010). **a** ventral view, approximate outline of sulcus marked with thinner line; **b** apical view; **c** cyst with accumulation bodies

1. *Borghiella dodgei* Moestrup, Gert Hansen & Daugbjerg 2008, p. 57 (**Fig. 277**)

Epi- and hypocone usually of equal size, the epicone typically somewhat cone-shaped, the hypocone rounded. The paired elongate anterior amphiesmal vesicles 5–7 µm long, lined on each side by 3–4 vesicles. Cingulum descending, displaced *ca.* one cingulum width. The epicone slightly flattened dorsoventrally, hypocone more strongly so. The sulcus widens posteriorly into a large concave area. With peripheral network of chloroplasts. Nucleus central, most of it located in the epicone. One or two pusules in the girdle region and a very small eyespot near the anterior end of the sulcus. Cells approximately 20 µm long (size range 12–22 µm) and 14–15 µm wide. Cysts smooth, spherical or ovoid.
SEM: Flaim *et al.* (2004, figs 31–33); Moestrup *et al.* (2008).
TEM: Dodge *et al.* (1987, as *Glenodinium sanguineum*); Moestrup *et al.* (2008).
DNA data: Moestrup *et al.* (2008).
Ecology: cold-water species found in the oligotrophic Lake Tovel in the Italian Alps. Highest growth rates were at temperatures < 7 ˚C and irradiance levels of *ca.* 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Highest encystment rates were at temperatures > 7 ˚C. Blooms occurred when large amounts of organic nitrogen were available (Flaim *et al.* 2010).
Geographical distribution: Italy.

2. *Borghiella andersenii* Daugbjerg, Andreasen, Happel, Pandeirada, Gert Hansen, Craveiro, Calado & Moestrup 2014, p. 439, figs 2–28 (**Fig. 278**)

Cells roundish, slightly longer than wide and somewhat compressed dorsoventrally. Epi- and hypocone rounded, epicone slightly wider just above the cingulum. Hypocone slightly more flattened than the epicone. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus in its upper end with ventral ridge. With many yellowish-green chloroplasts in the cell periphery. Nucleus central, extending

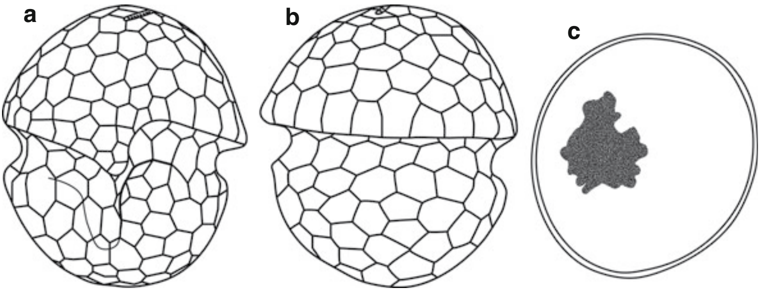

Fig. 278 *Borghiella andersenii* Daugbjerg, Andreasen, Happel, Pandeirada, Gert Hansen, Craveiro, Calado & Moestrup (**a**, **b** original, based on SEM images; **c** original, based on LM images). **a** ventral view showing amphiesmal vesicles, with the less abrupt posterior and right-hand side contour of the sulcus indicated by a thinner line; **b** dorsal view; **c** resting cyst

into the epicone. Eyespot present, but not readily visible in the light microscope. A narrow pair of elongate anterior amphiesmal vesicles, 3–4 µm long, lined by 2–3 vesicles on each side. Cell length *ca.* 20 µm, width *ca.* 15 µm and thickness *ca.* 13 µm. Cell division both in the motile stage and in non-motile division cysts. Sexual reproduction by formation of planozygotes with two longitudinal flagella. Cysts spherical to elongate, with smooth wall.
SEM: Daugbjerg *et al.* (2014).
TEM: Daugbjerg *et al.* (2014).
DNA data: Daugbjerg *et al.* (2014).
Ecology: presently known only from small pond in Scotland and from flooded stream area in Portugal. Maintained in culture at 15 °C and 18 °C.
Geographical distribution: Portugal; Scotland.

3. *Borghiella marylandica* (R. H. Thompson) Moestrup *comb. nov.* (Fig. 279)

Basionym: *Gymnodinium marylandicum* R. H. Thompson 1947, *Chesapeake Biol. Lab. Publ.* **67**, p. 7, pl. I, figs 7–9
Cells ovoid in face view, hypocone ventrally flattened. Cingulum descending, displaced 1–1.5× the width. Sulcus forming a sharp sinus at each end. Epi- and hypocone almost equal in size. Epicone broadly rounded, hypocone a truncated cone, narrow or broad, with rounded antapex. Upper margin of cingulum slightly flaring but rounded, lower margin rounded. Longitudinal flagellum 1–1.5× the cell length. Eyespot absent. Four to six golden-brown to brown discoidal chloroplasts, parietal. One to several orange-red to bright-red oil globules may be present. Cell length 17–22 µm, width 13–19 µm. Cysts oval, smooth, 18–24 µm long and 14–21 µm wide.
Ecology: in water flowing slowly from under the ice (in Belcamp, Maryland).
Geographical distribution: USA, MD.

Note: this species closely resembles *B. pascheri*, the main difference being the small number of chloroplasts and the equal size of epi- and hypocone.

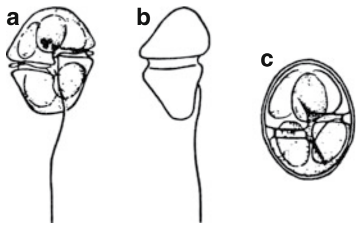

Fig. 279 *Borghiella marylandica* (R. H. Thompson) Moestrup (after Thompson 1947). **a** ventral view showing large chloroplasts; **b** outline of cell in right lateral view; **c** cyst (resting cyst?)

4. *Borghiella pascheri* (Suchlandt) Moestrup *comb. nov.* (**Fig. 280**)

Basionym: *Glenodinium pascheri* Suchlandt 1916, *Ber. Deutsch. Bot. Ges.* **34**, p. 246, text-figs A–F
Nomenclatural synonyms: *Gyrodinium pascheri* (Suchlandt) Er. Lindemann 1928a, p. 259 ≡ *Gymnodinium pascheri* (Suchlandt) J. Schiller 1954a, p. 269 ≡ *Woloszynskia pascheri* (Suchlandt) Stosch 1973, p. 133
Taxonomic synonym: *Gyrodinium nivale* Er. Lindemann 1929, p. 75, figs 55–60

Vegetative cells occur as two morphological types, a coccoid and a flagellated stage. In the flagellated stage cells are more or less oval, the epicone smaller than the hypocone. The epicone varies in shape, and is typically somewhat flattened dorsoventrally, hemispherical or slightly conical. The hypocone is strongly flattened, trapezoidal, in lateral view narrowing strongly toward the antapex. Cingulum descending, the two ends of the cingulum displaced 1–1 1/2 cingulum widths. Sulcus extends to the antapical end. The left side of sulcus is lined by a slight ridge along its proximal part. Amphiesma very thin, composed of numerous, usually hexangular, plates. Plates smooth. Longitudinal flagellum 1–3× the length of the cell. Nucleus anterior, dorsal. The central part of the cell carmine-red due to the presence of red pigment, obscuring the cingular-sulcal area. Many olive-green parietal chloroplasts, seen best in cells with little starch and little red pigment. Cells strongly positively phototactic but eyespot not seen in the light microscope. An eyespot of type B observed in the electron microscope. Cells 18–33 µm long. Cell division takes place in the swimming stage, mainly during the dark period.
Non-motile stage: cells without flagella occur at low temperature in ice or snow. Such cells are oval, surrounded by a wall. They contain olive-green chloroplasts and sometimes red pigment in the center, and measure *ca.* 26 × 21 µm. Lipid droplets occur in the cell periphery, red pigment mainly in the central part. These cells may transform into motile cells and represent temporary cysts. They are thought not to divide in this stage, but see Note 3 below.
Thick-walled cysts seen in old cultures, cyst wall up to 3 µm thick. They are formed after sexual reproduction and planozygotes have been observed. Germination of the cysts has not been studied.

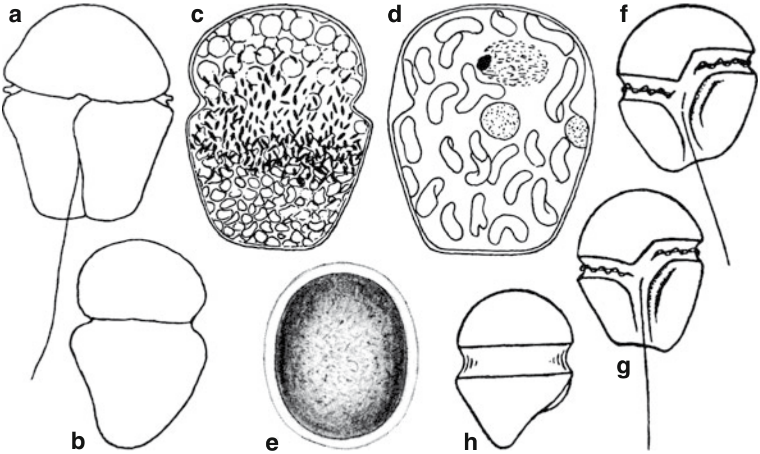

Fig. 280 *Borghiella pascheri* (Suchlandt) Moestrup (**a**–**e** after Suchlandt 1916; **f**–**h** after Lindemann 1929). **a**, **b** outlines of motile cells in ventral and lateral views, respectively; **c** contents of motile cell, with oil droplets in the anterior part, starch grains in the posterior and red fusiform bodies in the middle; **d** cell contents with numerous chloroplasts, the nucleus (with dark nucleolus) in the epicone and a vesicle (interpreted as a pusule) in the middle; **e** resting cyst; **f**, **g** ventral views of motile cells; **h** right lateral view

SEM: Moestrup *et al.* (in prep.).
TEM: Moestrup *et al.* (in prep.).
DNA data: Moestrup *et al.* (in prep.).
Ecology: in ice and snow, both as temporary cysts and as motile cells, forming red, sometimes extensive, patches on the snow. When the ice is melted in the laboratory, flagellated cells begin moving inside the cyst wall within a few minutes and escape, leaving an empty cyst wall behind. Cells then swim around among the ice crystals. Motile cells occur at 0–15 ˚C, with optimal growth at 1–8 ˚C.
Geographical distribution: Austria; Switzerland: the cause of red snow on the ice of frozen fish pond in the Austrian Alps (Traunsteiner 1914; Lindemann 1929), and frozen Lake Davos in the Swiss Alps (Suchlandt 1916). Most recently forming red snow in Ontario, Canada (Gerrath & Nicholls; Nicholls).

Note 1: This species is morphologically close to *Borghiella dodgei* and *B. andersenii*. It forms similar hypnocysts. The cells are of about the same size, the hypocone is also flattened dorsoventrally. It differs mainly in the presence of the red pigments in *B. pascheri*, located in vesicles in the cell, and in its ecology, *B. pascheri* being a snow and ice alga.

Note 2: Wilcox (1986) found the chloroplasts of cells from Wisconsin, identified as *Woloszynskia pascheri*, to contain numerous prokaryotes in an apparently stable symbiosis. Whether this material belongs to *B. pascheri* needs to be confirmed.

Note 3: Wołoszyńska (1937) reported the species from winter plankton in two lakes in the Tatra mountains in Poland. Her description agrees with Suchlandt's (1916) original description, only she found cells to divide in the non-motile stage and her material was from plankton. The identity of her material needs to be confirmed.

Note 4: Schiller (1954a, 1955) provided an extensive description of material identified by him as *Gymnodinium pascheri* from several localities in Vienna, Austria. It formed brown, not red patches on ice. Cells from some collections were found to form division cysts as in *Tovellia*. The material also formed horned cysts very similar to those described for *Gymnodinium tylotum*. Schiller's material may belong to a different species, or he may have collected a mixture of species.

5. *Borghiella silvatica* (Er. Lindemann) Moestrup *comb. nov.* (**Fig. 281**)

Basionym: *Spirodinium silvaticum* Er. Lindemann 1923a, *Hedwigia* **64**, p. 146, figs 1–3
Nomenclatural synonym: *Gyrodinium silvaticum* (Er. Lindemann) Er. Lindemann 1925c, p. 158

Cells approximately pentagonal, antapical end lobed. Epicone smaller than hypocone, triangular. Hypocone trapezoid, antapex sinuous, the right side of the cell slightly longer than the left side. Hypocone is irregularly conical in lateral view. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus extends to the antapex, at a slight angle to the longitudinal cell axis. Nucleus large, anterior. Numerous disc-shaped brown chloroplasts. Eyespot not observed. Lipid bodies are often common. Cell length 42–48 µm, width 36–43 µm. Cysts thick-walled, pentagonal-rounded.
Ecology: pond in forest.
Geographical distribution: Lissa, Poland.

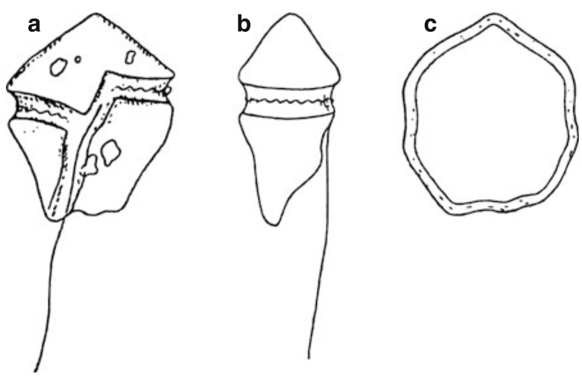

Fig. 281 *Borghiella silvatica* (Er. Lindemann) Moestrup (after Lindemann 1923a). **a** ventral view, with internal bodies identified as red oil droplets; **b** right lateral view; **c** resting cyst

Note: we include this species in *Borghiella* because of its general resemblance to *B. dodgei* and *B. woloszynskae*. It differs from these species in size and in the presence of antapical lobes on the cell.

6. *Borghiella tenuissima* (Lauterborn) Moestrup, Gert Hansen & Daugbjerg 2008, p. 74 (**Fig. 282**)

Basionym: *Gymnodinium tenuissimum* Lauterborn 1894, p. 396
Nomenclatural synonym: *Woloszynskia tenuissima* (Lauterborn) R. H. Thompson 1951, p. 290

Cells in ventral view angular-circular, dorsoventrally strongly flattened, disc-shaped. Epicone slightly larger than hypocone, asymmetrically pointed, right side more convex than left side. Hypocone angular, slightly excavated at the antapex. Cingulum descending but terminating ventrally midway on the cell's right side before reaching the sulcus. Cingulum formed of two horizontal rows of small plates. Sulcus on the hypocone only, extending to the antapex. Chloroplasts disc-shaped, yellow to yellowish-brown. Eyespot absent. Nucleus central, oval. Cell length 55–80 µm, width 45–72 µm, thickness 10–14 µm. Cells divide by binary fission in motile state (Stosch 1973). Cysts smooth, spherical (Stosch 1973).
TEM: Crawford *et al.* (1971).
Ecology: cold-water species, tolerant of low light intensities, favoring organic compounds, pH 7.2–7.4 (Höll 1928). Occurred in a pond in Vienna, in particular in February and April, disappearing when the temperature reached 4–6 ˚C (Schiller &

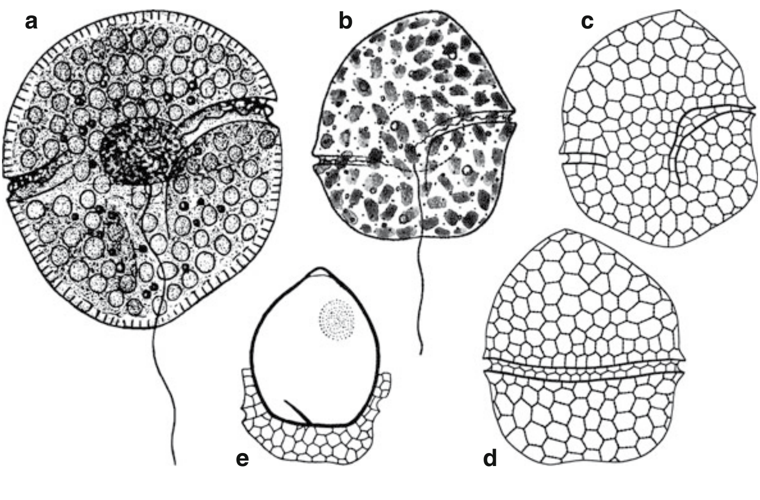

Fig. 282 *Borghiella tenuissima* (Lauterborn) Moestrup, Gert Hansen & Daugbjerg (**a** after Lauterborn 1899; **b** after Nygaard 1945; **c**–**e** after Wołoszyńska 1917). **a**, **b** ventral views showing cell contents; **c**, **d** ventral and dorsal views of cell cover; **e** cyst, still partially surrounded by cell cover, with the nucleus indicated

Stefan 1935; Steinberg 1981). Vertical migration was observed to take place under the ice, the cells moving away from the surface in the morning and returning in the afternoon. The movement was ascribed to the influence of light, the cells avoiding the strong light at mid-day (Schiller & Stefan 1935). In Westfalen, Germany, Schönhagen-Becker & Hegewald (1979) followed a population during two winters and found the cell size to change with the temperature of the water, from *ca.* 36 µm in length in November when the species started occurring, to *ca.* 65 µm under the ice in February. In a lake in Bavaria, Germany, Steinberg (1981) found the species to comprise 90% of the phytoplankton during its peak in March, numbering 2.8×10^6 cells per liter.
Geographical distribution: England (Crawford *et al.*; Lewis & Dodge); Germany (Lauterborn; Höll; Steinberg). Greenland (Moestrup *et al.*).

7. *Borghiella woloszynskae* (Pascher) Moestrup *comb. nov.* (**Fig. 283**)

Basionym: *Gymnodinium woloszynskae* Pascher 1923, *Arch. Protistenk.* **46**, p. 143, fig. 4 (new rank and replacement name for *Gymnodinium carinatum* var. *hiemale* Wołoszyńska 1917, p. 118, pl. 11, figs 1, 2, pl. 12, fig. 12 ["*hiemalis*"]; non *Gymnodinium hiemale* Wołoszyńska 1917, p. 118, pl. 11, fig. 4)
Nomenclatural synonyms: *Gymnodinium veris* Er. Lindemann 1925c, p. 155, *nom. illeg.* (name superfluous) ≡ *Woloszynskia veris* R. H. Thompson 1951, p. 290 ("*vera*"), *nom. illeg.*

Cells spherical to oval. Epi- and hypocone of almost the same size. Epicone conical, hypocone rounded, sometimes with a slight antapical indentation. Cingulum descending, with little displacement. A ridge is present along the left side of the sulcus. Amphiesma of hexangular vesicles, plates finely areolated. Chloroplasts numerous, yellow-brown. No eyespot. Nucleus rounded to oval, in the cell middle or in the epicone. Cells break open in the epicone. Cell length 18–30(–35) µm. Cysts oval, smooth, formed in late March after disappearance of the ice.

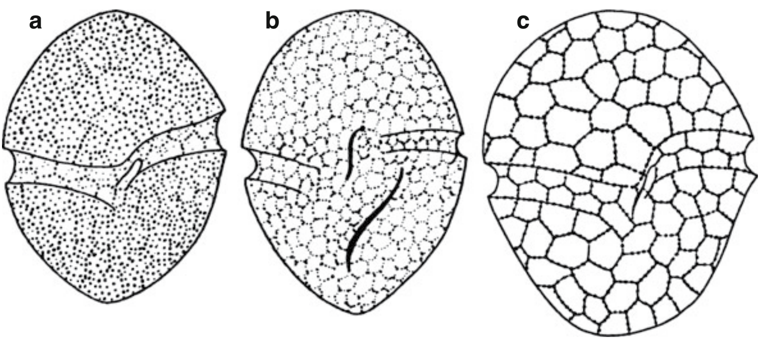

Fig. 283 *Borghiella woloszynskae* (Pascher) Moestrup (after Wołoszyńska 1917). **a**, **b** ventral views; **c** cell cover based on higher magnification (cell shape apparently deformed)

Ecology: very common in winter and during snow-melt in spring, in pools and ponds at pH 6.8–7.7; apparently favoring organic compounds in the water.
Geographical distribution: Czech Republic (Pascher); Germany (Lindemann; Baumeister); Ukraine (Wołoszyńska).

Note: very variable species, especially in size. It is closely related to *B. dodgei*, differing in the presence of a ridge along the right side of the sulcus.

Family 2. Hemidiniaceae Bourrelly *ex* P. C. Silva 1980, p. 61

Naked dinoflagellates, in which the cingulum is incomplete, extending from the cingulum-sulcus intersection and continuing to the dorsal side, terminating there. In the type of the single included genus, and the only species examined in the TEM, the amphiesmal vesicles are empty or with poorly defined contents (amphiesmal plates are absent). In this same species the cell possesses a very long line of narrow amphiesmal vesicles, the line extending from the ventral side of the epicone, past the apex to the dorsal side and continuing to the antapical end of the cell.

Genus 1. *Hemidinium* F. Stein 1878, pp 91, 97

Type species: *Hemidinium nasutum* F. Stein 1878

Cells rounded-elliptical in ventral view, asymmetric, more or less flattened dorsoventrally. Cingulum extends from the mid-ventral region towards the left side, terminating on the mid-dorsal side. Sulcus restricted to the hypocone, sometimes difficult to see. Amphiesmal plates not visible with the light microscope, and not staining with calcofluor. Chloroplasts discoid, in the peripheral part of the cell, sometimes connected to a central, compound pyrenoid. Cell division by fission in the motile stage. Resting cysts spherical.
Zoospores of *Gloeodinium* resemble *Hemidinium* but they are, as far as known, covered by amphiesmal plates that can be seen in a good light microscope. Most species of *Hemidinium* have been described without mentioning of plates, and some of these may turn out to constitute true *Hemidinium*. In a recently described species, *Hemidinium nephroideum*, the presence of plates was indicated, and it may therefore belong to *Gloeodinium*. However, the coccoid stage was not described. We are retaining it in *Hemidinium* for the time being.
Due to the confusion regarding the difference between *Hemidinium* and *Gloeodinium*, the taxonomy is presently in a chaotic state and the majority of species in the following list require careful examination before their taxonomy, phylogenetic affinity, distribution and ecology can begin to be understood. Many species were described incompletely and have never been refound. We have included below only species that we believe may be possible to identify. Skvortsov (1958, 1968) described a series of new *Hemidinium* species from eastern Asia, but all descriptions are so incomplete that identification to species level appears to be impossible. For a complete list of these species, see p. 473.

Key to species of *Hemidinium* reported from fresh water:

1a	Cells covered by plates	4. "*H. nephroideum*"
1b	Amphiesmal plates not visible in the light microscope	2
2a	Cells red	7. *H. purpureum*
2b	Cells colorless or yellowish-brown	3
3a	Chloroplasts absent	2. *H. bryophyticum*
3b	Chloroplasts present	4
4a	Cell with rostrum-like extension of the left side of the epicone	8. *H. soligenum*
4b	Cells without rostrum	5
5a	Many chloroplasts extending from cell center	6
5b	Chloroplasts 1–4	8
6a	Cells ovoid-rounded	"*H. ochraceum*"
6b	Cells elongate	7
7a	Cells rounded-elongate, 24–41 µm long	1. *H. nasutum*
7b	Cells almost rectangular, 38–45 µm long	5. *H. nobile*
8a	Cells with one laminate chloroplast, cell length 1.4–2× cell width	3. *H. montanum*
8b	Cells with 1–4 chloroplasts, cell length 1.3–1.4× cell width	6. *H. pseudochraceum*

Note: regarding "*H. ochraceum*" see p. 447.

1. *Hemidinium nasutum* F. Stein 1878, pp 91, 97 (first illustrated *in* Stein 1883, pl. II, figs 23–26) (**Fig. 284**)

Taxonomic synonyms: *Hemidinium tumidum* Skvortsov 1946, p. 13, pl. 1, fig. 3; *Hemidinium olivaceum* Skvortsov 1968, p. 100, pl. IV, fig. 8; *Hemidinium brasiliense* C. E. M. Bicudo & Skvortsov 1970, p. 16, figs 16, 19, 20

Cells elongate-rounded. Cells strongly dorsoventrally compressed. Cells almost kidney-shaped, left side of the cell almost straight to slightly convex, right side convex. Nucleus in the posterior part of the cell. With central, compound pyrenoid, from which the many chloroplasts extend towards the cell periphery. Proximal part of the sulcus located in a tube, not visible in the light microscope. External part of the sulcus extends from mid-region of hypocone to the antapex. With apical line extending from the ventral to the dorsal side, continuing to reach the antapex, and therefore *ca.* 20 µm long. Cells often swim with the broad sides towards the substrate. Mixotrophic (Stein 1878). Cell length 24–41 µm, width 15–25 µm, thickness 10–15 µm. Cyst bean-shaped or ellipsoid. The shape of the cysts recalls the flagellated cell. An additional, thin layer is formed inside and at some distance from the outer thick wall (Baumeister 1938a).
SEM: Dirchsen & Moestrup (in prep.).
TEM: Dirchsen & Moestrup (in prep.).
DNA data: (Moestrup & Daugbjerg 2007).
Ecology: acid bogs and ponds.
Geographical distribution: Czech Republic "bei Prag" (Stein); England (Lewis & Dodge); Finland (Levander; G. Hansen & Moestrup, unpubl.); Sweden (Skuja). Ivory Coast (Bourrelly). Brazil (Bicudo & Skvortsov). Manchuria, China (Skvortsov); Japan (Takano, pers. comm.). New Zealand (Thompson).

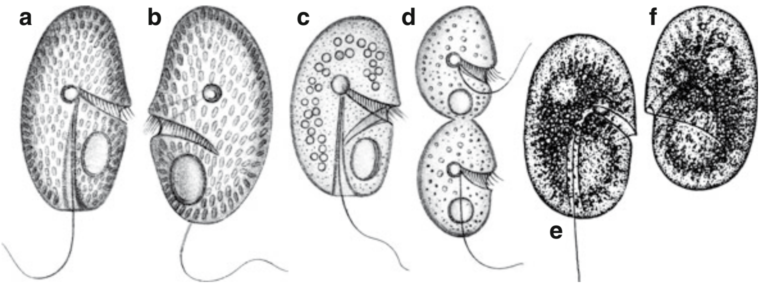

Fig. 284 *Hemidinium nasutum* F. Stein (**a**–**d** after Stein 1883; **e**, **f** after Skuja 1964). **a**, **b** ventral and dorsal views with cell contents (ellipsoid nucleus in left side of hypocone); **c** ventral view with dorsal part of cingulum also represented; **d** cell division; **e**, **f** ventral and dorsal views

Note: *Hemidinium kofoidii* Skvortsov (1968, p. 101, pl. IV, fig. 11) seems to differ only by having green chloroplasts.

2. *Hemidinium bryophyticum* Skvortsov 1958, p. 193, pl. 5, fig. 29 (**Fig. 285**)

Cells variable, spherical or oval, dorsoventrally very slightly compressed. Nucleus central. Chloroplasts absent. Cytoplasm hyaline. Longitudinal flagellum 2× length of the cell. Cell length 14–22 µm, width 14 µm.
Ecology: in *Drepanocladus* moss swamp, Manchuria.
Geographical distribution: Manchuria, China.

Note: several species described by Skvortsov are notoriously difficult to recognize. *Hemidinium animale* Skvortsov (1968, p. 99, pl. IV, fig. 6) differs by being distinctly compressed dorsoventrally. *Hemidinium kisselewii* Skvortsov (1968, p. 98, pl. IV, fig. 4) differs by possessing an eyespot. However, the position of the eyespot is not clear as there is no indication of orientation for the single drawing provided. The same applies to *Hemidinium mucosum* Skvortsov (1958, p. 194, pl. 5, fig. 21), described to possess green chloroplasts. *Hemidinium aquae-frigidae* Skvortsov (1968, p. 100, pl. IV, fig. 10) differs by measuring only 10–11 µm in length and 4–5 µm in width.

3. *Hemidinium montanum* C. E. M. Bicudo & Skvortsov 1970, p. 17, figs 17, 18 (**Fig. 286**)

Cells asymmetrical, globose to elliptical, 1.4–2× longer than wide, rather strongly dorsoventrally compressed. Epicone 2/3 the length of the cell. Chloroplast single, laminate, yellowish-green. Cells 11–26 µm long, 8–16.5 µm wide.
Ecology: in small temporary pool in a park (Parque do Estado de São Paulo) in the city of São Paulo, Brazil.
Geographical distribution: Brazil.

Note: *Hemidinium lindemannii* Skvortsov (1968, p. 102, pl. IV, fig. 12) differs by having four brown, “granular chloroplasts”.

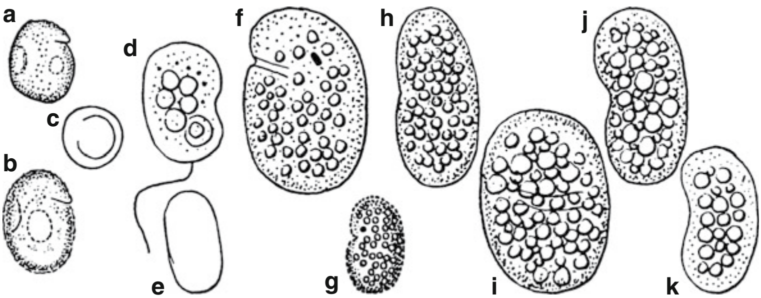

Fig. 285 *Hemidinium bryophyticum* Skvortsov and related species (**a**–**c**, **g** after Skvortsov 1958; **d**–**f**, **h**–**k** after Skvortsov 1968). The orientation of drawings on which these figures are based was not stated and must be presumed from the figures themselves. Both size and orientation follow the originals. **a**–**c** *Hemidinium bryophyticum*; **d**, **e** *Hemidinium animale* Skvortsov; **f** *Hemidinium kisselewii* Skvortsov; **g** *Hemidinium mucosum* Skvortsov; **h**–**k** *Hemidinium aquae-frigidae* Skvortsov

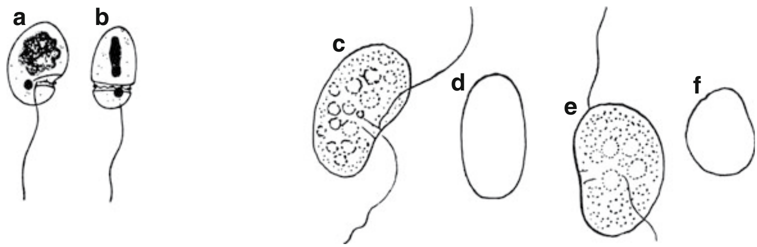

Fig. 286 *Hemidinium montanum* C. E. M. Bicudo & Skvortsov and *H. lindemannii* Skvortsov (**a**, **b** after Bicudo & Skvortsov 1970; **c**–**f** after Skvortsov 1968). **a**, **b** *Hemidinium montanum*, ventral and lateral views; **c**–**f** *Hemidinium lindemannii*

4. "***Hemidinium nephroideum***" Krakhmalny 2005, p. 365, figs 1, 2; SEM micrographs 1–4 (**Fig. 287**)

Cells reniform, slightly dorsoventrally compressed, the epicone exceeding the hypocone very slightly in length. The cingulum descending, the ends of cingulum slightly displaced only. Sulcus feebly marked, does not reach the antapex. Flagellar pores covered by a wing. Amphiesmal plates present. Cell length 22–33 μm, width 15–23 μm.
Ecology: pond of rainwater, June.
Geographical distribution: Israel.

Note: the presence of plates indicates that this is a zoospore of a species of *Gloeodinium* or some related genus. Since the coccoid stage is unknown, its generic affinity cannot be determined.

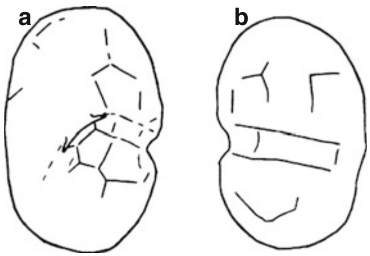

Fig. 287 "*Hemidinium nephroideum*" Krakhmalny (after Krakhmalny 2005). **a** ventral view; **b** dorsal view

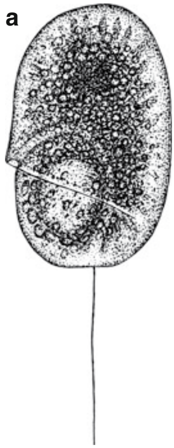

Fig. 288 *Hemidinium nobile* Skuja *ex* Moestrup & Calado (after Skuja 1964). **a** dorsal view, with the outline of the furrows on the ventral side marked as seen through the cell

5. *Hemidinium nobile* Skuja *ex* Moestrup & Calado *sp. nov.* (**Fig. 288**)

Skuja (1964, p. 352) regarded this as a previously undescribed species and gave it a name, but he did not validate it with a Latin description or diagnosis. Type: Skuja 1964, *Nova Acta Regiae Soc. Sci. Upsal., ser. IV*, **18** (3), pl. LXVII, fig. 11 (here designated).

Cells oval-rectangular, apex broadly rounded, antapex flat. Cingulum terminates dorsally near the right-posterior corner. Cell length 38–45 µm, width 24–28 µm, thickness 12–18 µm.
Ecology: in *Sphagnum* bogs near the railway at Abisko and in marshy waters of the western margin of Lake Torneträsk, northern Sweden.
Geographical distribution: Sweden.

Fig. 289 *Hemidinium pseudochraceum* C. E. M. Bicudo & Skvortsov and *H. woloszynskae* Skvortsov (**a**, **b** after Bicudo & Skvortsov 1970; **c** after Skvortsov 1968). **a**, **b** *Hemidinium pseudochraceum*; **c** *Hemidinium woloszynskae*

6. *Hemidinium pseudochraceum* C. E. M. Bicudo & Skvortsov 1970, p. 17, figs 21, 22 (**Fig. 289**)

Cells asymmetrical, subspherical to ovoid, slightly dorsoventrally compressed. Cell length 1.3–1.4× cell width. Epicone *ca.* 1/3 the length of the cell. Sulcus not observed. Chloroplasts 1–4, greenish-yellow, discoidal. Cells 11–14 µm long and 8–11 µm wide.
Ecology: in small temporary pool in a park (Parque do Estado de São Paulo) in the city of São Paulo, Brazil.
Geographical distribution: Brazil.

Note: *Hemidinium woloszynskae* Skvortsov (1968, p. 102, pl. IV, fig. 13) differs by having an eyespot.

7. *Hemidinium purpureum* Skvortsov 1968, p. 100, pl. IV, fig. 7 (**Fig. 290**)

Cells reniform, dorsoventrally compressed. Cell length 11–12 µm, width 4.5–5 µm. With 5 purple chloroplasts. Eyespot not seen. Nucleus central. Longitudinal flagellum *ca.* 1.5× cell length.
Ecology: in rice field, Sungari River, near Harbin, Manchuria.
Geographical distribution: Manchuria, China.

Note: the original description of this species is very incomplete and the inclusion here must therefore be preliminary.

8. *Hemidinium soligenum* Skuja 1964, p. 352, pl. LXVII, figs 12, 13 (**Fig. 291**)

Nomenclatural synonym: *Esoptrodinium soligenum* (Skuja) Javornický 1997, pp 39, 41

Cells ovoid, dorsoventrally flattened, with nose-like protruding upper edge of the cingulum. Cingulum located near the apex, curved, continuing in the sulcus, which extends almost to the antapex. Numerous elongate, yellowish-brown chloroplasts radiate from the cell center to the periphery. The rather large nucleus median, located just below the center. Cell length 24–29 µm, width 14–18 µm, thickness 7–13 µm.

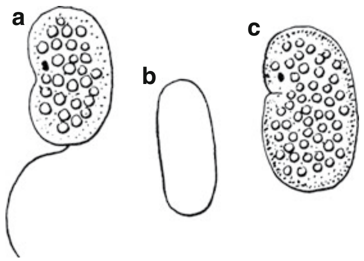

Fig. 290 *Hemidinium purpureum* Skvortsov (after Skvortsov 1968). **a**–**c** cells in different points of view, in **b** apparently from the side. What the dark spots on the left of **a** and **c** represent is unknown as an eyespot was stated to be absent

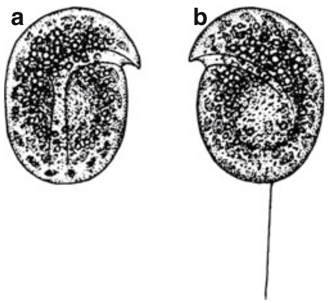

Fig. 291 *Hemidinium soligenum* Skuja (after Skuja 1964). **a** ventral view; **b** dorsal view

Ecology: in shallow ponds in North Sweden.
Geographical distribution: Sweden.

Family 3. Lophodiniaceae B. F. Osorio 1942, p. 119

Cells with longitudinal double ridges. All parts of the cell covered with small, usually hexangular plates.

Genus 1. *Lophodinium* Lemmermann 1910, pp 628, 637

Type species: *Lophodinium polylophum* (Daday) Lemmermann 1910

Cells covered with many hexangular plates. A double-ridged carina passes on the epicone from the mid-ventral side across the cell apex to the mid-dorsal side. Paired ridges extend longitudinally from the carina to the cingulum. Similar paired longitudinal ridges are present on the hypocone.

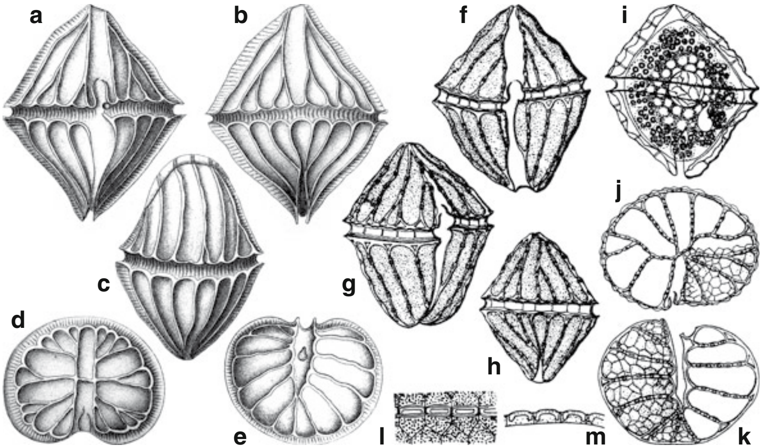

Fig. 292 *Lophodinium polylophum* (Daday) Lemmermann (**a**–**e** after Daday 1905; **f**–**m** after Osorio Tafall 1942). **a**–**e** ventral, dorsal, lateral, apical and antapical views of the cell surface, respectively; **f**–**h** ventral, ventral-right and dorsal views, respectively; **i** optical section showing cell contents; **j**, **k** apical and antapical views, respectively; **l** detail of amphiesmal vesicles with ridges; **m** side view of ridge

1. *Lophodinium polylophum* (Daday) Lemmermann 1910, p. 637 (**Fig. 292**)

Basionym: *Glenodinium polylophum* Daday 1905, p. 23, pl. I, figs 18–22
Taxonomic synonym: *Lophodinium dadayi* B. F. Osorio 1942, p. 116, figs 1–9

Cells biconical, 42–85 µm long and 31–67 µm wide. Slightly flattened dorsoventrally. Epi- and hypocone similar in size. Cingulum displaced one cingulum width, and cingulum margins slightly flared. Sulcus extends for a short distance onto the epicone and on the hypocone reaches the antapex forming a broad trough. Cell with numerous golden brown chloroplasts. Nucleus central, C-shaped in a transverse plane. Eyespot in the sulcal area. Cell division within the parental theca, oblique. Cysts unknown. No cysts were found in the sediment examined while vegetative cells were present in the water column.
SEM: Iltis & Couté (1984), Carty & Cox (1985).
Ecology: Lagoon in Paraguay (Estia Postillon), small pond in Texas, rivers in Mexico and the Bolivian lowlands.
Geographical distribution: thus far restricted to the Americas. USA, TX (Carty & Cox 1985). Bolivia (Iltis & Couté 1984); Mexico (Osorio Tafall 1942); Paraguay (Daday 1905).

Note: Carty and Cox (1985), after a detailed study, concluded that *Lophodinium dadayi* B. F. Osorio cannot be distinguished from *L. polylophum*. Iltis & Couté (1984) reached the same conclusion.

Family 4. Sphaerodiniaceae Moestrup & Calado *fam. nov.*

Cells covered by amphiesmal plates which are visible in the light microscope. Eyespot, where known, of type F *sensu* Craveiro *et al.* (2010), *i. e.* extraplastidic, the eyespot globules overlain by a series of vesicles with crystal- or brick-like contents. Apical complex of very small amphiesmal plates observed in *S. cracoviense*, one with a short line of protuberances.

Genus 1. *Sphaerodinium* Wołoszyńska 1916, p. 279

Type species: *Sphaerodinium polonicum* Wołoszyńska 1916 (see Loeblich & Loeblich 1966, p. 56)

Spherical or oval cells, amphiesma with nearly symmetrical plate arrangement. Epi- and hypocone of equal size or epicone slightly larger. Cells sometimes slightly dorsoventrally compressed. Cingulum descending. The sulcus appears to extend onto the epicone but SEM of *S. cracoviense* has shown that the apparent extension is formed by a separate amphiesmal plate, labelled plate Z by Craveiro *et al.* (2010), which may or may not be considered part of the sulcus. It is directly aligned with the first apical plate and may have originated by transverse division of an ancestral first apical plate extending from the cingulum to the apex. Plate formula: 4′, 4a, 7″, Z, 8c (?), 4s, 6‴, 2⁗, but an apical complex of 3 very small plates also present, one of which with a line of knob-like protuberances. The two antapical plates may be of slightly different size. With many brown, plate-like chloroplasts (or chloroplast lobes). Eyespot (if present) horseshoe-shaped, of type F. Resting cyst spherical or oval (*S. cracoviense*), smooth or papillate.
Species of this genus have been found only relatively few times but they have probably in addition been reported as *Glenodinium cinctum*. Except for *S. fimbriatum*, the described species differ in relatively minor features and the first four were merged by Huber-Pestalozzi (1950) into a single species with four varieties. Further studies are needed to clarify the taxonomy of the species/varieties.

Key to species of *Sphaerodinium*:

1a Sutures and plates on hypocone with fimbriate projections ... 3. *S. fimbriatum*
1b Sutures smooth or absent 2
2a Sulcus widens posteriorly 3
2b Sulcus narrows posteriorly, termination conical 5
3a Right rim of sulcus thickened on the epicone; intercalary bands usually distinctly papillate .... 1. *S. polonicum*
3b Right rim of sulcus not thickened on the epicone; not regularly papillate ... 4
4a Extension of the sulcus onto the epicone much longer than wide .... 1. *S. polonicum* var. *tatricum*
4b Extension of the sulcus onto the epicone of almost the same length and width .... 5. *S. limneticum*
5a Cells *ca.* 22 µm in diameter .... 4. *S. javanicum*
5b Cells 24–31 µm long .... 2. *S. cracoviense*

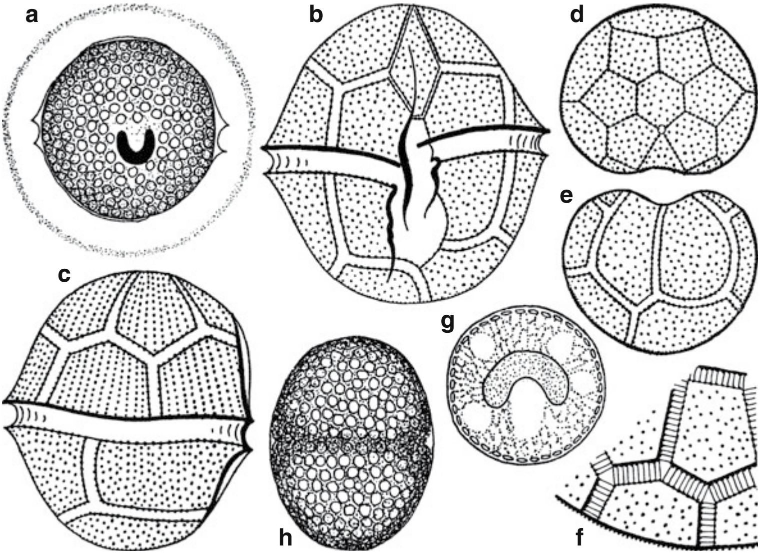

Fig. 293 *Sphaerodinium polonicum* Wołoszyńska (after Wołoszyńska 1916). **a** ventral view showing cell contents; **b**, **c** ventral and right-lateral views, respectively; **d**, **e** apical and antapical views; **f** detail of plate and suture ornamentation; **g** transverse section through middle of cell showing curved nucleus; **h** division in immotile stage

1. ***Sphaerodinium polonicum*** Wołoszyńska 1916, p. 280, pl. 14, figs 1–22 (**Fig. 293**)

Nomenclatural synonym: *Sphaerodinium cinctum* var. *polonicum* (Wołoszyńska) Huber-Pestalozzi 1950, p. 161

Cells spherical, rarely oval, not flattened. Cell length (25–)30–45 µm. Sulcus extends onto the epicone for a short distance. On the hypocone it widens posteriorly but does not reach the antapex. The left edge of the sulcus thickened anteriorly on the hypocone, the thickening continuing posteriorly into the sulcus. The right rim of the sulcus thickened on the epicone, the thickening continuing antapically into the sulcus. The right edge of the sulcus thickened on the hypocone. The first apical plate 5-sided but the proximal side near the cingulum is short. Plate 3′ regularly 6-sided. Periplast thin, with small papillae. Intercalary bands often distinct, with papillate edges. Nucleus central, horseshoe-shaped in a transverse plane. Chloroplasts parietal, radiating. Large horseshoe-shaped eyespot in the sulcus. Vegetative division into two cells within the parental amphiesma, which breaks open along the cingulum. Immobile cells embedded in thick mucilage.

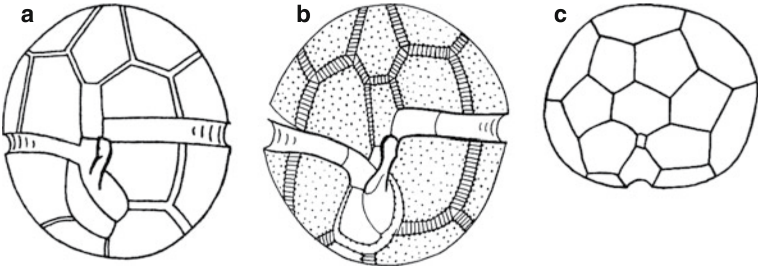

Fig. 294 *Sphaerodinium polonicum* var. *tatricum* Wołoszyńska (**a** after Wołoszyńska 1916; **b** after Wołoszyńska 1952; **c** slightly modified from Wołoszyńska 1952, to show precingular plates). **a**, **b** ventral views; **c** apical view

Ecology: found in plankton of pond in the Botanical Garden at Dubliany, Ukraine, in June and September (Wołoszyńska 1916); also reported in lakes and temporary ponds in July and August (Thompson 1951).
Geographical distribution: Ukraine (Wołoszyńska). USA, KS (Thompson)?

var. *tatricum* Wołoszyńska 1916, p. 280, pl. 14, fig. 23 ("*tatrica*") (**Fig. 294**)
Nomenclatural synonym: *Sphaerodinium cinctum* var. *polonicum* f. *tatricum* (Wołoszyńska) Huber-Pestalozzi 1950, p. 162 ("*tatrica*")

Differs from the nominal form by the sulcus (sa) extending further onto the epicone and in the thickening of the right side of the sulcus missing. Slightly dorsoventrally flattened. Plate 3′ irregularly 6-sided, elongated towards the right.
Ecology: peat bogs near Zakopane, Tatra Mountains, in August.
Geographical distribution: Poland (Wołoszyńska).

2. *Sphaerodinium cracoviense* Wołoszyńska 1916, p. 281, pl. 14, figs 28–30 (**Fig. 295**)

Cells spherical, rarely oval, slightly compressed dorsoventrally. Cingulum descending nearly its own width. Sulcus *ca.* 3× the width of the cingulum, narrowing posteriorly into a cone. Margins of the postcingular plates bordering the sulcus raised. Periplast relatively thick, usually smooth. Intercalary bands often indistinct. Nucleus almost central, hardly curved. Peripheral part of the cell with numerous yellowish-brown chloroplast lobes. Large horseshoe-shaped eyespot. Cells not embedded in mucilage. Vegetative bipartition within the parental amphiesma. Cell length 24–31 µm, width 22–28 µm, thickness 24–25 µm (Craveiro *et al.* 2010). Resting cysts spherical or oval.
SEM: Craveiro *et al.* (2010).
TEM: Craveiro *et al.* (2010).
DNA data: Craveiro *et al.* (2010).
Ecology: in vegetation-filled ponds near Cracow, Poland, June–November.
Geographical distribution: Poland (Wołoszyńska; Craveiro *et al.*); Portugal (Pandeirada *et al.*).

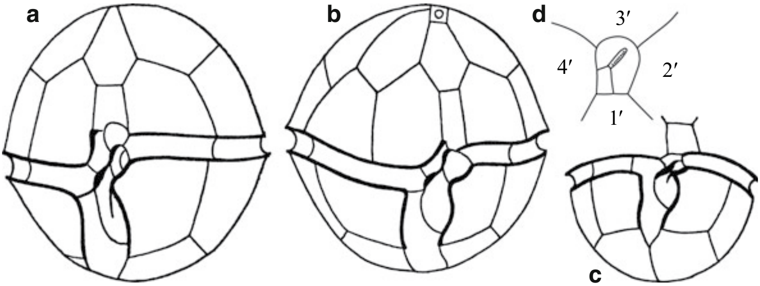

Fig. 295 *Sphaerodinium cracoviense* Wołoszyńska (**a**–**c** after Wołoszyńska 1916; **d** original drawing based on SEM information). **a**, **b** approximately ventral views; **c** ventral view of main plates on the hypocone, showing pointed posterior end of sulcus; **d** apical complex

3. ***Sphaerodinium fimbriatum*** R. H. Thompson 1951, p. 296, figs 63–67 (**Fig. 296**)

Cells ovate to elliptic. Large horseshoe-shaped eyespot, often with a posterior lobe. The sutures of the plates with fimbriate projections said to be present on both the epi- and hypocone, but visible only on the hypocone on an SEM illustration published by Carty (2003, p. 694). Each plate of the hypotheca with a central, elongate, fimbriate structure. USA material 42–53 μm long and 42–46 μm wide (Thompson 1951), Ivory Coast material 35–42 μm long and 34–40 μm wide (Couté & Iltis 1984).
SEM: Couté & Iltis (1984), Carty (2003, 2014).
Ecology: in temporary as well as permanent oxbows, and in Horseshoe Lake, Lawrence, Kansas, in July and August (Thompson 1951).
Geographical distribution: Ivory Coast (Couté & Iltis 1984). USA, KS (Thompson), OH (Carty).

4. ***Sphaerodinium javanicum*** Wołoszyńska *in* Schiller 1935a, p. 87, fig. 72 (**Fig. 297**)

Originally described (incompletely) as "*Sphaerodinium* sp.?" by Wołoszyńska (1930b, p. 168, fig. 7)
Nomenclatural synonym: *Sphaerodinium cinctum* var. *javanicum* (Wołoszyńska) Huber-Pestalozzi 1950, p. 162

Cells spherical, *ca.* 22 μm in diameter. Thickenings of the sulcal edges not mentioned. Sulcus narrows posteriorly to a cone. Antapical plates of almost equal size.
Ecology: in a crater lake at Danau Sindang, Sumatra.
Geographical distribution: Sumatra, Indonesia (Wołoszyńska).

Note: morphologically this species differs from *S. cracoviense* only in size, and studies on additional material are required to determine whether they are separate species. Material from Uttar Pradesh, India (Shyam & Sarma 1980) and from Sabah, Malaysia (Moestrup & Mohammad-Noor, unpublished) is probably identical.

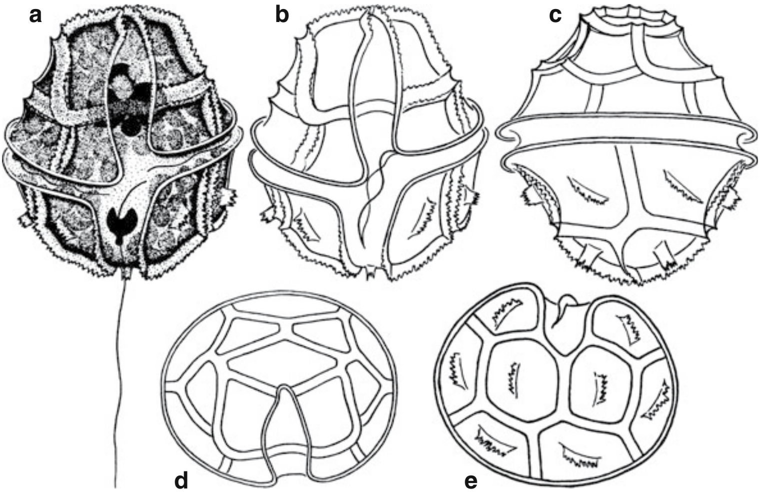

Fig. 296 *Sphaerodinium fimbriatum* R. H. Thompson (after Thompson 1951). **a** ventral view of live cell; **b**–**e** ventral, dorsal, apical and antapical views showing main amphiesmal plates

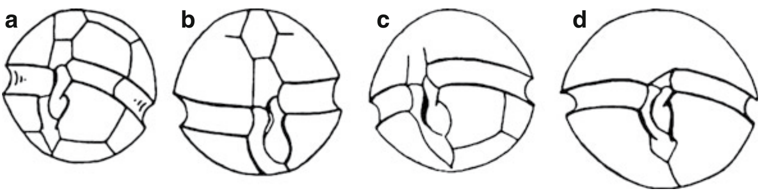

Fig. 297 *Sphaerodinium javanicum* Wołoszyńska (**a** after Wołoszyńska *in* Schiller 1935a; **b**–**d** after Wołoszyńska 1930b). **a** ventral-left view showing some of the main plates; **b**, **c** incomplete ventral plate patterns of two cells; **d** outline of a somewhat larger cell

5. ***Sphaerodinium limneticum*** Wołoszyńska 1916, p. 281, pl. 14, figs 24, 25 (**Fig. 298**)

Nomenclatural synonym: *Sphaerodinium cinctum* var. *limneticum* (Wołoszyńska) Huber-Pestalozzi 1950, p. 161

Cells spherical, rarely oval, 25–35 μm long. Sulcus reported to extend onto the epicone but identity of anterior limit of sulcus doubtful. On the hypocone it widens posteriorly but does not reach the antapex. The edges of the sulcus lack thickenings. First apical plate 5-sided, the proximal side sometimes longer than the adja-

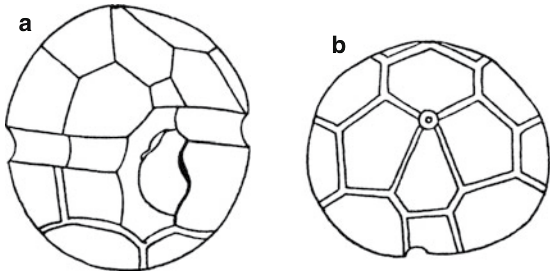

Fig. 298 *Sphaerodinium limneticum* Wołoszyńska (after Wołoszyńska 1916). **a** ventral view; **b** anterior-ventral view

cent sides. Periplast thick, smooth, rarely with papillae. Intercalary bands present. Nucleus small, rounded, central. Eyespot? Cells not embedded in mucilage.
Ecology and distribution: in a pond near Białogórski, Cracow, Poland. Only observed in fixed material (Wołoszyńska 1916). Höll (1928) mentions *Glenodinium cinctum* as characteristic of small, calcium-rich alkaline lakes and ponds (pH *ca.* 7.2) such as clay pits and ponds near tile factories. However, it is uncertain which *Sphaerodinium* species Höll found. Also mentioned from lake and swamp in New Zealand (Chapman *et al.* 1957).

Note: according to Wołoszyńska (1917) identical to *Glenodinium cinctum* Ehrenberg.

Family 5. Suessiaceae Fensome, F. J. R. Taylor, G. Norris, Sarjeant, Wharton & G. L. Williams 1993, p. 57

Eyespot, if present, of type E *sensu* Moestrup & Daugbjerg (2007), *i. e.* composed of a stack of cisternae with brick-like contents. Anterior furrow extends over the apical end from the dorsal to the ventral side but is usually not visible in the light microscope. It is formed by a single, elongate, narrow amphiesmal vesicle typically surrounded by 1–2 narrow amphiesmal vesicles on each side. Amphiesmal vesicles typically in 7–15 latitudinal series, or more irregular, in *Biecheleria pseudopalustris* with more than 20 latitudinal series.
Two genera occur commonly in fresh water (*Prosoaulax* and *Biecheleria*) and two other were recently described from ponds in Japan (*Asulcocephalium* and *Leiocephalium*). A fifth genus is a parasite on freshwater fish (*Piscinoodinium*). A sixth genus is marine but has occasionally been reported from fresh water (*Protodinium*).

Key to the genera of Suessiaceae found in fresh water:

1a Free living 2
1b Ectoparasitic on fish .... 4. *Piscinoodinium*

2a Epicone much smaller than the hypocone .... 5. *Prosoaulax*
2b Epicone and hypocone of almost the same size or epicone slightly smaller ... 3
3a Cells pentagonal or hexagonal in ventral view .... 3. *Leiocephalium*
3b Cells ovoid 4
4a Sulcus distinct 5
4b Sulcus barely visible in the light microscope .... 6. *Protodinium*
5a Cells 20 μm or less in length 6
5b Cells longer than 20 μm .... 2. *Biecheleria* p.p.
6a Nucleus in the apex, large pyrenoid in the center of the hypocone, distinct eyespot present in the sulcus .... 1. *Asulcocephalium*
6b Nucleus in the hypocone, eyespot absent .... *Biecheleria ordinata*

Genus 1. ***Asulcocephalium*** Kazuya Takahashi, Moestrup & Iwataki *in* Takahashi *et al.* 2015, p. 640

Type species: *Asulcocephalium miricentonis* Kazuya Takahashi, Moestrup & Iwataki

Cells covered by 9–12 series of amphiesmal vesicles. Small, laterally elongated intercalary amphiesmal vesicles present dorsally, two each on the epi- and hypocone. Apical furrow absent. Chloroplasts present.

1. *Asulcocephalium miricentonis* Kazuya Takahashi, Moestrup & Iwataki *in* Takahashi *et al.* 2015, p. 640 (**Fig. 299**)

Cells spherical to ovoid. Cingulum descending, the ends displaced *ca.* one cingulum width. Nucleus near the cell apex, sometimes almost filling the epicone. Chloroplasts yellow, located mainly in the hypocone. With single, central pyrenoid in the hypocone. Distinct eyespot in the sulcal region. Cell length 10–16 μm, width 7–14 μm. Cysts spherical, smooth.
SEM: Takahashi *et al.* (2015).
TEM: Takahashi *et al.* (2015).
DNA data: Takahashi *et al.* (2015).
Ecology: pond in Yamagata Prefecture, Japan.
Geographical distribution: Japan.

Genus 2. ***Biecheleria*** Moestrup, K. Lindberg & Daugbjerg 2009a, p. 213

Type species: *Biecheleria pseudopalustris* (J. Schiller) Moestrup, K. Lindberg & Daugbjerg 2009a

Cells surrounded by a thin periplast, the amphiesma comprising a large number of small vesicles, usually not visible in the light microscope. Cell division by binary fission. Resting cysts, where known, are spiny.
Presently four species in fresh water and three marine.

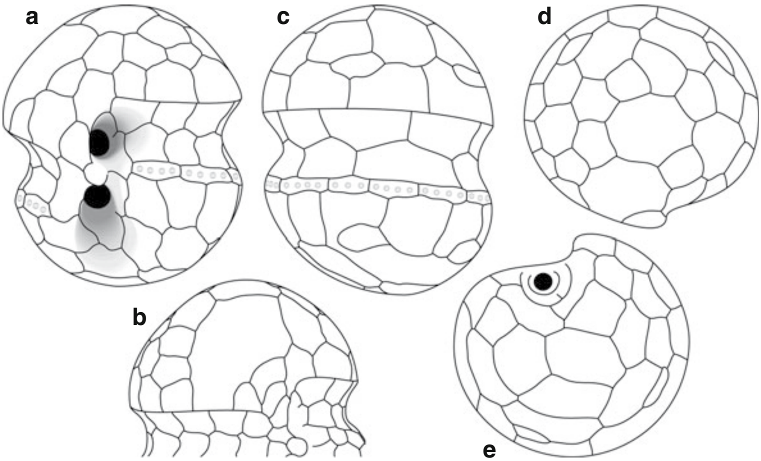

Fig. 299 *Asulcocephalium miricentonis* Kazuya Takahashi, Moestrup & Iwataki (original drawings, kindly provided by Kazuya Takahashi). **a** ventral view; **b** ventral-right side of epicone and cingulum; **c** dorsal view; **d**, **e** apical and antapical views, respectively

Key to freshwater species of *Biecheleria*:

1a Antapex excavate .... 1. *B. pseudopalustris*
1b Antapex rounded 2
2a Cell shorter than 20 µm .... 4. *B. ordinata*
2b Cell longer than 20 µm 3
3a Hypocone conical .... 3. *B. cestocoetes*
3b Hypocone hemispherical .... 2. *B. aesculus*

1. *Biecheleria pseudopalustris* (J. Schiller) Moestrup, K. Lindberg & Daugbjerg 2009a, p. 213 (**Fig. 300**)

Basionym: *Gymnodinium pseudopalustre* J. Schiller 1932, p. 400, fig. 418 (originally based on *Gymnodinium palustre* f. Wołoszyńska 1917, pp 115, 119, pl. 12, figs 7–9; pl. 13, figs A, B)
Nomenclatural synonym: *Woloszynskia pseudopalustris* (J. Schiller) Kisselev *ex* Elbrächter *in* Kremp *et al.* 2005, p. 635
Taxonomic synonyms: *Gymnodinium excavatum* Nygaard 1945, p. 52, text-fig. 20; “Gymnodinium acuminatum”, Christen 1959a, p. 75, fig. 12 (invalidly published for lack of type indication)

Cells ovoid, with distinct antapical indentation. Epicone slightly larger than the hypocone, hemispherical. Hypocone rounded. Cingulum descending, the ends displaced *ca.* one cingulum width. A short finger-like extension projects into the

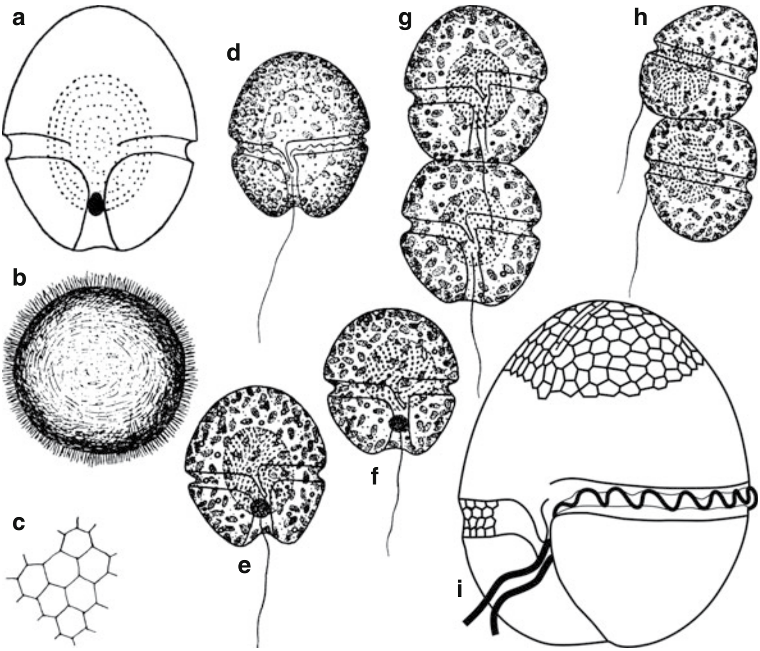

Fig. 300 *Biecheleria pseudopalustris* (J. Schiller) Moestrup, K. Lindberg & Daugbjerg (**a**–**c** after Wołoszyńska 1917; **d** after Nygaard 1945; **e**–**h** after Nygaard 1950; **i** original, based on SEM micrograph in Moestrup *et al.* 2009a). **a** ventral view, with eyespot and nucleus; **b** cyst; **c** detail of amphiesmal plates; **d**–**f** ventral views of vegetative cells (or gametes) with cell contents; **g**, **h** ventral and lateral views of cell division; **i** partial representation of amphiesmal organization in a planozygote, as indicated by the two longitudinal flagella

sulcus at the intersection between cingulum and sulcus. Cell surface covered with numerous small amphiesmal vesicles in more than 20 latitudinal series. Cingulum with 2–4 horizontal rows of vesicles. Many parietal chloroplasts with pyrenoids. Nucleus central. Cells 26–42 μm long and 21–34 μm wide. Cyst spherical with numerous, relatively short spines covering the entire surface, initially smooth.
SEM: Moestrup *et al.* (2009).
TEM: Moestrup *et al.* (2009).
DNA data: Moestrup *et al.* (2009).
Ecology: plankton of ponds, mainly in summer (Europe), occasionally bloom forming (Denmark).
Geographical distribution: Denmark (Nygaard; Lindberg *et al.*); England (Lewis & Dodge); Germany (Stosch); Hungary (Entz); Portugal (Pandeirada *et al.*); Sweden (Skuja); Ukraine (Wołoszyńska).

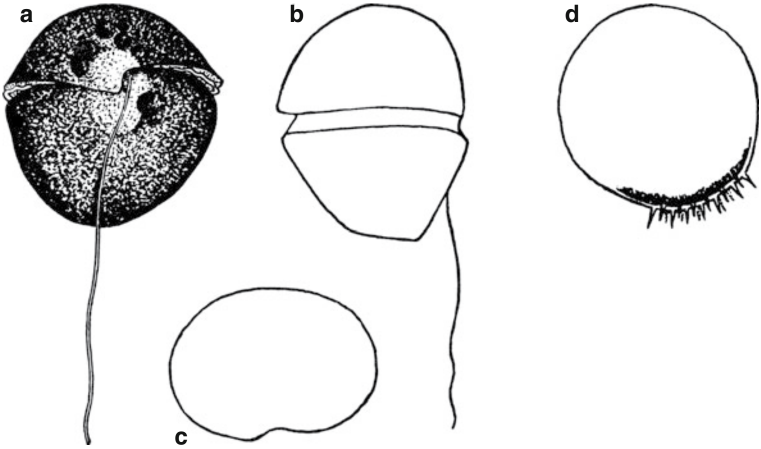

Fig. 301 *Biecheleria aesculus* (Baumeister) Moestrup (after Baumeister 1943a). **a** ventral view; **b** outline of cell in right lateral view; **c** cross-section; **d** cyst (ornamentation shown only in a small portion)

Note: *Gymnodinium concavum* Skvortsov (1968, p. 87, pl. I, figs 12, 13) from Manchuria may be identical. *Gymnodinium planctonicum* Skvortsov (1968, p. 89, pl. II, fig 5) from Manchuria is somewhat more flattened. Studies on additional material are needed to determine their identity.

2. *Biecheleria aesculus* (Baumeister) Moestrup *comb. nov.* (**Fig. 301**)

Basionym: *Gymnodinium aesculum* Baumeister 1943a, *Arch. Protistenk*. **96**, p. 334, fig. 2

Cells broadly-oval in ventral view, slightly compressed dorsoventrally. Epicone broadly flattened, helmet-shaped, smaller than the hemispherical hypocone. Left side of the cell more convex than right side, the cell therefore asymmetrical. Cingulum descending, the ends displaced 2–3× the cingulum width. Sulcus a flat trough, but difficult to see in the living cell. Cells brown. Chloroplasts or eyespot not reported. Cell length 25–34 µm, width 20–30 µm. Cyst spherical, 36 µm in diameter excluding the wall, covered throughout with 5-µm long colorless spines.
Ecology: in snow water-filled hollows in meadows, at neutral or slightly alkaline pH.
Geographical distribution: Germany.

3. *Biecheleria cestocoetes* (R. H. Thompson) Moestrup *comb. nov.* (**Fig. 302**)

Basionym: *Gymnodinium cestocoetes* R. H. Thompson 1947, *Chesapeake Biol. Lab. Publ.* **67**, p. 8, pl. I, figs 10–14
Nomenclatural synonym: *Woloszynskia cestocoetes* (R. H. Thompson) R. H. Thompson 1951, p. 291

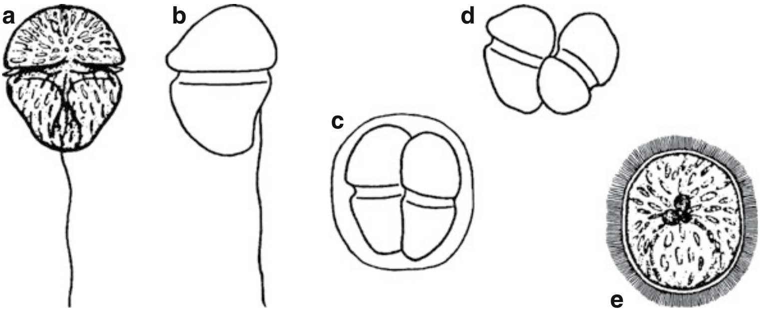

Fig. 302 *Biecheleria cestocoetes* (R. H. Thompson) Moestrup (after Thompson 1947). **a** ventral view showing radiating chloroplast lobes; **b** outline of cell in right lateral view; **c** division in immotile stage; **d** division in motile stage; **e** resting cyst

Cells ovoid in ventral view, somewhat dorsoventrally flattened. Epicone hemispherical, hypocone conical with rounded antapex. Cingulum circular. Sulcus indistinct near the cingulum, but broadening considerably. Longitudinal flagellum equal to cell length or slightly longer. Chloroplasts small, numerous, elongate, radially disposed at the periphery of the cell. Eyespot absent. Cell length 23–25 µm, width 19–21 µm. Cell division in the non-motile stage, completed within two hours. Cyst oval or broadly elliptic, with needle-like prickles. These are within or part of a homogenous gelatinous envelope that dissolves away, leaving a smooth exterior.
Ecology: in swamps, Maryland, USA, January–March 1947, also under the ice.
Geographical distribution: USA, MD (Thompson).

Note: the taxonomic position of this species is somewhat uncertain. The spine-covered resting cysts indicate phylogenetic affinity to the genus *Biecheleria*, but cell division in the non-motile state is unusual.

4. *Biecheleria ordinata* (Skuja) Moestrup *comb. nov.* (**Fig. 303**)

Basionym: *Gymnodinium ordinatum* Skuja 1939, *Acta Horti Bot. Univ. Latv.* **11/12**, p. 151, pl. X, figs 26–28
Nomenclatural synonym: *Woloszynskia ordinata* (Skuja) R. H. Thompson 1951, p. 291

Cells symmetrical, broadly ovoid, dorsoventrally flattened. Epicone slightly larger than hypocone, hemispherical. Hypocone conical-hemispherical. Cingulum circular, sulcus on the hypocone only, reaching the antapex. Longitudinal flagellum twice the length of the cell. Four yellowish-brown, disc-shaped chloroplasts, usually two in each half of the cell. The epicone often with 1–2 round eyespot-like bodies, but eyespot absent. Nucleus in the hypocone. Cell length 12–17.5 µm, width 11–14.5 µm, thickness 8–10 µm. Cyst oval, flattened, pale orange-brown, *ca.* 25 µm in diameter, surface covered with fine spines (Mertens *et al.* 2012).

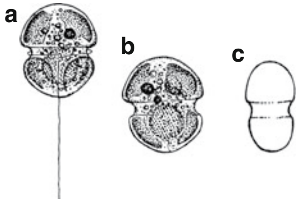

Fig. 303 *Biecheleria ordinata* (Skuja) Moestrup (after Skuja 1939). **a**, **b** ventral and dorsal views, respectively, showing the four chloroplasts; **c** outline of cell in lateral view

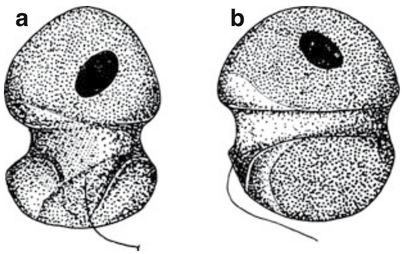

Fig. 304 *Biecheleria ordinata* var. *sparsa* (Popovský) Moestrup (after Popovský 1971b). **a** ventral view; **b** left lateral view. Dark body in epicone described as "large red-brown storage product"

Ecology: pool in May in Bohemia, ponds in spring in forest in Latvia, also reported from cold water in Lunzer Mittelsee, Austria and under the ice in Maryland, USA and in Lake Erken, Sweden. In Lake Erken, a large mesotrophic lake, *B. ordinata* occurred from February, with maximum occurrence in April at 70×10^3 cells per liter, disappearing in June.
Geographical distribution: Austria (Schiller); Latvia (Skuja); Czech Republic (Popovský); Poland (Popovský); Portugal (Nauwerck); Sweden (Skuja; Rengefors); Switzerland (Preisig). USA, MD (Thompson).

var. *sparsa* (Popovský) Moestrup *comb. nov.* (**Fig. 304**)
Basionym: *Gymnodinium ordinatum* var. *sparsum* Popovský 1971b, *Arch. Protistenk.* **113**, p. 279, pl. 35, figs 11, 12

One or two chloroplasts present. Cell length 5–9 µm, width 4–7 µm.
Ecology: in lake Flosek, Masuria, northern Poland.
Geographical distribution: Poland.

Note: the morphological differences described by Popovský (1971b), and the occurrence in Masuria, Poland 25 June 1965 indicate that this taxon may not be related to *B. ordinata*.

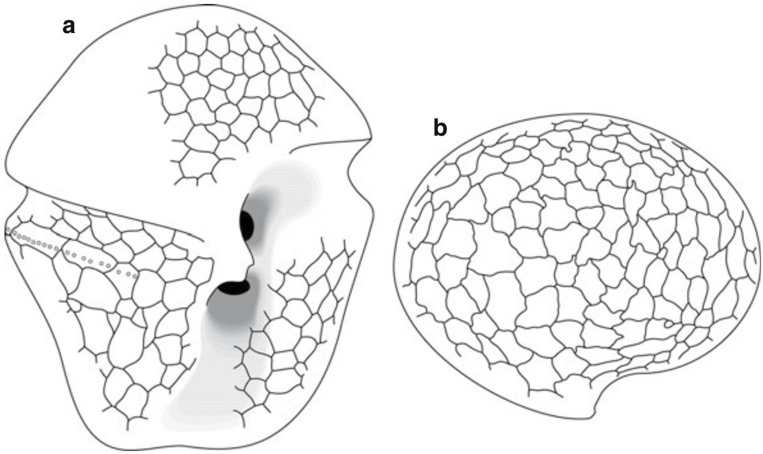

Fig. 305 *Leiocephalium pseudosanguineum* Kazuya Takahashi, Moestrup & Iwataki (original drawings based on SEM information, kindly provided by Kazuya Takahashi). **a** ventral view; **b** apical view

Genus 3. *Leiocephalium* Kazuya Takahashi, Moestrup & Iwataki *in* Takahashi *et al.* 2015, p. 641

Type species: *Leiocephalium pseudosanguineum* Kazuya Takahashi, Moestrup & Iwataki

Cells covered by more than 24 series of amphiesmal vesicles, not visible in the light microscope. Apical furrow absent. Chloroplasts present.

1. *Leiocephalium pseudosanguineum* Kazuya Takahashi, Moestrup & Iwataki *in* Takahashi *et al.* 2015, p. 642 (**Fig. 305**)

Cells pentagonal or hexagonal in ventral view, dorsoventrally flattened. Epi- and hypocone of nearly the same size. Epicone rounded, hypocone trapezoidal to pentagonal with antapical excavation, forming a bilobed antapex. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus widening towards the antapex. Nucleus U-shaped, located dorsally across the middle of the epicone. Yellowish-brown chloroplasts rod to ribbon shaped, radially arranged from the cell center. Pyrenoid absent. Eyespot in the sulcal region. More than 10 latitudinal rows of amphiesmal vesicles in both the epi- and the hypocone, 4–6 in the cingulum. Cell length 28–42 µm, width 22–34 µm. Cysts spherical, smooth in the light microscope, seen to be covered by fibrillary material in the SEM. Cyst diameter 32–38 µm.

SEM: Takahashi *et al.* (2015).
TEM: Takahashi *et al.* (2015).
DNA data: Takahashi *et al.* (2015).
Ecology: pond in Yamagata Prefectural Park, NE Japan.
Geographical distribution: Japan.

Genus 4. ***Piscinoodinium*** Lom 1981, p. 8

Type species: *Piscinoodinium pillulare* (Schäperclaus) Lom 1981

Ectoparasitic on gills and skin of freshwater fish, including aquarium fish (velvet disease). Cells (trophont) spherical to ovoid-pyriform, attached to fish with attachment disc containing numerous, up to 40 μm long, radiating rhizoid-like organelles, which penetrate into and are firmly embedded in the epithelial cells of the host. Often several trophonts together. Nucleus in the upper third of the cell. Numerous chloroplasts have been reported. Starch grains may be present in large numbers.
When the trophont has reached maturity it withdraws the rhizoids and detaches from the host. It then sinks to the lake bottom, rounds off and forms a walled Palmella stage (tomont). This divides by transverse divisions into progressively smaller cells, as many as 128, each of which divides into two gymnodinioid motile cells (zoospores). The zoospores represent the infectious stage, attacking and attaching to fish. The trophont possesses remains of the flagellar apparatus and, although not mentioned by the authors, an eyespot of suessiacean kind (type E) is visible in Lom & Schubert (1983, fig. 17, top left), indicating the suessiacean affinity of *Piscinoodinium*.
SEM: Lom & Schubert (1983), Levy *et al.* (2007).
TEM: Lom & Schubert (1983), Levy *et al.* (2007).
DNA data: Levy *et al.* (2007).
Two species have been described, but the species distinction, based mainly on size, has been questioned (Levy *et al.* 2007). Whether the two species are different needs to be determined. *Piscinoodinium pillulare* was further said to differ in the presence of an eyespot in the zoospores (Schäperclaus 1954) but such an eyespot was not refound by Lom (1981), although, as mentioned above, it is visible in Lom & Schubert (1983). The number of zoospores formed per trophont was also claimed to be different in the two species, up to 64 per trophont in *P. pillulare* and up to 256 in *P. limneticum*.

1. *Piscinoodinium pillulare* (Schäperclaus) Lom 1981, p. 9 (**Fig. 306**)

Basionym: *Oodinium pillulare* Schäperclaus 1954, p. 404, figs 225–229 ("*pillularis*")

Trophont 20–160 μm long, pyriform. Zoospore rounded-elongate with equatorial cingulum. Attaches to prey with longitudinal flagellum.

Ecology: at least 30 freshwater fish species are known to be affected, many infections reported of *Carassius carassius* (crucian carp) and *Colisa lalia* (dwarf gourami). Experimental infection also on tadpoles of *Rana temporaria* (European

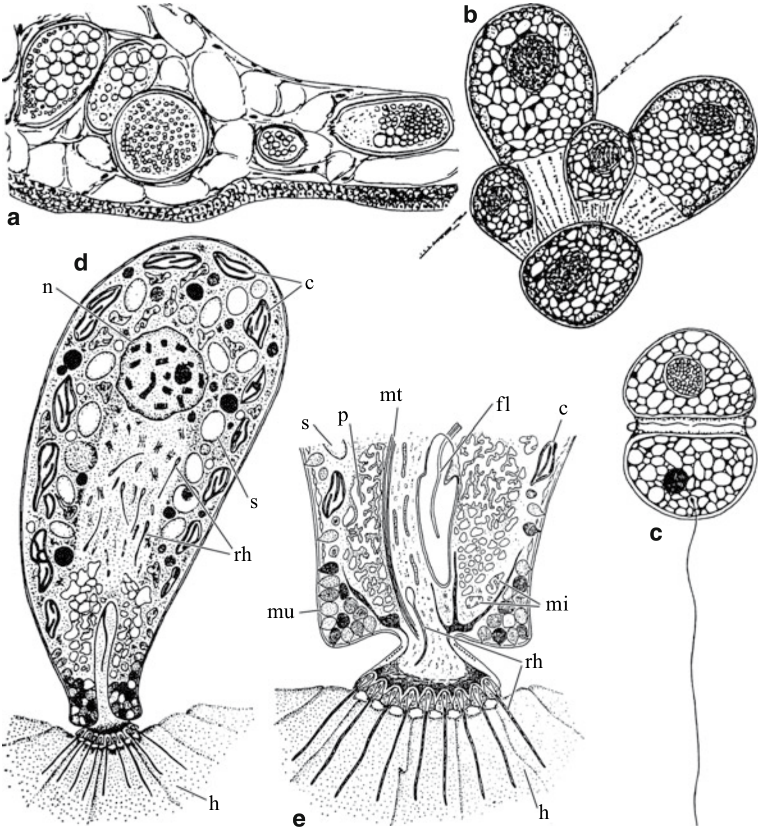

Fig. 306 *Piscinoodinium pillulare* (Schäperclaus) Lom (**a** after Reichenbach-Klinke 1956; **b**, **c** after Geus 1960; **d**, **e** after Lom 1981). **a** parasitic cells in subcutaneous connective tissue of fish gill cover; **b** group of cells attached to fish scale; **c** swarmer; **d**, **e** schematic representation of attached parasite and detail of attachment area, respectively, based on TEM observations (c chloroplasts; fl, flagellum in flagellar groove; h host cell; mi, mitochondrial profiles; mt, microtubular strand extending into attachment disk; mu, mucocysts; n nucleus; p, pusular system; rh, rhizocysts in special cytoplasm below the nucleus, migrating to attachment disk and embedded in the host cell; s, starch)

common frog) and *R. arvalis* (moor frog), and larvae of *Amblyostoma mexicanum* (axolotl). It is a serious pathogen that may result in loss of all fish in an aquarium unless treated. The trophont reaches maturity in 4 days at room temperature and then forms the tomont stage. Up to 64 zoospores are formed per trophont. The

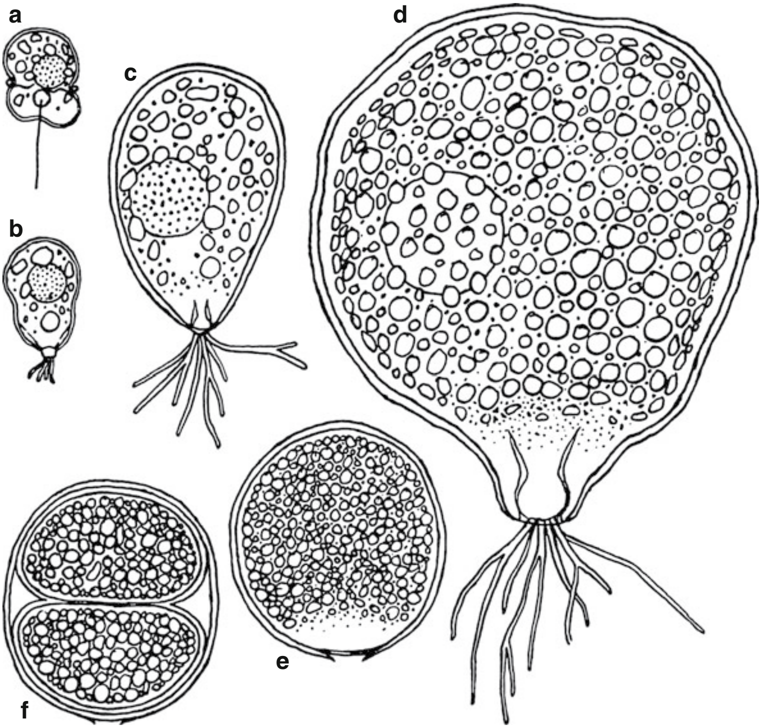

Fig. 307 *Piscinoodinium limneticum* (D. L. Jacobs) Lom (after Jacobs 1946). **a** swimming, infectious cell; **b** cell transformation following attachment; **c** young parasitic stage, 60 h after attachment; **d** nearly mature parasitic stage, seven days after attachment; **e** encysted stage; **f** first division within cyst wall

zoospores move very rapidly (up to 180 µm · s^{-1}), thus allowing them to settle on moving fish. They initially attach mainly at the base of the breast fins and the ventral fins and in cavities in the head, later on the gills and eventually on the entire body of the fish.
Geographical distribution: Czech Republic, Germany, attacking both local and tropical fish (disease named "Pillularis-Krankheit"; Schäperclaus; Geus).

2. *Piscinoodinium limneticum* (D. L. Jacobs) Lom 1981, p. 9 (**Fig. 307**)

Basionym: *Oodinium limneticum* D. L. Jacobs 1946, pp 1, 10, pls I–III (figs 1–15)

Trophont up to 96 µm long including the stalk, and 80 µm wide, pyriform when small, becoming slightly irregularly subspherical. Up to 256 zoospores are formed

per trophont. Each zoospore 10–19 µm long, 8–15 µm wide, covered with cellulosic wall, indented posteriorly. Epicone larger than hypocone. Sulcus does not extend onto epicone. With numerous yellowish-green chloroplasts but no eyespot. Nucleus spherical. Zoospores attach to the host with the longitudinal flagellum, form a protuberance from the lower part of the sulcus and from here extend short tentacles that appear to attach the cell to its host. The two flagella are shed.
Ecology: known from freshwater aquaria, attacking 9 species of exotic fish, belonging to the families Cyprinidae, Poecilidae and Anadantidae. Natural habitat not known. Observed to attach to all external parts of the fish, including fins, trunk, eyes, mouth and gills.
Geographical distribution: USA, MN, in aquaria (Jacobs).

Genus 5. ***Prosoaulax*** Calado & Moestrup 2005, p. 113

Type species: *Prosoaulax lacustris* (F. Stein) Calado & Moestrup 2005

Epicone much smaller than hypocone. Cells as long as wide or occasionally a little longer. Cingulum circular, both ends at the same level. Amphiesma comprises a few hundreds of mostly polygonal vesicles.
Species of this genus were previously included in *Amphidinium*, a genus that does not typically occur in fresh water. See Flø Jørgensen *et al.* (2004) for recircumscription of *Amphidinium*.

Key to species of *Prosoaulax*:

1a	Epicone sharply set off from the hypocone, semicircular	3. *P. viridis*
1b	Epicone only slightly narrower than hypocone, typically flat	2
2a	Sulcus extends shortly onto the epicone	2. *P. multiplex*
2b	Sulcus does not extend onto the epicone	1. *P. lacustris*

1. *Prosoaulax lacustris* (F. Stein) Calado & Moestrup 2005, p. 113 (**Fig. 308**)

Basionym: *Amphidinium lacustre* F. Stein 1883, p. 15, pl. XVII, figs 21–30
Taxonomic synonyms: *Amphidinium elenkinii* Skvortsov 1925, pp 146, 148, unnumbered text-figs ("*Elenkini*"); *Amphidinium larvale* Er. Lindemann 1928c, p. 291, figs 1–3; *Amphidinium hyalinum* Entz 1930, p. 207, figs 1, 2; *Amphidinium tatrae* Wołoszyńska 1937, p. 190, pl. IX, fig. 5; *Amphidinium tatrae* f. *achromaticum* Wołoszyńska 1937, p. 191, pl. IX, fig. 6; *Amphidinium gyrinum* T. M. Harris 1940, p. 18, fig. 5, N–S; *Amphidinium tenagodes* T. M. Harris 1940, p. 20, fig. 5, J–M; *Amphidinium turicense* Huber-Pestalozzi 1950, p. 104, fig. 80; *Amphidinium eucephalum* J. Schiller 1955, p. 23, pl. I, fig. 6; *Amphidinium inconstans* J. Schiller 1955, p. 25, pl. I, fig. 9; *Amphidinium sauerzopfii* J. Schiller 1955, p. 22, pl. I, fig. 4 ("*Sauerzopfi*"); *Gymnodinium stagnale* J. Schiller 1955, p. 29, pl. II, fig. 15; *Amphidinium skujae* Christen 1958b, p. 69, fig. 2; *Amphidinium vernale* Skvortsov 1946, p. 13, pl. 1, figs 1, 2; *Gymnodinium vernale* Skvortsov 1968, p. 86, pl. I, fig. 10

Cells approximately round, slightly flattened dorsoventrally, the epicone approximately 1/4 the cell length. Epicone slightly narrower than hypocone, its top almost

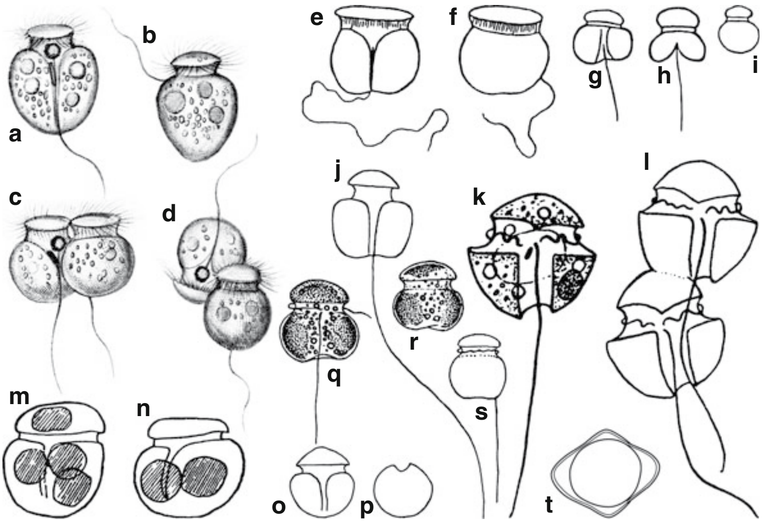

Fig. 308 *Prosoaulax lacustris* (F. Stein) Calado & Moestrup (**a**–**d** after Stein 1883; **e**, **f** after Skvortsov 1925; **g**–**i** after Lindemann 1928c; **j** after Wołoszyńska 1937; **k**, **l** after Entz 1930; **m**, **n** after Harris 1940; **o**, **p** after Huber-Pestalozzi 1950; **q**–**s** after Skuja 1939; **t**, original). **a**, **b** ventral and dorsal views; **c**, **d** aspects of gamete fusion; **e**, **f** ventral and dorsal views; **g** ventral view; **h**, **i** dorsal views, in **h** possibly a stage in division; **j**, **k** ventral views; **l** late cell division; **m**, **n** ventral views; **o**, **p** ventral view and outline of cross-section; **q**–**s** ventral and dorsal views showing plate-like chloroplasts, and outline of dorsal view, respectively (as *Amphidinium luteum*); **t** cyst (hypnozygote)

flat, occasionally convex or conical. Sulcus widening towards the posterior end. Nucleus in the left side of the hypocone. Elongated eyespot present along the right edge of the sulcus. Starved cells colorless, recently fed cells with food vacuoles of various sizes and shapes, in the hypocone or the epicone. Chloroplasts typically absent. Cells usually 8–14 μm long and 8–12 μm wide. Cysts thick-walled, four-angled.
TEM: Calado *et al.* (1998).
Ecology: winter and spring in Lake Haussersee, Switzerland. Later seen mainly in eutrophic ponds and lakes.
Geographical distribution: Denmark (Calado & Moestrup); England (Harris; Lewis & Dodge); Germany (Lindemann); Poland (Wołoszyńska); Switzerland (Christen). Manchuria (Skvortsov).

Note: *Amphidinium luteum* Skuja (1939, p. 148, pl. X, figs 18–20) was described with 3–4 parietal, discoid, golden-yellow chloroplasts. However, it is uncertain whether the chloroplasts are always present or may be lost, in which case the cells would be indistinguishable from *P. lacustris*.

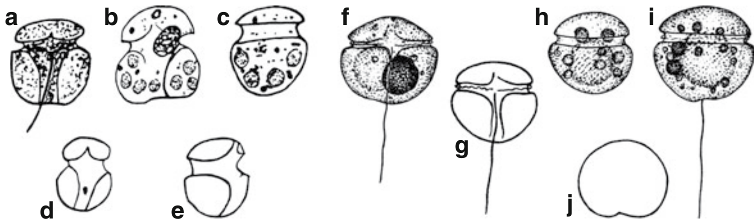

Fig. 309 *Prosoaulax multiplex* (J. Schiller) Calado & Moestrup (**a**–**e** after Schiller 1955; **f**–**j** after Skuja 1956). **a**, **b** ventral views; **c** dorsal view; **d**, **e** outline and furrows in ventral and ventral-lateral views; **f** ventral view with cell contents; **g** outline, furrows and flagella in ventral view; **h**, **i** dorsal views of different cells; **j** outline of vertical view

2. *Prosoaulax multiplex* (J. Schiller) Calado & Moestrup 2005, p. 115 (**Fig. 309**)

Basionym: *Amphidinium multiplex* J. Schiller 1955, p. 23, pl. I, fig. 7
Taxonomic synonyms: *Amphidinium vorax* J. Schiller 1955, p. 26, pl. I, fig. 11; *Amphidinium lohammarii* Skuja 1956, p. 354, pl. LXI, figs 18–22 ("*Lohammari*")

Epicone flat or cap-shaped. Approximately 8 chloroplasts observed which are difficult to see. Sometimes no chloroplasts visible. The sulcus extends onto the epicone. Cells 8–13 µm long and 6.5 µm wide.
Ecology: Lake Neusiedl, Austria, in winter. Later reported (as *A. lohammarii*) from numerous lakes in Sweden.
Geographical distribution: Austria (Schiller); Sweden (Skuja).

Note: this species differs from *P. lacustris* in the extension of the sulcus onto the epicone.

3. *Prosoaulax viridis* (J. Schiller) Calado & Moestrup 2005, p. 116 (**Fig. 310**)

Basionym: *Amphidinium viride* J. Schiller 1955, p. 21, pl. I, fig. 2

Epicone 4 µm long, very narrow, semicircular, sharply set from the wider hypocone. Six green chloroplasts present. Cells 12–14 µm long and 10–11 µm wide.
Ecology: Lake Neusiedl, Austria, summer to autumn.
Geographical distribution: Austria.

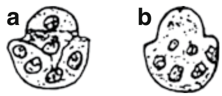

Fig. 310 *Prosoaulax viridis* (J. Schiller) Calado & Moestrup (after Schiller 1955). **a** ventral view; **b** dorsal view

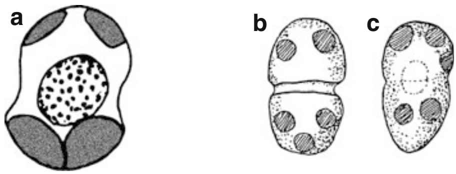

Fig. 311 *Protodinium simplex* Lohmann (**a** after Lohmann 1908; **b**, **c** after Dangeard 1939). **a** ventral (?) view showing central nucleus and four chloroplasts; **b**, **c** two aspects of cells with five chloroplasts and central nucleus (outlined in **c**)

Genus 6. ***Protodinium*** Lohmann 1908, p. 265

Type species: *Protodinium simplex* Lohmann 1908

1. *Protodinium simplex* Lohmann 1908, p. 265, pl. XVII, fig. 17 (**Fig. 311**)

Nomenclatural synonym: *Gymnodinium simplex* (Lohmann) Kofoid & Swezy 1921, p. 256
Taxonomic synonym: *Gymnodinium simplex* Dangeard 1939, p. 301, pl. XVII, figs 1–8, *nom. illeg.*

Cells broadly ellipsoidal, not dorsoventrally compressed. Cingulum circular. From four to many yellowish, disc-shaped chloroplasts, fewer in small cells. Cell length 10–20 µm, width *ca.* 13 µm.
Ecology: marine, planktonic. Recorded from fresh water in stream near Ségrie, France (Dangeard 1939).
Geographical distribution (freshwater record): France (Dangeard).

Note 1: whether the material from France is identical to the marine species *Protodinium simplex* needs to be confirmed.

Note 2: the species was also recorded from a small, temporary freshwater pool in São Paulo, Brazil (Bicudo & Skvortsov 1970). However this material was twice the size (35–45 µm long, 23–31 µm wide) and its identity is therefore questionable.

Order 9. TOVELLIALES Moestrup & Calado *ord. nov.*

Cells with many, often hexagonal, amphiesmal vesicles, which in some species contain thin plates whereas in others no firm material is present. The eyespot is composed of lipid globules that are not part of a chloroplast (eyespot type C).

Family 1. Tovelliaceae Moestrup, K. Lindberg & Daugbjerg *in* Lindberg *et al.* 2005, p. 438

As here circumscribed, the family includes the genus *Woloszynskia* R. H. Thompson. Bourrelly (1970, pp 53, 56) segregated *Woloszynskia* into a monotypic family but used a French ending for the family name. Starmach (1974, pp 163, 241) corrected the name to "Woloszynskiaceae", but did not provide a validating description in Latin.

Cells with many, often hexagonal, amphiesmal vesicles, which in some species contain thin plates (*Tovellia*, *Jadwigia*), while in others the vesicles are empty (*Bernardinium*). In *Woloszynskia* the hypocone is covered by amphiesmal plates with conspicuously raised rims. In four genera (*Tovellia*, *Jadwigia, Opisthoaulax, Woloszynskia*) the cingulum is complete, beginning and ending in the sulcus; in *Bernardinium,* however, the right side of the cell lacks a cingulum. The cingulum is typically covered by a single row of amphiesmal plates. The eyespot is composed of lipid globules that are not part of a chloroplast (Type C, see p. 19). It is located in the sulcus as in other dinoflagellates, associated with the longitudinal microtubular root R1, which supports the sulcal area. The anterior end of the cell was shown in *Tovellia* and *Jadwigia* to possess a linear anterior complex (LAC) comprising a row of very narrow plates (the anterior line of plates, ALP), which are difficult to see in the LM but readily visible by SEM. The ALP extends over the apical end of the cell, in contrast to the somewhat similar LAC of *Borghiella* which passes to the left of the apex. The so-called carina in *Woloszynskia* may be an ALP. Trichocysts observed in several species. Propagation by formation of 4–8 zoospores within the non-motile cell was observed in *Tovellia* and *Opisthoaulax* and is probably a family character. Sexual reproduction results in planozygotes with two longitudinal flagella. They develop into resting cysts, which are round and smooth (*Bernardinium, Jadwigia*) or bipolar with protuberances or spines (*Tovellia, Opisthoaulax*). Apparently a family restricted to fresh water.

Key to the genera of Tovelliaceae:

1a Cells with complete cingulum 2
1b Cingulum lacking on the right hand side .... 1. *Bernardinium*
2a Cells without chloroplasts .... 3. *Opisthoaulax*
2b Cells with chloroplasts 3
3a Cells distinctly flattened but not pointed apically and antapically; cysts smooth .... 2. *Jadwigia*
3b Cells barely flattened dorsoventrally or, if flattened (*Tovellia leopoliensis*), pointed apically and antapically; cysts bipolar, with protuberances or spines 4

4a Amphiesmal plates of hypocone with distinct raised rims .... 5. *Woloszynskia*
4b Amphiesma on hypocone without such ridges .... 4. *Tovellia*

Genus 1. *Bernardinium* Chodat 1924, p. 40

Type species: *Bernardinium bernardinense* Chodat 1924
Taxonomic synonym: *Esoptrodinium* Javornický 1997, p. 35

Cells somewhat longer than broad, epicone longer than hypocone. The cingulum restricted to the left side of the cell, starting near the sulcus and vanishing on the dorsal side. Chloroplasts absent or present, large eyespot present. The single species of this genus is truly naked, as the amphiesmal vesicles do not contain any trace of amphiesmal plates.

Note: the original illustrations of *Bernardinium* (Chodat 1924, fig. VII) show cells with the cingulum oriented toward the cell's right. Later authors generally regarded this as a misrepresentation justified by the swiftness of movement of the cells or shape deformation (Schiller 1935; Huber-Pestalozzi 1950). However, Javornický (1997) reported *Bernardinium*-like cells with a right-oriented cingulum from NE Germany, which he regarded as the true *Bernardinium*, and established the genus *Esoptrodinium* for the mirror-symmetrical types more commonly reported. The unlikeliness of this symmetry and the possibility of a mistake induced by microscope optics were addressed by Calado *et al.* (2006). Until the existence of *Bernardinium*-like cells with the cingulum extending to the right is confirmed we adopt the conservative view of considering *Esoptrodinium* as a synonym of *Bernardinium*.

1. *Bernardinium bernardinense* Chodat 1924, p. 41, fig. VII (**Fig. 312**)

Taxonomic synonyms: *Hemidinium kisselewii* Skvortsov 1968, p. 21, pl. IV, fig. 4; *Esoptrodinium gemma* Javornický 1997, p. 36, table II, fig. 2

Cells roughly obovoid, often slightly flattened dorsoventrally. Epicone longer and wider than hypocone. Apex rounded, more or less helmet shaped. Hypocone rounded. Cingulum deep, extending to the mid-dorsal region. Cell contents often obscured by food vacuoles. An eyespot present near the base of the longitudinal flagellum just below the proximal end of the cingulum. Sulcus difficult to see in the light microscope. One or two band-shaped chloroplasts may be present, but a strain with non-functional chloroplasts and a strain without chloroplasts are also known. Nucleus posterior. Cells mostly 10–19 µm long and 7–14 µm wide, but smaller cells (down to 8 × 5 µm) also seen. Cells swim rapidly, at velocities exceeding 200 µm/s. Food uptake by direct engulfment (Hansen & Calado 1999) through the ventral part of the hypocone, involving a wide, thin pseudopod apparently driven by a short peduncle. Cysts round, smooth-walled, 12–16 µm in diameter.
TEM: Calado *et al.* (2006).
DNA data: Calado *et al.* (2006), Fawcett & Parrow (2012).
Ecology: temporary pools, ponds, dams. According to Fawcett & Parrow (2013) this species is most likely a soil flagellate, which is present in the soil as a cyst. The species is heterotrophic or an obligate mixotroph, but all strains examined grow better in the light. It feeds on a wide range of prey, including diatoms, but material

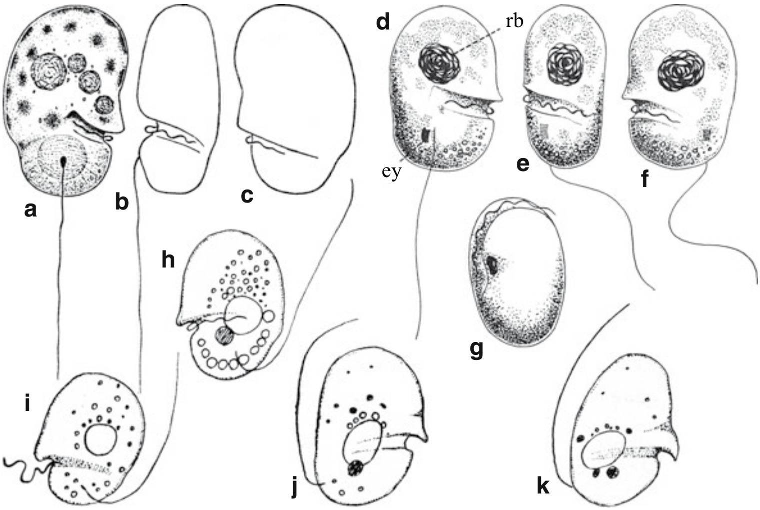

Fig. 312 *Bernardinium bernardinense* Chodat (**a**–**c** after Thompson 1951; **d**–**g** after Javornický 1962; **h**–**k** after Chodat 1924). **a**–**c** ventral, left, and dorsal views of the cell, respectively; **d**–**g** ventral, left, dorsal and antapical views of the cell, respectively (ey, eyespot; rb, reddish-brown body); **h**–**k** four of Chodat's original illustrations rotated 180º

from North Carolina examined for food preferences favored cryptomonads and *Chlamydomonas*.
Geographical distribution: Czech Republic (Javornický); Portugal (Calado *et al.*); Switzerland (Chodat). USA, KS (Thompson), NC (Fawcett & Parrow). Manchuria, China (Skvortsov).

Genus 2. *Jadwigia* Moestrup, K. Lindberg & Daugbjerg *in* Lindberg *et al.* 2005, p. 432

Type species: *Jadwigia applanata* Moestrup, K. Lindberg & Daugbjerg 2005

Cells covered with many, often hexagonal, amphiesmal plates which are usually difficult to see in the light microscope except after staining or in empty thecae. Anterior end with straight or slightly curved apical line of plates (ALP) that extends from the ventral to the dorsal side of the cell. The ALP is lined on each side by a row of pentagonal amphiesmal vesicles. Several or many golden-green or brown chloroplasts in the periphery of the cell. Hypnozygotes smooth, round. Only the type species, *Jadwigia applanata*, has been examined in detail. Three additional species are included here pending further studies. Three of the four species are known to possess an eyespot, whereas an eyespot has not been reported in *J. hiemalis.*

Key to species of *Jadwigia*:

1a Cells flattened, epicone not overhanging, many chloroplasts 2
1b Cells subspherical, epicone overhanging, 5–9 chloroplasts ..... 3. *J. limnetica*
2a Cells pentagonal, eyespot absent .... 2. *J. hiemalis*
2b Cells ovoid, eyespot present 3
3a Cells strongly flattened, epi- and hypocone of almost equal size ....
.... 1. *J. applanata*
3b Cells less strongly compressed, epicone larger than hypocone .... 4. *J. neglecta*

1. *Jadwigia applanata* Moestrup, K. Lindberg & Daugbjerg *in* Lindberg *et al.* 2005, p. 432, figs 39–69 (**Fig. 313**)

Taxonomic synonyms: *Glenodinium neglectum* A. J. Schilling *sensu* Wołoszyńska 1917, p. 115, pl. 11, fig. 5, pl. 12, figs 10, 11; *Gymnodinium neglectum* (A. J. Schilling) Er. Lindemann *sensu* Lindemann 1929, p. 60, figs 42–45; *Woloszynskia limnetica* Bursa *sensu* Roberts *et al.* 1995, p. 949, figs 1–38

Cells oval-round, strongly compressed dorsoventrally. Epi- and hypocone of almost equal size, the epicone sometimes marginally larger. With numerous golden-green discoid chloroplasts in the cell periphery. Nucleus sausage-shaped, mainly on the right side of the cell. Eyespot oval-elongate, in the sulcus. Cingulum descending, the ends displaced 1–3 cingulum widths. Apical line of narrow plates lined on each side by a row of pentagonal plates. Cell length 24–34 µm, width 24–32 µm. Cell division occurs at night in the non-motile stage: the cells stop swimming, lose the flagella and the cell contents divide into two cells, which are released from the mother cell cover. Cysts spherical, smooth but sometimes with remains of amphiesmal plates.
SEM: Lindberg *et al.* (2005).
TEM: Roberts *et al.* (1995), Lindberg *et al.* (2005).
DNA data: Lindberg *et al.* (2005).
Ecology: in small pond near Lochmühle, Germany (Lindberg *et al.* 2005); apparently eurytherm in Bavaria, at pH 5.6–7.5 (Lindemann 1929).
Geographical distribution: Denmark (Nygaard); Germany (Lindemann; Lindberg *et al.*); Sweden (Skuja)?; Portugal (Nauwerck)?; Ukraine (Wołoszyńska).

2. *Jadwigia hiemalis* (Wołoszyńska) Moestrup *comb. nov.* (**Fig. 314**)

Basionym: *Gymnodinium hiemale* Wołoszyńska 1917, *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math., Sér. B, Sci. Nat.* **1917**, p. 118, pl. 11, fig. 4; (again in Wołoszyńska 1918, *Rozpr. Wydz. Mat.-Przyr. Akad. Umiejetn., Dział B, Nauki Biol.* **17**, p. 28, text-fig. 2c, pl. 5, fig. 4)
Nomenclatural synonym: *Woloszynskia hiemalis* (Wołoszyńska) R. H. Thompson 1951, p. 290 ("*heimale*")

Cells pentagonal, dorsoventrally compressed. Epicone conical, hypocone trapezoidal, often slightly indented posteriorly. Epicone smaller than hypocone. Cingulum descending, the ends displaced *ca.* 4× the cingulum width. The sulcus does not extend onto the epicone. Amphiesma of numerous hexagonal plates. Plates finely

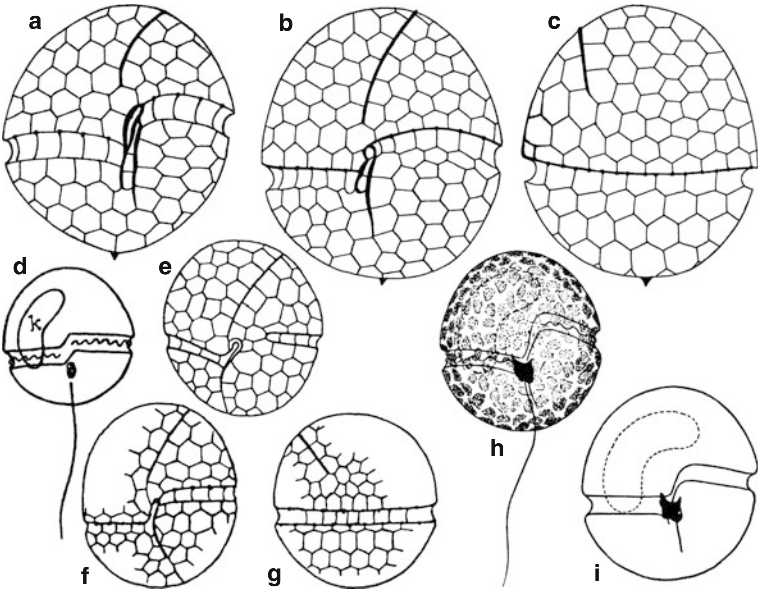

Fig. 313 *Jadwigia applanata* Moestrup, K. Lindberg & Daugbjerg (**a**–**c** after Wołoszyńska 1917; **d**–**g** after Lindemann 1929; **h**, **i** after Nygaard 1950). **a**, **b** ventral views showing limits of amphiesmal vesicles and apical line; **c** amphiesma in dorsal view, with dorsal end of apical line; **d** ventral view showing flagella, eyespot and the elongated nucleus on the right side of the epicone; **e**, **f** ventral views; **g** dorsal view; **h** ventral view with flagella, eyespot and chloroplasts; **i** outline of cell with elongate nucleus on the right side of the epicone

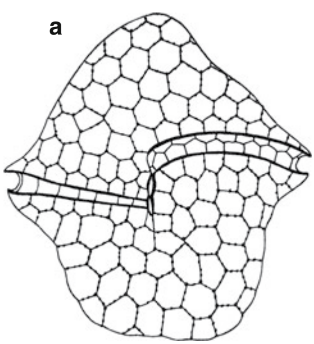

Fig. 314 *Jadwigia hiemalis* (Wołoszyńska) Moestrup (after Wołoszyńska 1917). **a** ventral view showing limits of amphiesmal vesicles

areolated. Numerous brown chloroplasts. Nucleus oval or spherical, in the epicone. Eyespot absent. The amphiesma opens for cell release on the epicone. Cell length *ca.* 45 µm, width 40 µm, sometimes much smaller.
Ecology: in plankton of ponds in Dublany, Ukraine, typical winterform.
Geographical distribution: Ukraine.

Note 1: epicone and hypocone both with 6–8 horizontal rows of plates, cingulum with 2 rows of plates.

Note 2: this species differs in very few features from *J. limnetica*, notably in the absence of an eyespot and in being a cold-water species. We are retaining both species as separate, pending further studies.

3. *Jadwigia limnetica* (Bursa) Moestrup *comb. nov.* (**Fig. 315**)

Basionym: *Woloszynskia limnetica* Bursa 1958, *J. Protozool*. **5**, p. 299, figs 1–12

Cells subspherical, epicone conical or dome-shaped, hypocone rounded angular. Hypocone sometimes slightly longer than epicone. Cingulum descending, the ends displaced *ca.* 4 cingulum widths. The anterior edge of the cingulum overhanging. Sulcus observed in some cells to continue onto the epicone as a double row of elongate pentagonal, hexangular or quadrilateral plates. In other cells this structure was not observed. Sulcus of minute rectangular plates in young cells, two rows in mature cells. Amphiesma in both epi- and hypocone of *ca.* 8 horizontal rows of hexagonal plates. Cingulum with 2 rows of plates. Five to nine spherical or subspherical chloroplasts. Nucleus in the epicone. Eyespot brown-red, V-shaped, U-shaped or irregular. Longitudinal flagellum 1.5–2× the cell length. Cell length 28–63 µm, width 31–60 µm. Cysts spherical or subspherical, with fine hexagonal reticulation or hyaline. Cyst diameter 35–69 µm.
Ecology: in a small pond near Cambridge, England.
Geographical distribution: England.

4. *Jadwigia neglecta* (A. J. Schilling) Moestrup *comb. nov.* (**Fig. 316**)

Basionym: *Glenodinium neglectum* A. J. Schilling 1891a, *Flora* **74**, p. 284, pl. X, fig. 17
Nomenclatural synonyms: *Gymnodinium neglectum* (A. J. Schilling) Er. Lindemann 1928a, p. 259 ≡ *Woloszynskia neglecta* (A. J. Schilling) R. H. Thompson 1951, p. 290
Taxonomic synonyms: (?) *Glenodinium australicum* Playfair 1920, p. 799, text-fig. 4; *Gymnodinium hiemale* Skvortsov 1927, p. 123, fig. 1, *nom. illeg.* (*non* Wołoszyńska 1917) ≡ *Gymnodinium skvortsowii* J. Schiller 1932, p. 415; *Gymnodinium neglectum* var. *astigmatum* Christen 1959b, p. 187 ("*astigmata*")

Cells oval, dorsoventrally compressed, the epicone larger than the hypocone. Epicone hemispherical, hypocone broadly rounded. Cingulum circular (Schilling 1891a) or descending, the ends displaced half a cingulum width (Thompson 1947). Chloroplasts numerous, parietal or radial at the periphery, light to dark yellowish-brown. Eyespot oval to elongate, in the sulcus. Amphiesma of hexangular plates

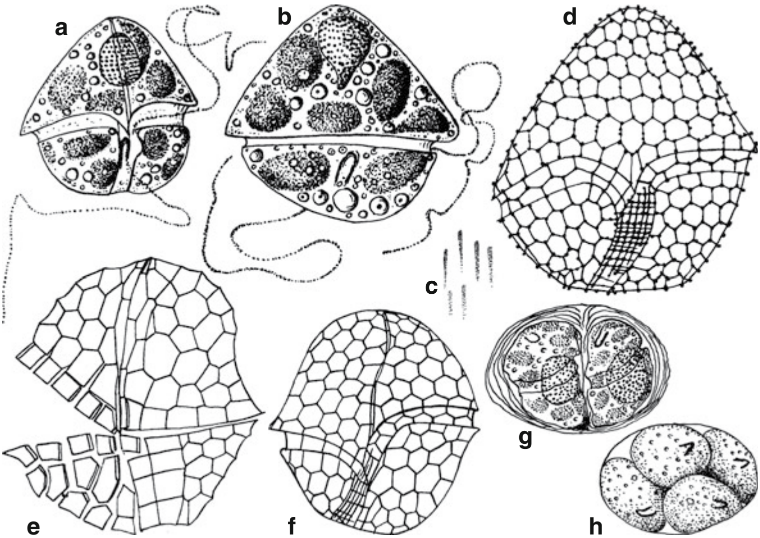

Fig. 315 *Jadwigia limnetica* (Bursa) Moestrup (after Bursa 1958). **a**, **b** ventral and dorsal views, showing subspherical chloroplasts, the apical nucleus and the V- or U-shaped eyespot; **c** alternative, elongate shape of chloroplasts; **d** ventral structure of thin amphiesma (presumably of young cell), with blebs interpreted as mitochondria protruding from within the sutures; **e**, **f** ventral structure of amphiesma (cell shown in **e** interpreted as old); **g** division in immotile stage within multilayered cyst; **h** division into 4 cells within a single-layered cyst

(Thompson 1947, Javornický 1967). Cell length 22–35(–45) μm, width 22–30 μm. Cysts spherical or slightly oval, with smooth wall.
Ecology: peat bogs, ponds and pools.
Geographical distribution: Czech Republic (Javornický); Switzerland (Schilling, Christen). USA, MD (Thompson). Manchuria, Russia (Skvortsov).

Note 1: the original description is very incomplete. Schilling (1891a) referred the production of spherical and horned cysts, which suggests that a mixture of cyst-forming *Jadwigia* and *Tovellia* species may have been involved.

Note 2: *Glenodinium australicum* Playfair differs from this species mainly in the absence of an eyespot. Playfair (1920) gave no information about chloroplasts.

Genus 3. *Opisthoaulax* Calado 2011, p. 646

Type species: *Opisthoaulax vorticella* (F. Stein) Calado 2011
Taxonomic synonyms: *Massartia* W. Conrad 1926, p. 70, *nom. illeg.* (*non* De Wildeman 1897, p. 27), *pro parte* ≡ *Katodinium* Fott 1957, p. 287, 313, *pro parte*

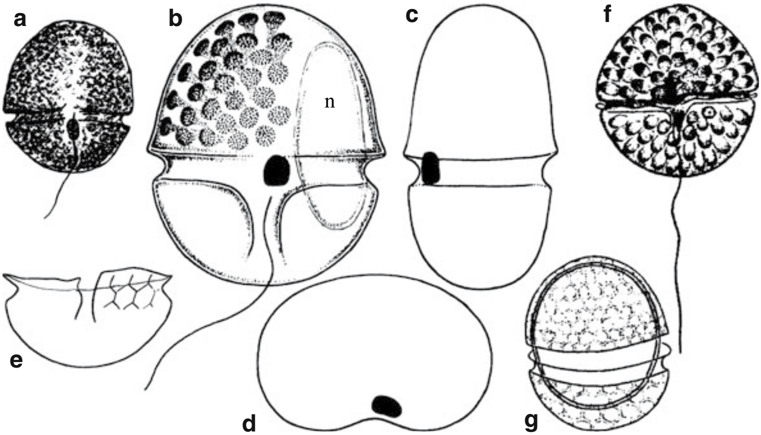

Fig. 316 *Jadwigia neglecta* (A. J. Schilling) Moestrup (**a** after Schilling 1891a; **b**–**e** after Javornický 1967; **f**, **g** after Thompson 1947). **a** ventral view; **b** ventral view, showing radial chloroplasts and an elongate nucleus (n) on the left side of the cell; **c**, **d** lateral view and cross-section of the hypocone; **e** amphiesmal structure of the posterior part of the cell; **f** ventral view with radial chloroplasts; **g** outline of oval cyst surrounded by the amphiesma of the vegetative cell

Epicone 1.5–2.5× the length of the hypocone, chloroplasts absent. Cells more or less dorsoventrally compressed. With distinct eyespot in the sulcus. Propagation by formation of 4–8 zoospores in the non-motile stage has been observed in *O. vorticella*, O. *musei* and *O. fastigata.* Cyst, where known, with paracingulum and two axial horns as in *Tovellia*. Although not examined with molecular methods, there is little doubt that *Opisthoaulax* is a close relative of *Tovellia*.

Key to species of *Opisthoaulax*:

1a Cells in ventral view longer than wide 2
1b Cells in ventral view approximately as long as wide; ends of the cingulum displaced two or more cingulum widths .... 7. *O. woloszynskae*
2a Antapex pointed .... 3. *O. fastigata*
2b Antapex rounded or concave 3
3a Antapex concave; cingulum with anterior edge overhanging .... 4. *O. musei*
3b Antapex rounded 4
4a Cingular ends displaced one cingulum width or less 5
4b Cingular ends displaced *ca.* two cingulum widths .... 6. *O. tetragonops*
5a Sulcal extension on the epicone displaced towards the left ... 2. *O. campylops*
5b Sulcal extension not displaced 6
6a Cingular ends displaced *ca.* one cingulum width, cell apex mostly rounded .. .. 1. *O. vorticella*
6b Cingular ends displaced less than one cingulum width, cell apex pointed, left side of hypocone concave .... 5. *O. piscinalis*

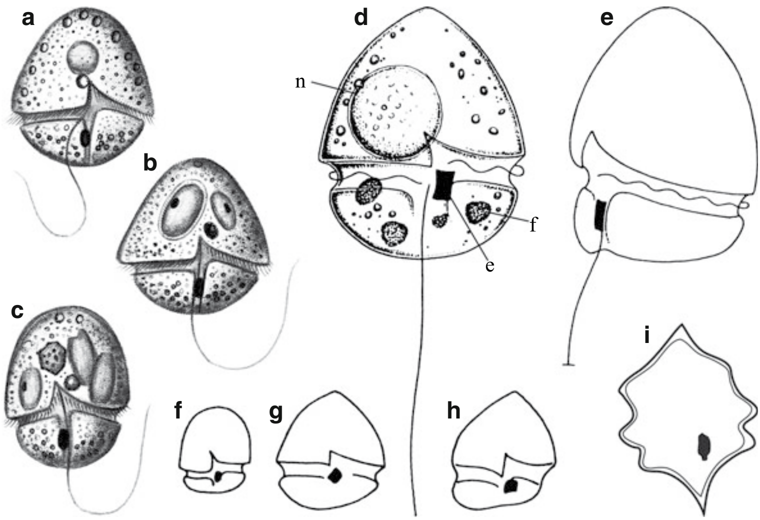

Fig. 317 *Opisthoaulax vorticella* (F. Stein) Calado (**a**–**c** after Stein 1883; **d**–**h** after Javornický 1967; **i** original). **a**–**c** ventral views, in **b** and **c** cells with ingested food in the epicone; **d**, **e** ventral and ventro-lateral views of a cell (e eyespot; f ingested food; n nucleus); **f**–**h** shape variation; **i** outline of recently formed resting cyst (hypnozygote), with the eyespot still clearly visible

1. *Opisthoaulax vorticella* (F. Stein) Calado 2011, p. 647 (Fig. 317)

Basionym: *Gymnodinium vorticella* F. Stein 1878, p. 90, 95; 1883, pl. III, figs 1–4
Nomenclatural synonyms: *Gyrodinium vorticella* (F. Stein) Er. Lindemann 1924e, p. 275 ≡ *Massartia vorticella* (F. Stein) J. Schiller 1933, p. 441 ≡ *Katodinium vorticella* (F. Stein) A. R. Loeblich 1965, p. 16
Taxonomic synonyms: *Gymnodinium stigmaticum* Er. Lindemann 1928c, p. 291, figs 5–7 ≡ *Massartia stigmatica* (Er. Lindemann) J. Schiller 1933, p. 441 ("*stigmaticum*") ≡ *Katodinium stigmaticum* (Er. Lindemann) A. R. Loeblich 1965, p. 16

Cells rounded, ovoid, usually dorsoventrally flattened. Epicone large, helmet-shaped, somewhat wider and about twice the length of the hypocone. Cingulum descending, ends displaced 1–1.5× the cingulum width. Sulcus extends for a short distance onto the epicone. Eyespot present in the sulcus. Nucleus rounded, in the apical part of the cell, or more centrally located. Cell length 21–33 µm, width 18–30 µm. Sexual reproduction known, with planozygotes gradually developing into hypnozygotes with equatorial constriction (paracingulum) and axial, pointed horns. TEM: Calado (2011).
Ecology: in vegetation-rich ponds and lakes, feeding on green algae, cryptomonads, etc.

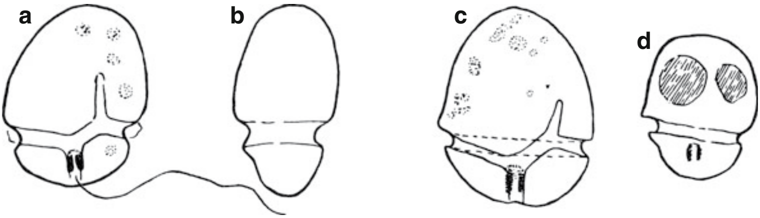

Fig. 318 *Opisthoaulax campylops* (T. M. Harris) Calado (after Harris 1940). **a**, **b** ventral and lateral views of one cell; **c**, **d** different cells in ventral and dorsal view, respectively. Stippled bodies are reserve granules, shaded bodies in **d** are ingested food items

Geographical distribution: Austria (Wawrik); Bohemia, Czech Republic (Stein; Javornický); Denmark (Huber-Pestalozzi); Hungary (Entz); Portugal (Calado); Switzerland (Christen). USA, KS (Thompson), IA (Prescott).

2. *Opisthoaulax campylops* (T. M. Harris) Calado 2011, p. 647 (**Fig. 318**)

Basionym: *Massartia campylops* T. M. Harris 1940, p. 13, fig. 4, A–D
Nomenclatural synonym: *Katodinium campylops* (T. M. Harris) A. R. Loeblich 1965, p. 15

Cell broadly ovoid, compressed dorsoventrally. Epicone 3× the length of the hypocone, rounded. Sulcus extends onto the epicone but is displaced towards the left side of the cell. Eyespot horseshoe-shaped, in the sulcus. With many colored inclusions, probably food vacuoles. Cell length 12–16 µm, width 10–13 µm, thickness 7 µm.
TEM: Wilcox (1989).
Ecology: in eutrophic pond near Reading, England, in May; during winter in Wisconsin (Wilcox 1989). Reported as phagotrophic.
Geographical distribution: England (Harris). USA, WI (Wilcox).

Note: the most characteristic feature of this species is the strongly deviated anterior extension of the sulcus. Somewhat surprisingly this was not mentioned in the original description but was illustrated in two of the drawings.

3. *Opisthoaulax fastigata* (B. Kirchhoff & Barbara Meyer) Calado 2011, p. 647 (**Fig. 319**)

Basionym: *Katodinium fastigatum* B. Kirchhoff & Barbara Meyer 1995, p. 181, figs 1–12

Cells elliptical in ventral view. The epicone pointed helm-shaped (miter-shaped), the hypocone conical with convex sides. Epicone 1.5–2.7× the length of the hypocone and slightly wider. Cingulum descending, the ends displaced 1–1.5× the cingulum width. The sulcus extends onto the epicone and is slightly deflected to the right, whereby a lobe which projects into the sulcus is formed. A bright-red eyespot

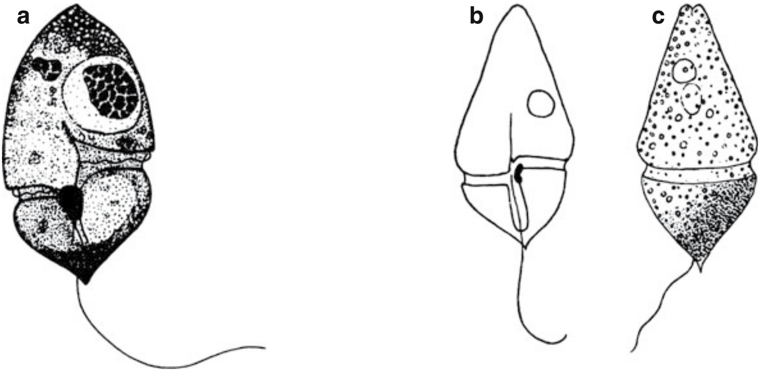

Fig. 319 *Opisthoaulax fastigata* (B. Kirchhoff & Barbara Meyer) Calado (**a** after Kirchhoff & Meyer 1995; **b**, **c** after Redeke 1919). **a** ventral view, with large food vacuole in the epicone, refractive granules in the apical region, nucleus in the hypocone and numerous small granules in the antapical region; **b**, **c** ventral and dorsal views, the right side of the hypocone in **c** with dark purplish-brown granules (as *Gymnodinium meervalli* Redeke, from lakes in Friesland, The Netherlands)

situated in the sulcal region. Food vacuoles present. The antapical region often filled with minute, brown, granular bodies. Nucleus in the hypocone. Longitudinal flagellum *ca.* 1.5× the cell length. Zoosporangia releasing their contents as a motile unit, the individual zoospores then dispersing. Cell 27–48 µm long, epicone 12–26 µm wide, hypocone 12–24 µm wide, thickness *ca.* 14 µm.
Ecology: plankton in small, hypertrophic shallow lakes in August–September in Northern Germany (surface area 0.2–0.46 km^2, max. depth 3.8 m, transparency 0.2–0.3 m, pH 8.4–9.7, temp. 16–20ºC, conductivity 269–409 µS m^{-1}) (Kirchhoff & Meyer 1995); in shallow eutrophic pond in September in NW Portugal (Pandeirada *et al.* 2013). Ingested cells of green algae and *Anabaena* observed.
Geographical distribution: Germany (Kirchhoff & Meyer); Portugal (Pandeirada *et al.*).

Note: *Gymnodinium meervalli* Redeke (1919, p. 128, figs 1, 2) was described as a colorless flagellate with a bright red eyespot, very similar to *O. fastigata*. It differs mainly in the position of the nucleus, stated to be in the epicone, and in the variable shape of the slightly metabolic tip of the epicone. Further observations are needed to determine whether it constitutes a separate species.

4. ***Opisthoaulax musei*** (Danysz) Calado 2011, p. 647 (Fig. 320)

Basionym: *Gymnodinium musei* Danysz 1886, p. 462
Nomenclatural synonyms: *Massartia musei* (Danysz) J. Schiller 1933, p. 438 ≡ *Katodinium musei* (Danysz) A. R. Loeblich 1965, p. 16
Taxonomic synonyms: *Massartia edax* J. Schiller 1954a, p. 266, fig. 23 ≡ *Katodinium edax* (J. Schiller) A. R. Loeblich 1965, p. 15–16

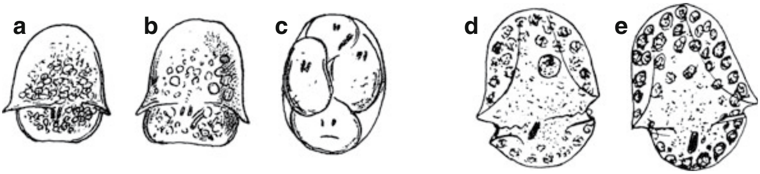

Fig. 320 *Opisthoaulax musei* (Danysz) Calado (**a**–**c** after Pouchet 1887; **d**, **e** after Schiller 1954a). **a**, **b** ventral views; **c** formation of four zoospores in the immobile stage; **d**, **e** ventral views of cells with ingested items scattered in the cytoplasm (as *Massartia edax* J. Schiller, from Lake Neusiedl)

Cell asymmetrically ellipsoidal, dorsoventrally flattened. Epicone twice the length of the hypocone. Epicone bell-shaped, wider than hypocone, with strongly overhanging sides. Hypocone short and wide, slightly concave at the antapex. Cingulum circular. With "double" eyespot in the sulcus (probably horseshoe- or trough-shaped). Longitudinal flagellum 1.5–2× the cell length. Cell colorless with numerous small grains in the hypocone. The nucleus is located in the hypocone. Cells 8–36 μm long (typically 30–36 μm), cell width one third less. Reproduction by formation of four zoospores in the cell. Cysts not described with certainty.
Ecology: in pond at the Botanical Garden in Paris in July 1886.
Geographical distribution: Austria (*M. edax*, Schiller); France (Danysz, Pouchet).

Note 1: whether this species has chloroplasts has been debated. Danysz (1886) mentions "grains of chlorophyll", Pouchet (1887) says that the cells are mainly transparent but contain spherical bodies of "green chlorophyll colour". Thompson (1947) mentions the presence of numerous dark-brown chloroplasts and lack of eyespot. However, his material (from Maryland, USA) somewhat resembles *Gymnodinium vernum* (syn. *Katodinium vernale*) and its pentagonal resting cyst indicates affinities to the *Gymnodinium tylotum* group.

Note 2: *Katodinium edax* appears morphologically identical but is said to be a cold-water species. Its cells lack chloroplasts but contain food vacuoles with bluish contents. We have merged the two taxa under the older name, pending additional studies.

5. *Opisthoaulax piscinalis* (Fott) Calado 2011, p. 647 (**Fig. 321**)

Basionym: *Katodinium piscinale* Fott 1957, p. 289, 314, text-fig. 3: 1–4

Cells egg-shaped, asymmetrical, dorsoventrally compressed. Epicone rounded-conical to miter-shaped. Hypocone about half the length of the epicone, left side concave, right side convex. Epi- and hypocone of the same width. Cingulum slightly descending. Sulcus extends widely onto the epicone, on the hypocone reaching the antapex. Eyespot on the left side of the sulcus. Cell length: 35 μm, width 28 μm, thickness 17 μm.
Ecology: plankton in small pond in Bohemia, Czech Republic.
Geographical distribution: Czech Republic.

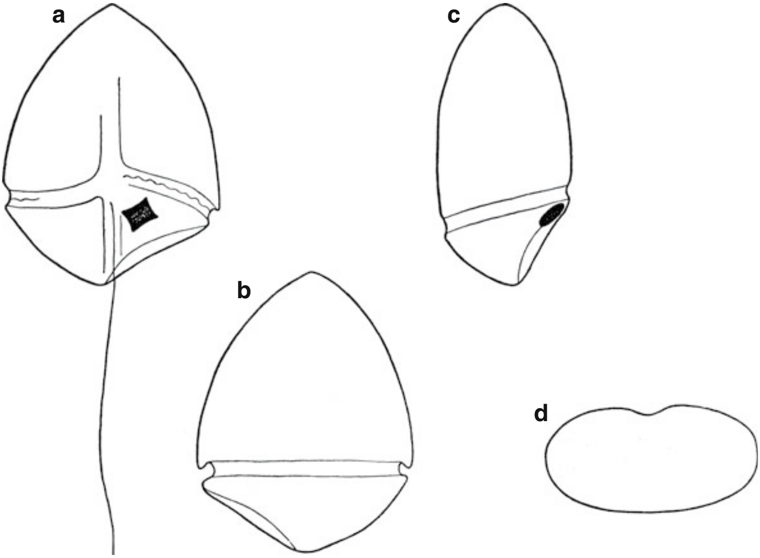

Fig. 321 *Opisthoaulax piscinalis* (Fott) Calado (after Fott 1957). **a** ventral outline, showing the eyespot and both flagella; **b** dorsal outline; **c** right lateral outline with eyespot; **d** cross section, with the sulcus upward

6. ***Opisthoaulax tetragonops*** (T. M. Harris) Calado 2011, p. 647 (**Fig. 322**)

Basionym: *Massartia tetragonops* T. M. Harris 1940, p. 15, fig. 4, G–L
Nomenclatural synonym: *Katodinium tetragonops* (T. M. Harris) A. R. Loeblich 1965, p. 16
Taxonomic synonyms: *Massartia ptyrtica* T. M. Harris 1940, p. 16, fig. 3, F–I ≡ *Katodinium ptyrticum* (T. M. Harris) A. R. Loeblich 1965, p. 16

Cells ovoid, dorsoventrally compressed. Epicone usually longer than hypocone but of the same width. Apex and antapex rounded. Cingulum clearly visible on the dorsal side of the cell, on the ventral side difficult to see, descending, the ends displaced 1.5–2× the cingulum width, sometimes more. Sulcus likewise difficult to see, extending apically to half the length of the epicone. Eyespot in the sulcus, square or rounded. Cell length 8–20 µm, width (7–)12–16 µm, thickness 7–11 µm.
Ecology: in eutrophic ponds and tanks, oxbows and ditch waters, at all times of the year. Claimed by Harris (1940) to be the most common heterotrophic gymnodinioid in the Reading area, England.
Geographical distribution: Czech Republic (Javornický); England (Harris). USA, KS (Thompson).

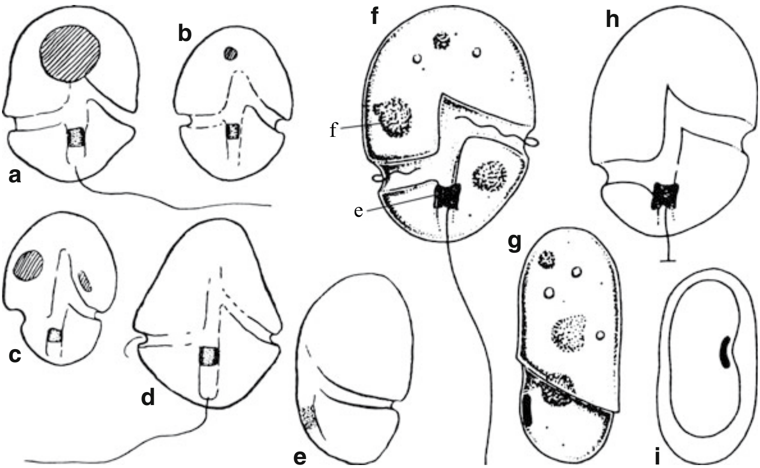

Fig. 322 *Opisthoaulax tetragonops* (T. M. Harris) Calado (**a**–**e** after Harris 1940; **f**–**i** after Javornický 1967). **a**–**c** ventral views of different cells with ingested food items (shaded areas); **d**, **e** ventral and left lateral views of the same cell; **f**, **g** ventral and left lateral views of a cell (f ingested food; e eyespot); **h** ventral view; **i** antapical view

7. *Opisthoaulax woloszynskae* (J. Schiller) Calado 2011, p. 647 (**Fig. 323**)

Basionym: *Massartia woloszynskae* J. Schiller 1933, p. 442 ("*woloszynskaae*"), a replacement name for *Spirodinium vorticella* Wołoszyńska 1917, p. 117, pl. 12, figs 19–22; pl. 13, figs F–H. The epithet "*vorticella*" is unavailable in *Massartia* and in *Opisthoaulax* because of *M. vorticella* (F. Stein) J. Schiller and *O. vorticella* (F. Stein) Calado, respectively.
Nomenclatural synonym: *Katodinium woloszynskae* (J. Schiller) A. R. Loeblich 1965, p. 16
Taxonomic synonyms: *Massartia woloszynskae* var. *notata* Skuja 1956, p. 361, pl. LXII, figs 4–7 ≡ *Katodinium woloszynskae* var. *notatum* (Skuja) A. R. Loeblich 1965 ("*notata*"), p. 16 ≡ *Katodinium notatum* (Skuja) Christen 1961, p. 327

Cells somewhat asymmetric, dorsoventrally compressed, about as long as wide. Epicone longer than hypocone. Epicone conical with convex sides, hypocone wide, the antapical end asymmetrical. Cingulum descending, the ends displaced at least two cingulum widths, sometimes more. Sulcus extends onto the epicone, and on the hypocone continues to the antapex. Cell colorless but containing remains of ingested algae and flagellates, especially in the hypocone, which may become brown due to the vacuoles. Distinct eyespot near the sulcus. Nucleus rounded or elongate, usually in the middle of the cell, sometimes on the left side. Cell length 20–50 µm, width 18–33 µm, thickness 10–18 µm.
Ecology: in claypits in western Ukraine in summer (Wołoszyńska 1917), in Norrviken (Sweden) in summer (Skuja 1956) and in small pools under the ice near

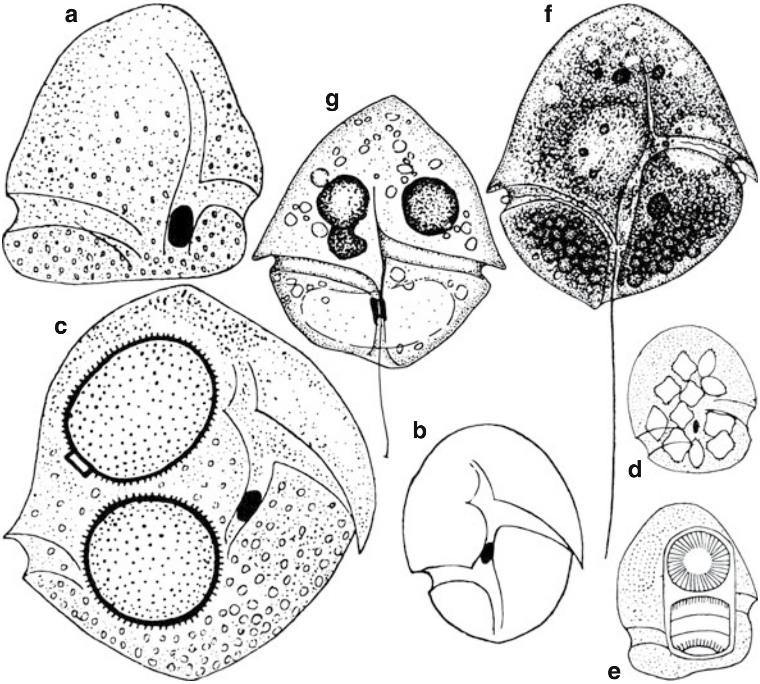

Fig. 323 *Opisthoaulax woloszynskae* (J. Schiller) Calado (**a**–**e** after Wołoszyńska 1917; **f** after Skuja 1956; **g** after Christen 1961). **a**, **b** ventral views; **c**–**e** different views of cells with recognizable ingested organisms (*Trachelomonas*, centric diatoms, chlorococcalean green algae); **f**, **g** ventral views displaying cell contents

Winterthur in winter (Christen 1961). Ukrainian material described to feed on *Trachelomonas* species, centric and pennate diatoms, and green algae.
Geographical distribution: Sweden (Skuja); Switzerland (Christen); Ukraine (Wołoszyńska).

Genus 4. *Tovellia* Moestrup, K. Lindberg & Daugbjerg *in* Lindberg *et al.* 2005, p. 427

Type species: *Tovellia coronata* (Wołoszyńska) Moestrup, K. Lindberg & Daugbjerg 2005

Cells covered with many, often hexagonal, amphiesmal plates which are usually difficult to see in the light microscope except after staining or in empty thecae that can be studied at high magnification using phase contrast or interference contrast microscopy. The plates are arranged in 6–17, more or less distinct latitudinal rows.

The cingulum generally comprises only a single row of plates but the postcingular row of plates curves over the cingulum edge into the cingulum. *Tovellia stoschii* was drawn with two rows of plates in the cingulum. The arrangement of the chloroplasts divides the genus into two: (1) those with chloroplasts radiating from the cell center (*T. apiculata*, *T. aveirensis*, *T. nygaardii*, *T. sanguinea*) and those in which the chloroplasts are parietal or more or less fill the cytoplasm (*T. coronata*, *T. glabra, T. paldangensis, T. stoschii*). There is some indication that in old or nutrient-depleted cells the radiating arrangement of the chloroplasts is lost, the arrangement becoming more irregular. In species with radiating chloroplasts, the central parts are often located close together and in *T. sanguinea* and *T. aveirensis* they form a compound pyrenoid. When known, cell division appears to take place within the non-motile cell, resulting in the formation of up to 8 zoospores. They are probably released through a slit in the epicone, corresponding to the position of the ALP. Cysts with paracingulum, two often very distinct opposite axial horns, and pre- and postcingular protuberances or with more evenly distributed, sometimes branched spines.

Key to species of *Tovellia*:

1a Cells strongly flattened dorsoventrally, almost disc-shaped ... 6. *T. leopoliensis*
1b Cells not or only very slightly compressed dorsoventrally 2
2a Cells shortly apiculate anteriorly, usually sharply pointed also at the antapex .... 2. *T. apiculata*
2b Cells rounded or somewhat conical but not pointed at apex or antapex 3
3a Cells (orange-)red or reddish due to the presence of red lipid globules 4
3b Cells brownish or greenish, one species with 2 large red bodies 6
4a Chloroplasts arranged radially .... 9. *T. sanguinea*
4b Chloroplasts parietal or filling most of the cytoplasm, not radially arranged .. 5
5a Cells with prominent antapical hexagonal amphiesmal plate ... 1. *T. coronata*
5b Cells lacking prominent antapical hexagonal plate .... 5. *T. glabra*
6a Cells with two large red bodies, one in the epi- and one in the hypocone; nucleus nearly filling the hypocone .... 8. *T. paldangensis*
6b Cells without such red bodies 7
7a Chloroplasts arranged radially 8
7b Chloroplasts parietal or filling most of the cytoplasm, not radially arranged 9
8a With *ca.* 6 horizontal rows of amphiesmal plates, cysts with paracingulum and two opposite, axial horns .... 7. *T. nygaardii*
8b With 10–14 horizontal rows of amphiesmal plates, cysts with branched processes, which are absent in the slightly constricted equatorial area .... 3. *T. aveirensis*
9a Cells with prominent antapical hexagonal plate .... 10. *T. stoschii*
9b Cells lacking prominent antapical hexagonal plate 10
10a Sulcus extends onto the epicone as a plough-shaped structure .... 4. *T. dodgei*
10b Sulcus does not extend onto the epicone .... 5. *T. glabra*

1. *Tovellia coronata* (Wołoszyńska) Moestrup, K. Lindberg & Daugbjerg *in* Lindberg *et al.* 2005, p. 427 (**Fig. 324**)

Basionym: *Gymnodinium coronatum* Wołoszyńska 1917, p. 115, 120, pl. 11, figs 10–19, pl. 13, figs I–L, N
Nomenclatural synonym: *Woloszynskia coronata* (Wołoszyńska) R. H. Thompson 1951, p. 290
Taxonomic synonym: *Glenodinium muricatum* Skuja 1964, p. 353, pl. LXVII, figs 17–19

Cells nearly spherical, very slightly dorsoventrally compressed. Epicone marginally larger than hypocone. Cingulum descending, the ends displaced *ca.* one cingulum width. Sulcus extends almost to the antapex. Cells typically with *ca.* 9 latitudinal series of plates, 4 on the epicone, one in the cingulum and 4 on the hypocone. Additional plates also occur. A nearly straight ALP extends anteriorly from the ventral to the dorsal side of the cell. About 30 pores observed in the ALP (material from Sweden). Hypothecal plates radially arranged around a single, centrally located, usually hexagonal plate, which may be ornamented with low projections. Cells with numerous, greenish or brownish, sausage-shaped chloroplasts in the outer part of the cell. Nucleus in the hypocone. Eyespot near the upper part of the sulcus, elongate or horseshoe-shaped. Trichocysts scattered over the entire surface. Cells with numerous carotenoid globules, giving the cell a red color, sometimes with a greenish tinge. Longitudinal flagellum extends more than the cell length behind the cell. Cells 25–30 μm long and 24–32 μm wide. Cell division by formation of 2–4(–8) zoospores within the cell. Cysts bright red.
SEM: Lindberg *et al.* (2005).
TEM: Lindberg *et al.* (2005).
DNA data: Lindberg *et al.* (2005).
Ecology: marl pits, bogs, lakes and ponds. Summer? In British Isles considered to be a cold-water species occurring in late winter and forming cysts when the water warms in March–April (Lewis & Dodge 2002).
Geographical distribution: Austria (Schiller); Denmark (Moestrup & Calado, unpubl.); Great Britain (Lewis & Dodge); Sweden (Lindberg *et al.* 2005; Skuja 1964, as *Glenodinium muricatum*); Ukraine (Wołoszyńska 1917).

Note: *Glenodinium muricatum* Skuja is probably identical to *T. coronata.* It was described to lack an eyespot and to have the posterior edges of the sulcus projecting as two minute spines. It agrees in size, color, presence of red globules in the cell, position of nucleus and chloroplasts, and can hardly be distinguished from *T. coronata*.

2. *Tovellia apiculata* (Stosch) Moestrup, K. Lindberg & Daugbjerg *in* Lindberg *et al.* 2005, p. 430 (**Fig. 325**)

Basionym: *Woloszynskia apiculata* Stosch 1973, p. 129, figs 33–41, 43–87

Cells pyriform or broadly pyriform, slightly flattened dorsoventrally. Epicone ovate-conical, slightly apiculate, hypocone conical-campanulate, more or less pointed at the antapex, slightly shorter than the epicone. Sulcus rather shallow, not

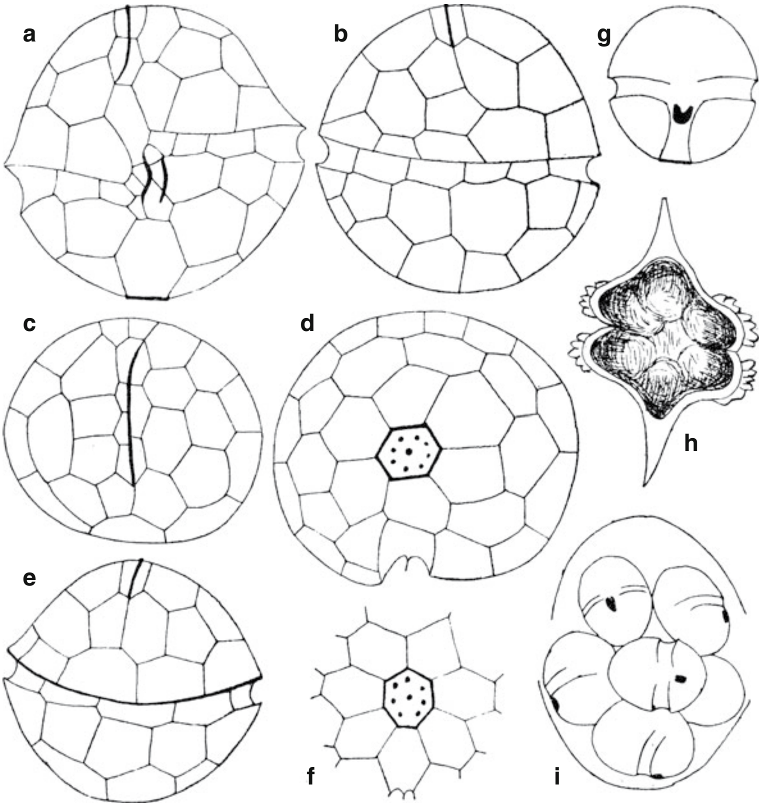

Fig. 324 *Tovellia coronata* (Wołoszyńska) Moestrup, K. Lindberg & Daugbjerg (after Wołoszyńska 1917). **a**–**d** ventral, dorsal, apical and antapical views of the cell showing the arrangement of amphiesmal vesicles; **e** dorsal view of a smaller cell, with less latitudinal series of amphiesmal vesicles; **f** variation in the arrangement of antapical vesicles; **g** outline of cell in ventral view, showing the eyespot; **h** cyst; **i** formation of zoospores

reaching the antapex. Cingulum descending, the ends displaced *ca.* one cingulum width. Cells covered with thin plates arranged in 11–13 latitudinal series, 6–7 on the epicone, one (apparently) in the cingulum and 4–5 on the hypocone (as seen in the drawings provided by von Stosch 1973, although he gives 5–6 in the description). Posterior apiculus formed by 3–4 plates. Chloroplasts brown, radiating from the center of the cell. Nucleus sausage or kidney-shaped, positioned in the dorsal side of the hypocone. Red eyespot in the anterior part of the sulcus. Cells 25–46 µm long and 18–36 µm wide. Asexual reproduction by formation of 2–8 zoospores. Hypnospores with paracingulum, a blunt or minutely biapiculate apex and a more

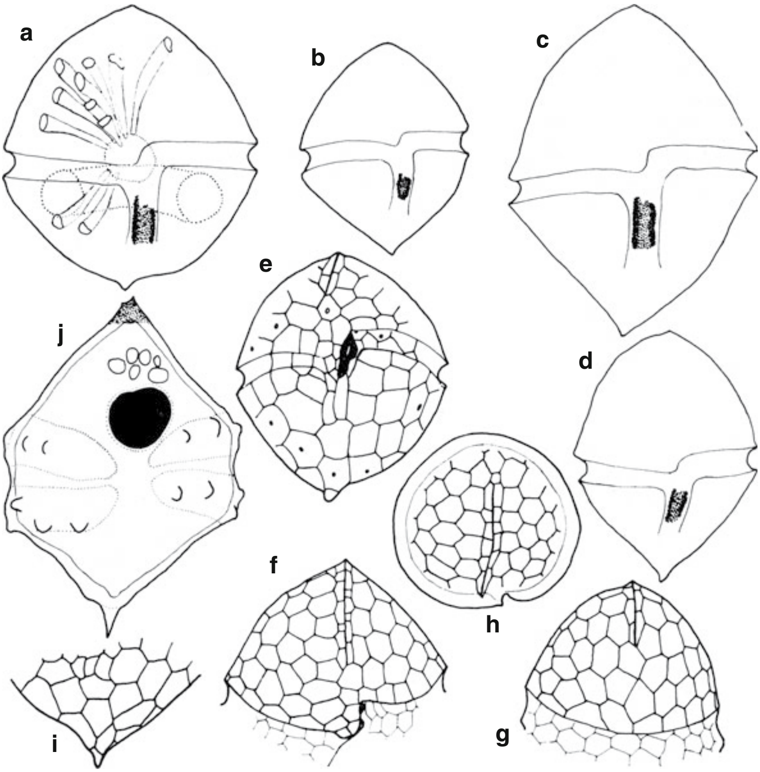

Fig. 325 *Tovellia apiculata* (Stosch) Moestrup, K. Lindberg & Daugbjerg (after Stosch 1973). **a**–**d** size and shape variation (**a**, **b** cells grown at 14,000 lx; **c**, **d** cells grown at 2000 lx; all drawings at the same scale); **e**–**i** amphiesma of vegetative cells, prepared by laurylsulphate (**e** ventral view with epicone tilted back; **f**, **g** anterior part in ventral and dorsal views, respectively; **h** apical line of plates; **i** antapex); **j** hypnozygote (cyst), ventral view, with surface punctae exemplified at the apex and a few starch grains indicated above the red oil globule (shown in black)

or less sharply pointed antapex. The hypnospores are slightly compressed, yellowish. The margins of the paracingulum swollen and ornamented with 1–2 rows of tubercles. Cyst surface minutely punctate. Hypnospores 41–49 μm long and 31–36 μm wide.
Ecology: pond at the Botanical Gardens, University of Marburg, Germany during spring and summer.
Geographical distribution: Germany (Stosch). Japan (Ibaraki, NIES Collection 619, as *W. leopoliensis*).

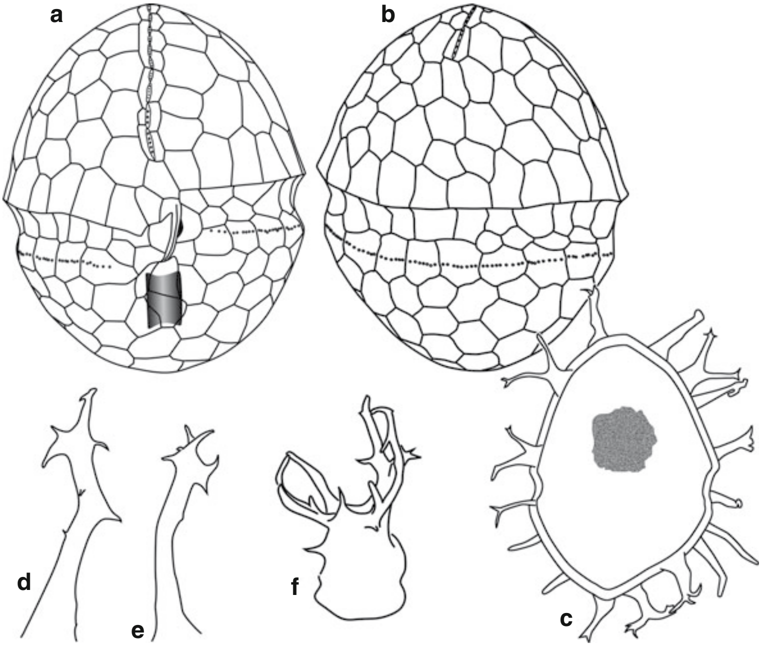

Fig. 326 *Tovellia aveirensis* Pandeirada, Craveiro, Daugbjerg, Moestrup & Calado (original drawings, based on information from LM and SEM images). **a** ventral view with the eyespot indicating the position of the sulcus and the ventral ridge marked by two parallel lines next to the transverse flagellar pore (dark spot in the middle); **b** dorsal view; **c** cyst (hypnozygote) with accumulation body (optical section); **d**–**f** examples of antler-like spines, in **f** a highly branched spine in oblique view

3. *Tovellia aveirensis* Pandeirada, Craveiro, Daugbjerg, Moestrup & Calado 2014, p. 232, figs 1–21 (**Fig. 326**)

Cells ovoid or nearly spherical, sometimes slightly dorsoventrally compressed. Cingulum descending, the ends displaced about one cingulum width. Epicone broadly round, slightly longer than wide and often somewhat longer than the obliquely flattened hypocone. Chloroplast lobes yellowish-green, radiating from the cell center towards the periphery. Nucleus in the hypocone. Eyespot nearly rectangular in ventral view, located in the sulcal area. Cell cover mainly formed by pentagonal or hexagonal amphiesmal vesicles roughly arranged in latitudinal series, 5–7 series on the epicone and 3–5 on the hypocone. Cingulum with 2 series of vesicles, the anterior vesicles abutting the sharply defined anterior cingulum edge whereas the roughly hexagonal vesicles of the posterior row extend into the hypocone over the rounded posterior cingulum edge. A row of knobs marks the posterior edge of the

cingulum. The initial part of the cingulum shows additional two or three nearly hexagonal vesicles intercalated between the two regular vesicle rows. A line of narrow vesicles starts near the proximal end of the cingulum, on the ventral side, and extends over the apex of the cell. Cells 25–34 µm long, 17–25 µm wide and 14–21 µm thick. Cysts yellowish-brown, ornamented by branched processes that are usually absent in the equatorial area, which is often slightly constricted.
SEM: Pandeirada *et al.* (2014).
TEM: Pandeirada *et al.* (2014).
DNA data: Pandeirada *et al.* (2014).
Ecology: in freshwater tank (conductivity *ca.* 300 µS) at Aveiro University, Portugal, 12 October 2009.
Geographical distribution: Portugal.

Note: a strain recently established from sediment in the Xipi Reservoir of Jiulong River in China was described as *T.* cf. *aveirensis* by Luo *et al.* (2016). If differs in having 7–10 latitudinal series of amphiesmal vesicles on the epicone versus 5–7 in the material from Portugal, and 10–11 plates along the apical line of plates versus 8–9 in the Portuguese material. The resting spore was also slightly different as the processes were rarely branched. The Portuguese and Chinese material are closely related but studies from elsewhere are needed to evaluate whether they represent different species or belong to a single, highly variable, species.

4. *Tovellia dodgei* (Sarma & Shyam) K. N. Mertens & H. Gu *in* Luo *et al.* 2016, p. 92 (**Fig. 327**)

Basionym: *Gymnodinium dodgei* Sarma & Shyam 1974, p. 21, figs 1–3, 9–12

Cells ovoid, dorsoventrally flattened. Epi- and hypocone of equal size. Epicone rounded conical, hypocone hemispherical. Cingulum descending, the ends displaced about half a cingulum width, sometimes more. Sulcus extends onto the epicone as a plough-shaped structure. Longitudinal flagellum *ca.* 1.5× cell length. Numerous yellow-brown discoid chloroplasts. Large comma-shaped eyespot in the sulcus. Nucleus in the hypocone. Cell length 31–36 µm, width 24–28 µm. Divides in the motile state. Cysts red, of the same shape as the vegetative cell, covered with numerous spines, each spine 3.5–10 µm long.
Ecology: in temporary and permanent ponds and in a reservoir, February–April, Uttar Pradesh, India.
Geographical distribution: India.

5. *Tovellia glabra* (Wołoszyńska) Moestrup, K. Lindberg & Daugbjerg *in* Lindberg *et al.* 2005, p. 429 (**Fig. 328**)

Basionym: *Gymnodinium coronatum* var. *glabrum* Wołoszyńska 1917, p. 115, 121, pl. 11, figs 20, 21 ("*glabra*")—LT: Wołoszyńska 1917, pl. 11, fig. 20 (see Moestrup *et al.* 2008)

Cells as in *T. coronata* but an antapical hexangular amphiesmal plate absent and cells slightly more dorsoventrally flattened. Chloroplasts light to dark brown. Am-

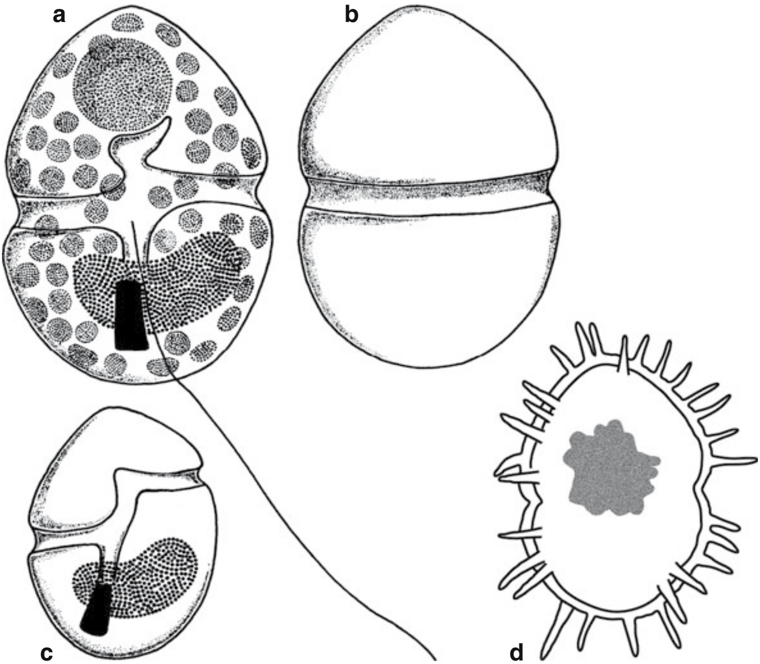

Fig. 327 *Tovellia dodgei* (Sarma & Shyam) K. N. Mertens & H. Gu (**a**–**c** after Sarma & Shyam 1974; **d** original, based on light micrograph in Sarma & Shyam 1974). **a** ventral view showing chloroplasts, eyespot, nucleus in the hypocone and a red body in the center of the epicone; **b** dorsal view; **c** ventral view of cell with larger displacement of the cingulum; **d** cyst

phiesmal plates very thin, striped areolated. Thompson (1951) illustrates at least 5 latitudinal rows of amphiesmal plates in the Kansas material, with two rows of plates in the cingulum. Cells 19–35 µm long and 14–32 µm wide (material from Kansas).
TEM: Crawford & Dodge (1974).
DNA data: Lindberg *et al.* (2005).
Ecology: marl pits, bogs, ponds and small lakes. Summer.
Geographical distribution: England (Crawford & Dodge); Ukraine (Wołoszyńska). USA, KS (Thompson).

Note: a new red species, *Tovellia diexiensis* Qi Zhang & G. X. Liu *in* Zhang *et al.* (2016, p. 208, figs. 3, 4) was recently described from Sichuan, China. It keys out in the *Tovellia* key above as *T. glabra* and has almost the same size and shape. It differs in having red cells, the color apparently due to astaxanthin and astaxanthin diesters.

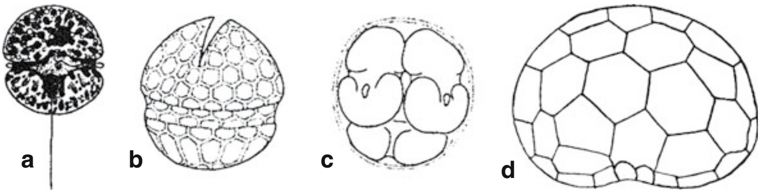

Fig. 328 *Tovellia glabra* (Wołoszyńska) Moestrup, K. Lindberg & Daugbjerg (**a**–**c** after Thompson 1951; **d** after Wołoszyńska 1917). **a** ventral view of live cell; **b** amphiesma in dorsal view; **c** formation of zoospores; **d** antapical view of the amphiesma (absence of a prominent, central antapical plate)

6. *Tovellia leopoliensis* (Wołoszyńska) Moestrup, K. Lindberg & Daugbjerg *in* Lindberg *et al.* 2005, p. 430 (**Fig. 329**)

Basionym: *Gymnodinium leopoliense* Wołoszyńska 1917, p. 115, 119, pl. 11, fig. 6; pl. 13, figs C–E
Nomenclatural synonym: *Woloszynskia leopoliensis* (Wołoszyńska) R. H. Thompson 1951, p. 290

Cells plate-like, strongly flattened dorsoventrally, shortly pointed apically and antapically. Epicone slightly larger than hypocone. Cingulum descending, slightly displaced. Cells covered with numerous, small, 6- or 7-sided plates in *ca.* 15, more or less distinct, latitudinal series, *ca.* 8 on the epicone, 1 in the cingulum, *ca.* 6 on the hypocone. Chloroplasts light yellow to brown, apparently somewhat radiating. Eyespot large, somewhat variable, wide or narrow horseshoe-shaped (Wołoszyńska) or comma shaped with long anterior bifid extension from the right hand side and a short one from the left side (G. Hansen, pers. comm.), located near the anterior end of the sulcus. Nucleus central or in the hypocone, horseshoe-shaped in a transverse plane. Cell length *ca.* 40 µm. Cell division not described. Resting cyst with paracingulum and two opposite axial spines; several shorter spines scattered on the cell surface.
When examined under a coverslip, cells of *T. leopoliensis* readily shed the amphiesma, which may remain attached to the cell for some time.
Ecology: ponds, marl pits, oxbows; spring and summer form.
Geographical distribution: Denmark (G. Hansen, pers. comm.); Poland, Ukraine (Wołoszyńska; Moestrup, unpubl.).

Note 1: this species has been confused with *Borghiella tenuissima*, a cold-water species that differs in lacking a distinct eyespot (it is present but usually difficult to see in the light microscope). In addition, *Borghiella tenuissima* has an incomplete cingulum on the ventral side and a different type of resting cyst. The two species belong in different families.

Note 2: *Gymnodinium lens* Fott (1957, p. 286, 313, text-fig. 3, figs 5, 6), described from the Czech Republic, was said to differ in lacking visible amphiesmal plates when observed in the light microscope. In other respects it appears to be similar, and is probably identical to *T. leopoliensis* (cell length 34–35 µm, width 28–30 µm).

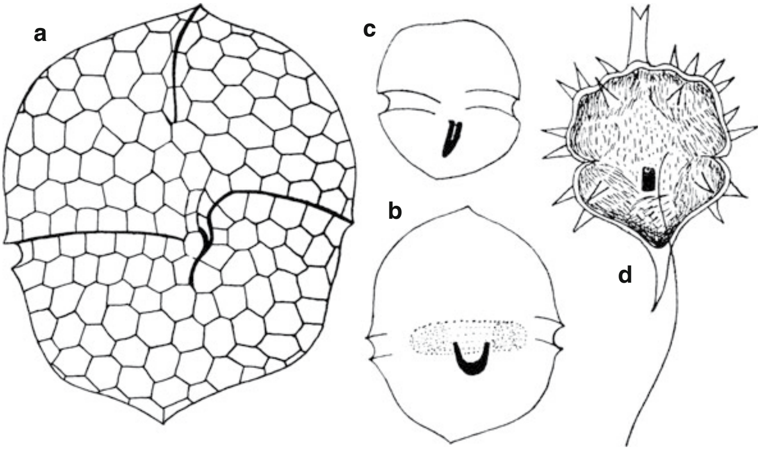

Fig. 329 *Tovellia leopoliensis* (Wołoszyńska) Moestrup, K. Lindberg & Daugbjerg (after Wołoszyńska 1917). **a** ventral view, showing arrangement of amphiesmal vesicles; **b** outline of cell, showing the eyespot and the position of the nucleus; **c** outline of a recently released zoospore; **d** immature cyst, still with eyespot and longitudinal flagellum

7. *Tovellia nygaardii* Moestrup, K. Lindberg & Daugbjerg *in* Moestrup *et al.* 2008, p. 76 (**Fig. 330**)

Based on the description of "*Gymnodinium nygaardi* Christen (1958a, p. 47, figs a–i)", a designation not validly published (type not designated).—T: Christen 1958a, fig. b (see Moestrup *et al.* 2008)

Epicone and hypocone rounded or somewhat conical. Epicone usually slightly larger than the hypocone. Cells slightly flattened dorsoventrally. Cells covered with small number of amphiesmal plates in *ca.* 6 latitudinal rows, usually 3 on the epicone, 1 in the cingulum and 2 on the hypocone. Amphiesmal plates on the hypocone radially arranged around a small antapical plate. Plates smooth. Cingulum descending, displaced up to one cingulum width. Sulcus wide, extending to the antapex. Nucleus elongate, in the hypocone. Chloroplasts greenish-brown, radially arranged, in old or stressed cells more irregular. Eyespot elongate, at the right-hand rim of the sulcus. Cells usually 20–28 µm long, 20–24 µm wide. Cell division in the immotile stage but details unknown. Cysts with paracingulum and two opposite horns, the wall also with hyaline thickenings.
Ecology: in mesotrophic-eutrophic lakes and ponds in Denmark and in Canton Zürich and Luzern, Switzerland. Spring-summer.
Geographical distribution: Denmark (Nygaard); Switzerland (Christen).

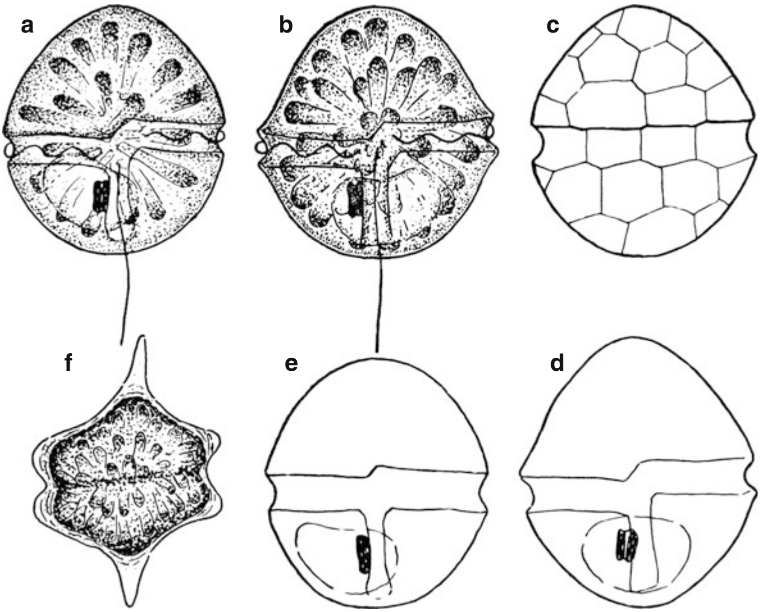

Fig. 330 *Tovellia nygaardii* Moestrup, K. Lindberg & Daugbjerg (after Christen 1958a). **a**, **b** ventral views, showing radial arrangement of chloroplasts; **c** dorsal view, showing amphiesmal vesicles; **d**, **e** variations in cell outline, with position of eyespot and nucleus indicated; **f** cyst

8. *Tovellia paldangensis* Zhun Li, M. S. Han & H. H. Shin *in* Li *et al.* 2015, p. 69, figs 1–24 (**Fig. 331**)

Cells ovoid or nearly spherical, slightly dorsoventrally compressed. Epicone slightly longer than hypocone, both epi- and hypocone somewhat conical. Amphiesmal plates in 3–4 latitudinal rows on the epicone, 1 in the cingulum and 2–3 on the hypocone. With distinct edge in the epicone-cingulum boundary. A ring of knobs usually mark the posterior edge of the cingulum, absent in some cells. Cingulum ends displaced *ca.* one cingulum width. A nearly straight ALP extends anteriorly from the ventral to the dorsal side of the cell, the length varying between 0.5 and 2.9 µm. It comprises 3–4 very narrow plates with a row of pores, lined on each side by 4–5 elongate plates. Antapical plate usually hexagonal. Numerous small ovoid greenish-yellow chloroplasts along the cell periphery. Nucleus fills most of the hypocone. A prominent red body on each side of the cingulum. Cells positively phototactic. Cells bright green in color, 20–27 µm long, 18–23 µm wide and 17–21 µm thick. Cysts 25–31 µm long and 20–23 µm wide, of yellowish color, with shallow paracingulum and ornamented by numerous short, solid spines.

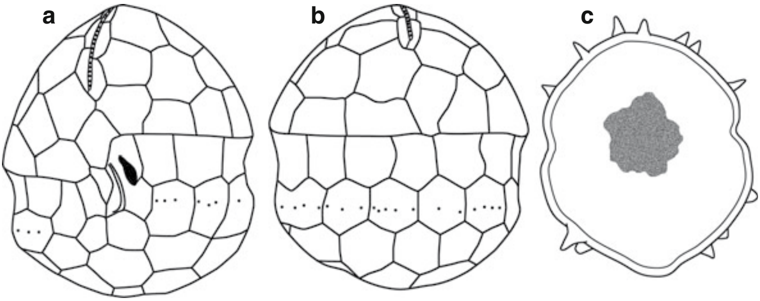

Fig. 331 *Tovellia paldangensis* Zhun Li, M. S. Han & H. H. Shin (original drawings, based on information from LM and SEM images in Li *et al.* 2015). **a**, **b** ventral and dorsal views with ventral ridge and transverse flagellar pore near the middle of the cell in **a** and a row of knobs along the posterior margin of the cingulum (not visible in all cells); **c** cyst with red body

SEM: Li *et al*. (2015).
DNA data: Li *et al.* (2015).
Ecology: known from a dam lake in Korea.
Geographical distribution: Paldang Dam Lake, Korea.

9. *Tovellia sanguinea* Moestrup, Gert Hansen, Daugbjerg, Flaim & d'Andrea 2006, p. 50, figs 2–37 (**Fig. 332**)

Taxonomic synonym: *Glenodinium sanguineum* Marchesoni 1941, p. 17, *nom. illeg.* (non *Glenodinium sanguineum* (H. J. Carter) Diesing 1866, p. 391)

Epicone and hypocone more or less conical, almost equal in size. Cells covered with amphiesmal plates in *ca.* 8 latitudinal series, *ca.* 5 on the epicone, 1 in the cingulum and 2 on the hypocone. Antapical amphiesmal plate usually hexagonal, sometimes protruding slightly from the cell. Cingulum descending, displaced *ca.* one cingulum width. Cells usually bright red due to the presence of numerous red-pigmented bodies. The pigments have been shown to be astaxanthin esters (Frassanito *et al.* 2006). Chloroplasts greenish-yellow, radiating from the central part of the cell. Central part of each chloroplast with pyrenoid. Nucleus posterior. A prominent eyespot located next to the sulcus. Cells on average 24 µm long and 19 µm wide. Cysts bright red, with bipolar horns and a central constriction (paracingulum), sometimes with knobs along the paracingulum. Planozygotes with two longitudinal flagella observed in Swiss material (Gert Hansen, pers. comm.).
SEM: Moestrup *et al.* (2006).
TEM: Moestrup *et al.* (2006).
DNA data: Moestrup *et al.* (2006).
Ecology: known from 3 oligotrophic-mesotrophic lakes in the Italian Alps, and from Lake Seealpsee, Switzerland, at temperatures below 15 ˚C. Lake Tovel was famous for blooms of *T. sanguinea* during the summer, which gave the lake wa-

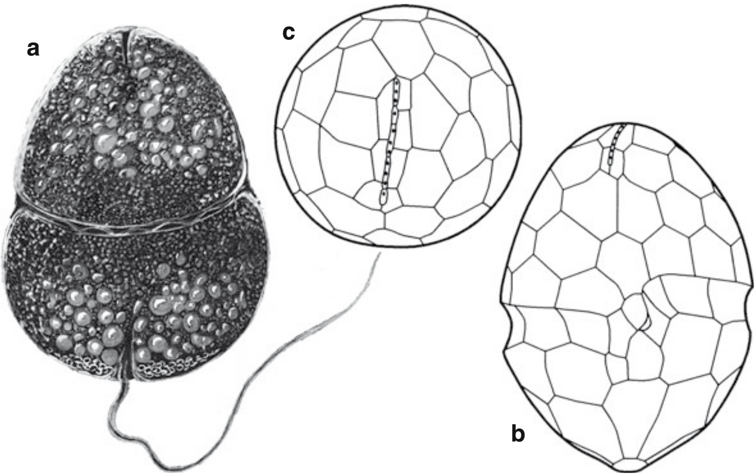

Fig. 332 *Tovellia sanguinea* Moestrup, Gert Hansen, Daugbjerg, Flaim & d'Andrea (**a** after Baldi 1938; **b**, **c** after Moestrup *et al.* 2006). **a** grayscale rendering of aquarelle of live cell (the numerous globules originally painted red); **b**, **c** ventral and apical views, showing the arrangement of amphiesmal vesicles

ter a striking, tomato-red color. The color phenomenon disappeared after 1964. Historical data indicate that the color first appeared in 1845, when cattle was introduced in the area. The cattle was removed in 1964. A strong red color occurred, for the first time, in Lake Seealpsee, Canton Appenzell, Switzerland, in July and August 2009, caused by the same species (Preisig & Moestrup, unpubl.)
Geographical distribution: known only from the 3 lakes in the Italian Alps and the Swiss mountain lake.

10. *Tovellia stoschii* (Shyam & Sarma) Moestrup, K. Lindberg & Daugbjerg *in* Lindberg *et al.* 2005, p. 430 (**Fig. 333**)

Basionym: *Woloszynskia stoschii* Shyam & Sarma 1976, p. 206, figs 1–9, 16–20

Cells somewhat ovoid or conical, slightly flattened dorsoventrally. Epicone conical, hypocone rounded, slightly larger than epicone. Cells covered with amphiesmal plates in *ca.* 17 latitudinal rows, (7–)8 on the epicone, 2 in the cingulum and 6–7 on the hypocone. Central antapical plate hexagonal, with small knobs. Cingulum descending, very slightly displaced. Sulcus extends very slightly onto the epicone; posteriorly it proceeds along *ca.* half the length of the hypocone. Nucleus more or less triangular, located centrally towards the epicone. Chloroplasts numerous, parietal, elongate to ellipsoid, yellowish-brown. Eyespot prominent, elongate quadrangular, located in the anterior part of the sulcus. Longitudinal flagellum *ca.* 1.5× the cell length. Cell 30–37 μm long and 28–35 μm wide. Propagation by formation of 2–8 zoospores. Cysts not described.

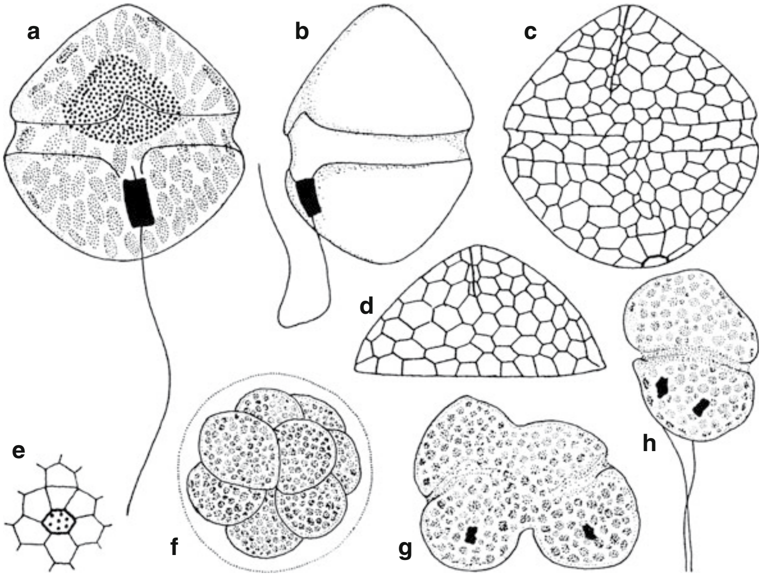

Fig. 333 *Tovellia stoschii* (Shyam & Sarma) Moestrup, K. Lindberg & Daugbjerg (after Shyam & Sarma 1976). **a** ventral view, showing eyespot, chloroplasts and nucleus; **b** outline of cell viewed from the ventral-left side; **c** ventral view, showing the arrangement of amphiesmal vesicles; **d** amphiesmal vesicles on the epicone in dorsal view; **e** detail of the antapical amphiesmal vesicles; **f** formation of zoospores; **g** fusion of gametes; **h** planozygote

Ecology: pond in Company Garden, Varanasi, India.
Geographical distribution: India (Shyam & Sarma).

Note: this species is closely related to *T. coronata* and differs mainly in the more numerous plates. A red color has not been reported in *T. stoschii*.

Genus 5. *Woloszynskia* R. H. Thompson 1951, p. 286

Type species: *Woloszynskia reticulata* R. H. Thompson 1951 (see Loeblich & Loeblich 1966)

Cells covered by many amphiesmal plates, of which those on the epicone are thin, smooth, whereas those on the hypocone are thicker, with distinct raised rims, giving the hypocone a honeycomb appearance. Cysts spherical or slightly rhomboid, covered by amphiesmal plates. The plates remain attached along one margin, thereby standing at right angles to the periphery of the cell. This gives the cyst a spiny appearance. Monotypic.

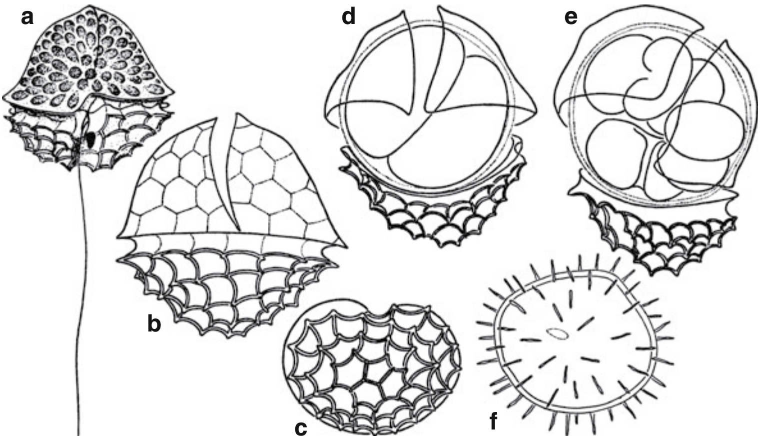

Fig. 334 *Woloszynskia reticulata* R. H. Thompson (after Thompson 1951). **a** ventral view of swimming cell; **b** dorsal view with amphiesma split open on the epicone; **c** antapical view; **d**, **e** stages in cell division (zoospore production); **f** cyst surrounded by old amphiesma

1. *Woloszynskia reticulata* R. H. Thompson 1951, p. 288, figs 15–20 (**Fig. 334**)

Cells rhomboid-ovoid in ventral view, dorsoventrally flattened. Epi- and hypocone of approximately the same size. Epicone bell-shaped or conical, hypocone hemispherical. Cingulum descending, the ends displaced *ca.* one cingular width. Amphiesma on the epicone delicate, smooth, with a ridge (carina) over the apex, extending from the ventral to the dorsal margin of the cingulum. This almost certainly represents an ALP. Splitting of the amphiesma occurs along this carina as well as along the cingulum. Amphiesmal plates on the epicone in 4 or 5 series. Amphiesma of the hypocone composed of four series of smooth, thick, concave plates. The typical arrangement of plates has been identified as 19(–20) postcingular, 14 postintercalary, 9 antapical intercalary and (3–)4 antapical plates, but some variation occurs. Chloroplasts yellowish-brown. Obovate or V-shaped eyespot in the sulcus. Longitudinal flagellum 1–1.5× cell length. Cell length 25–52 µm, width 21–46 µm. The protoplast may escape from the amphiesma through the split along the carina and cingulum and form a thin wall. Alternatively, it may form the wall while still within the amphiesma. The cytoplasm then divides into 2–4 zoospores, which escape by dissolution of the thin wall.
SEM: Pfiester *et al.* (1980), Carty (2003; 2014).
Ecology: in ponds, oxbows and small lakes, Kansas, June–August 1949–1950; in Crystal Lake, Norman, Oklahoma, Aug.-Sept. 1978, bloom-forming.
Geographical distribution: USA, KS (Thompson), OK (Pfiester *et al.*), FL, OH, TX (Carty 2014). Reported from Ukraine in estuaries and other water bodies near the river Danube. We have not seen documentation for this unexpected report. The Ukrainian material considered to be euryhaline.

Order 10. PHYTODINIALES A. R. Loeblich 1970, p. 905

As presented here the order contains an assemblage of species for which an immotile stage is predominant. Phylogenetic studies are needed for most of these taxa, which may well reveal that some species described below belong in other dinoflagellate orders.

Family 1. Phytodiniaceae G. A. Klebs 1912, p. 404, 443

Vegetative cells coccoid, non-flagellated. Flagella present only in reproductive stages. Many species reproduce by forming 2–4 zoospores, which germinate rapidly into new coccoid cells. Some taxa, in which reproduction is unknown, may turn out to be resting cysts of other dinoflagellates. Pascher (1914) described – without illustrations – that in *Hypnodinium* small gymnodinioid gametes were formed within the cells. They fused and the zygote grew to the size of the vegetative cells. The contents of the zygote divided into four cells, indicating that meiosis took place. Each cell was at first naked, with furrow(s), but subsequently formed a cell wall and grew into normal vegetative cells. If this can be confirmed in other genera, the life cycle comprises an asexual and a sexual cycle, the vegetative cell being haploid. More recently, in *Cystodinium bataviense*, Timpano & Pfiester (1985a) reported fusion of zoospore-like gametes, resulting in the formation of thick-walled cysts. Their fate was apparently not followed.
Very few genera and species have been examined in detail and the concepts of genera and species are likely to change.
Establishment of unialgal cultures in the laboratory has been successful in a few cases but most reports rely on observations of material in nature. Very complex life cycles have been suggested in some genera, involving both various types of heterotrophic protozoa and autotrophic stages (Pfiester & Popovský 1979, Popovský & Pfiester 1982), but none of these were based on culture studies.
Many species of the Phytodiniaceae are attached to filamentous algae, detritus, etc. Unattached species often seem to be tychoplanktonic, and are rarely observed in plankton samples unless the samples are taken near vegetation of macrophytes or filamentous algae. A few species appear to be more or less parasitic on filamentous algae, some lacking chloroplasts, and the sole member of the genus *Haidadinium* is parasitic on fish. The ecology of the species is generally very poorly known.

Key to the genera of Phytodiniaceae:

1a Cells attached 2
1b Cells not attached 10
2a Cells attached to or embedded in the surface of fish ...... 5. *Haidadinium* p.p.
2b Cells attached to algal filaments, detritus, etc., but not to fish 3
3a Cells attached by a stalk 6
3b Cells attached by one of the long sides, but stalk absent 4

4a Cells brick-like, cell ends not rounded .... 3. *Dinastridium* p.p.
4b Cell ends rounded 5
5a Cells more or less heteropolar .... 1. *Cystodinedria*
5b Cells isopolar .... 7. *Phytodinedria*
6a Cells tetrahedral .... 10. *Tetradinium*
6b Cells spherical or elongate 7
7a Cells spherical or elongate, the stalk in the latter from one of the cell poles ... 8
7b Cells elongate, stalk attached to the middle of one of the long sides ....
.... 4. *Dinococcus*
8a Both ends of the cell with extensions, one extension may serve as a stalk .....
.... 2. *Cystodinium* p.p.
8b Distinct stalk from one end, the other stalk-less 9
9a Stalk short, with cytoplasmic contents .... 5. *Haidadinium* p.p.
9b Stalk shorter or longer and always without cytoplasmic contents ....
.... 9. *Stylodinium*
10a Cells with short spines .... 3. *Dinastridium* p.p.
10b Cells without spines 11
11a Cells spherical or ellipsoidal 12
11b Cells bipolar, ends pointed or (rarely) rounded .... 2. *Cystodinium* p.p.
12a Dividing cells with cingulum .... 6. *Hypnodinium*
12b Cells always lack cingulum .... 8. *Phytodinium*

Genus 1. *Cystodinedria* Pascher 1944a, p. 378, 380

Type species: *Cystodinedria brunnea* Pascher 1944 (see Loeblich Jr. & Loeblich III 1966)

Cells usually more or less bean- or kidney-shaped, the flat or concave ventral side attached to filamentous algae, macrophyte leaves, *Lemna* roots, etc. The two ends of the cell unequal (cells heteropolar), one end thicker and rounded, the other more narrow. Cells without furrows. Chloroplasts band-shaped, brown. Pyrenoids present in some species. Propagation by division of the cytoplasm into 2–4 cells, which are released as gymnodinioid zoospores or as wall-covered autospores or aplanospores.

Key to species of *Cystodinedria*:
1a Broad end of the cell obliquely obtuse .... 4. *C. obtusata*
1b Broad end of the cell rounded 2
2a Chloroplasts radially arranged 3
2b Chloroplasts parietal .... 1. *C. brunnea*
3a Cells 17–24 µm long .... 2. *C. inermis*
3b Cells 42–88 µm long .... 3. *C. maxima*

1. *Cystodinedria brunnea* Pascher 1944a, p. 384, text-fig. 7 (**Fig. 335**)

Cells bean-shaped or somewhat kidney-shaped. With very thin attachment organelle, extending in the longitudinal direction of the cell and up to 13 µm long. Chloroplasts irregularly band-shaped, parietal, dark brown. Reproduction by formation of 2 zoospores with V-shaped eyespot. Cell length up to 30 µm, width up to 20 µm.

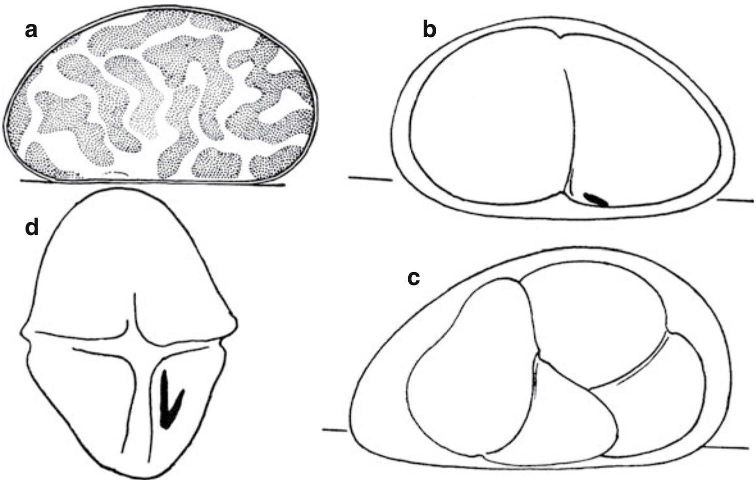

Fig. 335 *Cystodinedria brunnea* Pascher (after Pascher 1944a). **a** vegetative cell with contents; **b** cell contents before division, with furrows and eyespot; **c** formation of zoospores; **d** zoospore

Ecology: attached to *Oedogonium*, *Utricularia* and roots of *Lemna*.
Geographical distribution: pool in a sandpit near Prague, Czech Republic (Pascher). Lake in New Zealand (Thompson).

2. *Cystodinedria inermis* (Geitler) Pascher 1944a, p. 381 (**Fig. 336**)

Basionym: *Raciborskia inermis* Geitler 1943, p. 173, figs 2e–m, 3d–m, 4a–e
Nomenclatural synonym: *Dinococcus inermis* (Geitler) Fott 1960, p. 150
Taxonomic synonym: *Cystodinium brevipes* Geitler 1928b, *pro parte excl. typo*, p. 68, 81, text-figs 1b, 1c, 2, 3, pl. 7, fig. 2

Cells similar to those of *C. brunnea* but chloroplast arrangement stellate, with central pyrenoid and peripheral net. Eyespot present but furrows missing. Reproduction by two (rarely 1) zoospores or two autospores with furrows. Reproduction by autospores may result in 2- or 4-celled colonies. Cells (17–)19–22(–24) µm long and 11–14 µm wide.
Ecology: Attached to *Nitella*, *Oedogonium*, *Spirogyra* and *Rhizoclonium*. A characteristic of this species is the formation, at least on *Spirogyra*, of more or less structured ingrowths into the cytoplasm of the filament cells.
Geographical distribution: Austria (Geitler).

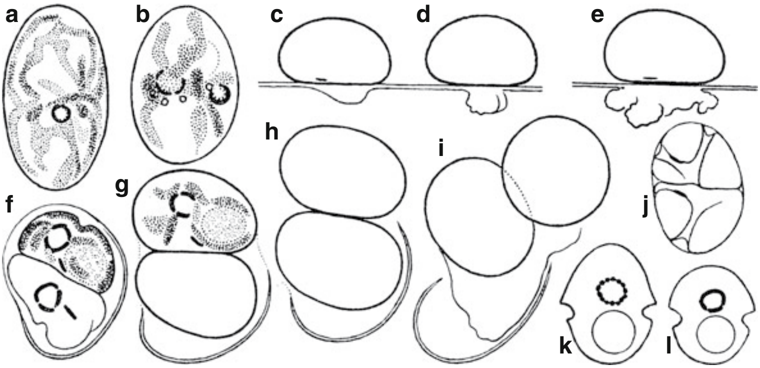

Fig. 336 *Cystodinedria inermis* (Geitler) Pascher (after Geitler 1943). **a**, **b** vegetative cells with contents; **c**–**e** outlines of cells on *Spirogyra grevilleana* (in **c** and **e** the eye-spot is visible); **f**–**i** formation of autospores, **g** and **h**, 3 and 10 min after **f** respectively; **j** formation of zoospores; **k**, **l** zoospores

3. *Cystodinedria maxima* Popovský 1961, p. 295, text-fig. 1, pl. XIX, figs 1–5 (**Fig. 337**)

Cells kidney-shaped and more or less asymmetric, attached to algal filaments with the central part of the slightly concave or straight ventral side. Cells with band-shaped, radially arranged chloroplast extending from a central pyrenoid. Cell length 42–88 μm, width 34–62 μm. Propagation by formation of two zoospores. The epi- and hypocone of the same size, the epicone rounded, the hypocone cone-shaped. An eyespot seen on one occasion only. Length of the zoospore 37–56 μm, width 28–40 μm.
Ecology: in shallow concrete container, attached to *Oedogonium*.
Geographical distribution: Botanical Garden, Prague, Czech Republic (Popovský). USA, OH (Carty, as *C. inermis sensu lato*).

4. *Cystodinedria obtusata* Pascher 1944a, p. 382, text-fig. 6 (**Fig. 338**)

Cells broadly egg-shaped to plump bean-shaped, the narrow side rounded and usually more pointed than the broad side, which is obliquely obtuse. The side of attachment flattened. Pyrenoid large, central, strands of cytoplasm extending from the pyrenoid to the cell periphery. Chloroplasts light brown or yellow-brown, located in the cell periphery, disc-shaped to shortly band-shaped, rarely one of them located in a radial strand of cytoplasm. Large vacuoles located between the strands. Nucleus next to the pyrenoid. Red oil droplets often present. Propagation by formation of 2–4 gymnodinioid zoospores in which epi- and hypocone are of almost the same size. Epicone rounded semicircular when seen from the broad side, hypocone more triangular. The ends of the cingulum not displaced. Sulcus wide, extending onto the

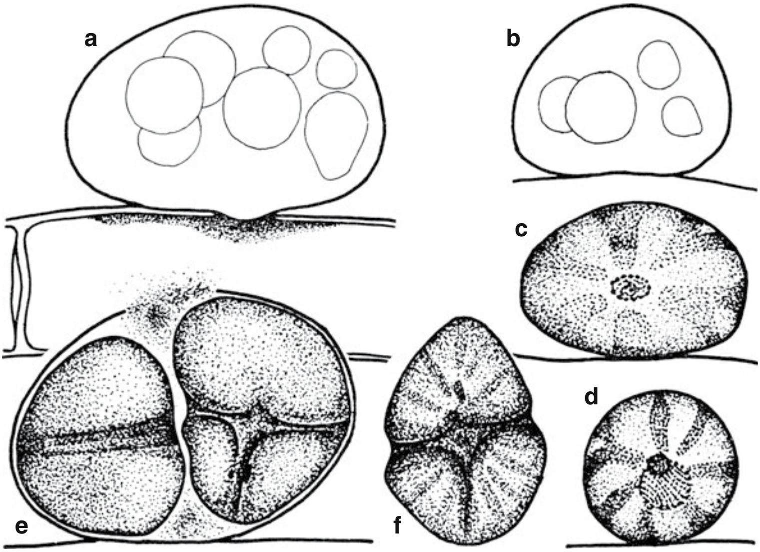

Fig. 337 *Cystodinedria maxima* Popovský (after Popovský 1961). **a**, **b** outlines of empty cells with large oil droplets; **c**, **d** optical sections of cells with band-shaped chloroplasts radiating from central pyrenoid (**d** young cell); **e** formation of zoospores; **f** zoospore

epicone. Eyespot elongate. Cells with very thick wall also seen (resting cells?). Cell length up to 30–38 µm, width 20–25 µm.
Ecology: oxbows and bogs, epiphytic on *Microspora pachyderma* and *Oedogonium*.
Geographical distribution: Austria (Pascher, Ettl).

Genus 2. *Cystodinium* G. A. Klebs 1912, p. 376, 441

Type species: *Cystodinium bataviense* G. A. Klebs 1912 (see Loeblich Jr. & Loeblich III 1966)

Cells elongate, unattached or only feebly so, in some species with a spine at each end. Chloroplasts band-shaped, occasionally absent. Cells typically reproduce by the formation of two zoospores which remain motile for a very short time before developing into the coccoid stage. Aplanospores are also known. Zoospores and aplanospores are released by gelatinization and dissolution of the cell wall. Klebs (1912) described zoospore germination in *C. bataviense*, the zoospore settling and increasing in length from 60 µm to 148 µm in 4 min. In some species, formation of a higher number (8–16) of 6–10-µm long cells has been observed, perhaps gametes. Fusion of zoospore-like cells has been reported in a single case, resulting in thick-walled cysts (Pfiester & Lynch 1980).

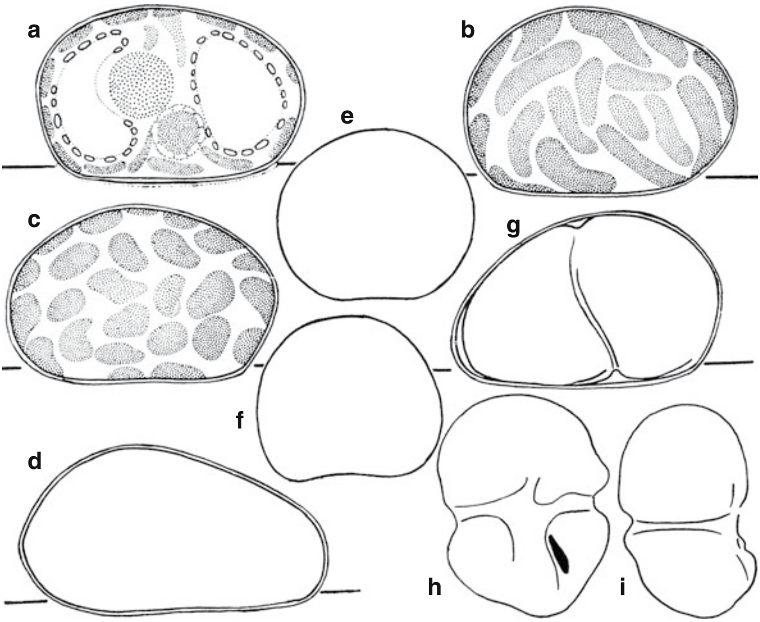

Fig. 338 *Cystodinedria obtusata* Pascher (after Pascher 1944a). **a**–**d** vegetative cells (**a** optical section, **d** outline); **e**, **f** cells seen from an end; **g** cell contents before division, usually with furrows and eyespot; **h**, **i** zoospore (**i** lateral view)

Note: Species of *Cystodinium* fall into several groups, which differ notably in the presence or absence of terminal horns. Species without horns resemble *Cystodinedria* and *Phytodinedria*, whose cells are attached to filamentous algae by one of the long sides. Molecular studies are needed to determine whether *Cystodinium* as presently circumscribed is monophyletic.

Key to species of *Cystodinium*:

1a Cell with terminal spines (sometimes on 1 end only) or with pointed ends ... 13
1b Cell without terminal spines, cell ends rounded 2
2a Cell distinctly heteropolar, one end more rounded than the other or pointed ... 5
2b Cell isopolar or very slightly heteropolar 3
3a Cell rotationally symmetrical 4
3b One of the long sides almost straight, the other convex .... 3. *C. closterium*
4a Cell ellipsoid, 18–20 µm long, 8 µm wide, chloroplasts pale blue-green .... 8. *C. dominii*
4b Cell slightly heteropolar, 33–42 µm long, 20–25 µm wide, chloroplasts yellowish-brown .... 4. *C. conchaeforme*
5a Cell colorless .... 12. *C. hyalinum*

5b Cell with yellow to brown chloroplasts 6
6a Cell ends blunt 7
6b Cell with short, terminal blunt horn, sharp point or process, or cell tapering .
.... 10
7a Cell 13–15 µm long .... 14. *C. minimum*
7b Cell 25 µm long or longer 8
8a Cell bean-shaped or slightly concave-convex 9
8b Cell approximately mussel-shaped .... 6. *C. dimorphe*, morph I
9a Chloroplasts extending from central pyrenoid .... 4. *C. conchaeforme*
9b Pyrenoid absent .... 17. *C. phaseolus*
10a Cell tapers gradually into a colorless process, cells straight or nearly so ....
.... 2. *C. acerosum*
10b Cell with a short, blunt terminal horn or a sharp point 11
11a Cell lemon-shaped, very shortly pointed at each end ....
.... 6. *C. dimorphe*, morph II
11b Cell more or less pointed 12
12a Cell terminates in a blunt short horn .... 13. *C. lunare*
12b Cell terminates in a sharp point .... 1. *C. bataviense*
13a Cell with distinct spine at one end, the other end rounded or attenuated ....
.... 19. *C. unicorne*
13b Cell with distinct spines at both ends 14
14a Terminal spines bent and directed towards each other, nearly touching ....
.... 10. *C. guttatum*
14b Terminal spines at right angles, diverging or more irregularly oriented 15
15a Cell nearly round, almost colorless .... 15. *C. pallidulum*
15b Cell ovoid or more elongate 16
16a Longitudinal spine with basal swelling .... 16. *C. papilionaceum*
16b No swelling on the longitudinal spine 17
17a Terminal spines long tapering extensions of the cell, often elegantly curved
.... 18
17b One or both spines short 19
18a Both spines long, one consistently *ca.* twice the length of the other (tropical species) .... 18. *C. sonfonense*
18b Spines variable, but one not consistently twice the length of the other ....
.... 5. *C. cornifax*
19a Cell lunate, one side convex, the other concave 20
19b Cell nearly ovoid, both sides convex .... 11. *C. heterorhamphos*
20a One cell end extended into a long, thin spine almost as long as the cell is wide, zoospores flattened like a coin .... 9. *C. grabenseei*
20b Both ends attenuating into short spines .... 7. *C. dirhamphos*

1. *Cystodinium bataviense* G. A. Klebs 1912, p. 337, 441, text-fig. 2 (**Fig. 339**)

Cells broadly lunate, with short, blunt, hyaline corners. Numerous small, parietal, brown, elliptic chloroplasts. Nucleus excentric. One or more red lipid bodies may be present. Propagation by formation of two, rarely three, gymnodinioid zoospores or aplanospores. Epi- and hypocone of the zoospore of the same size, nucleus in the cell middle. Cingulum descending, the ends displaced about one cingulum width.

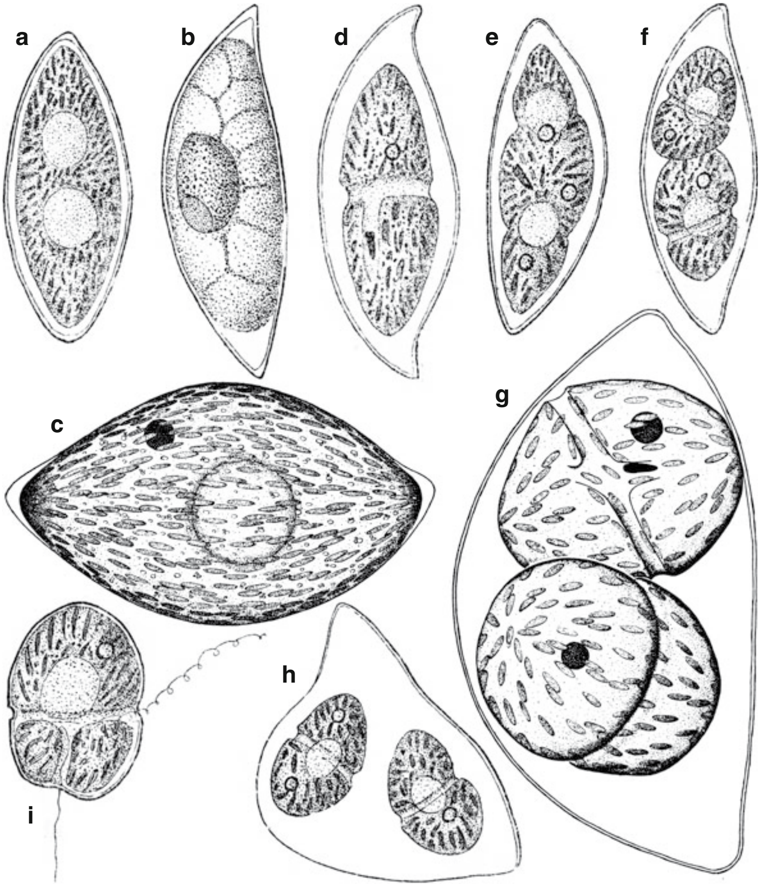

Fig. 339 *Cystodinium bataviense* G. A. Klebs (**a**, **b**, **d**–**f**, **h**, **i** after Klebs 1912; **c**, **g** after Thompson 1949). **a**–**c** vegetative cells; **d** cell with *Gymnodinium*-like protoplast; **e**, **f**, **g** formation of zoospores (**e** early division stage); **h** swelling of parental cell wall prior to release of zoospores; **i** zoospore

Distinct elongate eyespot present near the sulcus. Numerous chloroplasts. Coccoid cell 60–200 µm long and 36–62 µm wide, length of zoospore 44–60 µm, width 38–48 µm. Sexual reproduction by fusion of zoospore-like cells also observed, resulting in thick-walled cyst (Pfiester & Lynch 1980).
SEM: Timpano & Pfiester (1985a).
TEM: Timpano & Pfiester (1985b).

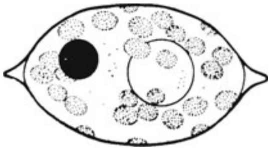

Fig. 340 *Cystodinium bataviense* var. *brasiliense* C. E. M. Bicudo & Skvortsov (after Bicudo & Skvortsov 1968)

Ecology: in plankton or in floating masses of surface scum in swamps and ponds with extensive macrophyte vegetation.
Geographical distribution: Indonesia (Klebs). USA, MD, KS, OH, OK (Thompson; Carty; Timpano & Pfiester).

var. *brasiliense* C. E. M. Bicudo & Skvortsov 1968, p. 33, fig. 2 (**Fig. 340**)
Cells broadly elliptic with each pole prolonged into short stout spine. With many disc-shaped chloroplasts. Cells 25–30 μm long, 12–15 μm wide.
Ecology: in temporary pool in São Paulo, Brazil.
Geographical distribution: Brazil (Bicudo & Skvortsov).

2. *Cystodinium acerosum* R. H. Thompson in Thompson & Meyer 1984, p. 88, fig. 3 (**Fig. 341**)

Cells narrowly fusiform, straight or slightly curved. The wall at each end extended into a colorless process. Cell length including processes 67–72 μm, 15–18 μm thick. Chloroplasts numerous, fusiform, parietal. Reproduction unknown.
Ecology: boggy pond.
Geographical distribution: USA, MD (Thompson).

3. *Cystodinium closterium* Pascher 1927, p. 39, fig. 35 (**Fig. 342**)

Cells semi-lunar, one side almost straight, the other side convex. No terminal horns. Eyespot seen. The cell content divides into two *Katodinium*-like swarmers (probably zoospores), each with an eyespot in the hypocone. Cell size unknown. This species was illustrated by Stein (1883, pl. XII, figs 7, 8), who identified it as the cyst of *Peridinium umbonatum*.
Ecology: bogs.
Geographical distribution: Czech Republic (Pascher).

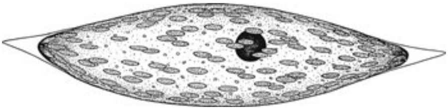

Fig. 341 *Cystodinium acerosum* R. H. Thompson (after Thompson & Meyer 1984)

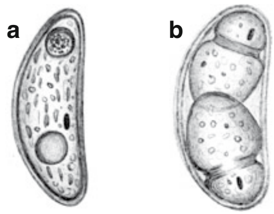

Fig. 342 *Cystodinium closterium* Pascher (after Stein 1883). **a** vegetative cell; **b** formation of zoospores

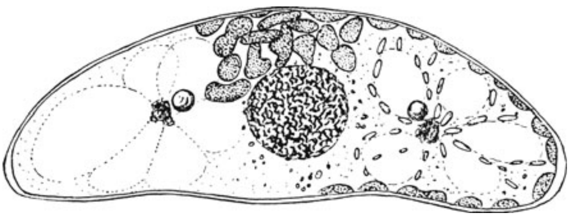

Fig. 343 *Cystodinium closterium* var. *crassum* Bourrelly (after Bourrelly 1961). The upper part shows the chloroplasts in surface view, the rest is an optical section

var. *crassum* Bourrelly 1961, p. 297, 353, pl. 3, fig. 17 ("*crassa*") (**Fig. 343**)
Cells convex on one side, the other side almost straight with a slight central bulge. Ends rounded with slight thickening of the wall. Nucleus central, on each side with a pyrenoid (?) from which extend a number of vacuoles and starch grains. A lipid globule is located next to each pyrenoid. Numerous parietal, disc-shaped chloroplasts. Cells 85–90 µm long, 30–38 µm wide.
Ecology: in a marshy forest in Ivory Coast.
Geographical distribution: Ivory Coast (Bourrelly).

4. *Cystodinium conchaeforme* Baumeister 1963, p. 545, 547, fig. 6 (**Fig. 344**)

Cells ellipsoid, slightly asymmetrical laterally. Many golden-brown chloroplasts radiating from centrally located compound pyrenoid. Nucleus near one end or lateral. Cells may be highly vacuolated, and sometimes contain red lipid droplets. Cells 32–42 µm long and 16–25 µm wide. Propagation by formation of two zoospores within the cell, each zoospore with centrally located compound pyrenoid from which extend a number of elongate chloroplasts, and a very small eyespot. Nucleus in the posterior end.
Ecology: in peat bog attached to *Sphagnum* leaves, Bavaria, in Lunzer Obersee, Austria. Grown in culture at 15ºC, in DY IV and L16.
Geographical distribution: Austria (Moestrup & Daugbjerg); Germany (Baumeister).

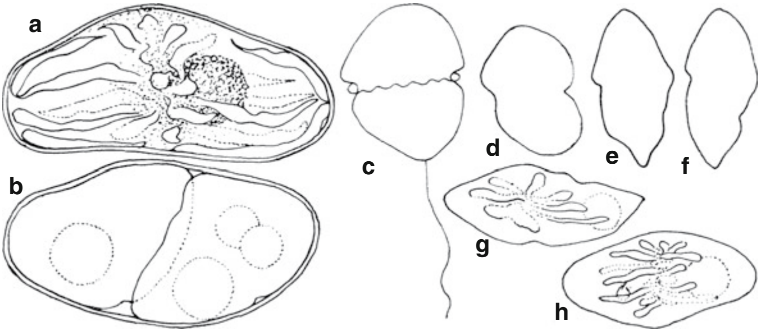

Fig. 344 *Cystodinium conchaeforme* Baumeister (after Baumeister 1963). **a** vegetative cell showing chloroplasts radiating from a central pyrenoid; **b** formation of zoospores; **c** zoospore; **d**–**g** transformation of a zoospore into a vegetative cell; **h** young vegetative cell

5. *Cystodinium cornifax* (A. J. Schilling) G. A. Klebs 1912, p. 384, 442 (**Fig. 345**)

Basionym: *Glenodinium cornifax* A. J. Schilling 1891a, p. 285, pl. VIII, fig. 1, pl. X, figs 1–5, 18
Nomenclatural synonyms: *Gymnodinium cornifax* (A. J. Schilling) Er. Lindemann 1928b, p. 43 ≡ *Gymnodinium fuscum* var. *cornifax* (A. J. Schilling) Playfair 1913, p. 545
Taxonomic synonyms: *Closterium cancer* Playfair 1907, p. 167, pl. II, fig. 16; *Cystodinium steinii* G. A. Klebs 1912, p. 381, 442, text-fig. 3, pl. X, fig. 2 ≡ *Gymnodinium steinii* (G. A. Klebs) Er. Lindemann 1928b, p. 43; *Gymnodinium bisaetosum* Er. Lindemann 1928c, p. 291, fig. 4 ≡ *Cystodinium bisaetosum* (Er. Lindemann) Huber-Pestalozzi 1950, p. 292; *Cystodinium iners* Geitler 1928a, p. 5, figs 2, 3 ≡ *Gymnocystodinium iners* (Geitler) Baumeister 1958a, p. 246; *Gymnodinium novaculosum* Baumeister 1939b, p. 401, fig. 3a–c ≡ *Cystodinium novaculosum* (Baumeister) Huber-Pestalozzi 1950, p. 294; *Cystodinium steinii* var. *dimidiominus* Baumeister 1958b, p. 261, figs 1–3 ("*dimidio-minor*"); *Gymnocystodinium gessneri* Baumeister 1957a, p. 10, 19, Abb. 3, figs 1–10, 12; *Cystodinium schilleri* Baumeister 1958a, p. 252, 256, figs 4–6

Cells lunate with thin extension from each end. Length and orientation of the extensions very variable. Commonly one extension continues at right angles to the cell, while the other bends back distally. Length of coccoid stage *ca.* 50–130 µm, including extensions, width 17–41 µm. The cytoplasmic part of the cell usually *ca.* 30–65 µm long. Chloroplasts usually numerous, oblong, parietal, 2.5–4 µm long and *ca.* 1 µm wide. Nucleus located at one end of the cell. Propagation by formation of two zoospores, each 25–44 µm long, 21–35 µm wide. Epi- and hypocone of almost the same size, hypocone somewhat cone-shaped, epicone more rounded. With eyespot near the sulcus. The two ends of the cingulum are barely displaced, the sulcus appears to continue onto the epicone. Nucleus in the posterior end or

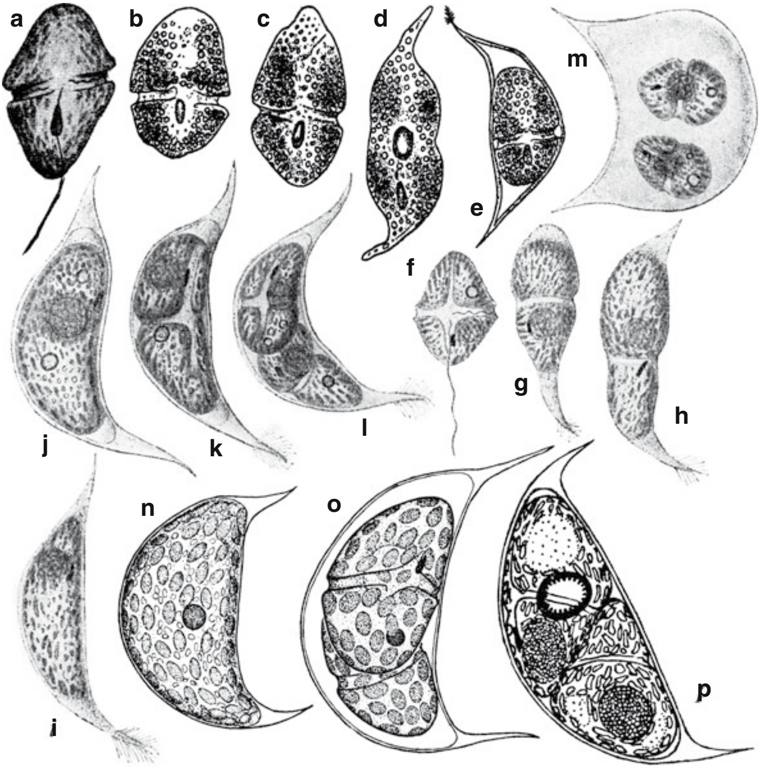

Fig. 345 *Cystodinium cornifax* (A. J. Schilling) G. A. Klebs (**a**–**e** after Schilling 1913; **f**–**m** after Klebs 1912; **n**, **o** after Thompson 1949; **p** after Geitler 1928). **a** motile stage (zoospore); **b**–**e**, **f**–**i** transformation from zoospore (**b**, **f**) to vegetative stage (**e**, **i**); **j**–**m**, **n**–**p** formation of zoospores starting from vegetative cell (**j**, **n** vegetative cells; **k** cell with *Gymnodinium*-like protoplast; **l**, **o**, **p** cell contents divided into two zoospores; **m** swollen cell wall prior to zoospore release)

near the center of the cell. The eyespot is retained for some time after the zoospore has transformed into the coccoid stage.

Ecology: bogs, ponds, attached by one of the terminal spines to other algae, detritus, etc. Höll (1928) and Nygaard (1977, as *C. iners*) in central and northern Europe found this species in small slightly acid ponds (Höll: organotrophic, Nygaard: humic), pH 5.8–6.6; Thompson (1949, as *C. iners*) gives the localities in the USA as peaty, with pH 6.0.

Geographical distribution: Albania, Montenegro (Rakocevic-Nedovic & Rakaj); Austria (Geitler); Denmark (Nygaard, Ettl); England (Jane; Lewis & Dodge); Germany (*e. g.*, Klebs, Höll, Baumeister); Portugal (Rodrigues); Spain (Álvarez Co-

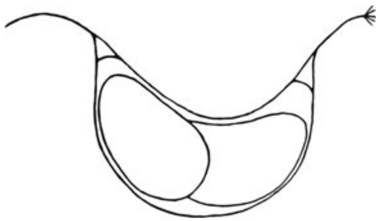

Fig. 346 *Cystodinium cornifax* var. *tenuirostre* (Wołoszyńska) Moestrup & Calado (after Wołoszyńska 1919a)

belas); Sweden (Moestrup, unpubl.); Switzerland (Ettl). USA, KS, MA, MD, MN, NC, WI (Thompson; Prescott; Whitford & Schumacher; Meyer & Brook). Brazil (Borics *et al.*). Japan (Akiyama – nice drawing of zoospore formation); Turkey (Atici *et al.*). New Zealand (Thompson; Cassie).

Note 1: a few small specimens were described by Baumeister (1958b) as a separate variety, var. *dimidio-minor* Baumeister. Whether this is justified must await observations on more plentiful material, as the shape of the cell has resulted in some confusion regarding how to measure the length of the cell.

Note 2: Baumeister claimed having observed division of the motile cell, which is therefore not a zoospore. This caused him to consider his material as belonging to the separate genus *Gymnocystodinium* Baumeister 1957a, *nom. illeg*. These findings need to be confirmed.

var. *tenuirostre* (Wołoszyńska) Moestrup & Calado *comb. nov.* (**Fig. 346**)
Basionym: *Cystodinium steinii* f. *tenuirostre* Wołoszyńska 1919a, *Rozpr. Wydz. Mat.-Przyr. Akad. Umiejetn., Dział B, Nauki Biol.* **18**, p. 319, pl. 13, fig. 20; 1919b, *Bull. Int. Acad. Sci. Cracovie, Cl. Sci. Math., Sér. B, Sci. Nat.* **1918,** p. 198, pl. 14, fig. 20 ("*tenuirostris*")

With very long and thin terminal spines.
Ecology: small lake in Tatra; squeezed from *Sphagnum* and *Drepanocladus* in small pools in Czech Republic.
Geographical distribution: Poland (Wołoszyńska); Czech Republic (Popovský).

6. *Cystodinium dimorphe* (Baumeister) Huber-Pestalozzi 1950, p. 298 (**Fig. 347**)

Basionym: *Gymnodinium dimorphe* Baumeister 1938b, p. 462, figs 1, 2
Nomenclatural synonym: *Gymnocystodinium dimorphe* (Baumeister) Baumeister 1957b, p. 21

Two types (morphs) of coccoid cells:
Morph 1. Mussel-shaped (like the mussel *Ensis*), 49–53 µm long and 24–27 µm wide. With small projection at each end of the cell.
Morph 2. Lemon-shaped, 34–37 µm long and 22–25 µm wide. Slightly pointed at each end.

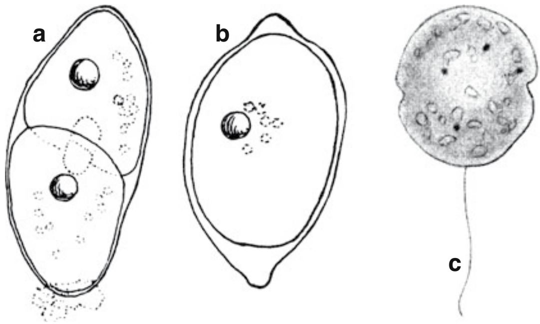

Fig. 347 *Cystodinium dimorphe* (Baumeister) Huber-Pestalozzi (**a**, **b** after Baumeister 1957b; **c** after Baumeister 1938). **a** mussel-shaped morph; **b** lemon-shaped morph; **c** zoospore

The two morphs share a mainly colorless peripheral zone, and a greenish-yellow middle zone. Zoospores 22 μm long and 17 μm wide. Epi- and hypocone almost equal-sized, with very thin periplast. Nucleus in the epicone. Mussel-shaped type: cell contents divided into two autospores. No division was seen in the lemon-shaped cell type. Furrows or eyespots not seen in the coccoid cells.
Ecology: during winter in a peat bog.
Geographical distribution: Southern Germany (Baumeister).

Note 1: there is no proof that the two types of coccoid cells belong to the same species, nor is it certain that the zoospore described is part of this life cycle.

Note 2: the mussel-shaped cells can hardly be distinguished from *C. phaseolus*.

7. *Cystodinium dirhamphos* Baumeister 1957b, p. 35, 42, Abb. 4, fig. 1 (**Fig. 348**)

Cells moon-shaped, the concave side less curved than the convex side. Cells gradually narrowing into two horns, one horn straight, the other curved, beak-like. Cell contents dark-brown, often with darker central region, chloroplasts dark-brown. Cell also contains refractile grains. With very small comma-shaped eyespot near the concave side. Nucleus near the eyespot. Cell length 73–79 μm, width 26–30 μm.
Ecology: in nearly dried-out pond near Taubenbach, Bavaria.
Geographical distribution: Germany (Baumeister).

8. *Cystodinium dominii* Fott 1933, p. 166, pl. II (**Fig. 349**)

Cells ellipsoidal, rounded at the ends, symmetrical. Sometimes with slight central constriction. Eyespot present. With parietal, plate-like, pale blue-green chloroplasts. A single, large brown pyrenoid present (6 μm in diameter). Cells 18–20 μm long and 8 μm wide. Cell contents divide into two cells with furrows. Release of these cells not observed, propagation is apparently only by formation of autospores.
Ecology: found along the banks of the oligotrophic-mesotrophic Lake Ohrid in August 1933.

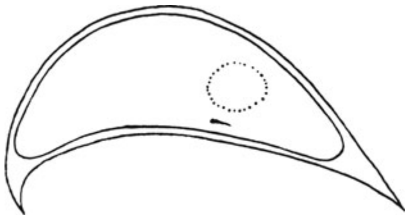

Fig. 348 *Cystodinium dirhamphos* Baumeister (after Baumeister 1957b)

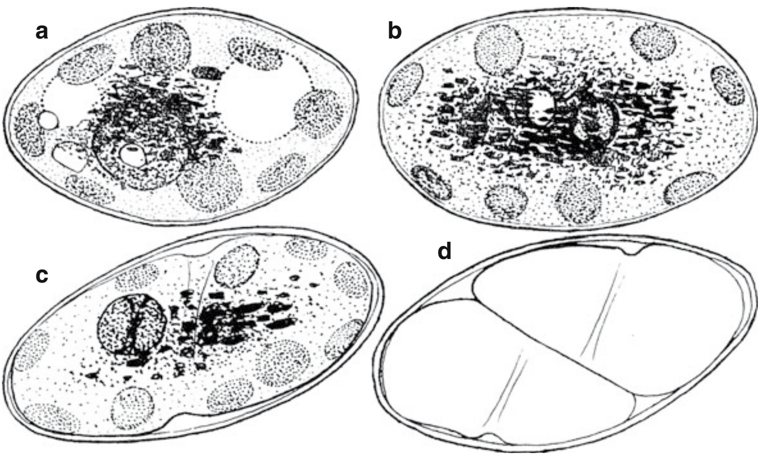

Fig. 349 *Cystodinium dominii* Fott (after Fott 1933). **a** vegetative cell with disc-shaped chloroplasts, large, dark pyrenoid, three starch grains, an eyespot on the upper-right side, two vacuoles and red oil droplets; **b** elliptical vegetative cell with larger quantity of red oil droplets; **c** cell contents with furrows, pyrenoid (on the left) apparently dividing; **d** formation of two autospores with furrows

Geographical distribution: Lake Ohrid, on the border between Macedonia and Albania (Fott).

Note: the blue-green chloroplasts are unique within the genus and deserve further examination.

9. *Cystodinium grabenseei* Baumeister 1957a, p. 7, 19, Abb. 2, fig. 9 (**Fig. 350**)

Cells resembling *C. cornifax* but one end (the posterior end) drawn out into a narrow, straight spine, the other (anterior) short, sickle-shaped, at right angles to the first. Length 50 µm, width 18 µm. Zoospores extremely flattened, dark-brown, both ends rounded, without eyespot.

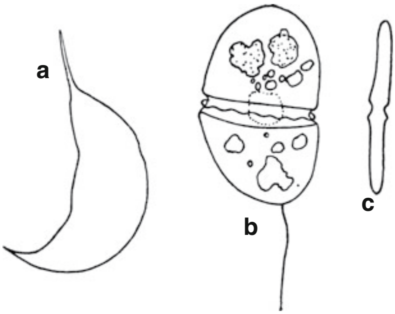

Fig. 350 *Cystodinium grabenseei* Baumeister (after Baumeister 1957a). **a** vegetative cell outline; **b**, **c** dorsal and lateral views of the flat zoospore

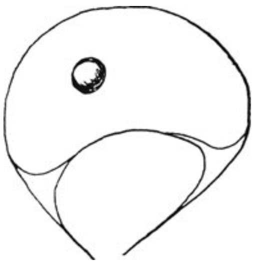

Fig. 351 *Cystodinium guttatum* Baumeister (after Baumeister 1957b)

Ecology: in peat bog.
Geographical distribution: Bavaria, Germany (Baumeister).

Note: in the coccoid stage, this species can hardly be distinguished from *C. cornifax*. However, the extremely flattened zoospore of *C. grabenseei* is unique and indicates a separate species.

10. *Cystodinium guttatum* Baumeister 1957b, p. 33, 41, Abb. 1, fig. 2 (**Fig. 351**)

Brown bean-shaped cells with terminal spines, each spine bent inwards, one slightly more than the other. The ends of the spines are almost touching. Cells 43 μm long and 41 μm wide. Reproduction unknown.
Ecology: only reported once, in a lime-containing pond.
Geographical distribution: Bavaria, Germany (Baumeister).

Note: whether this is a distinct species is somewhat uncertain.

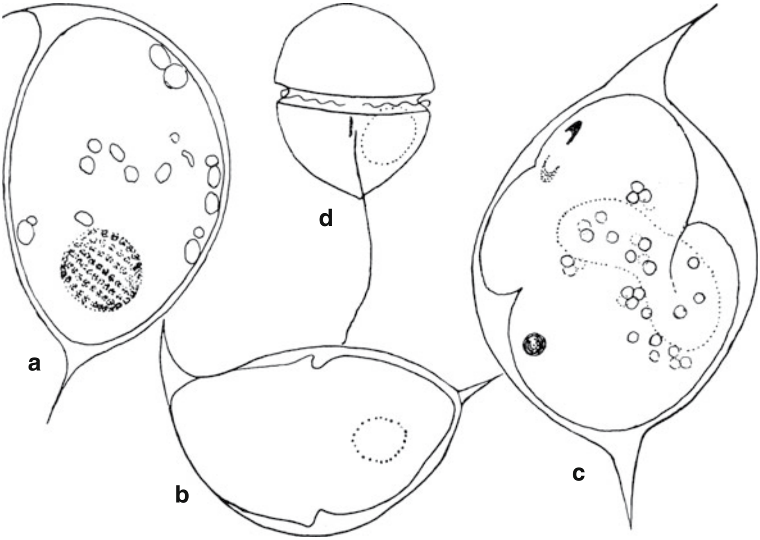

Fig. 352 *Cystodinium heterorhamphos* Baumeister (after Baumeister 1957b). **a** vegetative cell; **b** cell with *Gymnodinium*-like protoplast; **c** formation of zoospores; **d** zoospore

11. *Cystodinium heterorhamphos* Baumeister 1957b, 37, 42, Abb. 4, fig. 4, Abb. 5 (**Fig. 352**)

Cells with one side more strongly curved than the other. With two terminal spines, one (the anterior) curved like an eagle's beak, the other almost aligned with the cell. Cells 45–50 µm long and 28–29 µm wide. Zoospores spherical, 20 µm in diameter, epi- and hypocone of equal size, with eyespot, nucleus posterior. The zoospore was said by Baumeister (1957b) to resemble *Peridiniopsis berolinensis*. However, the drawing provided shows a cell with a rounded epicone and a pointed hypocone as in *C. cornifax*.
Ecology: in small waterbodies in Bavaria.
Geographical distribution: Germany (Baumeister).

Note: this taxon differs in the spherical shape of the zoospore and therefore possibly represents a distinct species. A conclusion on this question requires examination of additional material.

12. *Cystodinium hyalinum* Pascher 1944b, p. 397, text-fig. 1, pl. VI, fig. a (**Fig. 353**)

Cells colorless, without indication of chloroplasts. Cells plump or short bean-shaped, hardly longer than wide. Cells heteropolar, both ends rounded, one end broader than the other. Terminal spines missing. Ventral side most straight, rarely

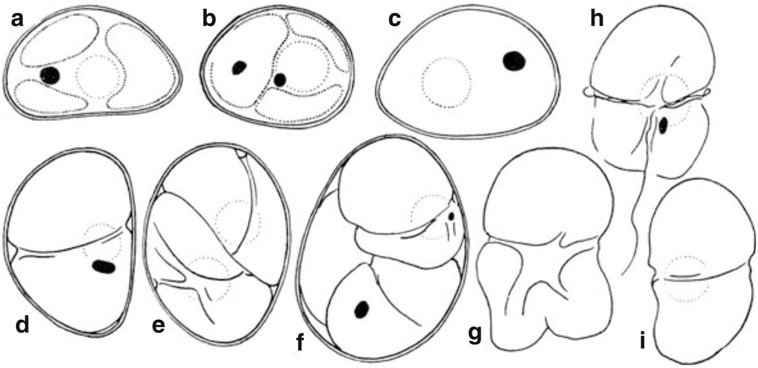

Fig. 353 *Cystodinium hyalinum* Pascher (after Pascher 1944b). **a**–**c** vegetative cells (**a**, **b** optical section); **d** cell protoplast before formation of zoospores, with furrows and eyespot; **e**, **f** formation of two (**e**) and four (**f**) zoospores; **g** zoospore with amoeboid movement; **h**, **i** zoospore (**i** lateral view)

slightly concave. Cell wall thick but apparently not layered. Red oil droplets nearly always present in the cell. Mature cells without furrows. Cells 17–22 µm long. Reproduction by division into two or four colorless zoospores, each with a pale, yellow, line-shaped eyespot. Zoospores have tendency to amoeboid movements. Other stages of the life cycle unknown.
Ecology: small pools.
Geographical distribution: Czech Republic: Franzensbad, Graben bei Natalienquelle, Soosgräben, in a small pool in Böhmerwald (Pascher).

Note 1: it seems unlikely that a purely heterotrophic species of *Cystodinium* exists. The presence of an eyespot is also an indication that a chloroplast may be present, at least in a reduced form. For the time being, however, we retain this very small taxon as a separate species.

Note 2: *Cystodinium achroum* Baumeister (1957b, p. 33, 42, Abb. 1, fig. 5), was described on the basis of a single cell. It was said to differ in being slightly smaller (14 µm long and 8.5 µm wide) and in having a red rather than a yellow eyespot. Its identity is obscure.

13. *Cystodinium lunare* Pascher 1927, p. 53, fig. 34 (**Fig. 354**)

Cells curved, spindle-shaped, slightly narrowed towards the ends, which bear a short horn. Furrows, eyespot and zoospores not seen. Cells 80–120 µm long. The cell content divides into 2 autospores with the same morphology as the parent cell.
Ecology: in peat bogs.
Geographical distribution: Southern Bohemia, Czech Republic (Pascher).

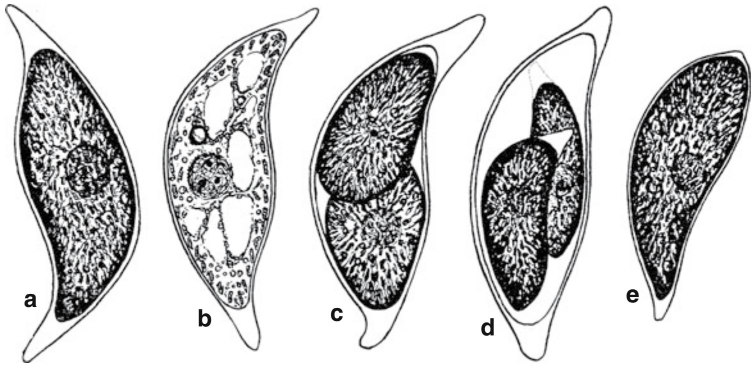

Fig. 354 *Cystodinium lunare* Pascher (after Pascher 1927). **a**, **b** vegetative cells (**b** optical section); **c**, **d** formation of autospores; **e** young vegetative cell

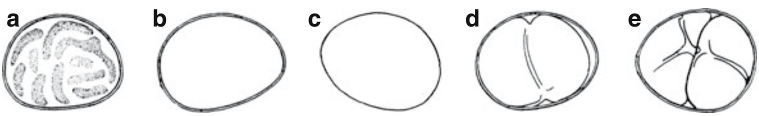

Fig. 355 *Cystodinium minimum* Pascher (after Pascher 1944b). **a**–**c** vegetative cells (**a** cell contents from a combination of focusing planes); **d**, **e** formation of zoospores

14. *Cystodinium minimum* Pascher 1944b, p. 399 (footnote), text-fig. 2, pl. VI, fig. b (**Fig. 355**)

Cells short kidney-shaped or bean-shaped, up to one quarter longer than wide, with an almost flat ventral side and a strongly convex dorsal side. Terminal spines absent. One end of the cell almost hemispherical, the other slightly narrowed. Furrows or eyespot not seen. With many dark-brown chloroplasts (apparently parietal). Cells 13(–15) μm long, 9–11 μm wide. Reproduction by formation of 2, more rarely 4, swarmers with furrows and eyespot, in which the hypocone is slightly larger than the epicone. Autospore formation by division into 2–4 cells within the mother cell wall, resulting in the formation of groups of 2–4 cells.
Ecology: bog species.
Geographical distribution: Franzensbad, Stobl, Böhmerwald, Czech Republic (Pascher).

15. *Cystodinium pallidulum* Baumeister 1957b, p. 32, 41, Abb. 1, fig. 1 (**Fig. 356**)

Cells with terminal horns. Dorsal side of the cell strongly convex, ventral side much less so. Both spines curved, almost at a right angle. The shorter spine used for attachment. Cell content hyaline. Eyespot seen. Cells 64 μm long and 36 μm wide.
Ecology: only reported once, in a lime-containing pond.
Geographical distribution: Bavaria, Germany (Baumeister).

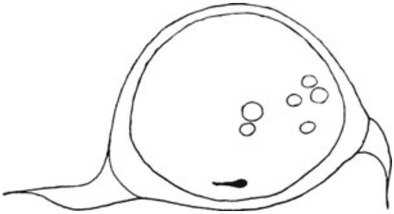

Fig. 356 *Cystodinium pallidulum* Baumeister (after Baumeister 1957b)

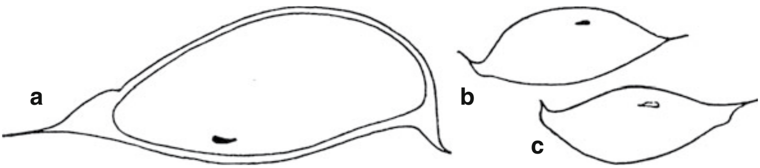

Fig. 357 *Cystodinium papilionaceum* Baumeister (after Baumeister 1957a). **a**–**c** outlines of vegetative cells, showing eyespot

16. ***Cystodinium papilionaceum*** Baumeister 1957a, p. 15, 19, Abb. 4 (**Fig. 357**)

Cells with the two ends unequal. One end with a short, longitudinally directed spine, which is swollen at the base. The other end with a short, bent spine at an angle to the first spine, slightly curved. Cell contents brown, with eyespot. Cells 35–45 µm long, rarely longer, 14 µm wide. Reproduction by formation of two zoospores in each cell.
Ecology: in peat bog.
Geographical distribution: Bavaria, Germany (Baumeister).

17. ***Cystodinium phaseolus*** Pascher 1928, p. 253, figs 1–7 (**Fig. 358**)

Cells bean-shaped, often heteropolar with one end more rounded than the other. One of the long sides convex, the other slightly concave, rarely flat. Cytoplasm with or without furrows. Numerous parietal chloroplasts, band-shaped to elongate disc-shaped. Pyrenoid absent. Cells 18–40 µm long, 13–30 µm wide. Reproduction by formation of two (rarely one) zoospores, with horseshoe-shaped eyespot. Small swarmers (6–10 µm long, probably gametes) sometimes formed, 8 or 16 in each parental cell, with notably long longitudinal flagellum. These cells lack eyespot.
Ecology: in *Sphagnum* pools and ponds among zygnemataleans and *Oedogonium* filaments; in reservoir of river.
Geographical distribution: Czech Republic (Pascher, Popovský); Austria (Ettl); Tatra Mountains, Poland (Wołoszyńska).

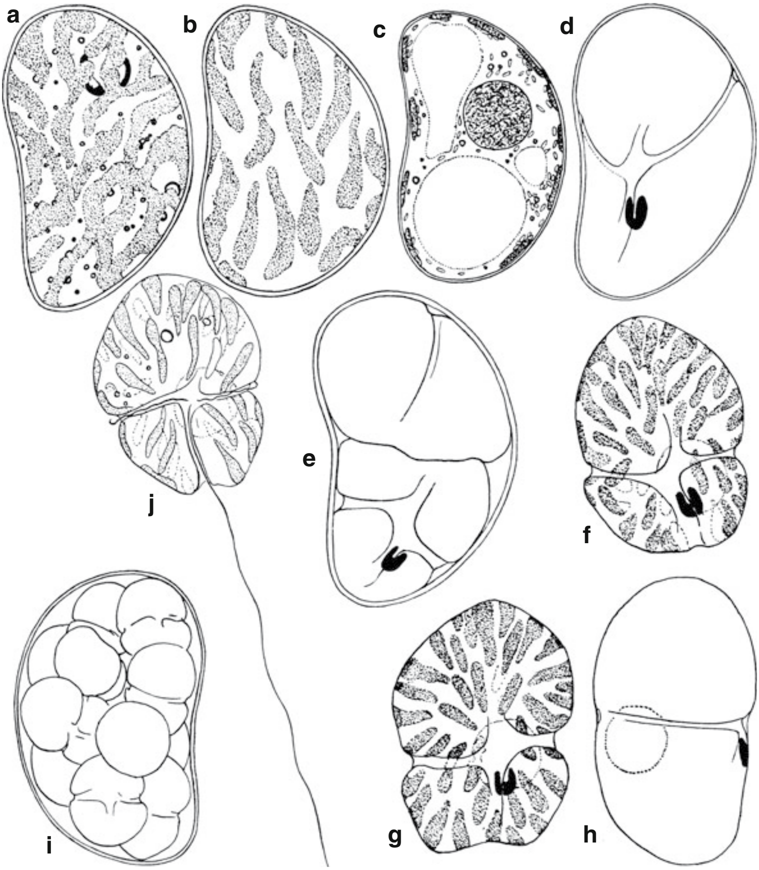

Fig. 358 *Cystodinium phaseolus* Pascher (after Pascher 1928). **a** vegetative cell with band-shaped, anastomosing, parietal chloroplasts; **b** vegetative cell with isolated, band-shaped chloroplasts; **c** vegetative cell, optical section; **d** cell with *Gymnodinium*-like protoplast; **e** formation of zoospores; **f**–**h** zoospores, with eyespot (**h** lateral view); **i** formation of a larger number of swarmers (more than 8); **j** small swarmer without eyespot (gamete?)

var. *brasiliense* C. E. M. Bicudo & Skvortsov 1968, p. 34, fig. 24 (**Fig. 359**)
Cells bean-shaped, with many disc-shaped chloroplasts. Cell length 11–18(–25) µm, width 6–10(–12) µm.
Ecology: in temporary pool in São Paulo, Brazil.
Geographical distribution: Brazil (Bicudo & Skvortsov).

Fig. 359 *Cystodinium phaseolus* var. *brasiliense* C. E. M. Bicudo & Skvortsov (after Bicudo & Skvortsov 1968)

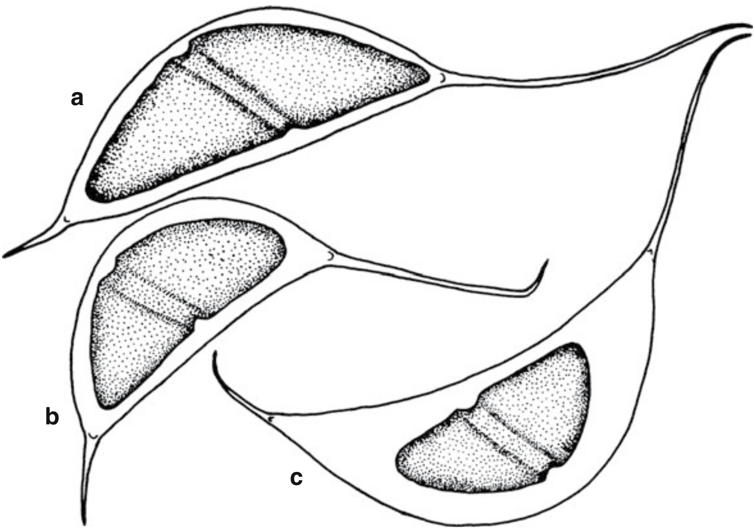

Fig. 360 *Cystodinium sonfonense* Gerrath & Denny (after Gerrath & Denny 1981). **a**–**c** shape variations of cells with *Gymnodinium*-like protoplast

18. *Cystodinium sonfonense* Gerrath & Denny 1981, p. 943, pl. 3, figs 6–8 (**Fig. 360**)

Cells slightly to strongly lunate. One end with short, straight or curved spine, 15–20 µm long, the other end with long spine, 40–55 µm long, which may be straight, slightly curved or curved only at the tip. Cell length without spines 75–80 µm, with spines 115–140 µm. Width 28–30 µm.
Ecology: in tropical Lake Sonfon at 26 °C, pH 6.6 and conductivity 46 µS · cm^{-1}.
Geographical distribution: Sierra Leone (Gerrath & Denny).

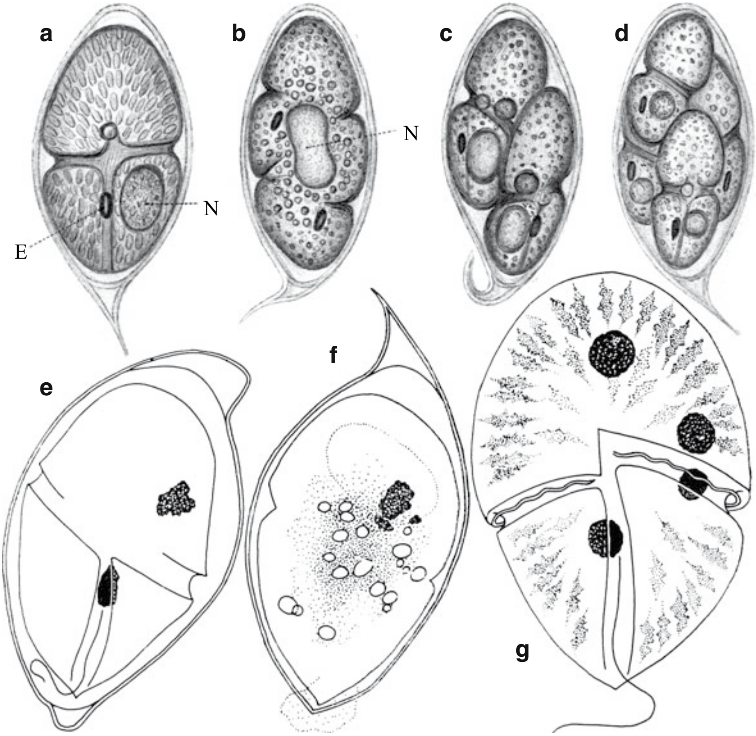

Fig. 361 *Cystodinium unicorne* G. A. Klebs (**a**–**d** after Stein 1883; **e**–**g** after Baumeister 1964). **a** cell with *Gymnodinium*-like protoplast showing radial arrangement of chloroplasts, the nucleus (N) on the left side of the hypocone and the eyespot (E); **b**–**d** formation of zoospores; **e**, a single zoospore within parental cell wall; **f** rearrangement of cytoplasm during conversion from zoospore to vegetative stage; **g** zoospore

19. *Cystodinium unicorne* G. A. Klebs 1912, p. 385, 442 (Fig. 361)

Nomenclatural synonyms: *Gymnodinium unicorne* (G. A. Klebs) Er. Lindemann 1928c, p. 291 ≡ *Gymnocystodinium unicorne* (G. A. Klebs) Baumeister 1957a, p. 14
Taxonomic synonym: *Gymnodinium rotundatum* G. A. Klebs 1912, p. 392, 439, fig. 5 (?) ≡ *Gymnodinium uberrimum* var. *rotundatum* (G. A. Klebs) Popovský 1968, p. 253

Cells broadly elliptical, with one terminal horn. The horn is rather short and stout, straight or curved. Cell size, according to Baumeister (1943b), 46 µm long and

24 µm wide. Each cell may produce 1, 2 or 4 zoospores. Zoospores with equally-sized epi- and hypocone, descending cingulum, the ends of which displaced *ca.* one cingulum width (Baumeister 1964). With numerous radially arranged chloroplasts and 3–4 pigment globules. Large, drop-shaped eyespot in the sulcus. Nucleus in the left side of the hypocone. Zoospores 34 µm long and 23 µm wide.
Seen and illustrated by Stein (1883, pl. XII, figs 20–28) as a possible cyst of *Peridinium cinctum*.
Ecology: bogs.
Geographical distribution: Bohemia, Bavaria (Baumeister).

Note 1: this taxon has sometimes been claimed to be a *C. cornifax* in which one of the horns could not be seen or did not develop. The detailed study by Baumeister (1964) has shown that *C. unicorne* is a distinct species.

Note 2: Klebs (1912) described *Gymnodinium rotundatum* as "double cysts", *i. e.*, immobile stages producing two swarmers; he noted the affinity with *Cystodinium* but did not classify his material in that genus because the swarmers were enveloped by a mucilaginous vesicle before being released. However, he noted swimming periods of 15–65 min before transition to the resting stage, a zoospore-like behavior. Swimming cells of *G. rotundatum* lacked an eyespot and may therefore represent a different species.

Genus 3. *Dinastridium* Pascher 1927, p. 27, 53

Type species: *Dinastridium sexangulare* Pascher 1927
Taxonomic synonym: *Bourrellyella* Baumeister 1957b, p. 31, 41

Probably an artificial genus, in which two of the three known species are characterized by either being bipolar with 3 spines at each end, or by having 5–6 spines (sometimes bipartite) scattered on the cell surface. In one species the wall is irregularly wavy, but no clear spines were described.

Note: Baumeister (1957b, p. 26, Abb. 1, fig. 3) described *Dinastridium verrucosum* Baumeister, but its identity needs to be confirmed. It may be a resting cyst. Bourrelly (1970, p. 95) illustrated one cell referred by him as *Dinastridium* sp., indicating that more species exist within this little-studied group.

Key to species of *Dinastridium*:
1a Cells bipolar with 3 spines at each end .... 2. *D. armatum*
1b Cells with 4–6 corners 2
2a Each corner with 1 or 2 short spines .... 1. *D. sexangulare*
2b Spines absent .... 3. *D. inerme*

1. *Dinastridium sexangulare* Pascher 1927, 53, figs 25–29 (**Fig. 362**)

Cells compressed, when seen from the flat sides with 6, more rarely 5 corners, each with 1–2 short spines. Spines often layered. Cells with thin cytoplasmic layer beneath the wall, the central vacuole transversed by cytoplasmic strands. Numerous disc-shaped chloroplasts, mostly parietal, some in the strands, unevenly distributed, leaving parts of the wall free. Nucleus near the wall. Reproduction by 2–4

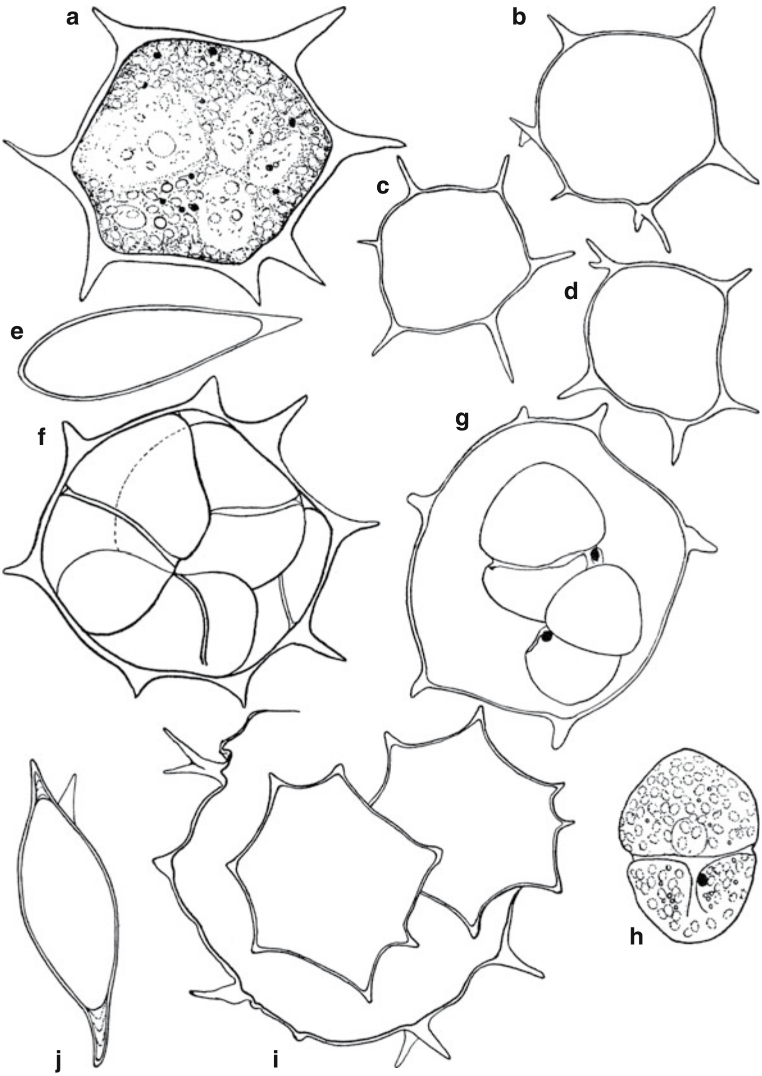

Fig. 362 *Dinastridium sexangulare* Pascher (after Pascher 1927). **a** vegetative cell with contents; **b**–**d** shape variation of cells seen from the wide side; **e** outline of optical section seen from the thin side, showing one spine; **f**, **g** formation of zoospores; **h** zoospore; **i** release of autospores; **j** layered wall (not always visible) of cell seen from the thin side

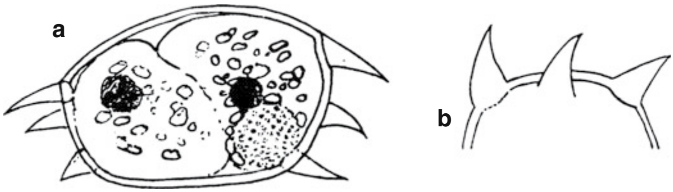

Fig. 363 *Dinastridium armatum* (Baumeister) Bourrelly (after Baumeister 1957b). **a** vegetative cell in advanced division stage; **b** shape and arrangement of the spines

Fig. 364 *Dinastridium inerme* Thérézien (after Thérézien 1989). **a**–**d** lateral views of attached cells; **e**, **f** vertical views

autospores or zoospores. The epicone of the zoospore is slightly larger than the hypocone, the ends of the cingulum not displaced, and a distinct circular eyespot is present near the sulcus. Chloroplasts sometimes indistinct. Zoospores very fragile. Coccoid cells 35–57 µm in diameter (without the spines).
Ecology: ponds, bogs.
Geographical distribution: Germany, Austria (Pascher). USA, MN (Ngô & Pfiester).

2. *Dinastridium armatum* (Baumeister) Bourrelly 1970, legend to pl. 21, fig. 12 (p. 94), p. 96 (**Fig. 363**)

Basionym: *Bourrellyella armata* Baumeister 1957b, p. 31, 41, Abb. 4, Fig 8

Cells longer than wide, with three thick spines at each end. Cell length including spines 28 µm, without spines 21 µm, width 13 µm.
Ecology: in small waterbodies in Bavaria.
Geographical distribution: Germany (Baumeister).

3. *Dinastridium inerme* Thérézien 1989, pp 41, 47, pl. V, fig. 11 (**Fig. 364**)

Cells brick-like, the sides somewhat irregular. The upper part often slightly wider than the lower part. Gymnodinioid zoospores observed in the cell. Cell height 8–10(–12) µm, width 11–13(–15) µm.
Ecology: cells observed fairly commonly attached to filaments of the cyanobacterium *Scytonema*, more rarely to *Oedogonium*, in clear-water pond, October 1985.
Geographical distribution: Amazonian part of Bolivia.

Genus 4. *Dinococcus* Fott 1960, p. 149

Substitute name for *Raciborskia* Wołoszyńska (1919a, p. 321; 1919b, p. 199), *non* Berlese *in* Saccardo (1888, p. 400; Myxomycetes).
Type species: *Raciborskia bicornis* Wołoszyńska 1919, herein considered synonymous with *Dinococcus oedogonii* (P. G. Richter) Fott 1960

Cells bipolar, usually with a single spine at each pole, attached by a central stalk or disc to filamentous algae or charophytes.

Key to species of *Dinococcus*:
1a Lateral sides of the cell almost perpendicular to dorsal side, dorsal side strongly concave .... 2. *D. incus*
1b Cells biconvex, plano-convex or rarely concavo-convex .... 1. *D. oedogonii*

1. *Dinococcus oedogonii* (P. G. Richter) Fott 1960, p. 149 (**Fig. 365**)

Basionym: *Rhizophydium oedogonii* P. G. Richter 1897, p. 12, fig. 6
Nomenclatural synonym: *Raciborskia oedogonii* (P. G. Richter) Pascher 1932, p. 566
Taxonomic synonyms: *Raciborskia bicornis* Wołoszyńska (1919a, p. 321, pl. 13, figs 15–17; 1919b, p. 199, pl. 14, figs 15–17) ≡ *Cystodinium bicorne* (Wołoszyńska) Huber-Pestalozzi 1950, p. 299 ≡ *Dinococcus bicornis* (Wołoszyńska) Fott 1960, p. 150; *Cystodinium brevipes* Geitler 1928b, *pro parte incl. typo*, p. 68, 81, text-fig. 1a, 1d, pl. 7, fig. 1

Note: Geitler (1943) stated that *Cystodinium brevipes* had been described from a mixture of two species, *Raciborskia oedogonii* and *R. inermis*, but did not define the type of *C. brevipes*. To preserve current usage of names we here designate pl. 7, fig. 1 in Geitler (1928b) as lectotype of *Cystodinium brevipes* Geitler.

Solitary or forming colonies with up to 16 cells. Cells up to 35 µm long, incl. spines, and up to 20 µm high. Cells seen from above oval, with a short spine at each end, in side view typically biconvex, but the dorsal side is sometimes flat or even slightly concave. The dorsal side extends as two opposite short spines, sometimes slightly curved, which may be rudimentary or missing. Cell circular in transverse section. A very short, wide stipe or attachment disc extends from the mid-ventral side of the cell. With central pyrenoid and radiating plus peripheral network of chloroplasts. Forms 1–2 *Gymnodinium*-like zoospores within the cell. Zoospore with almost equally sized epi- and hypocone. Cingulum descending, displaced *ca.* one cingulum width. Nucleus in the posterior end, eyespot in the anterior part of the sulcus. Chloroplasts and pyrenoid as in vegetative cells. Zoospores positively phototactic, mostly released during the morning hours. The furrows and the eyespot are retained for some time after germination.
Ecology: Attached to *Spirogyra*, *Oedogonium*, *Tribonema*, *Microspora*, *Mougeotia* and *Nitella*, sometimes so densely that “man stellenweise die Fäden gar nicht sehen konnte” (Richter 1897, material from Greenland), in a variety of ponds, swamps and lakes. Studies on autecology have apparently not been performed.

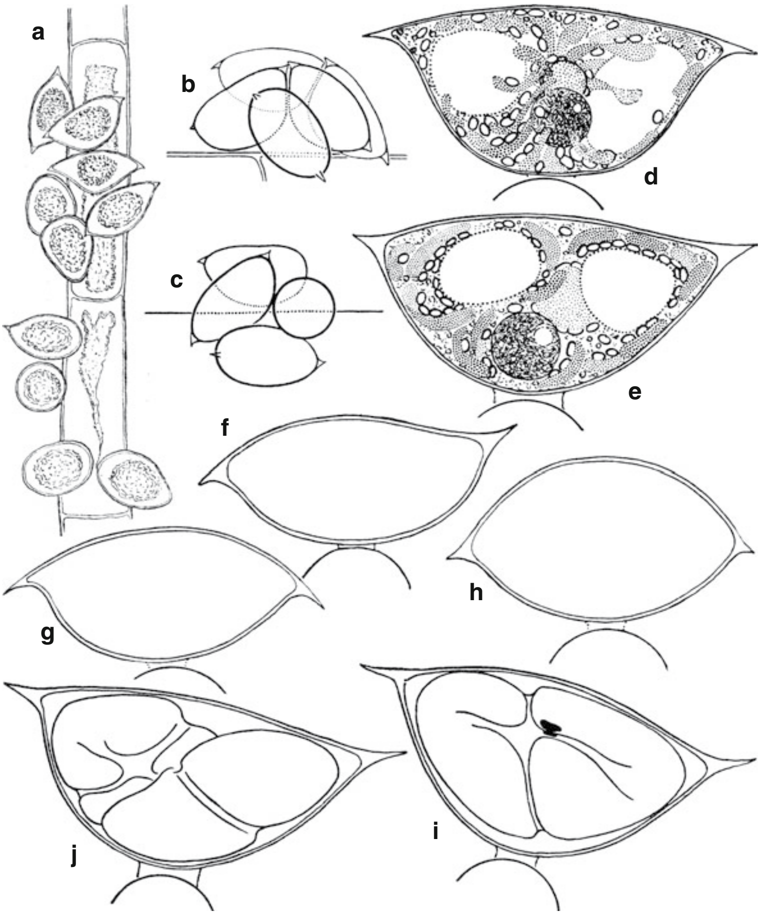

Fig. 365 *Dinococcus oedogonii* (P. G. Richter) Fott (**a** after Richter 1897; **b**, **c** after Geitler 1943; **d**–**j** after Pascher 1932). **a**–**c** groups of cells attached to *Oedogonium*; **d**, **e** optical sections, showing the nucleus, a central pyrenoid, band-shaped chloroplasts, numerous starch grains and two large vacuoles; **f**–**h** variations in cell shape; **i** cell with *Gymnodinium*-like protoplast; **j** formation of zoospores

Geographical distribution: Umanak, Greenland (Richter); Austria (Geitler – pond in the Botanical Garden, cold house at the Biological Station at Lunz; Ettl – acid waters, also slowly running waters); England (Williams & Lund; Lewis & Dodge); Germany (Pascher); Poland (Wołoszyńska); Portugal (Rino; M. F. Santos); Sweden (Teiling; Skuja – attached to *Aulacoseira ambigua*). Ivory Coast (Bourrelly –

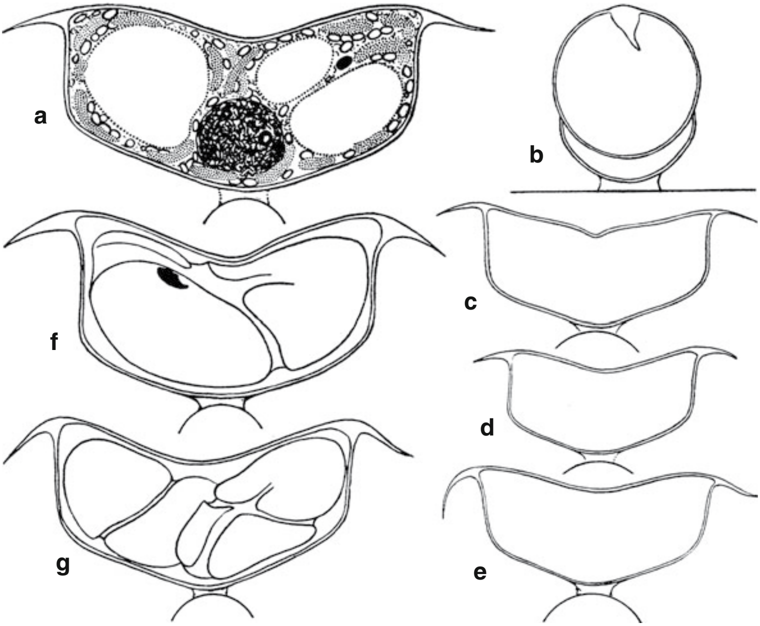

Fig. 366 *Dinococcus incus* (Pascher) Fott (after Pascher 1932). **a** vegetative cell, optical section; **b** lateral view (cell seen from the narrow side); **c**–**e** variations in cell shape; **f** cell with *Gymnodinium*-like protoplast; **g** formation of zoospores

savannah swamp, cells somewhat larger, 50 × 20 µm incl. terminal spines). New Zealand (Thompson).

Note: Narrow cells (9–12 µm wide), in which the spines appear to be more sharply attached rather than narrowing from the cell, and the dorsal side is less convex, are sometimes considered a separate species, *D. bicornis* (Wołoszyńska) Fott. However, following Geitler (1943), we regard it as a synonym of *D. oedogonii*.

2. ***Dinococcus incus*** (Pascher) Fott 1960, p. 150 (**Fig. 366**)

Basionym: *Raciborskia incus* Pascher 1932, p. 554, 566, text-figs 10, 11, pl. VII, fig. e

Cells more than twice as long as wide. Dorsal side deeply concave. Ventral side parallel to the dorsal side. Lateral sides at right angles to the dorsal and ventral sides, each with a spine inserted perpendicularly. Pyrenoid lacking. Propagation by 2 zoospores, each with an eyespot. The ends of the cingulum not displaced, the sulcus extends onto the epicone. Cell up to 22 µm long (rarely up to 28 µm), 10–14 µm high.

Ecology: in acid waters, on thick-walled *Oedogonium* and filamentous cyanobacteria.
Geographical distribution: Czech Republic (Pascher).

Genus 5. ***Haidadinium*** Buckland-Nicks, Reimchen & Garbary 1997, p. 1937

Type species: *Haidadinium ichthyophilum* Buckland-Nicks, Reimchen & Garbary 1997

Ectoparasitic coccoid cells on stickleback (*Gasterosteus aculeatus*).

1. *Haidadinium ichthyophilum* Buckland-Nicks, Reimchen & Garbary 1997, p. 1937, figs 1–6. (**Fig. 367**)

Coccoid cells on the epithelium of stickleback. Cells spherical or somewhat elongate, 20–150 µm in diameter, sometimes with a short terminal stalk at one end. Attachment to filamentous algae also seen. Structures identified as chloroplasts present in swarmer and cysts stages, pyrenoids also reported. Multiplication by division of the coccoid cell or by formation of aplanospores (many in each cell) or zoospores (two in each cell). Zoospores apparently naked. Reproduction by several stages of colorless, bacteria-ingesting amoebae also reported, each amoeba with a non-dinokaryotic nucleus and lacking chloroplasts.
TEM: Buckland-Nicks *et al.* (1990); Buckland-Nicks & Reimchen (1995).
Geographical distribution: known from two acid lakes in British Columbia, Canada.

Note: Whether there is a phylogenetic relationship between this species and the Phytodiniales needs to be confirmed.

Genus 6. ***Hypnodinium*** G. A. Klebs 1912, p. 399, 443

Type species: *Hypnodinium sphaericum* G. A. Klebs 1912

Cells symmetrical, spherical, with radiating cytoplasmic strands. Nucleus central. Yellow chloroplasts, eyespot also present. Cingulum and sulcus present just prior to and during cell division, when the cell contents divide into two gymnodinioid cells that lack flagella. Zoospores unknown.

Note: *Hypnodinium lefevrei* Bourrelly (1987) deviates from the generic diagnosis of *Hypnodinium* in several respects; see further under *Phytodinium simplex*.

1. *Hypnodinium sphaericum* G. A. Klebs 1912, p. 399, 443, text-fig. 8., pl. X, 1a, b (**Fig. 368**)

Nomenclatural synonym: *Gymnodinium klebsii* Er. Lindemann 1928b, p. 43 (non *Gymnodinium sphaericum* [G. N. Calkins] Kofoid & Swezy 1921, p. 258)

Cells spherical, 72–122(–133) µm in diameter, with yellow or brown chloroplasts. Chloroplasts in small parietal rosettes, which form a distinctive network. Nucleus

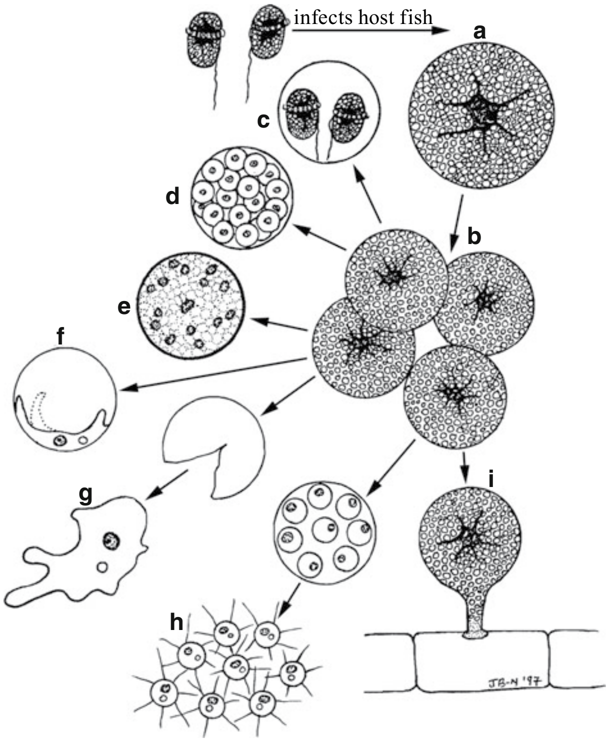

Fig. 367 *Haidadinium ichthyophilum* Buckland-Nicks, Reimchen & Garbary (after Buckland-Nicks *et al.* 1997). **a** primary vegetative cyst on fish host; **b** cysts produced by repeated divisions, with sizes down to 20 μm; **c** flagellated cells, which may infect host; **d** formation of aplanospores by palintomic reproduction within a vegetative cyst; **e** multinuclear resting cyst; **f** spheroidal amoeba; **g** lobose amoeba; **h** rhizopodial amoebae; **i** trophont stage attached to filamentous alga by a stalk-like extension

central, cytoplasmic strands radiating from the nucleus towards the cell wall. One or more lipid droplets usually present. The cytoplasm contracts somewhat from the cell wall before division into two immotile gymnodinioid cells. Young cells pelagic near the water surface. Pascher (1914) mentions fusion of two smaller gymnodinioid gametes.
Ecology: planktonic in ponds and swamps; cells sink to the bottom to be found between leaves (*e. g.*, *Utricularia*).
Geographical distribution: Baden, Germany (Klebs); “Hanflöcher” near Freiburg, Switzerland (Huber-Pestalozzi). USA, MD (Thompson).

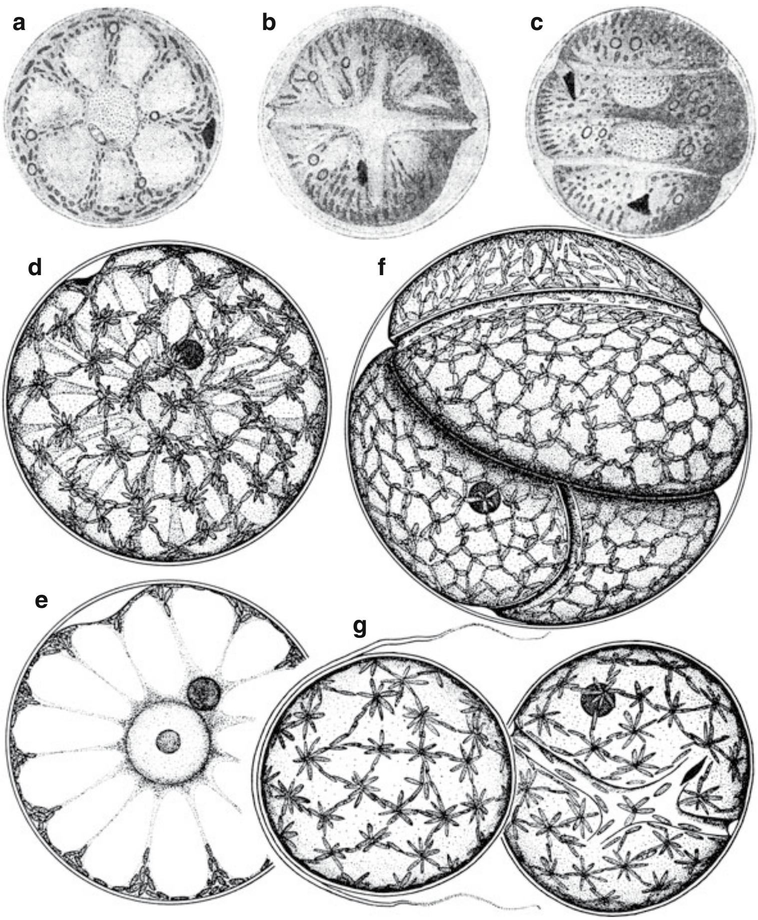

Fig. 368 *Hypnodinium sphaericum* G. A. Klebs (**a**–**c** after Klebs 1912; **d**–**g** after Thompson 1949). **a** vegetative cell without furrows (optical section, showing central nucleus and radiating cytoplasmic strands); **b** cell with *Gymnodinium*-like contents; **c** formation of spores; **d**, **e** two views of the same vegetative cell (**e** optical section); **f** *Gymnodinium*-like spores within parental cell wall; **g** release of spores from ruptured parental cell wall

Note: *Hypnodinium asiaticum* Skvortsov (1958, p. 197, pl. 5, fig. 43) was described to be related to *Hypnodinium sphaericum* but only 33–35 µm in diameter. The description is very incomplete, and the identity of this species, found in a swamp near Harbin in Manchuria, is uncertain.

Genus 7. *Phytodinedria* Pascher 1944a, p. 379, 384

Type species: *Phytodinedria aeruginea* Pascher 1944 (see Loeblich Jr. & Loeblich III 1966)

Cells hemispherical to bean-shaped or kidney-shaped with flattened ventral side (in *P. reniformis* concave). Cells isopolar. Cells without stalk, attached to filamentous algae with the flattened side. A layer of attachment is sometimes very distinct between the cell and the substrate. Band-shaped chloroplasts, pyrenoid sometimes present. Furrows absent, eyespot present in some species. Multiplication by formation of 2–4 zoospores or perhaps autospores.

Key to species of *Phytodinedria*:

1a Chloroplasts blue-green .... 1. *P. aeruginea*
1b Chloroplasts brown or chloroplasts absent 2
2a Cell surface smooth 3
2b Cell surface covered with setae .... 7. *P. setosa*
3a Cells colorless, chloroplasts absent 4
3b Cells with chloroplasts 5
4a Cells bean-shaped in lateral view, twice as long as high .... 6. *P. reniformis*
4b Cells elliptic in lateral view, 1/3–1/4 longer than high .... 4. *P. hyalina*
5a Cells hemispherical 6
5b Cells flattened semicircular .... 2. *P. adpressa*
6a Cells up to 30 µm long and 24 µm high .... 5. *P. procubans*
6b Cells 14–17 µm long, up to 14 µm high .... 3. *P. hemisphaera*

1. *Phytodinedria aeruginea* Pascher 1944a, p. 388, Abb. 11 (**Fig. 369**)

Cells more or less ovoid, attached to the substrate with one of the long sides. Cell typically 1.5–2 times longer than wide with rounded ends. Chloroplasts large, often parietal, band-shaped, sometimes branched, distinctly blue-green. Large pyrenoid present. A large refractile oil droplet often present. Cell wall thin or thick, in the latter case often layered. Propagation by 2–4 zoospores. Each zoospore with epi- and hypocone of the same size. Epicone rounded triangular-hemispherical, hypocone narrowing towards the flat antapex. With large eyespot along the sulcus. Following germination, the young cell retains the furrows and the eyespot for some time, but these eventually disappear. Cell length 18–27 µm (usually ca. 23 µm), height 10–14 µm. Both smaller and much larger cells have been observed.
Ecology: epiphytic on filamentous algae: *Spirogyra*, *Zygnema*, *Rhizoclonium*. According to Pascher a heat-loving species.
Geographical distribution: locality not given (Germany?).

2. *Phytodinedria adpressa* Pascher 1944a, p. 387, Abb. 10 (**Fig. 370**)

Cells flattened semicircular, attached with the ventral side to the substrate. Cells 0.75–2 times as long as wide. Cell wall thick, often slightly reddish in color. Chloroplasts more or less band- or net-shaped, converging towards the relatively large pyrenoid. No furrows but eyespot present. One or two red droplets present. Propa-

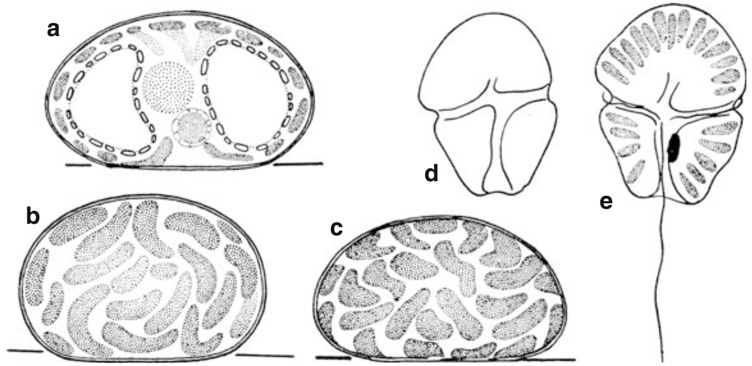

Fig. 369 *Phytodinedria aeruginea* Pascher (after Pascher 1944a). **a**–**c** vegetative cells (**a** optical section); **d**, **e** zoospores

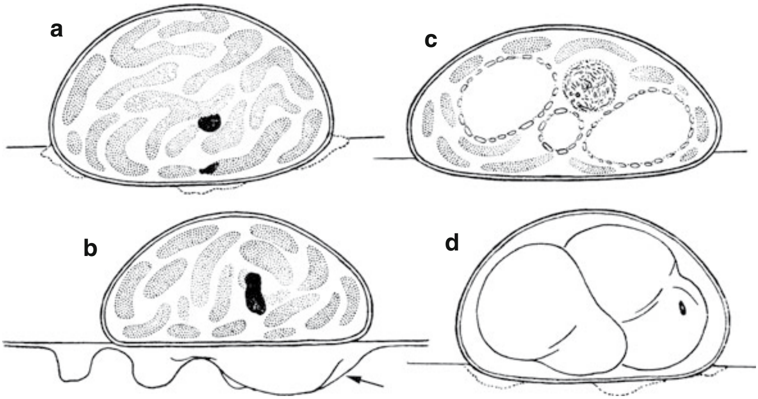

Fig. 370 *Phytodinedria adpressa* Pascher (after Pascher 1944a). **a**–**c** vegetative cells (**c** optical section); **d** formation of zoospores. The dotted lines that protrude from the base of the cell in **a** and **d** mark the contour of the adhesion layer. The arrow in **b** marks the wall thickening of the underlying *Vaucheria*

gation by 2–4 zoospores, each with an eyespot. Sulcus only extends for a short distance onto the epicone. Compared to other species, the zoospores remain motile for longer time. Cell length 20–30 μm, height 12–18 μm.
Ecology: On floating filaments of *Rhizoclonium* and *Vaucheria*. Cell wall of *Vaucheria* with distinct thickenings on the point of attachment of *Phytodinedria*. Any damaging effect of *Phytodinedria* not known.
Geographical distribution: locality not provided (Germany?).

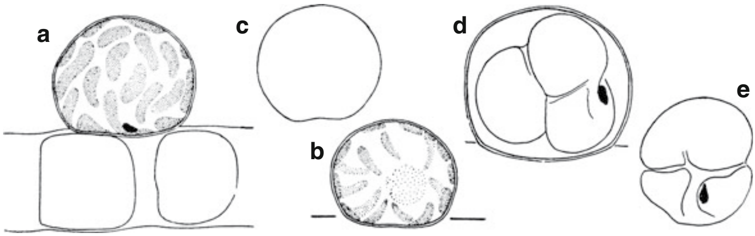

Fig. 371 *Phytodinedria hemisphaera* Pascher (after Pascher 1944a). **a**, **b** vegetative cells on *Binuclearia* (**b** optical section); **c** cell seen from an end; **d** formation of zoospores; **e** zoospore

3. *Phytodinedria hemisphaera* Pascher 1944a, p. 386, Abb. 9, pl. VI, fig. d (**Fig. 371**)

Cells hemispherical, almost isodiametric. Cell wall thin, chloroplasts deep brown, more or less band-shaped, parietal. Nucleus excentric. A large vacuole, often excentric, takes up most of the cell volume. Pyrenoid apparently absent. Eyespot present but furrows absent. Propagation by formation of 2 zoospores, in which the sulcus extends for a short distance onto the epicone but in the hypocone widens strongly towards the antapex. Epi- and hypocone of almost the same size. Chloroplasts in the zoospores elongate, radiating from the center. Eyespot distinct. Cell length 14–17 µm, height 10–14 µm.
Ecology: epiphytic on *Binuclearia* and *Microspora* during the colder parts of the year. Filaments of *Microspora* were often seen to be covered with a dense, continuous layer of *Phytodinedria* cells. *Microspora* appeared to respond by forming wall thickenings, but mostly on the transverse walls.
Geographical distribution: Austria (Ettl); Southern Germany? (Pascher).

4. *Phytodinedria hyalina* Pascher 1944b, p. 400, Abb. 3, pl. VI, fig. e (**Fig. 372**)

Cells shortly elliptic with evenly rounded ends. Cells 1/3–1/4 longer than high. Cells colorless, apparently lacking chloroplasts and transparent. Cell wall relatively thin, refractile. Secondary layers of wall material not observed. Nucleus large, pyrenoid absent. In mature cells no furrows or stigma. Propagation by 1–2 zoospores, in which the epi- and hypocone are of the same size, the epicone rounded hemispherical, the hypocone oblique, cone-shaped. A large, pale-yellow eyespot present. Cells 18–22 µm long, to 16 µm high.
Ecology: On filamentous desmids (*Hyalotheca*, *Desmidium*) and more rarely on filamentous zygnemataleans.
Geographical distribution: Southern Germany (Pascher).

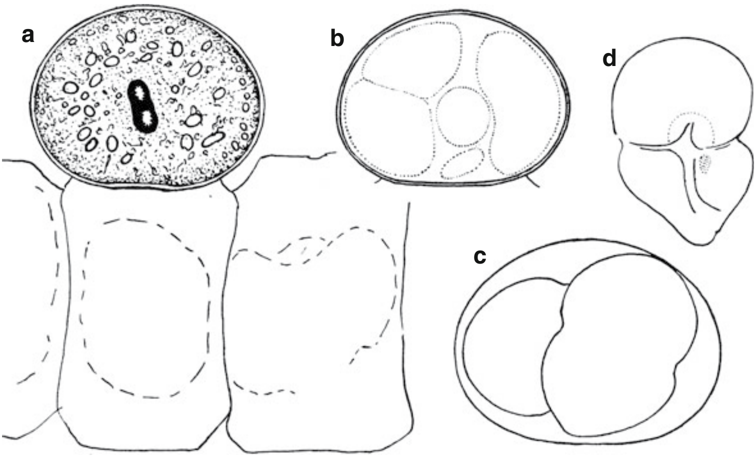

Fig. 372 *Phytodinedria hyalina* Pascher (after Pascher 1944b). **a**, **b** vegetative cell on *Desmidium* (**b** optical section); **c** formation of zoospores; **d** zoospore

5. *Phytodinedria procubans* Pascher 1944a, p. 386, Abb. 8, pl. VI, fig. c (**Fig. 373**)

Cells in lateral view hemispherical with wide, flat ventral side attached to filamentous algae, in top view elliptical. Cells 0.2–0.25 as high as long. Chloroplasts band-shaped, brown, large pyrenoid present. Furrows and eyespot absent in mature cells. Propagation mostly by two zoospores, each with an eyespot. Epicone of the zoospores larger than hypocone, semicircular. Ends of cingulum not displaced. Sulcus extends for a short distance onto the epicone. Cells up to 30 µm long and 24 µm high. Larger and smaller cells also occur.
Ecology: in acid waters, on filaments of *Microspora*, *Tribonema*, *Geminella*, *Oedogonium*. The host filaments are obviously damaged, wall thickenings are formed by the cells, chloroplasts are discolored, the cytoplasm eventually contracts and the filaments bend in the affected region. This bending is readily observed even at low magnification. Neighboring cells appear unaffected.
Geographical distribution: Germany (Pascher, Baumeister?).

Note: the species is very similar to *P. hemisphaera* but differs by its larger size (twice as large).

6. *Phytodinedria reniformis* Baumeister 1957b, p. 31, 41, Abb. 4, fig. 5 (**Fig. 374**)

Cells bean-shaped in lateral view, cocoon-shaped from above. Cell twice as long as high. Chloroplasts absent. The cell contents comprise the large nucleus, an orange lipid droplet and numerous grains. Mode of propagation unknown. Cell length 28 µm, height 15 µm.

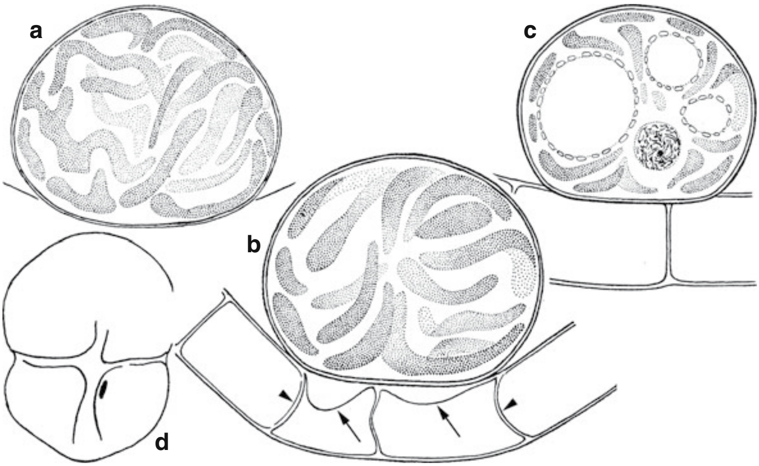

Fig. 373 *Phytodinedria procubans* Pascher (after Pascher 1944a). **a**–**c** vegetative cells (**c** optical section; pyrenoid not shown); **d** zoospore. The arrows in **b** mark the wall thickenings of the underlying filament cells; arrowheads mark the apparently inward pressed cross-walls of the affected filament cells

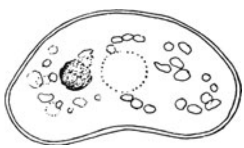

Fig. 374 *Phytodinedria reniformis* Baumeister (after Baumeister 1957b)

Ecology: found among algae, host (if any) not known.
Geographical distribution: Germany (Baumeister).

Note: *Phytodinedria* (*Cystodinium*?) *coconiformis* Baumeister (1957b, p. 32, 41, Abb. 4, fig. 7) may belong to this taxon or to *P. hemisphaera*. It was described as brown but chloroplasts were not mentioned. The 5 known cells were described as bean-shaped, 20 µm long and 13 µm wide, in detritus associated with filaments of *Oedogonium*.

7. *Phytodinedria setosa* Pascher 1944a, p. 390, Abb. 12, pl. VI, fig. f (Fig. 375)

Cells in lateral view elliptic. Cell wall thin, not lamellated, with numerous but not closely located, slightly curved, attenuating, unevenly long setae. The length of the setae 1/6–1/8 the cell diameter. The setae are cellulosic. Cells with numerous band-shaped or more rarely discoid parietal chloroplasts, which converge on the pyrenoid. Large nucleus present. A large oil droplet also usually present. Furrow

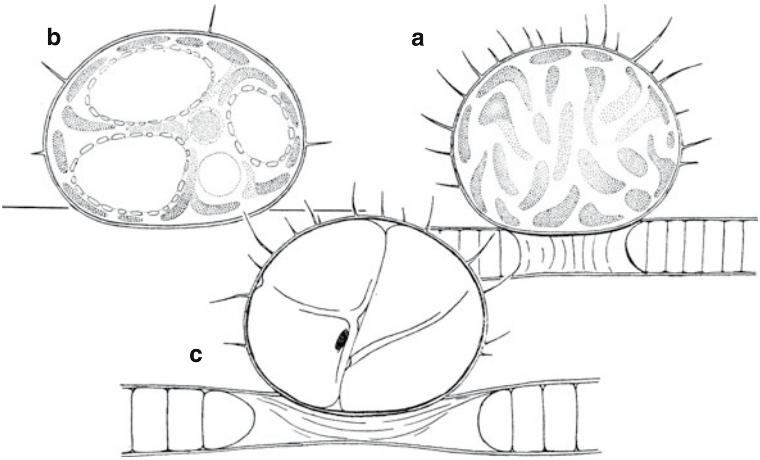

Fig. 375 *Phytodinedria setosa* Pascher (after Pascher 1944a). **a**, **b** vegetative cells (**b** optical section); **c** formation of zoospores. In **a** the underlying *Phormidium* cells are dead

system and eyespot absent. Propagation by 2–4 zoospores. Each zoospore with epi- and hypocone of nearly the same size. Cingulum oblique. Sulcus extends onto the epicone and on the hypocone widens towards the antapex. Eyespot present. At germination the zoospore forms a thin wall and the wall with the setae is formed beneath the initial wall. Cells 25–30 µm long, 18–22 µm high.
Ecology: epiphytic, especially on thin filamentous algae (thick-walled *Phormidium*, thin filaments of *Tribonema*, *Oedogonium*, *Zygnema*), in spring and autumn. The host filaments of cyanobacteria are strongly affected by the presence of *Phytodinedria*, large cell wall thickenings are formed, and the cells eventually die. The green algae appear to be less affected.
Geographical distribution: Southern Germany (Pascher); Czech Republic? (Popovský).

Note: the Czech material was larger than the original German material, measuring 32–44 µm in length and 29–32 µm in width (Popovský 1971b).

Genus 8. ***Phytodinium*** G. A. Klebs 1912, p. 406, 444

Type species: *Phytodinium simplex* G. A. Klebs 1912

Cells free-living, symmetrical, spherical or ellipsoidal. Chloroplasts yellow, parietal, disc-shaped or stellate, eyespot absent. Cell wall very thin. The coccoid cell elongates before cell division and a transverse wall is formed at right angles to the long axis. The cell contents do not contract prior to cell division but the daughter cells are released as autospores when the parent cell wall disappears. Stigma, cingulum and sulcus not observed. Zoospores unknown.

Fig. 376 *Phytodinium simplex* G. A. Klebs (**a**, **b** after Klebs 1883; **c** after Pascher 1927). **a** optical section of vegetative cell; **b** formation of autospores; **c** autospores inside ruptured wall of parental cell

Key to species of *Phytodinium*:

1a	Chloroplasts disc-shaped, parietal	2
1b	Chloroplasts stellate	4. *P. stellatum*
2a	Cells spherical	3. *P. globosum*
2b	Cells elongate	3
3a	Cell length 8–12 µm	2. *P. aureum*
3b	Cell length 20–50 µm	1. *P. simplex*

1. *Phytodinium simplex* G. A. Klebs 1912, p. 406, 444, text-fig. 10 (**Fig. 376**)

Cells spherical or broadly ovoid with many parietal chloroplasts. Cell length 42–50 µm, width 30–45 µm.
Ecology: ?
Geographical distribution: Tübingen, Germany (Klebs); Belgium (Conrad)?. New Zealand (Thompson).

Note: the cells found in large numbers in the hyaline cells of *Sphagnum* by Conrad (1943) are slightly smaller and may belong to another species.

f. *minus* C. E. M. Bicudo & Skvortsov 1968, p. 37, figs 9–11 (**Fig. 377**)
Cells broadly elliptical. Cell length 20–30 µm, width 13–16 µm.
Ecology: in temporary pool in São Paulo, Brazil.
Geographical distribution: Brazil (Bicudo & Skvortsov).

Note 1: *Hypnodinium lefevrei* Bourrelly (1987, p. 46, pl. XIV, fig. 26, pl. XV, fig. 29, pl. XVII, figs 1–3, 36) from the Lunz am See region, Austria, agrees in morphology

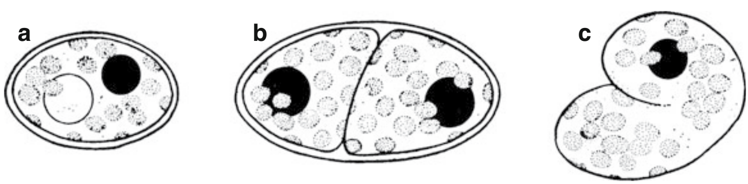

Fig. 377 *Phytodinium simplex* f. *minus* C. E. M. Bicudo & Skvortsov (after Bicudo & Skvortsov 1968). **a** vegetative cell; **b** formation of autospores; **c** aberrant form

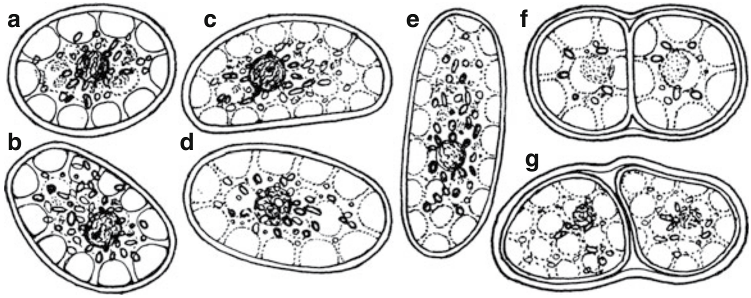

Fig. 378 *Phytodinium aureum* Starmach (after Starmach 1963). **a**–**e** vegetative cells; **f**, **g** formation of autospores

and size with *Phytodinium simplex* f. *minus* (cell length 18–25 µm, width 12–16 µm). It propagated by division of the cell during summer and by forming a single zoospore within each cell in winter. It is probably closely related or identical.

Note 2: *Cystodinium interspersum* Baumeister (1957b, p. 40, 42, Abb. 4, fig. 3) is similar but was described without chloroplasts. Only few cells were observed and their identity is obscure.

2. ***Phytodinium aureum*** Starmach 1963, p. 338, text-fig. 1, pl. I (**Fig. 378**)

Cells elliptical, sometimes curved, bean-like, after cell division spherical or broadly elliptical. With numerous discoid, parietal, golden-yellow (rarely greenish-yellow) chloroplasts. Cell size: 8–12 µm long.
Ecology: On the damp walls of Twardowski Cave, a limestone cave in the banks of the Vistula River in Southern Poland.
Geographical distribution: Poland (Starmach).

3. ***Phytodinium globosum*** Pascher 1927, p. 52, fig. 16 (**Fig. 379**)

Cells spherical, with many disc-shaped chloroplasts. Cell diameter up to 30 µm.
Ecology: in slightly acid pools in meadows.
Geographical distribution: Czech Republic (Pascher, Huber-Pestalozzi). USA (MN) (Ngô & Pfiester). Brazil (Bicudo & Skvortsov).

4. ***Phytodinium stellatum*** C. E. M. Bicudo & Skvortsov 1968, p. 38, figs 22–23 (**Fig. 380**)

Cells broadly elliptical with chloroplasts extending from the cell center. Cell length 20–30 µm, width 12–15 µm.
Ecology: in temporary pool in São Paulo, Brazil.
Distribution: Brazil (Bicudo & Skvortsov).

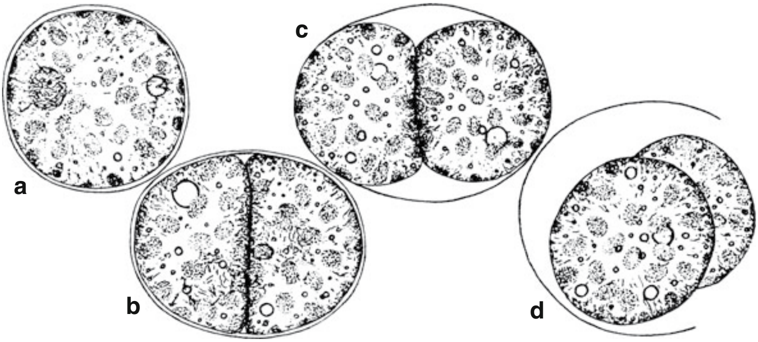

Fig. 379 *Phytodinium globosum* Pascher (after Pascher 1927). **a** vegetative cell; **b**, **c** formation of autospores; **d** autospores inside ruptured wall of parental cell

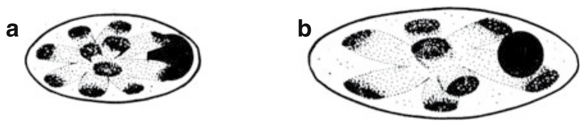

Fig. 380 *Phytodinium stellatum* C. E. M. Bicudo & Skvortsov (after Bicudo & Skvortsov 1968). **a**, **b** two vegetative cells of different sizes

Genus 9. *Stylodinium* G. A. Klebs 1912, p. 410, 445

Type species: *Stylodinium globosum* G. A. Klebs 1912 (see Loeblich Jr. & Loeblich III 1966)
Taxonomic synonym: *Dinopodiella* Pascher 1944a, p. 380, 392

Cells globular to oval, attached by a stipe (stalk, pedicel) to other algae or macrophytes. Species concept very uncertain.
Baumeister (1943b) described stipe formation in *Stylodinium tarnum* and provided outlines of mobile, flagellate cells of *S. globosum*, *S. truncatum*, *S. cerasiforme* and *S. tarnum*.
In two of the species below, the coccoid cell and the zoospores have been described to be covered with amphiesmal plates, visible in the light microscope. Amphiesmal plates are not known to occur in other freshwater members of the order Phytodiniales and in this and several other respects the two species resemble the marine species *Halostylodinium arenarium* T. Horiguchi & Yoshizawa-Ebata and *Stylodinium littorale* T. Horiguchi & Chihara from Japan and the Philippines. There are minor differences in plate formula between the freshwater and the marine species, indicating that the freshwater species may belong to a separate, new genus. All these species show some similarity to the thecate *Staszicella dinobryonis* Wołoszyńska, presently included in the Peridiniaceae.

Key to species of *Stylodinium*:

1a	Cells covered with thin amphiesmal plates	12
1b	No amphiesmal plates	2
2a	Cells more or less quadrangular, bean-shaped, triangular or conical	3
2b	Cells spherical to ovoid or obpyriform	9
3a	Cells more or less conical or triangular	4
3b	Cells bean-shaped or quadrangular	6
4a	Distal side concave	13. *S. truncatum*
4b	Distal side convex	5
5a	Cell sides slightly constricted below the apex	2. *S. africanum*
5b	Cell sides even, not constricted	4. *S. cerasiforme*
6a	Cells quadrangular	7
6b	Cells bean-shaped	8
7a	Stipe long (6–36 µm)	7. *S. longipes*
7b	Stipe very short (less than 2 µm)	10. *S. quadrangulare*
8a	Cells 8–12 µm wide	5. *S. gracile*
8b	Cells 17–19 µm wide	8. *S. phaseolus*
9a	Cells globose to ovoid	10
9b	Cells obpyriform, the lower part narrower than the upper part	3. *S. baumeisteri*
10a	Cells spherical, stipe very short and conical towards the basal disc	11
10b	Cells spherical to ovoid, stipe evenly thick, not cone-shaped at the base	1. *S. globosum*
11a	Cells 25–30 µm in diameter	11. *S. sphaera*
11b	Cells *ca.* 50 µm in diameter	6. *S. grande*
12a	Cells 18–27 µm in diameter	9. *S. polymorphum*
12b	Cells 31–34 µm long, 28–31 µm wide	12. *S. tarnum*

1. *Stylodinium globosum* G. A. Klebs 1912, 410, 445, text-fig. 12, a–c (**Fig. 381**)

Taxonomic synonyms: *Stylodinium bavariense* Baumeister 1943b, p. 362; *Stylodinium lindemannii* Baumeister 1943b, p. 362, Table

Cells globular to ovoid, 21–40 µm in diameter. Stipe mostly 24–36 µm long. With parietal, disc-shaped to elliptic, yellow to golden-brown chloroplasts. Nucleus basal, cytoplasmic strands extend from the nucleus to the cell wall. Conspicuous lipid globule present near the nucleus. Stipe of very variable length, with basal disc and with thickening at the junction with the cell. Cell wall without any structure. Reproduction by the expulsion of aplanospore-like cell (Klebs 1912); division of cell contents into two cells of unknown fate (Thompson 1949).
Ecology: in ponds and swamps. On *Oedogonium* (Maryland) and among root hairs of *Azolla* (Indonesia), also seen in the plankton (Denmark: May–July at temperatures of 11–22 °C, pH 4.6–5.4 and a conductivity of 72–76 µS · cm^{-1}).
Geographical distribution: Denmark (Nygaard); Germany (Lindemann, Baumeister). Sierra Leone (Gerrath & Denny). USA, MD (Thompson – stipe up to 15 µm long only), OH (Carty). Bolivia (Thérézien). Botanic Garden Buitenzorg, Java (Klebs).

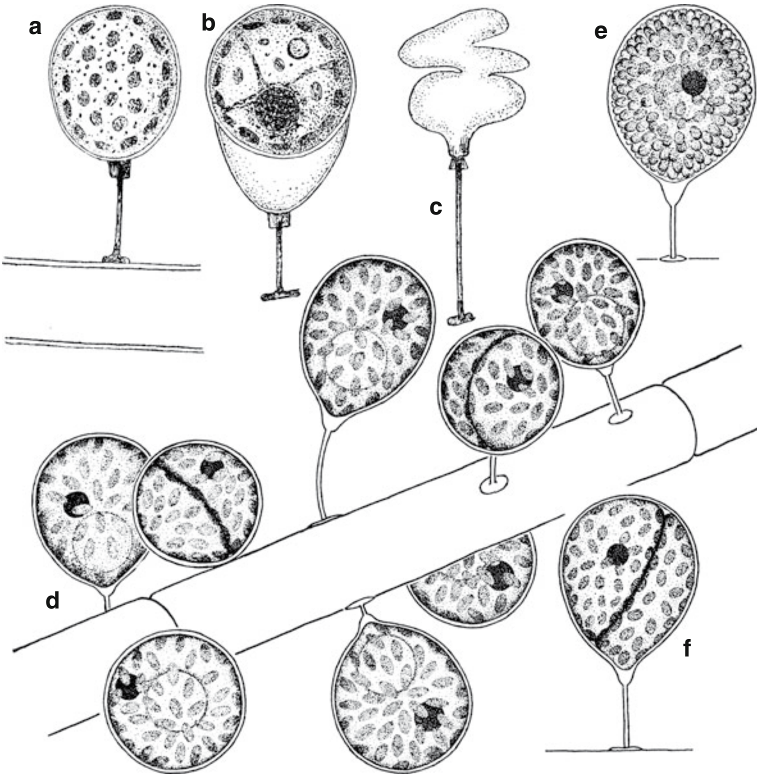

Fig. 381 *Stylodinium globosum* G. A. Klebs (**a**–**c** after Klebs 1912; **d**–**f** after Thompson 1949). **a** vegetative cell attached to root hair of *Azolla*; **b** release of cell contents surrounded by a wall; **c** empty wall from cell with long stipe; **d** group of vegetative and dividing cells attached to filamentous alga; **e** cell with radial arrangement of chloroplasts seen during initial phases of division; **f** cell with divided contents

2. *Stylodinium africanum* Bourrelly 1961, p. 297, 353, pl. 3, fig. 18 (Fig. 382)

Cells more or less conical, distal part convex, the sides with humps. Basally the cell extends to a slightly thicker part, which continues into a stipe with a basal disc. Cells 26–27 µm long (without stipe), 20–22 µm wide. Stipe 12–15 µm long. Nucleus basal, numerous parietal chloroplasts, irregularly disc-shaped. Apparently a central pyrenoid from which vacuoles and starch grains extend.
Ecology: in swamps, attached to filamentous algae.
Geographical distribution: Ivory Coast (Bourrelly). Bolivia (Thérézien).

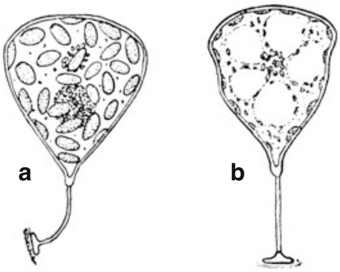

Fig. 382 *Stylodinium africanum* Bourrelly (after Bourrelly 1961). **a** surface view of vegetative cell; **b** optical section

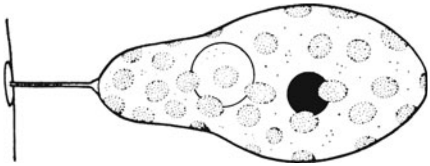

Fig. 383 *Stylodinium baumeisteri* (C. E. M. Bicudo & Skvortsov) Moestrup & Calado (after Bicudo & Skvortsov 1968)

3. *Stylodinium baumeisteri* (C. E. M. Bicudo & Skvortsov) Moestrup & Calado *comb. nov.* (**Fig. 383**)

Basionym: *Dinopodiella baumeisteri* C. E. M. Bicudo & Skvortsov 1968, *Anais Congr. Soc. Bot. Brasil XIX*, p. 36, fig. 19

Cells obpyriform, with numerous disc-shaped chloroplasts, 33–37 µm long and 18–20 µm wide. Stipe thin and delicate, with distinct discoidal holdfast, stipe length not given (*ca.* 9.5 µm, as measured in the original figure).
Ecology: in temporary pool, attached to *Oedogonium*.
Geographical distribution: Pinheiros River, São Paulo, Brazil (Bicudo & Skvortsov); Guadeloupe? (Bourrelly & Manguin).

Note: the cells from Guadeloupe (Bourrelly & Manguin 1952, as *S.* cf. *cerasiforme*) show the constriction characteristic of *S. baumeisteri*, but the distal part is slightly shorter.

4. *Stylodinium cerasiforme* Pascher 1927, p. 21, 52, fig. 19 (**Fig. 384**)

Note: Pascher (1927) noted the strong resemblance to *Characium cerasiforme* B. Eichler & Raciborski (1893, p. 299, "*cerassiforme*"), although he referred it in error to Rostafinski & Eichler and to Eichler & Rostafinzski.

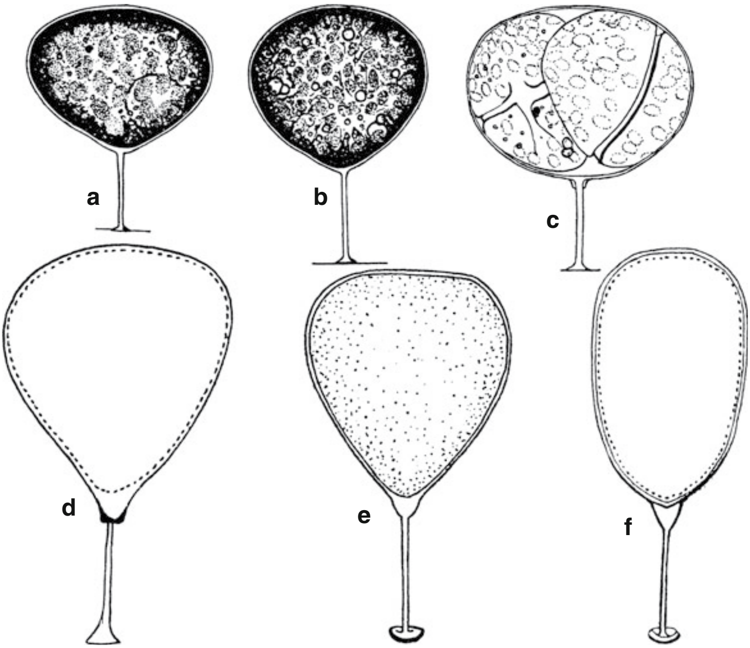

Fig. 384 *Stylodinium cerasiforme* Pascher (**a**–**c** after Pascher 1927; **d**–**f** after Wołoszyńska 1952). **a**, **b** vegetative cells with contents; **c** division stage, with two *Gymnodinium*-like zoospores before release; **d**, **e** outline of vegetative cells seen from the larger side (**d** asymmetrical cell); **f** outline of vegetative cell seen from the narrow side

Cells widely ovoid, almost as long as wide, 21–45 µm long, 17–43 µm wide. Stipe as long as, or shorter than cell. Distally widely to almost flatly rounded. Rapidly narrowing proximally. Chloroplasts very variable in size, discoidal. Propagation by formation of two *Gymnodinium*-like zoospores with eyespot.
Ecology: Pools, in Brazil attached to *Oedogonium* and occasionally *Myriophyllum.*
Geographical distribution: Holstein, Germany (Pascher); Poland (Wołoszyńska). Sierra Leone (Gerrath & Denny). Brazil (Bicudo & Skvortsov).

5. *Stylodinium gracile* (Pascher) Starmach 1974, p. 434 (**Fig. 385**)

Basionym: *Dinopodiella gracilis* Pascher 1944a, p. 393, text-fig. 14

Cells 20–30 µm long, 8–12 µm wide, bean- to kidney-shaped, cell length more than twice the cell width. Chloroplasts light brown. Pyrenoid small. Eyespot present. Stipe short (*ca.* one tenth of total cell length, as estimated from the original illustrations).

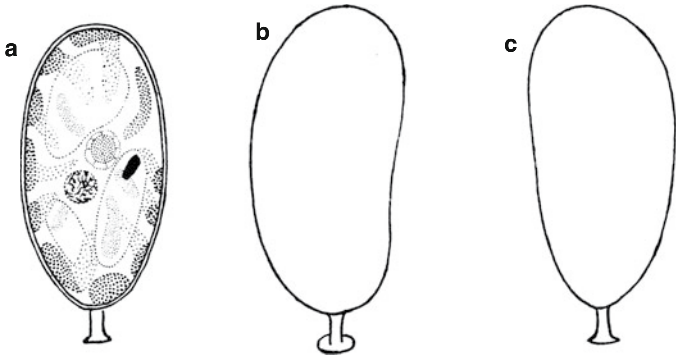

Fig. 385 *Stylodinium gracile* (Pascher) Starmach (after Pascher 1944a). **a** ventral view, cell contents from a combination of focusing planes; **b**, **c** outlines of cells in lateral view

Ecology: in ponds, epiphytic on zygnemataleans, notably *Spirogyra*.
Geographical distribution: Germany, Czech Republic (Pascher).

6. *Stylodinium grande* Jane 1945, p. 88, fig. 46 (**Fig. 386**)

Cells spherical, ca 50 µm in diameter, surrounded by thick wall, in older cells with an outer sheath visible. The sheath eventually sloughs off. Stalk 4–8 µm long, of variable thickness, arising from a little boss on the wall of the cell. The stalk terminates in a conspicuous brownish-colored pad. Numerous discoid chloroplasts in the cell periphery, sometimes extending in strands across the central vacuole. Nucleus relatively large, excentric.
Ecology: in pool in Llandegfan Common, Wales, February 1944, epiphyte chiefly on *Zygogonium ericetorum*.
Geographical distribution: Wales (Jane).

7. *Stylodinium longipes* R. H. Thompson 1949, p. 308, figs 30–34 (**Fig. 387**)

Cells more or less quadrangular in face view, elliptical or obovate in side view, oval from above, 12–28 µm wide, 15–38 µm long, 8–22 µm thick. Stipe very slender, 6–36 µm long, with conspicuous basal disc and distal thickening at the junction with the cell. Chloroplasts strap-shaped, radially arranged, golden-brown. Nucleus large, excentric. A small red lipid body usually present. Reproduction by division of cytoplasm into two cells observed, but no further details.
Ecology: in ponds and swamps.
Geographical distribution: USA, MD (Thompson). New Zealand (Thompson).

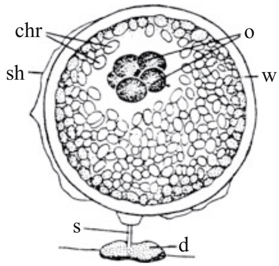

Fig. 386 *Stylodinium grande* Jane (after Jane 1945). chr, chloroplasts; d attaching disc; o oil; s, stalk (stipe); sh, sheath; w, wall

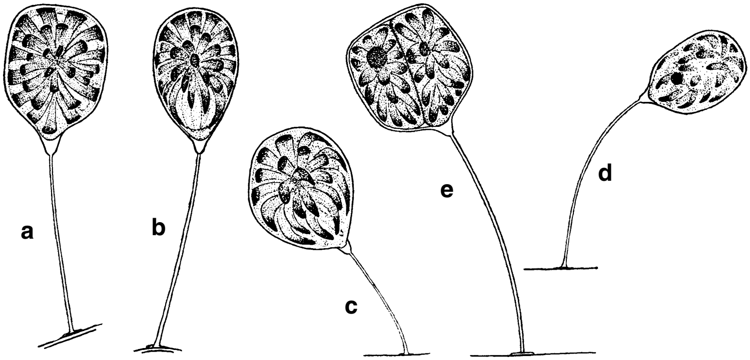

Fig. 387 *Stylodinium longipes* R. H. Thompson (after Thompson 1949). **a**–**d** vegetative cells (**a** and **b** wide and narrow side view, respectively, of the same cell); **e** division stage

8. *Stylodinium phaseolus* (Pascher) Bourrelly 1970, legend to pl. 21, figs 17–19 (**Fig. 388**)

Basionym: *Dinopodiella phaseolus* Pascher 1944a, p. 392, text-fig. 13, pl. VI, fig. g
Isonym: *Stylodinium phaseolus* (Pascher) Starmach 1974, p. 436

Cells 24–28 µm long, 17–19 µm wide, plump bean-shaped, *ca.* 1.5 times as long as broad. Stipe short, up to one tenth of the cell length. Eyespot not seen in vegetative stage. Reproduction by two zoospores with almost equal, triangular-shaped epicone and hypocone. Eyespot present in the zoospores.
Ecology: on large *Closterium*, *Spirogyra*, *Utricularia*, and on detritus.
Geographical distribution: Czech Republic (Pascher).

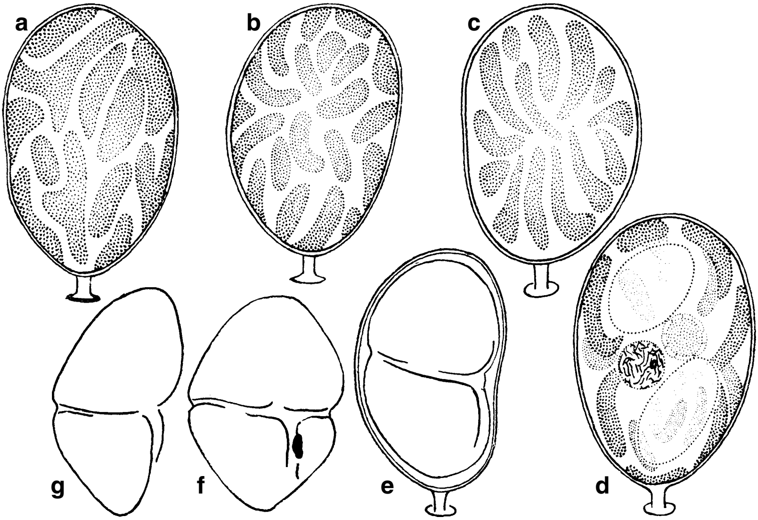

Fig. 388 *Stylodinium phaseolus* (Pascher) Bourrelly (after Pascher 1944a). **a**–**c** vegetative cells in lateral view; **d** vegetative cell in ventral view with cell contents drawn from a combination of focusing planes; **e** before formation of zoospores, already with furrows and eyespot (not shown); **f**, **g** zoospore (**g** lateral view)

9. *Stylodinium polymorphum* Baumeister 1957b, p. 27, 41, Abb. 3 (**Fig. 389**)

Cells spherical, broadly ovoid or somewhat angular. Stipe short, cone-shaped, increasing in width towards the attachment disc. Cell wall covered with amphiesmal plates, but the plate formula unknown. Cells leather brown, eyespot absent. Cell diameter 18–27 µm. Zoospores almost spherical, epi- and hypocone of similar size, central part of the cell described as brick-red ("Ziegelrot"), 20 µm long and 17 µm wide.
Ecology: epiphytic on *Oedogonium*, *Mougeotia* and other filamentous algae, apparently in a pond.
Geographical distribution: found once only, Bavaria, Germany (Baumeister).

10. *Stylodinium quadrangulare* Moestrup & Calado *nom. nov.* (**Fig. 390**)

Replaced synonym: *Dinococcus africanus* Bourrelly 1961, *Bull. Inst. Franç. Afrique Noire, A* **23,** p. 296, 352, pl. 3, fig. 16 ("*africanum*") ≡ *Stylodinium africanum* (Bourrelly) Bourrelly 1970, p. 94, *nom. illeg.* (non *Stylodinium africanum* Bourrelly 1961)

Cells 14–18 × 14–18 µm, 11 µm in thickness. Cells quadrangular in side view, the sides slightly concave, the base convex, the distal part convex or concave. Cells

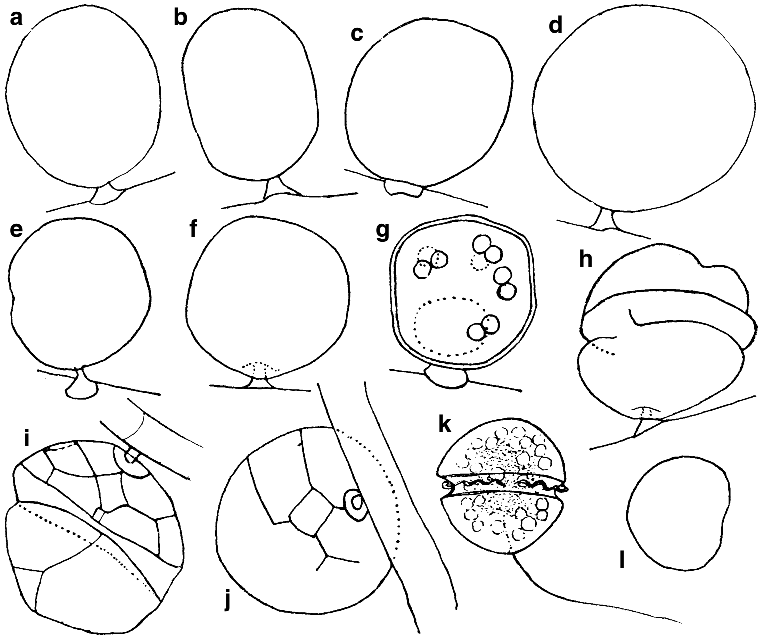

Fig. 389 *Stylodinium polymorphum* Baumeister (after Baumeister 1957b). **a**–**g** shape variation of attached cells (**g** showing cell contents); **h** non-tabulated cell envelope with furrows (presumably an old stage after zoospore attachment, in which swelling of the cell rendered plates undetectable); **i**, **j** empty cell envelopes with transverse furrow and amphiesmal plates; **k** zoospore with the central region brick-red; **l** transverse optical section of zoospore

flattened, elliptic in transverse section. Nucleus basal, chloroplasts disc-shaped, brown, extending from a centrally located pyrenoid. Attached with very short stalk that extends into an attachment disc.
Ecology: in a marshy forest.
Geographical distribution: Ivory Coast (Bourrelly).

11. ***Stylodinium sphaera*** Pascher 1944a, p. 393, text-fig. 15, pl. VI, fig. h (Fig. 391)

Cells spherical, 25–30 μm in diameter, with stalk measuring up to one fourth of the cell diameter. Eyespot present but pyrenoid not seen with certainty. Old cells with distinct red oil body. Zoospore with epicone larger than hypocone.
Ecology: on *Spirogyra*, more rarely on *Mougeotia*.
Geographical distribution: Czech Republic (Pascher).

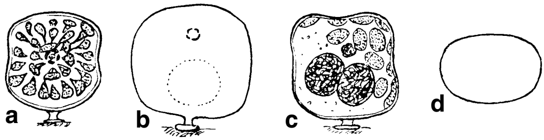

Fig. 390 *Stylodinium quadrangulare* Moestrup & Calado (after Bourrelly 1961). **a**–**c** cells viewed from the broad side (**a** radiating chloroplasts; **c** cell with two nuclei); **d** outline of apical view

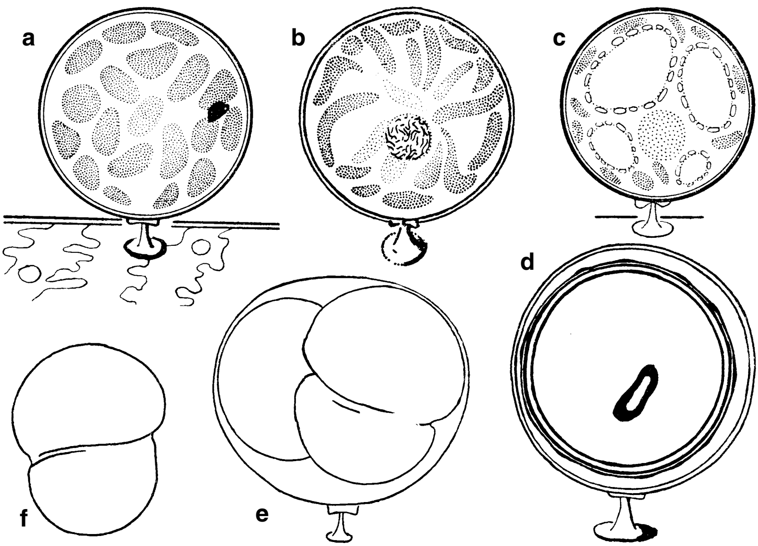

Fig. 391 *Stylodinium sphaera* Pascher (after Pascher 1944a). **a**–**c** vegetative cells with contents (**c** optical section); **d** thick-walled cyst formed inside the vegetative cell wall; **e** formation of zoospores; **f** zoospore

12. ***Stylodinium tarnum*** Baumeister 1943b, p. 354, figs 3, 4 (**Fig. 392**)

Cells globose, somewhat pointed towards the base. Stipe 7–8 µm long, delicate, widening slightly distally, forming a wide attachment disc proximally. Cells covered by amphiesmal plates, of which the plate formula was given as 5′, 3a, 8″, 7‴, 1p, 2⁗. The stipe attaches to the epicone, apparently to the apex. Cells 30–56 µm in diameter. Zoopores more or less globular, epi- and hypocone of almost the same size. Cingulum almost circular. Zoospores blackish-brown, slow swimming, 31–34 µm long, 28–31 µm wide, covered with distinct amphiesmal plates, with the same plate formula as the coccoid cell.

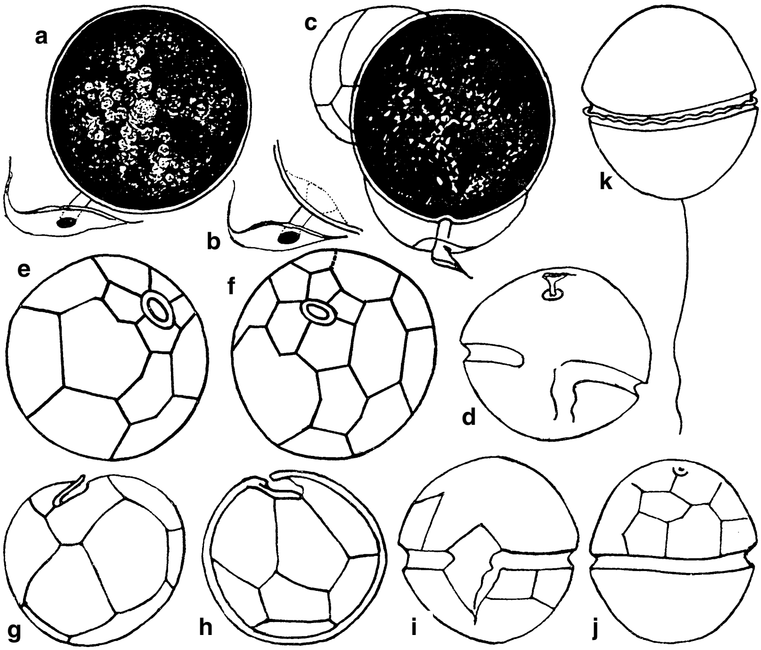

Fig. 392 *Stylodinium tarnum* Baumeister (after Baumeister 1943b). **a**, **b** cell with radial structure of protoplast, stipe and wide, flat attachment disc (**b** stipe structure); **c** cell with detaching tabulated envelope; **d** complete cell envelope with stipe attached to epitheca; **e**, **f** two views of epitheca; **g**, **h** two views of hypotheca; **i** ventral side of the theca; **j** dorsal side of the theca; **k** dorsal view of zoospore

Ecology: found under ice in a small peat pond at a pH of 5–5.5.
Geographical distribution: Bavaria, Germany (Baumeister).

Note: Bicudo & Skvortsov identified material from Brazil as belonging to this species. Cells were 21–45 µm long and 17–43 µm wide, with a stipe length of 8–15 µm. Numerous disc-shaped chloroplasts were present and cells were attached to *Utricularia* and submerged *Typha* leaves in temporary pools and water reservoirs in São Paulo (Bicudo & Skvortsov 1968). Amphiesmal plates were not mentioned. Considering the ecology of the original material from Germany, the material from Brazil may belong to a different species. Cells from Guadeloupe (Bourrelly & Mangin 1952), said to be covered with amphiesmal plates, may be similar. They also resemble *S. cerasiforme* which has not been described to be covered with amphiesmal plates (cell length 33–40 µm, width 27–37 µm, stipe length 10–11 µm).

Fig. 393 *Stylodinium truncatum* G. A. Klebs (after Klebs 1912)

13. *Stylodinium truncatum* G. A. Klebs 1912, p. 411, 445, text-fig. 12D, pl. X, fig. 4 (**Fig. 393**)

Cells somewhat compressed, triangular in side view, distal surface slightly concave. With short stipe. Cells 24–40 µm long, 20–35 µm wide, *ca.* 25 µm thick, stipe 12–20 µm long.
Ecology: in marshes and small lakes.
Geographical distribution: Mittl. Toporowy See, Tatra, Poland (Wołoszyńska). Near Batavia, Indonesia (Klebs).

Genus 10. *Tetradinium* G. A. Klebs 1912, p. 408, 444

Type species: *Tetradinium javanicum* G. A. Klebs 1912

Tetrahedral cells with 1–2 spines at each corner. Attachment stalk sometimes present, the species mainly occur as epiphytes. Reproduction by 2 autospores or zoospores seen in *T. minus* Pascher.

Note: the species concept is in need of study. Species of *Tetradinium* have apparently never been established in culture.

Key to species of *Tetradinium*:
1a Cells triangular in top view, with single spine at each corner, 12–25 µm in diameter, attached to filamentous algae by short stalk .... 3. *T. simplex*
1b Cells 20–73 µm in top view, with or without stalk, 1–2 spines at each corner 2
2a Cells distinctly tetrahedral, with a single spine at each end (rarely 2), stalk absent, cells 27–35 µm in diameter .... 2. *T. minus*
2b Cells more irregular, usually two spines at each end, a stalk often present, cells 20–73 µm in diameter .... 1. *T. javanicum*

1. *Tetradinium javanicum* G. A. Klebs 1912, p. 408, 444, pl. X, fig. 3, text-fig. 11 (**Fig. 394**)

Taxonomic synonym: *Tetradinium intermedium* Geitler 1928a, p. 2, fig. 1

Cells more or less tetrahedral, but highly variable. Cell wall dark, at each of the four corners with two, usually unequal, slightly curved spines. Often with shorter or longer stalk, which widens distally into an attachment disc (cf. *Stylodinium*). Spines are used for attachment. Nucleus located centrally or closer to the cell wall. Numerous yellow, parietal chloroplasts. Cell contents seen to divide into two naked cells. Cell size 20–73 µm in diameter, excluding horns.
Ecology: in wooden water container in the Botanical Garden at Buitenzorg, Java, attached to root hairs of *Azolla*, in small ponds attached to *Oedogonium*, *Myriophyllum* and *Potamogeton* (Maryland, Thompson), ponds and temporary pools, acid sphagnum bogs, small lakes.
Geographical distribution: Austria (Geitler); France (Bourrelly); Tatra, Poland (Wołoszyńska). Ivory Coast (Bourrelly); Mali (Bourrelly); Sierra Leone (Gerrath & Denny). USA, MD (Thompson), OH (Taft, Carty). Brazil (Bicudo & Skvortsov). China (Liu & Hu); Indonesia (Klebs); Japan (Akiyama). New Zealand (Thompson).

Note: Thérézien (1985, p. 34, pl. IV, fig. 8) created *Tetradinium intermedium* var. *longipes* for cells from French Guiana with stipe length 18–22 µm.

2. *Tetradinium minus* Pascher 1927, p. 22, 52, figs 21, 23, 24 (**Fig. 395**)

With single (rarely two) spines at each corner. One side flat or sometimes concave, the others convex. Chloroplasts discoid, somewhat angular. Zoospores released through a slit in the wall, epicone slightly larger and more elongate than the nearly hemispherical hypocone. Sulcus continues for a short distance onto the epicone. With distinct eyespot. Coccoid cells 27–35 µm wide.
Ecology: ponds and bogs; Danish material found at 20–22 °C and pH 6.6–6.8.
Geographical distribution: Austria (Pascher); Denmark (Nygaard).

3. *Tetradinium simplex* Prescott *in* Prescott *et al.* 1949, p. 89, 93, pl. 2, figs 13, 14 (**Fig. 396**)

Cells inversely triangular in lateral view, with very short central stipe. Dorsal margin broadly convex in lateral view. In top view cells triangular, each corner with downward pointing short spine. Reproduction unknown. Cells 12–25 µm in diameter, 12–20 µm high.
Ecology: On filamentous algae in shallow acid pond.
Geographical distribution: USA, MI (Prescott).

Note: very incompletely described species.

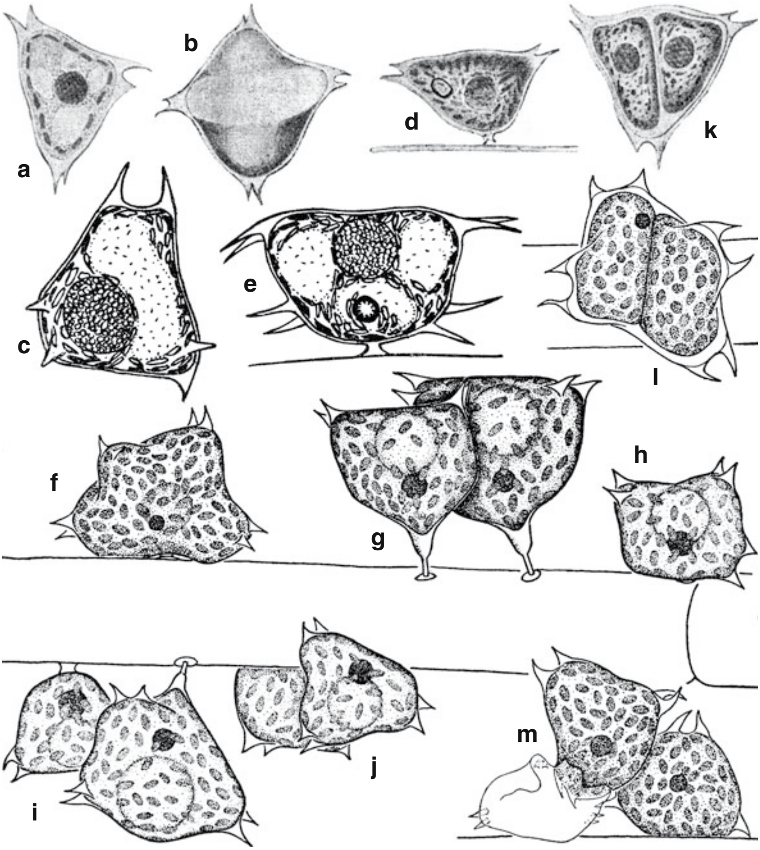

Fig. 394 *Tetradinium javanicum* G. A. Klebs (**a**, **b**, **d**, **k** after Klebs 1912; **c**, **e** after Geitler 1928a; **f**–**j**, **l**, **m** after Thompson 1949). **a**–**c** unattached vegetative cells; **d**–**j** attached vegetative cells (**d** wall spine attached to root hair of *Azolla*); **k**, **l** dividing cells; **m** release of autospores from ruptured parental cell wall

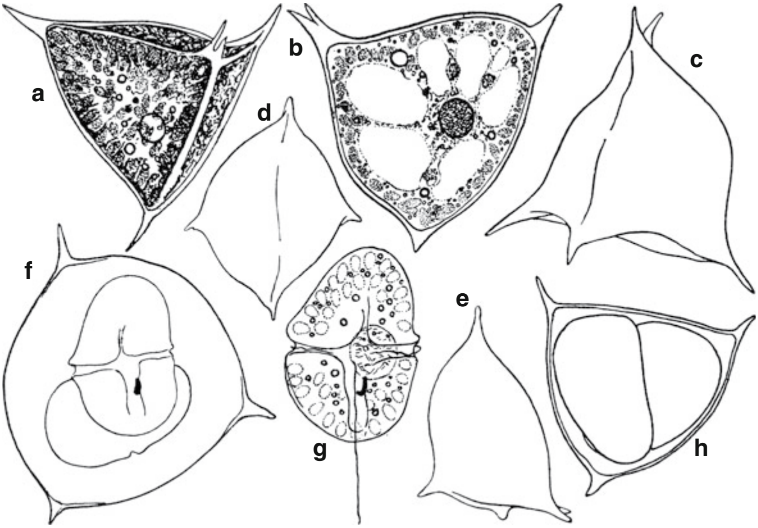

Fig. 395 *Tetradinium minus* Pascher (after Pascher 1927). **a**, **b** vegetative cells with contents (**b** optical section); **c**–**e** outlines of vegetative cells; **f** the two zoospores inside a swollen cell; **g** zoospore; **h** division stage, cell not yet swollen

Fig. 396 *Tetradinium simplex* Prescott (after Prescott *et al.* 1949). **a**, **b** front view of vegetative cells; **c** top view of vegetative cell

Order 11. GLOEODINIALES A. R. Loeblich 1970, pp 880, 903

Coccoid dinoflagellates covered by thick multi-layered wall. In one genus, reproduction is by zoospores, but the life cycle is not known. In 1924, Killian discovered that the zoospores resemble the genus *Hemidinium* and this resulted in the belief that *Hemidinium* was part of the life cycle of *Gloeodinium*. It is now known that they constitute two different genera, which are only distantly related (Moestrup & Daugbjerg 2007). In *Gloeodinium* the motile cells are short-lived zoospores, covered with amphiesmal plates, while species of *Hemidinium* are true flagellates that lack plates. Superficially they are similar. The coccoid stage is the dominant stage and may not represent a resting stage.

Family 1. Gloeodiniaceae Pascher *ex* J. Schiller 1937, p. 482

With the characters of the order.
Whether the two genera *Gloeodinium* and *Rufusiella* can be contained in the same family in future classifications awaits additional information.

Key to genera of Gloeodiniaceae:
1a Cells embedded in mucilage .... 1. *Gloeodinium*
1b Cells located at the end of mucilage tubes .... 2. *Rufusiella*

Genus 1. *Gloeodinium* G. A. Klebs 1912, pp 411, 445

Type species: *Gloeodinium montanum* G. A. Klebs 1912

Reproduces by zoospores that rapidly germinate into new coccoid cells. The zoospores are covered with distinct, often fairly large plates, but plate pattern is not readily interpreted following the Kofoidian system.

Key to species of *Gloeodinium*:
1a Cells 25–43 µm long, in peat bogs and mountain puddles .... 1. *G. montanum*
1b Cells 7–14 µm long, on damp walls .... 2. *G. cracoviense*

1. *Gloeodinium montanum* G. A. Klebs 1912, p. 414, 445, text-fig. 13, pl. X, fig. 5 (**Fig. 397**)

Cells spherical or ellipsoid, surrounded by thick cell wall of cellulose and mucilage. Cells may be solitary or form colonies of 2–4, or occasionally more cells. Numerous brown chloroplasts, close together, individual chloroplasts not always distinguishable, but the chloroplasts often appear to be radially arranged. No eyespot, nor any sign of furrow and cingulum. Nucleus near the wall. Orange-red lipid droplets occur commonly. Cell division by fission. The two daughter cells form new walls inside the parent cell wall, which persists as a layered structure. Cell length (without wall) 25–43 µm, width 19–25 µm. The colonies may reach 60 µm or more.
Zoospores are elongate kidney-shaped. The cingulum extends from the mid-ventral side to the mid-dorsal side, somewhat descending. Sulcus reaches almost to the antapex, widening antapically. Asexual reproduction by *Hemidinium*-like zoospores, which rapidly germinate into new coccoid cells. Length of zoospores (24–)30–40 µm, rarely 50 µm, width 16–17 µm. Each zoospore with periplast of plates which are visible in the light microscope, at least following staining. Nearly 20 plates present, excluding those of the cingulum and sulcus, but plate pattern is not readily interpreted following the Kofoidian system. Right rim of the sulcus lined by three plates, of which the middle one is the shortest. Cingulum composed of 4–5 plates, sulcus probably also of 4–5 plates.

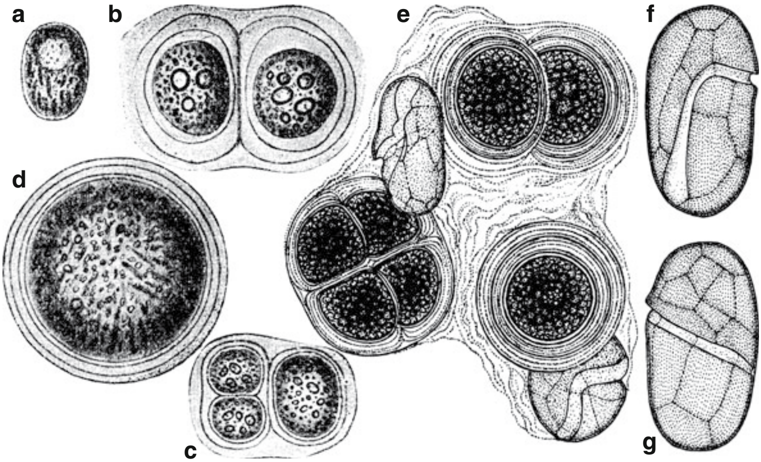

Fig. 397 *Gloeodinium montanum* G. A. Klebs (**a**–**d** after Klebs 1912; **e**–**g** after Skuja 1976). **a** young cell with band-shaped chloroplasts and the nucleus near one end; **b**, **c** groups of cells embedded in layered mucilage; **d** large cell in layered mucilage; **e** groups of cells in mucilage, with remnants of the amphiesma of mobile cells; **f**, **g** ventral and dorsal views of the amphiesma of mobile cells showing plate arrangement

Ecology: typical of acid (pH down to 3.6), brown-watered peat bogs, growing on the peat together with desmids, etc.; also in somewhat acidic mountain puddles. Tolerates low nutrients, low light and seasonal drought (Hosiaisluoma 1975).
Geographical distribution: Austria (Ettl); Denmark (Moestrup, unpublished); Finland (Hosiaisluoma); France (Killian; Frémy & Guinochet); Germany (Höll; Baumeister); Poland (Wołoszyńska); Portugal (Rino; Pandeirada *et al.*); Switzerland (Klebs). USA (Thompson; Kelly & Pfiester?; Pfiester & Highfill?). Brazil (Bicudo & Skvortsov). Java, Sumatra (Lindemann). New Zealand (Skuja).

Note: available evidence suggests that the described species of this genus are primarily coccoid and that the zoospore is a short-lived reproductive stage. Empty thecae embedded in the mucilage of the coccoid cells have been illustrated from several parts of the world (Killian 1924; Popovský 1971; Skuja 1976; Pfiester & Highfill 1993). True flagellates with a visible plate pattern somewhat like that of the zoospore of *Gloeodinium montanum* have been described from marine waters, but their phylogenetic relationship to *Gloeodinium* is unknown.

var. *tatricum* (Wołoszyńska) Moestrup *comb. nov.* (**Fig. 398**)
Basionym: *Hemidinium nasutum* var. *tatricum* Wołoszyńska 1930a, *Acta Soc. Bot. Poloniae* **7**, pp 500, 504, pl. XXVII, figs 1–8

In the motile cells, the right edge of the sulcus is lined by 3 plates of which the middle one is very long.

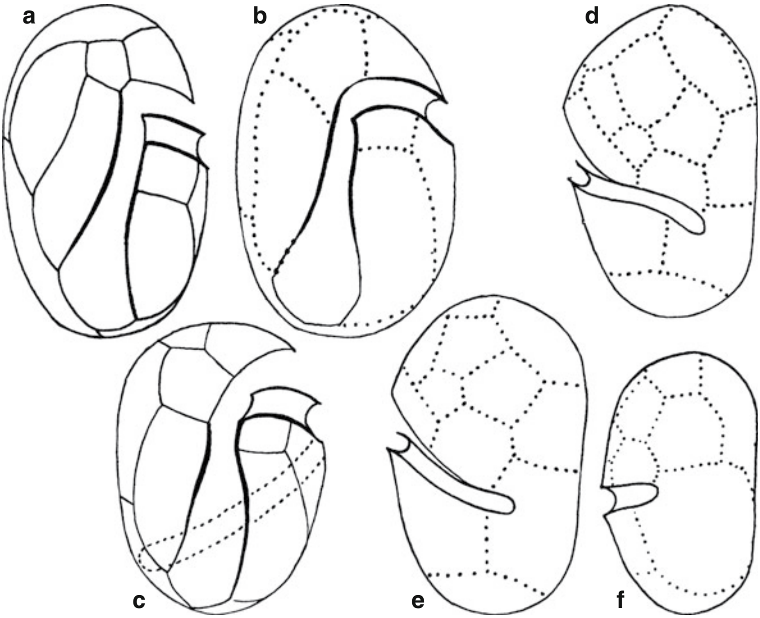

Fig. 398 *Gloeodinium montanum* var. *tatricum* (Wołoszyńska) Moestrup (after Wołoszyńska 1930a). **a**–**c** ventral views with main amphiesmal plates and dorsal path of cingulum marked with dotted line in **c**; **d**–**f** dorsal views with outline of main plates

Ecology: in peat bogs.
Geographical distribution: Poland.

2. *Gloeodinium cracoviense* Starmach 1963, p. 339, text-fig. 2, pl. II (**Fig. 399**)

Cells globular to elliptic, surrounded by several lamellate wall layers and forming loose aggregates or colonies. Chloroplasts golden-yellow, indistinct. Large filiform nucleus at the center or near the wall. Outer layers inflated, peeling off. Cell size without wall layers 7–10 µm, with wall layers 9–14 µm. Reproduction by cell division and by formation of 2–8 autospores. At cell division the daughter cells form new wall layers within the mother cell. They gradually increase in size and the mother cell wall eventually ruptures. Motile cells unknown.
Ecology: between cyanobacteria on the damp walls of Twardowski Cave in Poland, a limestone cave in the banks of the Vistula River.
Geographical distribution: Poland.

Note: *Gloeodinium cracoviense* was also reported from Cuba, with cells up to 25 µm long (Popovský 1970). However, it was found in a 2.5-ha pond with surface temperature 32 °C and pH 7.4, and it is therefore uncertain whether it was the same species.

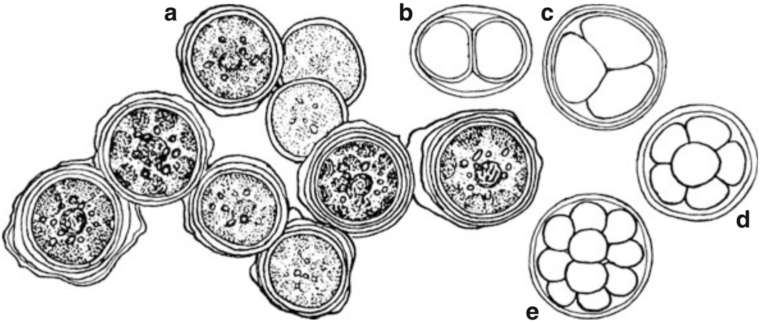

Fig. 399 *Gloeodinium cracoviense* Starmach (after Starmach 1963). **a** group of cells with the outermost cover layers peeling off; **b**–**e** reproduction by formation of 2, 4, 8 and 16 autospores, respectively

Genus 2. *Rufusiella* A. R. Loeblich *in* Christensen 1978, p. 68

Type species: *Rufusiella insignis* (Hassal) A. R. Loeblich

Cells spherical or ovoid, embedded in multilayered wall and successively discarding old walls in one direction, thus becoming located at the end of a stalk of discarded walls. Cells often with red globules. Propagation by bipartition or by division into 4 cells. Zoospores have been described as gymnodinioid or hemidinioid. Insufficiently studied genus with a single species in fresh water and one in the sea.

1. ***Rufusiella insignis*** (Hassall) A. R. Loeblich *in* Christensen 1978, p. 68 (**Fig. 400**)

Basionym: *Haematococcus insignis* Hassall 1845, p. 324, pl. LXXX, figs 6a, 6b
Nomenclatural synonyms: *Urococcus insignis* (Hassall) Kützing 1849, p. 207 ≡ *Hassallia insignis* (Hassall) Trevisan 1848, p. 67 ≡ *Ouracoccus insignis* (Hassall) Loeblich & A. R. Loeblich 1966, p. 43

Cells spherical, embedded in multilayered mucilage and located at the end of layered, mucilaginous tubes.
Ecology: found in scrapings from wet rocks, sometimes growing on filamentous algae (usually *Trentepohlia* sp.), or mosses. Also found on lichens growing on the bark of beech trees (Handa *et al.* 2013).
Geographical distribution: England (Hassall). USA, KS, TN (Carty 2014). Japan (Handa *et al.*).
On the basis of unpublished information, the species known as *Hemidinium ochraceum* Levander is here included in the Gloeodiniales. A more complete description of the species is being prepared for publication. We postpone a name change because it is still not clear to which genus the species belongs.

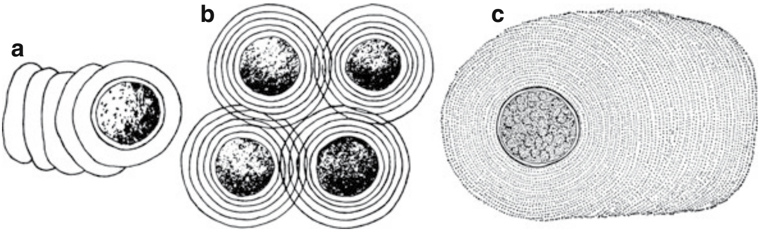

Fig. 400 *Rufusiella insignis* (Hassal) A. R. Loeblich (**a**, **b** after Hassal 1845; **c** after Thompson *in* Smith 1950). **a** cell at the end of a series of consecutively formed layers; **b** group of cells embedded in multiple layers (top view?); **c** cell in asymmetrically arranged layered envelope

2. "*Hemidinium ochraceum*" Levander 1900, p. 103, fig. 2 ("*ochraceus*") (**Fig. 401**)

Cells occur in two stages, a coccoid stage and a zoospore stage. Coccoid cells are spherical, occasionally elongate, the latter probably in preparation for division. Cells yellowish green with reddish brown center. With central stellate chloroplast with thin arms that reach the cell periphery, frequently flattening towards the surface. Chloroplast with central pyrenoid. Cells on average *ca.* 31 µm in diameter.
The zoospores are rounded-oval, slightly flattened dorsoventrally. Epicone smaller than hypocone. Cingulum incomplete, its origin is relatively close to the cell apex, and on the dorsal side it is directed towards the antapical end but reaching only half way. Nucleus in the posterior end. With red body near the apex of the epicone. Brown deposit fills most of the epicone and hypocone, leaving only the posterior part of the hypocone free. Cell length 26–33 µm, width 23–26 µm. Cells may swim for long periods, rotating around the longitudinal axis.
Divides during the coccoid stage.
SEM: Hansen *et al.* (in prep.).
TEM: Hansen *et al.* (in prep.).
DNA data: Hansen *et al.* (in prep.).
Ecology: typically in ephemeral rainwater rock pools without vegetation, forming a rust-colored line near the water line of the pools, and extending for some centimeters down into the pool. Occasionally in pools with some vegetation, or in pools above the sea level receiving some splash from the very low-salinity seawater. Survives desiccation when the pool dries out and will form zoospores if rewetted.
Geographical distribution: south-western Finland (Levander, Droop).

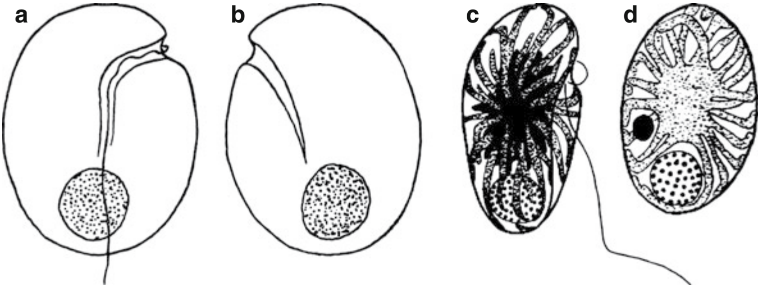

Fig. 401 "*Hemidinium ochraceum*" Levander (**a**, **b** after Levander 1900; **c**, **d** after Droop 1953). **a** ventral view; **b** dorsal view; **c** lateral view showing chloroplast lobes and orange-pigmented oil (represented in black); **d** optical section

Order 12. PROROCENTRALES Lemmermann 1910, p. 679 ("Prorocentrineae")

Cells surrounded by two lateral, watchglass-shaped plates and a number of very small plates around the two flagella, which insert anteriorly. One flagellum moves anteriorly, the other transversely or posteriorly. During cell division, each cell takes over one amphiesmal plate and forms a new one (Fensome *et al.* 1993). Occasionally, both plates are shed as the cell forms a whole new amphiesma inside the old one.

Family 1. Prorocentraceae F. Stein 1883, p. 8, 17 ("Prorocentrinen")

With the characters of the order.

Genus 1. *Prorocentrum* Ehrenberg 1834, p. 307

Type species: *Prorocentrum micans* Ehrenberg 1834, p. 307 (marine)

Cell body surrounded by two large amphiesmal plates (valves). Cells flattened, with two flagella inserting in an anterior notch, the notch covered by a number of small amphiesmal plates. Usually with two parietal chloroplasts and 0–2 centrally located pyrenoids.

A genus of mainly marine species, three species described from fresh water. One of these, *Prorocentrum manshuricum* Skvortsov (1958, p. 193, pl. 5, fig. 28), was described as non-compressed and with many chloroplasts. It is unlikely to belong in *Prorocentrum*, but its identity is uncertain. Thompson (1951) reported "*Exuviaella compressa*" from fresh water in Maryland. However this name is based on *Pyxidic-*

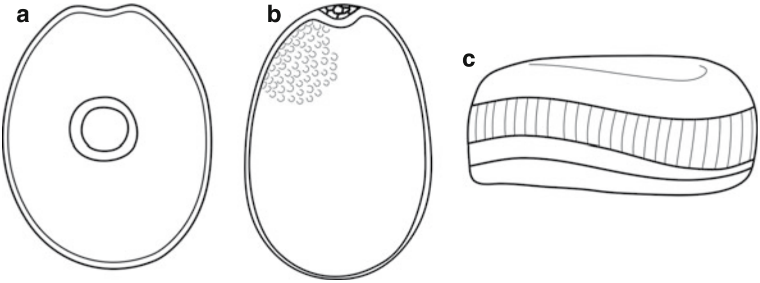

Fig. 402 *Prorocentrum foveolatum* Croome & P. A. Tyler (**a**, **c** original drawings from LM and SEM information in Croome & Tyler 1987; **b** original, from SEM information in Pearce & Hallegraeff 2004). **a** cell outline with central pyrenoid; **b** cell surface with nearly contiguous depressions (marked only on top left); **c** lateral view with intercalary band transversely striated and sinuous (striations on rim of lower valve not visible)

ula compressa Bailey (1851, p. 40, pl. 2, figs 13, 14), a diatom (Cowan & Huisman 2015). The identity of Thompson's material is uncertain. Playfair (1920, 1923) reported "*Exuviella lima*" from several freshwater bodies in Australia and one in New Zealand, but the finding of this marine species in freshwater environments such as Centennial Park and Sydney Botanical Gardens needs to be confirmed.

Key to species of *Prorocentrum* occurring in fresh water:

1a Cells with 1–2 central pyrenoids, 25–30 µm long; intercalary band generally sinuous and not projecting laterally .... 1. *P. foveolatum*

1b Cells without pyrenoids, 39–51 µm long; intercalary band straight, projecting as a smooth flange around the cell .... 2. *P. playfairii*

1. *Prorocentrum foveolatum* Croome & P. A. Tyler 1987, p. 71, figs 3, 4, 12–16 ("*foveolata*") (**Fig. 402**)

Taxonomic synonym: *Exuviaella lima* var. *scrobiculata* Playfair 1920, p. 817

Cells ovate to elliptical in valve view with rounded posterior end. Flagellar end with central notch. Cells slightly arcuate in dorsal and ventral view. With 1–2 central pyrenoids. Valve surface evenly ornamented with depressions (scrobiculate). Intercalary band broad, transversely striated, sinuous. Cell length 25–30 µm, width 18–25 µm, thickness 13 µm.
SEM: Croome & Tyler (1987), Ling *et al.* (1989), Pearce & Hallegraeff (2004).
DNA data: Pearce & Hallegraeff (2004), Logares *et al.* (2007b).
Ecology: in coastal lagoons (salinity 0–4 psu) in Tasmania (Croome & Tyler 1987; Pearce & Hallegraeff 2004), in fresh water in south-eastern Australia (Playfair 1920) and New Zealand (Playfair 1923). In culture *P. foveolatum* grew successfully at salinities between 0 and 20 psu and temperatures 10–20(–25)˚C, but tolerated salinities up to 30 psu. Maximum growth rate observed was 0.47 divisions per

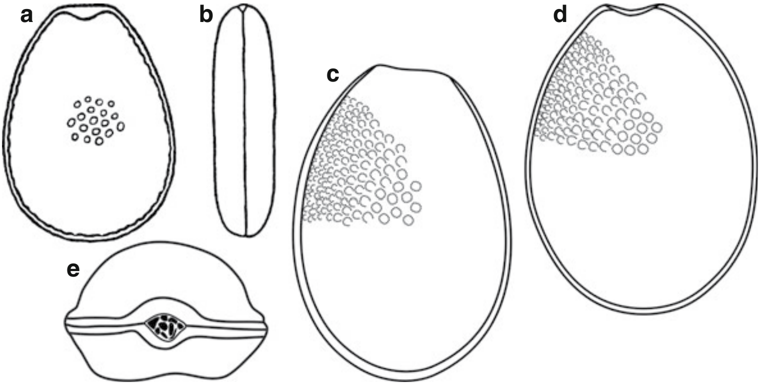

Fig. 403 *Prorocentrum playfairii* Croome & P. A. Tyler (**a**, **b** after Playfair 1920; **c**–**e** original, from SEM information in Croome & Tyler 1987). **a** cell outline with surface depressions marked in the central area of the plate (valve); **b** lateral view; **c**, **d** valve views with ornamentation partially represented; **e** front view showing platelets in the flagellar emergence area, the convex-concave outline and the somewhat projecting rim at the edge of one of the valves

day (Pearce & Hallegraeff 2004). Cells occurred in the water column and were not obviously associated with aquatic vegetation. *Prorocentrum foveolatum* was found to be phylogenetically related to the *P. lima* group of *Prorocentrum*, but no toxicity was found (Pearce & Hallegraeff 2004).
Geographical distribution: Australia. North Island of New Zealand.

2. *Prorocentrum playfairii* Croome & P. A. Tyler 1987, p. 68, figs 2, 5–11 ("*playfairi*") (**Fig. 403**)

Taxonomic synonym: *Exuviaella lima* var. *major* Playfair 1920, p. 818, text-figs 18c, 18d

Cells broadly ovate in valve view. Flagellar end with central notch where the flagella insert. The left valve convex, the right valve slightly concave in its mid region. Both valves with evenly scattered depressions on the entire surface. The intercalary band appears as a smooth flange around the cell. One flagellum held straight, *ca.* 50 µm long, the other sinuous, *ca.* 35 µm long. A prominent nucleus present near the antapical end. Two reticulate chloroplasts, pyrenoids not observed. The two valves frequently separate. Cell length 39–51 µm, width 29–40 µm, *ca.* 20 µm thick.
SEM: Croome & Tyler (1987), Ling *et al.* (1989), Pearce & Hallegraeff (2004).
DNA data: Pearce & Hallegraeff (2004), Logares *et al.* (2007b).

Ecology: in freshwater lakes and dystrophic coastal lagoons, pH 4.2–5.6, conductivity 42–950 $\mu S \cdot cm^{-1}$. It occurs in the water column but was found in higher numbers associated with aquatic vegetation. At its localities in Tasmania the highest concentration of cells was during the austral summer (November), nearly always in fresh water. In laboratory experiments it grew at salinities of 0–5 psu and temperature 10–30 °C and did not tolerate higher salinities. Maximum growth rate was 0.09 divisions per day. *Prorocentrum playfairii* was found to be phylogenetically related to the *P. lima* group of *Prorocentrum*, but no toxicity was found (Pearce & Hallegraeff 2004).
Geographical distribution: Australia. North Island of New Zealand.