

Life cycles, phylogeny and taxonomy of *Dissodinium* and *Pyrocystis* (Dinophyta)

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ABSTRACT: Life cycles of several species belonging to the marine genera *Dissodinium* Klebs in Pascher and *Pyrocystis* Murray ex Haeckel are described. The two known species of *Dissodinium*, *D. pseudolunula* Swift ex Elbr. & Dreb., (= *D. lunula* auct. nonnull.) and *D. pseudocalani* (Gönnert) Dreb. ex Elbr. & Dreb. are ectoparasites of copepod eggs. In this genus, sporogenesis, with obligate sequence from primary cyst to secondary cyst to dinospores, occurs by palintomy. *Dissodinium* is placed into the order Blastodinales Schiller and its position in this order is discussed. The asexual life cycle of *Pyrocystis* spp. represents an alternation between a dominating coccoid stage and a morphologically different transitory reproductive stage. The reproductive bodies may be either athecate aplanospores, athecate uni- or biflagellate planospores or thecate biflagellate planospores. Thecal morphology of thecate planospores resembles those of *Gonyaulax* Diesing. The occurrence of both, athecate aplanospores and thecate planospores in the same species, is discussed. *Pyrocystis* is regarded as belonging to the order Pyrocystales Apstein. The possible derivation from the Gonyaulacaceae Lindemann is suggested. In addition, the genera *Dissodinium* and *Pyrocystis* are redefined. A description of *D. pseudolunula* as well as a list of synonyms and references for detailed descriptions of *P. lunula* (Schütt) Schütt, not including *D. pseudolunula*, is given.

INTRODUCTION

The occurrence of lunate cysts of somewhat similar size and shape during certain stages in the life cycles of *Dissodinium pseudolunula* Swift ex Elbr. & Dreb. and *Pyrocystis lunula* (Schütt) Schütt misled Schütt (1895, 1896) to include stages of both species in his original description of the latter, and so have done most subsequent authors. *D. pseudolunula* was not separated at the species level before 1973, however, even in this description not all the features included apply to *D. pseudolunula* (Swift, 1973). Until now, there has been a discussion as to whether these two species should be separated at the genus level. Furthermore, the characters for separating the genera *Dissodinium* Klebs in Pascher and *Pyrocystis* Murray ex Haeckel are still under discussion (Taylor, 1972, 1976). As only a few investigators are familiar with both genera, and the species *D. pseudolunula* and *P. lunula* are particularly confusing, taxonomic use is unsettled.

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The following review of the life cycles determined from species of both genera, is based on personal knowledge of *D. pseudolunula* and *P. lunula* as well as of some other species in this group, on fixed material of several *Pyrocystis* clones cultivated by Dr. Swift (Kingston, Rhode Island, USA) and on an intensive literature survey. One purpose of this paper was to show the probability that *D. pseudolunula* may be a parasite. And indeed, during completion of the manuscript, the second author was fortunate to discover the parasitic stage of this species. Details of the latter will be communicated in a separate paper (Drebes, in prep.).

This review leads us to some taxonomic conclusions and phylogenetic suggestions. In the chapter 'Taxonomy' new definitions of the genera *Dissodinium* and *Pyrocystis*

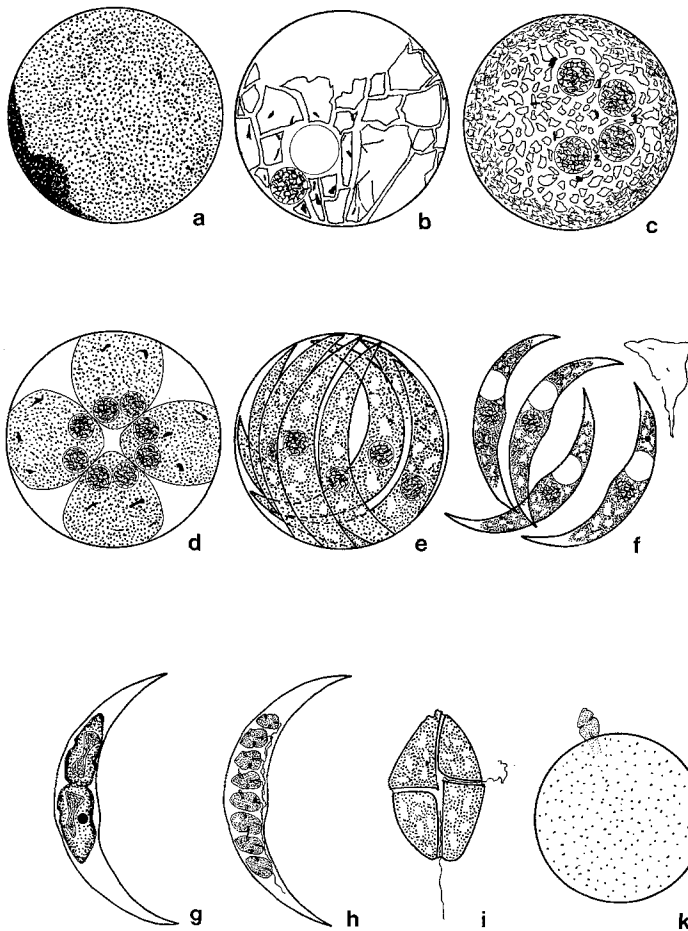


Fig. 1: *Dissodinium pseudolunula*, asexual life cycle. *a* young primary cyst filled with host material; *b* primary cyst, progressive resorption of the host material; *c* primary cyst starting nuclear divisions to form secondary cysts; *d-e* formation of lunate secondary cysts; *f* release of the secondary cysts by lysis of the primary cyst wall; *g-h* secondary cyst forming dinospores; *i* structure of a dinospore; *k* dinospore attached to a copepod egg (host)

are given and there is a revised description of *Dissodinium pseudolunula*. The synonymy of *D. pseudocalani* and *Pyrocystis lunula* is provided.

In the following, the names we consider to be correct are used, regardless what the cited author has called the species. This serves to clarify the confusing material. As complete references are given in the literature cited, the reader can follow these changes.

ON THE HISTORY OF THE GENERA *PYROCYSTIS* AND *DISSODINIUM*

Murray (1876) described two organisms which he named *Pyrocystis pseudonoctiluca* (Wyville Thomson) and *P. fusiformis* (Wyville Thomson). These names are not validly published (International Code of Botanical Nomenclature = ICBN, art. 34, 41; Stafleu, 1972). Murray (1885) published the same figures but replaced the name *P. pseudonoctiluca* by *P. noctiluca*. Haeckel (1890) separated *P. fusiformis* at genus level from *P. noctiluca*. Giving a short diagnosis for the now monotypic genus *Pyrocystis*, the date of valid publication of *Pyrocystis* is 1890. The correct citation has to be *Pyrocystis* Murray ex Haeckel (ICBN art. 41, 46 rec. C.). Haeckel (1890) used the combination *P. notiluca*. Thus the correct name of this species has to be *Pyrocystis noctiluca* Murray ex

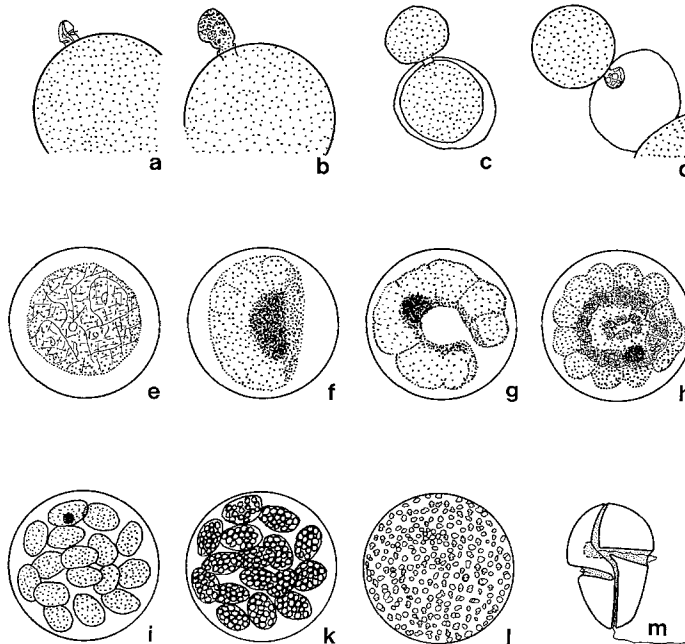


Fig. 2: *Dissodinium pseudocalani*, asexual life cycle. *a* dinospore attached to a copepod egg (host); *b-d* hypertrophic life phase, the dinospore forms a sucker organelle by which the egg material is incorporated, the parasite swells to a large spherical bladder; *e* primary cyst; *f-i* formation of secondary cysts; *k* cyst with 16 secondary cysts just forming dinospores; *l* after lysis of the secondary cyst walls the dinospores are swarming around inside the still intact primary cyst wall; *m* structure of a dinospore

Haeckel (ICBN art. 6, 12, 43, 46 rec. C.). Nevertheless, the name *P. pseudonocutiluca* has been used extensively. Haeckel created the new monotypic genus *Murracystis* Haeckel for *P. fusiformis*. Thus the date of valid publication of this species is 1890, and hence the correct name would be *M. fusiformis* Wyville Thomson in Murray ex Haeckel. Blackman (1902) was the first author after the valid species description who redescribed the species but using *Pyrocystis* as generic name. If this species is regarded as congeneric with *P. noctiluca*, as generally accepted today, the correct citation has to be *P. fusiformis* (Wyville Thomsen ex Haeckel) Blackman. These nomenclatural problems were also discussed by Taylor (1972, 1976) but with different results. As to other *Pyrocystis* species described later by various authors, see Schiller (1937), Sournia (1973), and Taylor (1976).

In his plates 24 and 25, Figs 80₁₋₁₄, Schütt (1895) figured, what he called *Gymnodinium lunula* n. sp. These figures comprise at least two different species. In 1896, he renamed his *G. lunula*, *Pyrocystis lunula*. In his Figure 2 F he reproduced a figure originating from Pouchet (1885) as "Kyste en forme croissant". Unfortunately, this form does not belong to *P. lunula* (Schütt) Schütt but to what is now named *Dissodinium pseudolunula*. The same applies to the species Schütt (1895) figured on his plate 24 Figs 80₂, 80₅. As these two species include a similar shaped lunate stage (see Figs 1, 5) in their quite different life cycles, subsequent authors applied the name *Pyrocystis* (*Gymnodinium*) *lunula* to different species. About the same time Apstein (1906, as *P. lunula*), Dogiel (1906, as *Gymnodinium lunula*) and Wright (1907, as *P. lunula*) independently published figures of the species now called *Dissodinium pseudolunula*. But Apstein (1906, 1909) included in his description the observations of Schütt for *P. lunula*. Figures 18–20 of Dogiel, 1906, also apply to *P. lunula*.

Klebs (1912) recognized that the species of Dogiel (1906) did not belong to the same genus as the species figured by Murray. Therefore, he established the new genus *Diplodinium*, including the species with *Gymnodinium*-like planospores. He restricted *Pyrocystis* to those species which reproduce by aplanospores. But he designated all figures given by Dogiel (1906) as type of *Diplodinium lunula*, including *Pyrocystis lunula*. As *Diplodinium* Klebs 1912 is a later homonym of *Diplodinium* Schubert 1888 and *Diplodinium* Fiorentini 1890, this genus was renamed *Dissodinium* Klebs in Pascher (Pascher, 1916). Since that time the names *Pyrocystis* and *Dissodinium* have been used as synonyms. Schiller (1937), discussing this problem, added to the species of *Pyrocystis* the generic name *Dissodinium* in parenthesis.

Taylor (1972) discovered unpublished figures of Kofoid and Michener representing thecate stages inside the coccoid cells of *Pyrocystis noctiluca* and *P. fusiformis*. In samples from the Indian Ocean he found additional material of such thecate planospores of both species. Based on this, Taylor (1972) emended the genera *Pyrocystis* and *Dissodinium*. *Pyrocystis* was characterized by those species with "Motile stage visibly thecate, with a tabulation resembling *Gonyaulax* Diesing" and "Motile cells . . . arise within secondary cysts, which in turn arise from primary cysts". *Dissodinium* was characterized by having *Gymnodinium*- or *Gyrodinium*-like planospores. As type of *Dissodinium*, Taylor designated *D. lunula* (Schütt) Pascher, synonym: *Pyrocystis lunula* (Schütt) Schütt . . . The latter taxon is now known (since Swift, 1973) to be a mixture of different species which we regard to belong even to different orders. Taylor (1976),

following his conception of both genera, introduced some new combinations, restricting the genus *Pyrocystis* to those taxa possessing a thecate motile stage, and assigning the remainder to *Dissodinium*.

Culture investigations on the life cycles of *Pyrocystis lunula* and of several other species of the genus *Pyrocystis* (as recognized here) by Swift & Durbin (1971), Bouquaheux (1972), Swift & Wall (1972), and Drebes (1974a) have shown that normal asexual reproduction involves simple alternation of a coccoid cell and a morphologically different transitory reproductive stage. It is evident, that the species figured and described by Apstein (1906, 1909), Dogiel (1906), Wright (1907) and Drebes (1970) is different from *P. lunula* (Schütt) Schütt, described in more detail by Swift & Durbin (1971) and Drebes (1974a). Swift (1973) separated this species and named it *Dissodinium pseudolunula*. According to ICBN (art. 32, 33) this taxon is invalid as neither a figure nor a reference to any previous published figure has been given. As in the definition and diagnosis of that species some features did not apply to *D. pseudolunula*, in the chapter "Taxonomy" a valid redescription is given. Swift did not separate *D. pseudolunula* from *P. lunula* on the genus level, and Taylor (1976) kept both species in the same genus, *Dissodinium*, although he noted that revisions would be required if the latter genus were restricted to parasitic species.

The first to suggest that *Dissodinium pseudolunula* might be a parasite was v. Stosch (in Ettl et al., 1967). Drebes (1969, 1972, 1974b) also regarded this species as most probably parasitic. Loeblich (1974) — after Swift's description of *D. pseudolunula* — studied the development of *Pyrocystis lunula* and of an organism corresponding to that of Dogiel (1906). He concluded that the latter may be parasitic and has to be congeneric with the species Gönner (1936) described as *Sporodinium pseudocalani*, but he did not propose new combinations.

The species of Gönner has been discovered and described independently by three authors: Wright (1907) as *Pyrocystis* sp., by Gönner (1936) as *Sporodinium pseudocalani* and by Drebes (1969) with a complete life cycle as *Dissodinium pseudocalani*. Drebes (1974) established the combination *D. pseudocalani* (Gönner) Drebes. However, giving no full reference of the basionym, this combination is invalid (ICBN art. 33, for validation see chapter "Taxonomy"). Sournia et al. (1975) raised some doubt about the identity of *S. pseudocalani* Gönner and *D. pseudocalani* Drebes, without giving reasons. Comparing both species descriptions — based on material from the same locality (Helgoland, North Sea) — there appear to be differences because Gönner misinterpreted some developmental stages of the parasite. He considered the species to be an endoparasite with sporogenesis inside copepod eggs. However, his figures, as well as the text, make it obvious that Gönner confused the primary cyst wall with the egg membrane of the host. The reason for establishing the new genus *Sporodinium* was because of an absence of palin sporogenesis present in *Chytriodinium* Chatton. The development from primary cysts to secondary cysts to zoospore formation is, apart from minor differences, identical in *D. pseudolunula* and *S. pseudocalani* Gönner; therefore the genus *Sporodinium* is considered a later synonym of *Dissodinium* Klebs in Pascher.

MATERIAL AND METHODS

Primary cysts of *Dissodinium pseudolunula* and *D. pseudocalani* were isolated from net samples taken from the plankton near Helgoland and Sylt (German Bight, North Sea). *Pyrocystis lunula*, isolated by Dr. Swift (Kingston, R. I.) from the Atlantic, was supplied by Dr. R. Zingmark (Columbia, S. C.). The organisms were cultivated in Guillard's f/2 medium (McLachlan, 1973) in Petri dishes. The development was docu-

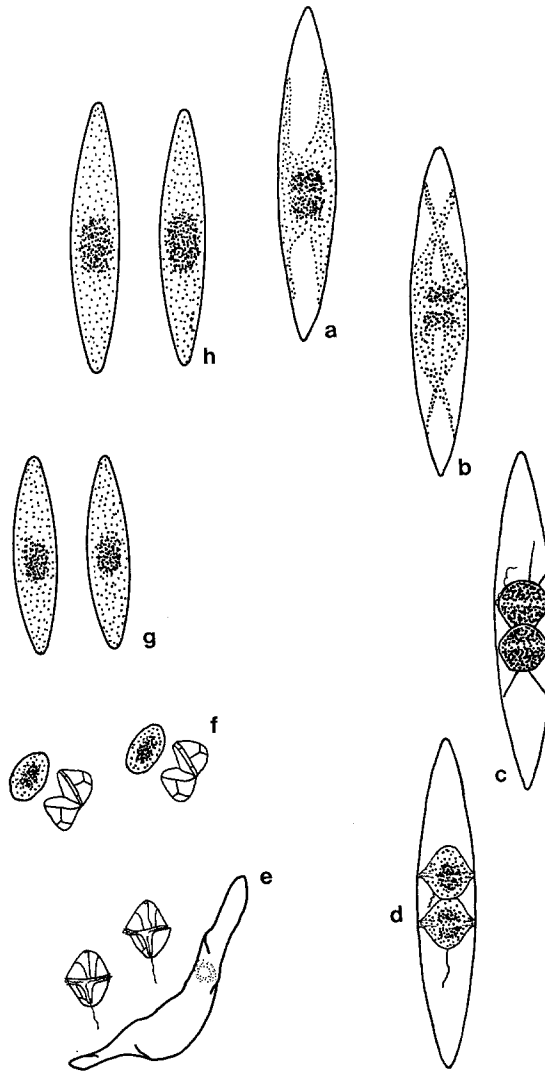


Fig. 3: *Pyrocystis acuta*, asexual life cycle. *a-d* coccoid cell forming two planospores; *e* two thecate biflagellate planospores released from the mother cell; *f-h* germination of planospores and development to fusiform coccoid cells. Combined after Swift & Wall (1972)

mented by photos or films using sea water immersion objectives (Leitz). Further details are given by Drebes (1969, 1970, 1972, 1974a). During the cruises 26 (1972), 36 (1975), 44 (1977) of R. V. *Meteor* to the Northwest African upwelling area, individuals of *D. pseudolunula*, *P. lunula* and *P. noctiluca* were isolated on board and their development documented. Cultures were lost during the transport from the investigation area to the laboratory.

Formalin-fixed samples of several clones of *Pyrocystis acuta* Kofoid, *P. fusiformis*, *P. lunula* and *P. noctiluca* were supplied by Dr. Swift. From each of these samples individuals were stained with ferric carmine acetic acid in order to get microphotos of the nuclear shape (see Fig. 8).

The life cycles of *Dissodinium pseudolunula*, *D. pseudocalani*, and *Pyrocystis lunula* were drawn from photos made by the authors. Further details were taken from the Drebes' films (1970, 1972, 1974a). The life cycle of *P. acuta* was combined from

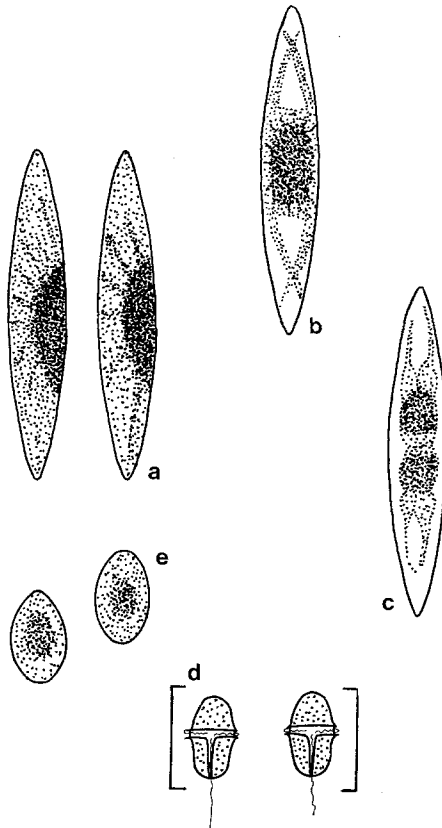


Fig. 4: *Pyrocystis lanceolata*, asexual life cycle. *a* coccoid cells; *b-c* formation of planospores; *d* athecate biflagellate planospores; *e* planospores germinating to form coccoid cells. Combined after text (planospore morphology) and figures of Bouquaheux (1972). Bouquaheux has called her organism *P. fusiformis*. The figures and description are in contradiction to those of Murray (1876, 1885), Blackman (1902), and Swift & Durbin (1971) given for *P. fusiformis* (compare Fig. 6), but they are in accordance with the original description of *P. lanceolata* Schröder

photos given in Swift & Wall (1972), those of *P. noctiluca* and *P. fusiformis* from photos given in Swift & Durbin (1971) and Meunier & Swift (in press), and that of *P. lanceolata* Schröder from the photos and the text given in Bouquaheux (1972) for *P. fusiformis* (see legend of Fig. 4).

LIFE CYCLE OF *DISSODINIUM*

Asexual reproduction of *Dissodinium* species is shown in Figures 1–2. The large spherical primary cysts, more or less filled with granular nutritive material, are floating in the plankton. If isolated, they become gradually transparent during progressive resorption of the food material. The parietal cytoplasm with the spherical nucleus is concentrated peripherally at one pole of the cell. After some hours the nucleus starts to divide, resulting in at least four nuclei, before the first cytoplasmic division follows. The cyst wall is not involved in the fission. Normally, 8 or 16 lunate or oval secondary cysts are formed within the primary cyst wall. Extremely small primary cysts, resulting usually from multi-infection, develop in very rare cases with only 4 or even 2 secondary cysts; 32 or even more secondary cysts may develop in some cases. In *D. pseudolunula* the lunate secondary cysts are liberated from the cyst wall and are found floating free in the plankton. This stage caused the mix-up with the lunate coccoid cells of *Pyrocystis lunula* and related species.

Immediately after liberation of the lunate secondary cysts of *Dissodinium pseudolunula*, the cell contents begin to divide repeatedly, forming 5 to 8 or more small biflagellate dinospores. In very rare cases (multi-infection?) only 2, 3 or 4 dinospores are formed. The development of girdle, sulcus, and flagella does not take place until the last cell division has finished. The dinospores are liberated from the secondary cysts by partial lysis of the secondary cyst wall. The liberated dinospores may swim for some time in the medium. The time between the first nuclear division in the primary cyst and dinospore liberation is about 2 to 3 days. By this time, 40 to 200 or more dinospores are formed by palintomy. In very rare cases less than 40 dinospores may arise. The liberated dinospores swim actively searching for copepod eggs. After infection and subsequent uptake of the egg content, new primary cysts are formed. Only after separation from the host does the primary cyst start with nuclear division forming secondary cysts and dinospores. Sporogenesis in *D. pseudocalani* differs in that the oval secondary cyst wall first undergoes lysis inside the primary cyst wall which is still intact. Thus, after rupture of the primary cyst wall the dinospores are released from the primary cyst.

In culture vessels, dinospores may encyst some time after active swimming. Binary fission in these cysts, as reported by Lebour (1925), was observed only once by the present authors. Infection of the host seems not to involve prior encystment of the dinospores. The meaning of binary fission inside these cysts is, up to now, unknown. According to our observations, encystment of the dinospores is tentatively interpreted as a reaction to missing a host. Binary fission of the dinospores in the motile stage has not been observed by the present authors. All developmental stages observed on isolated primary cysts have been found in plankton as well.

The sporogenesis in *Dissodinium* by the mode of palintomy is typical for parasitic flagellates (Dogiel, 1965). Palintomy as defined by Sachwatkin in Dogiel (1965): binary fission repeated over and over again, without the intermediate stage of nutrition and growth, leading to the formation of complete identical products of reproduction.

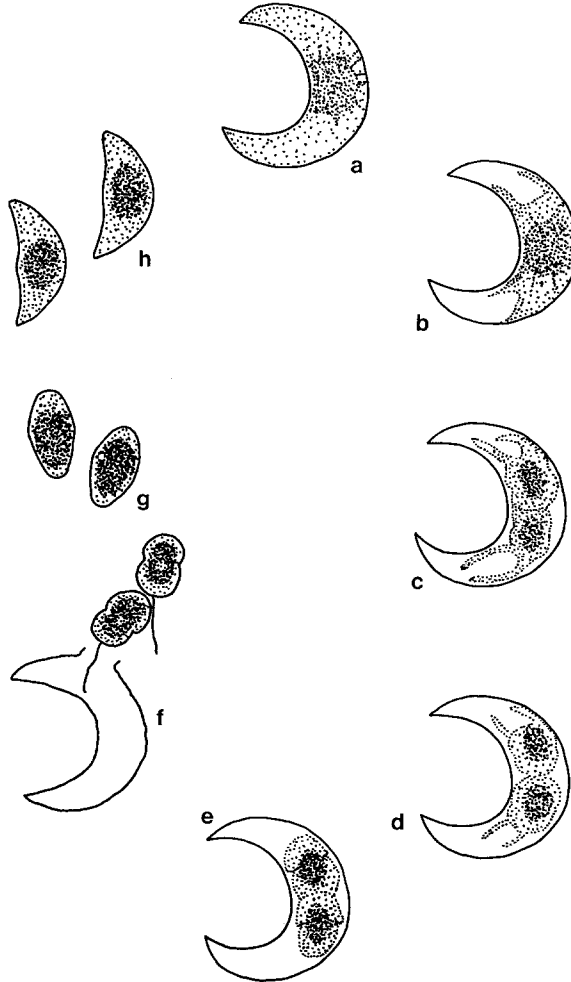


Fig. 5: *Pyrocystis lunula*, asexual life cycle. *a* coccoid cell; *b–e* formation of planospores; *f* two athecate uniflagellate planospores just released from the mother cell; *g–h* germination of the planospores and development to coccoid cells

By contrast, palinsporogenesis is defined: repeated . . . pseudotransverse division with a trophic differentiation into unequal daughter individuals: the trophocyte, which remains associated with the host, continuing to feed and grow, and the gonocyte which continues to divide by linear palintomy while the trophocyte continues to give new gonocytes.

The asexual life cycle of *Dissodinium* resembles that of the parasitic *Chytriodinium* Chatton, Blastodinales Schiller. However, the family of Chytriodiniaceae Cachon & Cachon is restricted to those members showing sporogenesis during feeding osmotrophically on the host (Cachon & Cachon, 1968). Consequently *Dissodinium* cannot be included in the Chytriodiniaceae. The family Apodiniaceae Chatton is re-

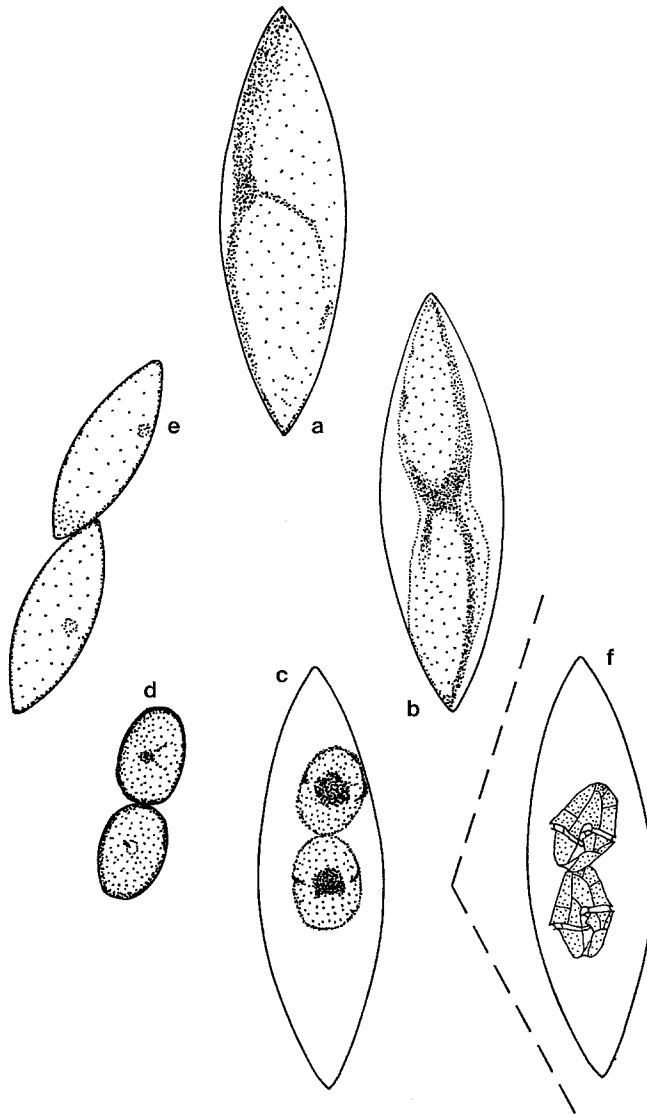


Fig. 6: *Pyrocystis fusiformis*, asexual life cycle. *a* coccoid cell; *b-c* formation of two athecate aplanospores; *d-e* germination of the aplanospores and development to fusiform coccoid cells; *f* in rare cases, thecate planospores may be developed. Combined after Swift & Durbin (1971) and Meunier & Swift (in press)

stricted to members showing typical palinsporogenesis (Cachon & Cachon, 1973). The life cycle of *Dissodinium* has some similarities to that of the parasitic *Oodinium* Chatton. Thus, it may be related to the family Oodiniaceae Chatton.

In conclusion, we can state that *Dissodinium* is a parasitic dinophyte belonging to the order *Blastodinales*, which are regarded as derived from the Gymnodiniales Lemmermann (see Kofoid & Swezy, 1921). There is no close relationship to the Pyrocystales Apstein in which they were included up to now. The lunate stage in the life cycle of

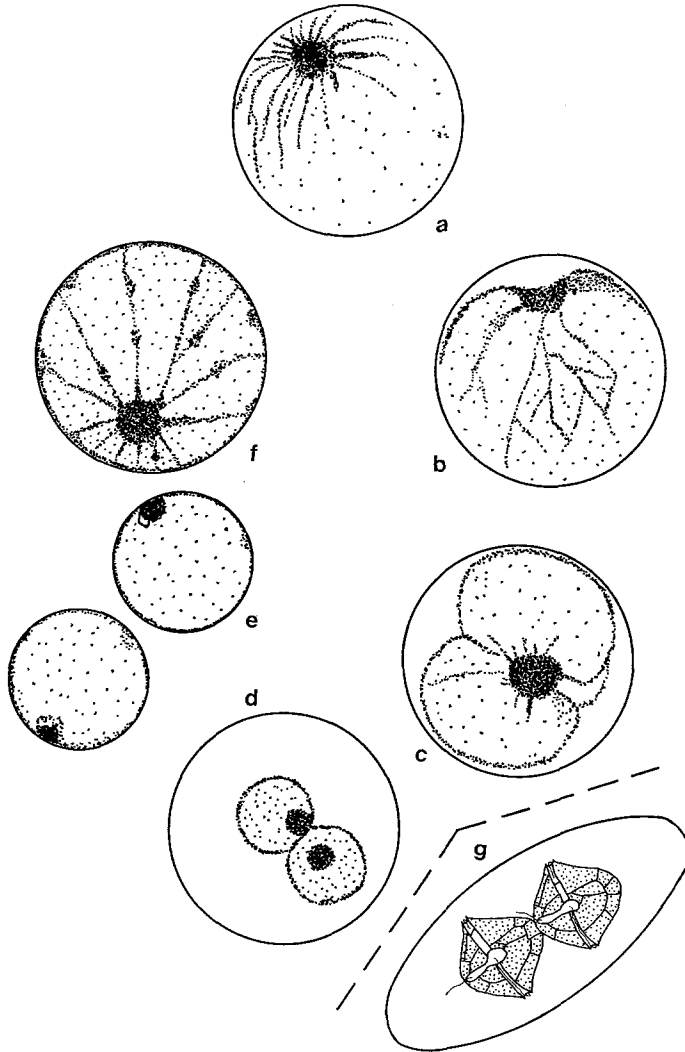


Fig. 7: *Pyrocystis noctiluca*, asexual life cycle. *a* coccoid cell; *b-d* formation of athecate aplanospores; *e-f* germination of the aplanospores and development to spherical coccoid cells; *g* in very rare cases, thecate planospores may be developed in oval coccoid cells. Combined after Swift & Durbin (1971) and Meunier & Swift (in press)

Dissodinium pseudolunula and that of some *Pyrocystis* species are not regarded as phylogenetically related but as a polyphyletic development, a view also advocated by Taylor (1976).

LIFE CYCLE OF *PYROCYSTIS*

During normal asexual reproduction, the genus *Pyrocystis* shows a simple alternation of a coccoid cell and a morphologically differing transitory reproductive stage. These 1 or 2 reproductive bodies grow within a few minutes to several hours into coccoid cells again. The time between subsequent formations of reproductive bodies is at least 2 to 3 days. At this time 1 or 2 daughter cells are produced. The reproductive bodies may be thecate-biflagellate (*P. acuta*), athecate-biflagellate (*P. lanceolata*), athecate-uniflagellate planospores (*P. lunula*) or athecate aplanospores (*P. fusiformis*, *P. noctiluca*) (see Figs 3–7).

When a coccoid cell starts with the formation of reproductive bodies, the cellular plasm retracts from the cell wall and then two daughter cells are formed by binary fission. Occasionally, in cultures as well as in the sea, only one daughter cell is formed. Thus, reproduction is not always combined with multiplication. In very rare cases, the formation of 4 reproductive bodies has been reported.

We recommend avoiding the use of the term "cyst" in connection with asexual reproduction of the coccoid organized *Pyrocystis* because it may be confused with the cysts of *Dissodinium*. In *Pyrocystis* there is no obligate succession of "primary cyst" to "secondary cyst" leading to dinospores.

This normal mode of asexual reproduction is occasionally complicated in *Pyrocystis fusiformis* and *P. noctiluca* by the occurrence of thecate biflagellate planospores, although normally these species reproduce by athecate aplanospores (see Figs 6, 7). Hitherto, however, the formation of these thecate planospores is still unknown. Meunier & Swift (in press) only observed that these thecate biflagellate planospores seemed to behave like normal aplanospores, i. e., they grow into vegetative coccoid cells. However, further development of these cells has not been studied so far. We do not know whether these coccoid cells form normal aplanospores again.

In order to deal with this phenomenon one should consider the possibility of sexual reproduction. To support the idea that the thecate planospores of *Pyrocystis noctiluca* and *P. fusiformis* could perhaps represent sexual stages, the following arguments can be given: (1) the occurrence of two different modes of asexual reproduction within one species appears quite unusual. (2) In contrast to asexual reproduction, sexual processes are normally rare. Thus the chance to observe sexual processes is low. (3) Many examples are known among the algae and fungi, where sexual reproduction is induced by a change from conditions which favour vegetative growth to unfavourable ones. For example, in *Ceratium horridum* (Cleve) Gran and *Gymnodinium pseudopalustre* Schiller, sexual reproduction occurs in ageing cultures with high cell densities, in the latter species even abundantly when day length and temperature have been previously reduced (v. Stosch, 1964, 1973). In *Peridinium cinctum* f. *ovoplanum* Lindemann sexual reproduction is induced when exponentially growing cells are inoculated into a nitrogen deficient medium (Pfiester, 1975). In both *Pyrocystis* species mentioned above,

Meunier & Swift (in press) observed thecate stages only in rare cases, in *P. noctiluca* in only three instances during several years of culture work. Although until now the factors causing formation of the thecate stages are unknown, they found these stages in relatively high concentrations in *P. fusiformis* when kept under conditions outside the normal range of population growth. (4) Morphology of sexual stages often recapitulate morphological details of their ancestors. If the relationship between *Pyrocystis* and *Gonyaulax* (see below) is accepted, the resemblance of thecal morphology of the thecate *Pyrocystis* planospores to *Gonyaulax* species may be a further indication for the possibility that the thecate planospores of *P. fusiformis* and *P. noctiluca* may be involved in sexual processes.

If the suggestion of sexual process would prove to be true, which stage is represented by the thecate planospores? Are they complete gametes or are they transitional stages? If they are complete gametes, it seems possible that all the gametes of a clonal culture are of one mating type and, because of lacking a compatible type dedifferentiate into the "vegetative form" again. For example, in the diatom *Rhabdonema arcuatum* (Lyngbye) Kützing the spermatogonia can be converted back into vegetative cells (v. Stosch, 1967). A very remarkable fact is that the 3 cells of *P. noctiluca* containing thecate planospores were not spherical but elliptical in shape (Meunier & Swift, in press), corresponding to *P. fusiformis* forma *biconica* Kofoid. Thus, putting all facts together, the possibility that here sexuality might be involved must be seriously kept in mind.

However, all this is pure speculation, as long as the details of the ontogeny of the thecate planospores are lacking, as well as the further development of those coccoid cells deriving from thecate planospores. This also applies to the suggestion made by Meunier & Swift (in press), that the thecate planospores may have the same function in the asexual life cycles of *P. fusiformis* and *P. noctiluca* as the commonly occurring athecate aplanospores.

A further complication of the life cycles of *Pyrocystis* is reported by Ballantine (1961) for *P. robusta* Kofoid. Taylor (1976) did not accept her figure as being *P. robusta*. Ballantine described large spherical cysts in which the formation of lunate cells should be formed (her Figs 64, 65). It is not stated whether she followed the formation of the lunate cells out of the large spherical cells on life material or whether all transitional stages were found in the fixed material. Therefore, it remains uncertain that the two stages belong to the same organism, and we do not like to speculate on these observations. The same applies to the organism shown by Sournia (1967; Fig. 6) as *P. lunula*.

Regarding the different species of *Pyrocystis*, the different forms of reproductive bodies may be considered a serial reduction (Figs 3–7). This, as well as the different shape of the species, may lead in the future to a splitting of the genus into several genera or subgenera. However, we do not recommend splitting the genus until the problems mentioned above have been solved. A premature splitting would perhaps result in a number of confusing and superfluous names.

The suggested morphological reduction of the reproductive bodies among the *Pyrocystis* group may be listed as follows:

<i>Pyrocystis acuta</i> :	thecate biflagellate planospores
<i>P. lanceolata</i> :	athecate biflagellate planospores

<i>P. lunula</i> :	athecate uniflagellate planospores
<i>P. noctiluca</i> :	athecate aplanospores
<i>P. fusiformis</i> :	athecate aplanospores

As the thecate planospores reveal a tabulation similar to that of *Gonyaulax*, *Pyrocystis* may be phylogenetically related to the family Gonyaulacaceae Lindemann. This hypothesis is strongly supported by the fact that all species of *Pyrocystis* investigated so far, have a sausage-like or horseshoe-shaped nucleus (Fig. 8 c–f). This applies to *P. fusiformis* as well, which was reported by Blackman (1902) and Apstein (1909) to contain a spherical nucleus. As the nucleus of this species is masked by cytoplasm, the visible part of the nucleus appears to be spherical in unstained cells, and measures about 16 to 20 μm in diameter. Apstein reported a spherical nucleus with a diameter of about 18 μm . Various species of *Gonyaulax* also have a sausage-like nucleus (see Loeblich & Loeblich, 1974; Loeblich et al., 1974). Another property is bioluminescence “which exists in many or all species of *Gonyaulax*” (Loeblich, 1966; p. 240) as well as in *Pyrocystis* spp. (Swift et al., 1973; Murray, 1876).

To summarize, there are good reasons to regard *Pyrocystis* as derived from the Gonyaulacaceae. In *Gonyaulax* and related genera the motile phase dominates during vegetative phase and the occurrence of resting spores and other features clearly separates these members of the Peridiniales Haeckel from *Pyrocystis*. We prefer to keep this genus in a separate order Pyrocystales Apstein, because in *Pyrocystis* the coccoid phase dominates during the vegetative phase. The same course is followed in the Chrysophyta and Chlorophyta for those taxa with a predominant coccoid life phase.

The relationship to some freshwater genera, like *Cystodinium* Klebs, *Phytodinium* Klebs, and related genera remains to be discussed. Members of the genus *Cystodinium* have a life cycle similar to the *Pyrocystis* species. In the former genus one can observe a reduction in the formation of reproductive bodies from athecate biflagellate planospores to aplanospores (Fott, 1971). Thecate planospores are unknown. As the nucleus in the freshwater species is always spherical — not sausage-like or horseshoe-shaped as in *Pyrocystis* — and bioluminescence is unknown, it is unlikely that they have also developed from members of the Gonyaulacaceae. Lacking any detailed personal knowledge of the freshwater species and their life cycles, we do not recommend the inclusion of *Pyrocystis* with *Cystodinium* and related genera in the same order.

TAXONOMY

Dissodinium

Definition of the genus *Dissodinium* Klebs in Pascher, emend. herein (Pascher, 1916, p. 132).

Synonyms: *Gymnodinium* Stein 1878, pro parte, non auct; *Diplodinium* Klebs 1912, non Schubert 1888, nec Fiorentini 1890; *Pyrocystis* Murray ex Haeckel 1890, pro parte, non auct; *Sporodinium* Gönner 1936.

Description: Marine ectoparasitic dinophytes, host: crustacean eggs. Asexual reproduction (sporogenesis) by obligate sequence of primary cysts, secondary cysts,

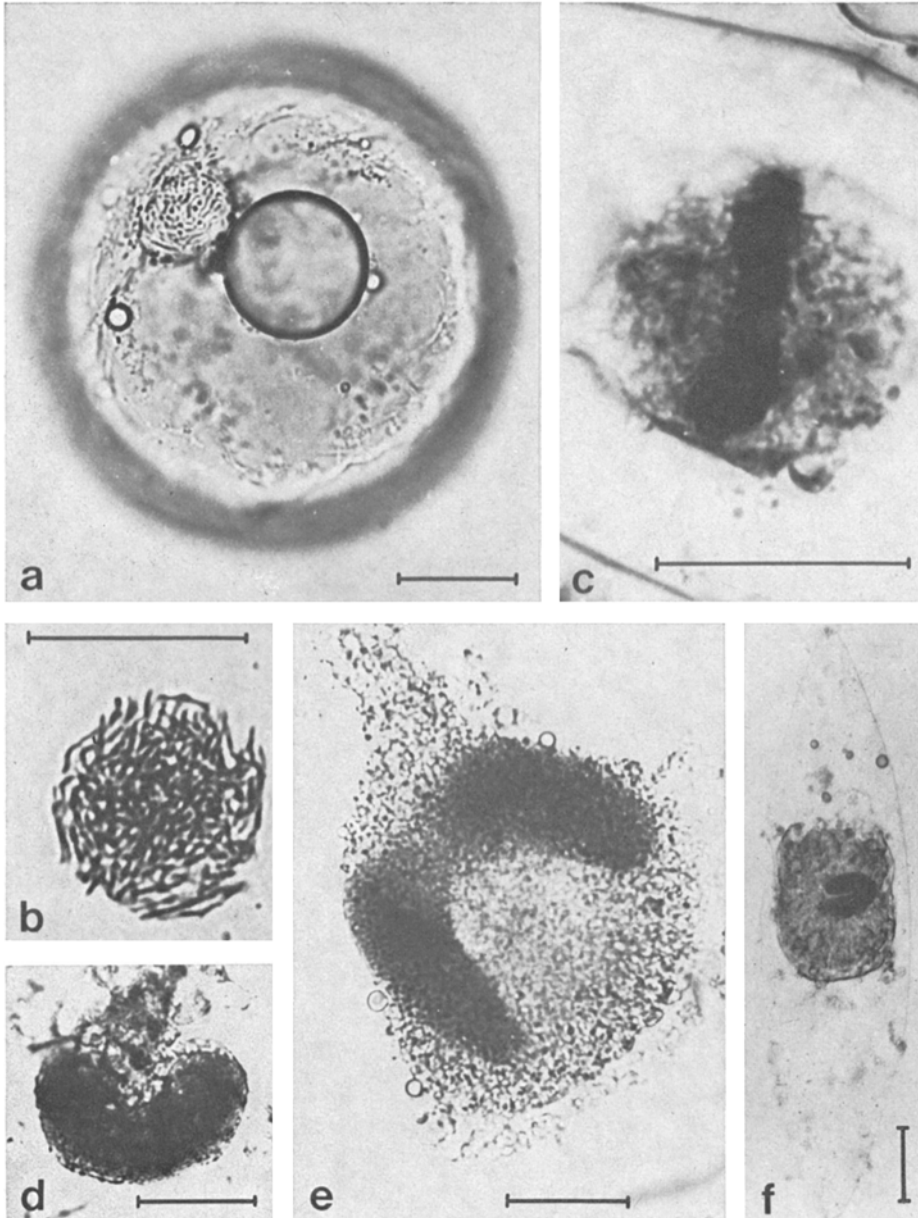


Fig. 8: *Dissodinium* and *Pyrocystis*, nuclear shape. *a* *Dissodinium pseudolunula*, primary cyst with spherical nucleus; *b* *D. pseudocalani*, dinospore nucleus, spherical, stained and slightly squashed; *c* *Pyrocystis lunula*, sausage-like nucleus, stained; *d* *P. fusiformis*, sausage-like nucleus, stained and squashed out of the cytoplasm; *e* *P. noctiluca*, horseshoe-shaped nucleus, stained and slightly squashed; *f* *P. acuta* horseshoe-shaped nucleus, stained. (Scales: *a*, *c-f*: 25 μm ; *b*: 20 μm)

and formation of planospores (dinospores). Primary cyst spherical, with large food vacuole. Nucleus spherical, located in the parietal cytoplasm. Chromatophores present or lacking. Inside the primary cyst wall the protoplast divides by repeated binary fission (palintomy) into 2, 4, 8, 16, or more secondary cysts. The secondary cysts form 5 to 16 or more (rarely less than 5) dinospores. Dinospores small, *Gymnodinium*- or *Gyrodinium*-shaped, biflagellate, athecate. The dinospores attach to the host, lose their motility and form a sucker organelle. Hypertrophic growth by phagotrophic uptake of host material. Finally, the growth phase terminates with formation of a primary cyst. No bioluminescence.

Type species: *Dissodinium pseudolunula* Swift ex Elbr. & Drebes.

Dissodinium is included in the Blastodiniales Schiller. It differs from the similar osmotrophic feeding at the host. The family Chytriodiniaceae Cachon & Cachon is genus *Chytriodinium* Chatton, as in the latter nuclear division already starts during restricted to those members showing these features. In *Dissodinium* sporogenesis begins a long time after phagotrophic feeding has finished. When the primary cyst detaches from the host, it lasts for several hours until the first nuclear division takes place.

Dissodinium pseudolunula

Dissodinium pseudolunula Swift ex Elbrächter & Drebes, hic

B a s i o n y m : *Dissodinium pseudolunula* Swift 1973; *Dissodinium pseudolunula* n. sp. (Phycologia 12, p. 90–91); invalid (ICBN art. 32, 33).

S y n o n y m s : *Gymnodinium lunula* Schütt, pro parte; Schütt 1895, Pl. 24 Figs 80₂, 5, non Figs 80₁, 3, 4, 6–12 (= *Pyrocystis lunula* (Schütt) Schütt); Dogiel 1906, Pl. 1 Figs 1–17, 21–25, non Figs 18–20 (= *P. lunula*); Kofoid & Swezy 1921, Pl. 5 Fig. 55, text Fig. 1; Lebour 1925, Pl. 4 Figs 1a–g; auct. nonnull.; *Diplodinium lunula* (Schütt) Klebs, pro parte; Klebs 1912, Figs after Dogiel 1906, Figs A–F, H, non Fig. G = Dogiel's Fig. 20 (= *Pyrocystis lunula*); *Dissodinium lunula* (Schütt) Klebs in Pascher, pro parte, Pascher 1916, Figs after Dogiel 1906, Figs 3b_A, c, d, non Fig. 3b_B = Dogiel's Fig. 20 (= *P. lunula*); *Dissodinium lunula* (Schütt) Pascher, auct. nonnull.; *Pyrocystis lunula* (Schütt) Schütt, pro parte; Schütt 1896 Fig 2f (partly after Pouchet 1885), non Figs 2B–E (= *Pyrocystis lunula* auct.); Apstein 1906, Pl. X; Wright 1907, Pl. 1 Figs 3–5; auct. nonnull.

D i a g n o s i s : Ectoparasite of copepod eggs. Sporogenesis by two successive cyst stages terminating with formation of dinospores. Primary cyst spherical, 60–100–130 μm in diameter. Cytoplasm parietal, surrounding a large vacuole filled with nutritional material. Nucleus spherical, lying in a peripheral cytoplasmic aggregation. A few greenish yellow chromatophores present, multiplying during sporogenesis. The primary cyst divides to form 8 or 16 (rarely 2 or 4) lunate secondary cysts which are liberated from the decaying primary cyst wall. The secondary cysts, about 100–140 μm from tip to tip across, contain a large nutritional vacuole. The secondary cysts form usually 5–8 (range 2–16) dinospores. Dinospores measuring 23–28 μm in length, 18–21 μm in width, athecate, biflagellate, of the *Gymnodinium* type, greenish yellow pigmented by numerous chromatophores. In each secondary cyst one dinospore con-

tains the residue of the large vacuole as a red globule. After release from the secondary cysts the dinospores may either infest a new host or may become non-motile with following encystment. Distribution: marine plankton.

Lectotype: Apstein, C. (1906). *Pyrocystis lunula* und ihre Fortpflanzung. Wiss. Meeresunters. (Abt. Kiel) 9, 263–269, Pl. 10 Figs 1b–27.

Dissodinium pseudocalani

Dissodinium pseudocalani (Gönnert) Drebes ex Elbrächter & Drebes, hic

Basionym: *Sporodinium pseudocalani* Gönnert; Gönnert, R. 1936: *Sporodinium pseudocalani* n. g., n. sp., ein Parasit auf Copepodeneiern. Z. Parasitenkunde 9, 140–143, Figs 1–7.

Synonyms: *Pyrocystis* sp. Wright 1907, Pl. 1, Fig. 6; *Dissodinium pseudocalani* Drebes; Drebes 1969, p. 58–67, Figs 1–4; *Dissodinium pseudocalani* (Gönnert) Drebes; Drebes 1974, p. 152 (invalid: ICBN art. 33).

Pyrocystis

Definition of the genus *Pyrocystis* Murray ex Haeckel emend. herein (Haeckel 1890, p. 30).

Synonyms: *Gymnodinium* Stein 1878, pro parte, non auct.; *Murracystis* Haeckel 1890; *Diplodinium* Klebs 1912, pro parte; *Dissodinium* Klebs in Pascher 1916, pro parte; Vix *Photocystis* Haeckel 1890, *Nectocystis* Haeckel 1890.

Description: Marine dinophytes, photoautotrophic, bioluminescent, coccoid stage dominating during vegetative life phase. Coccoid cells large, fusiform, lunate, or spherical. Cell wall smooth, unsculptured; cytoplasm parietal, concentrated at one pole of the cell; nucleus sausage-like or horseshoe-shaped; chromatophores numerous, yellowish. Asexual reproduction by formation of 1 or 2 aplanospores/planospores. The planospores are either athecate, *Gymnodinium*-like (uni- or biflagellate), or thecate biflagellate, with a tabulation resembling that of *Gonyaulax* Diesing. Shortly after release of the spores they swell up to form a new coccoid stage.

Type species: *Pyrocystis noctiluca* Murray ex Haeckel.

Pyrocystis is regarded as the type of the family *Pyrocystaceae* Apstein, *Pyrocystales*. By the tabulation of the thecate planospores, resembling that of *Gonyaulax*, and other features *Pyrocystis* is considered as related to the *Gonyaulacaceae* Lindemann, *Peridinales* Haeckel.

Pyrocystis lunula

Pyrocystis lunula (Schütt) Schütt.

Schütt 1896, Figs 2B–E; non Fig. 2F (= *Dissodinium pseudolunula*, Fig. after Pouchet 1885).

Basionym: *Gymnodinium lunula* Schütt, 1895 Pl. Figs 80₃₋₄, 80₆₋₈; non Figs

80₂, 5 (= *D. pseudolunula*) as to Figs 80₁, 9-14 it is questionable whether these belong to *P. lunula*.

Synonymy: *Gymnodinium lunula* Schütt, pro parte; Dogiel 1906, Pl. 1 Figs 18-20; non Figs 1-17, 21-25 (= *D. pseudolunula*); *Diplodinium lunula* (Schütt) Klebs, pro parte; Klebs 1912, Figs after Dogiel 1906, only Fig. G = Dogiel's Fig. 20; non Figs A-F, H (= *Dissodinium pseudolunula*); *Dissodinium lunula* (Schütt) Klebs in Pascher, pro parte; Pascher 1916, Figs after Dogiel 1906, only Fig. 3b_v = Dogiel's Fig. 20; non Fig. 3b_a, c, d (= *D. pseudolunula*); *Dissodinium lunula* (Schütt) Pascher, auct. nonnull.; *Dissodinium lunula* (Schütt) Taylor, Swift & Meunier 1976; non: *Pyrocystis lunula* sensu Apstein (1906) Wright (1907).

Good descriptions and figures of *Pyrocystis lunula* without mixing it with *Dissodinium pseudolunula* are given by Swift & Durbin (1971) and Drebes (1974a).

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