

## FISH INVADING DINOFLAGELLATES: A SYNOPSIS OF EXISTING AND NEWLY PROPOSED GENERA

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*Dedicated to Academician B. Ryšavý on the occasion of his 60th birthday*

**Abstract.** The paper reviews the dinoflagellate genera invading marine and freshwater fishes, presents their diagnostic features, points out the difference from tunicate-invading genus *Oodinium* Chatton, 1912 and comments on their pathogenicity. The genus *Crepidoodinium* Lom and Lawler g.n. is proposed for *Oodinium cyprinodontum* Lawler, 1967 from marine cyprinodontids, and *Piscinoodinium* g.n. is proposed to accommodate freshwater *Oodinium pillularis* Schäperclaus, 1954 and *O. limneticum* Jacobs, 1964. The most important diagnostic character is the structure of the attachment organelle which is depicted along with some other morphological features.

The first dinoflagellate parasite ever recorded from a fish host was *Oodinium ocellatum* Brown, 1931 described from the gills of fish kept in the Aquarium of the Zoological Society of London. In 1934, Brown extended her observation on the morphology and biology of the parasite. Nigrelli (1936) described in detail the morphology and life cycle of this parasite as found in the New York aquarium. In some points, his conclusions differed from Brown's (1934) observations. In 1946, Brown and Hovasse published a paper in which they stressed the differences between their fish *Oodinium* and a typical *Oodinium* species, *O. poucheti* Lemmerman, 1899 from the tunicate *Oikopleura* (they did not designate, however, *Oodinium poucheti* as a type species). Consequently, they erected a new genus *Amyloodinium* for the *Oodinium* from marine fish. In 1973, Lom and Lawler published an account on the ultrastructure of an *Amyloodinium* sp. found in natural habitats which corroborated the existence of essential morphological differences between *Amyloodinium* and species of the genus *Oodinium*. The structure of flagellates of the genus *Oodinium* including the type species *O. fritillariae* Chatton, 1912 had been described by Cachon and Cachon (1971a, 1971b). The reason why Lom and Lawler (1973) did not identify the species which they have investigated with *Amyloodinium ocellatum* (Brown, 1931) was the possible yet unproven existence of more than one *Amyloodinium* species on marine fishes.

The first parasitic dinoflagellate from freshwater fishes was described by Jacobs (1946) from aquarium fish in the United States under the name of *Oodinium limneticum*\*) Unaware of this paper, Schäperclaus (1951) recorded a dinoflagellate parasite from an aquarium fish, *Colisa lalia*. He himself had no idea about the possible taxonomic affinities of the parasite and therefore he described his „*Colisa*-Parasit” in a curious way, using only a specific name “*pillularis*” without generic allotment. Hirschmann and Partsch (1953) studying the same parasite decided that it belonged to the genus

\*) The claim of Reichenbach—Klinke (1955) that Weiser (1949) was the first to find a freshwater *Oodinium* in Europe, i.e. in trout, is erroneous — Weiser does not say a word on *Oodinium* in that paper.

*Oodinium* without, however, determining the species. In 1954, Schäperclaus followed their conclusions and called the species which he had previously described as *Oodinium pillularis* Schäperclaus, 1954. Although this way of description of a new taxon is very strange, it is not in dire contradiction to the International Code of Zoological Nomenclature and the species can be considered valid.

In 1976, studying freshwater *Oodinium*, evidently *O. pillularis*, Lom (the paper appeared as an abstract in 1977) found that in the structure of the attachment apparatus and in the presence of well developed chloroplasts this species markedly differed from both *Oodinium* and *Amyloodinium* and had to be placed in a new, separate genus. His findings are elaborated in greater detail by Schubert and Lom (in press).

In 1967, Lawler described from the euryhaline cyprinodontids of the U.S. Atlantic coast the species *Oodinium cyprinodontum*. It was later shown in an ultrastructural study by Lom and Lawler (1973) to possess morphological feature opposing those of both *Oodinium* and *Amyloodinium*. The authors suggested it should be transferred into a new, separate genus.

In the following paragraphs, we would like to clear up the chaotic situation in the taxonomy of fish invading dinoflagellates by giving adequate diagnosis of the individual genera. In view of the present importance of parasitic dinoflagellates as pests of aquarium fish — and potentially also of fish in marine aquaculture (Paperna and Laurencin 1979) — this may be of help in future research and in elaboration of practical control measures.

#### CHARACTERIZATION OF FISH INFECTING DINOFLAGELLATES

The characteristics are based chiefly on the morphology of the trophont, since the dinospores do not yield sufficiently differentiating features except for the presence or absence of the eye spot. The number of dinospores produced may vary in relation to the size of detached trophont and temperature. With the exception of the genus *Ichthyodinium*, all fish invading genera belong into the family Blastodiniaceae, order Dinococcales. This is a botanical classification, zoological classification allots them to the tribe Blastodinida, order Dinoflagellida. Their life cycle comprises three stages. The invasive stage, dinospore, resembles free living dinoflagellates of the genus *Gymnodinium* (hence the frequently used name gymnospor), has two flagella and moves freely in water in search for a fish host. Having attached itself to the fish surface, it transforms into a sac-like trophont (Chatton 1952, Cachon 1964) which is equipped with an elaborate attachment apparatus. It feeds and grows (Plate I, Fig. 3); it has not been ascertained thus far if in this stage loses one or both of its two flagella. The trophonts which have reached their final size detach themselves from the host, sink to the bottom, assume a spherical shape and encyst to form a palmella stage (Plate II, Fig. 2). This starts a series of division — either within a common cystic envelope or the old envelope may dissolve after each division. The last division produces again the dinospore (Plate I, Fig. 2).

##### a) Ectoparasitic genera

The most important feature for generic differentiation is the morphology of the attachment apparatus and the mode of nutrition as indicated by the absence or presence of food vacuole and chloroplasts.

For comparison, we also list here an abbreviated characteristic of the genus *Oodinium* invading marine tunicates and probably also polychaetes, and whose characters are at variance with features of the fish invading genera.

**Genus *Oodinium* Chatton, 1912**

Parasites of tunicates and possibly polychaetes.

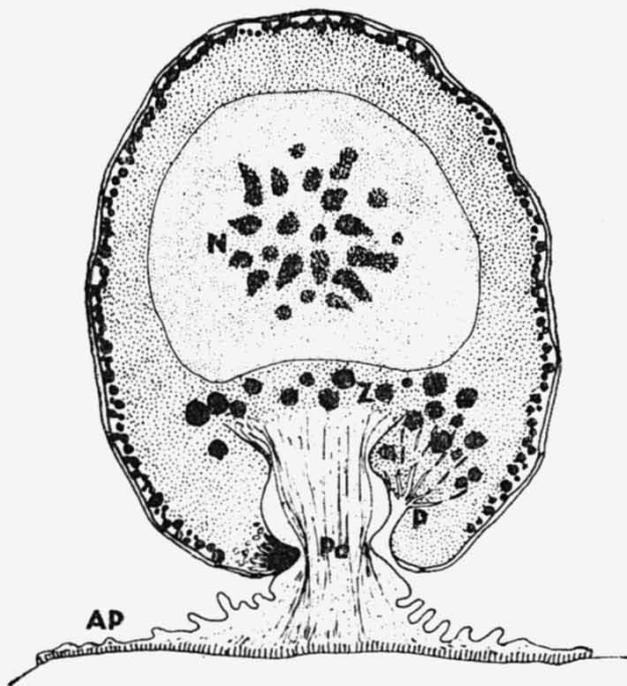
The trophont is sac-like and is attached to the host by a stout peduncle (Fig. 1) with a very large, flat attachment surface closely adhering to but not penetrating into the epithelial cells of the host. The cell membrane of the attachment surface has numerous thin and long invaginations serving for increased absorption of the nutrients by osmotrophy. There are no chloroplasts, the trophont's theca has plates filling its alveoli and constituting together the dinoflagellate "armour" of the cell. There are no starch grains. The nucleus contains stout coiled chromosomes only in young individuals. The dinospore is a gymnospor.

Type species: *O. fritillariae* Chatton, 1912

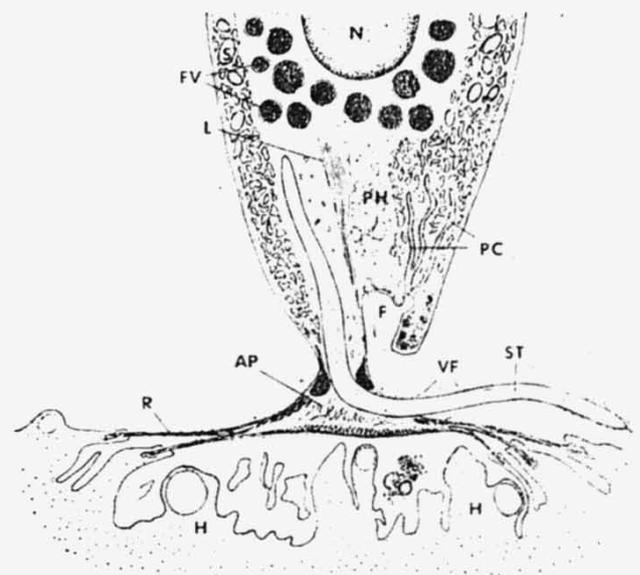
**Genus *Amyloodinium* Brown et Hovasse, 1946**

Synonym: *Oodinium* Chatton, 1912, pro parte.

Ectoparasitic on gills but also on the rest of the surface of most various species of marine fishes. Lawler (1979) states that the number of hosts has reached 111 species from 46 families of fishes. The trophont has an attachment disc with a very short peduncle, the circumference of the disc radiates into long filiform projections embedded deeply into the epithelial cells of the host (Fig. 2). A special tentacle-like movable organ, stomopode, extends along with the peduncle of the attachment disc from the basal end of the cell; its function may be food ingestion and/or injection of lytic bodies into the host cells. No chloroplasts. Thecal alveoli with plates. Cytoplasm contains large



**Fig. 1.** Diagram of *Oodinium fritillariae* Chatton (from Cachon and Cachon 1971). N — nucleus, Z — zone of subnuclear cytoplasm, P — pusular system, Pd — peduncle, bearing an extremely large attachment plate (AP) adhering closely to the surface of the host's tissue, but not penetrating into it.



**Fig. 2.** Diagram of the basal portion of an attached *Amyloodinium* (from Lom and Lawler 1973). N — nucleus, S — starch grain, VF — food vacuole, L — ribbon of micronuclei along the zone of phagocytic cytoplasm (PH), PC — pusular canals, F — flagellum, AP — attachment plate, ST — stomopode, R — rhizoids, H — destroyed host cells.

digestive vacuoles with particulate food, starch grains, spindle-shaped bodies, clove-like bodies and lytic bodies and subthecally located mucocysts and acontobolocysts. Size of trophont does not exceed 150  $\mu\text{m}$ .

Division of the palmella (tomont) stage takes place within a common cyst wall; up to 256 gymnospires produced. Gymnospire with stigma (eye spot).

Type species: *A. ocellatum* (Brown, 1931) Brown et Hovasse, 1946 by monotypy. (Syn. *Oodinium ocellatum* Brown, 1931).

The question of how many species there may be is open to further study. Lom and Lawler (1973) hesitated to identify the *Amyloodinium* they have studied with *A. ocellatum* because of the lack of interphase chromosomes in the nuclei of the former in addition to the reason quoted in the introduction to this paper. In some specimens, there were positively no chromosomes, while in some there were formations impossible to identify as chromosomes (Plate III, Fig. 1). The importance of interphase chromosomes as generic character of *Amyloodinium* is therefore questionable.

The differences separating this genus from the genus *Oodinium* (presence of stomopode, different attachment apparatus, presence of starch reserves, phagotrophy) fully warrant its independence and corroborate thus Brown and Hovasse's (1946) decision.

Thus far, no mortal infections could be observed in nature; in aquaria, this parasite thrives on fishes stressed by captivity or other factors and becomes a serious pathogen.

### Genus *Crepidoodinium* Lom et Lawler g. n.

Synonym: *Oodinium* Chatton, 1912, pro parte.

Ectoparasitic on gills of estuarine and marine fishes of the family Cyprinodontidae. Lawler (1968) lists 5 species of cyprinodontids as hosts.

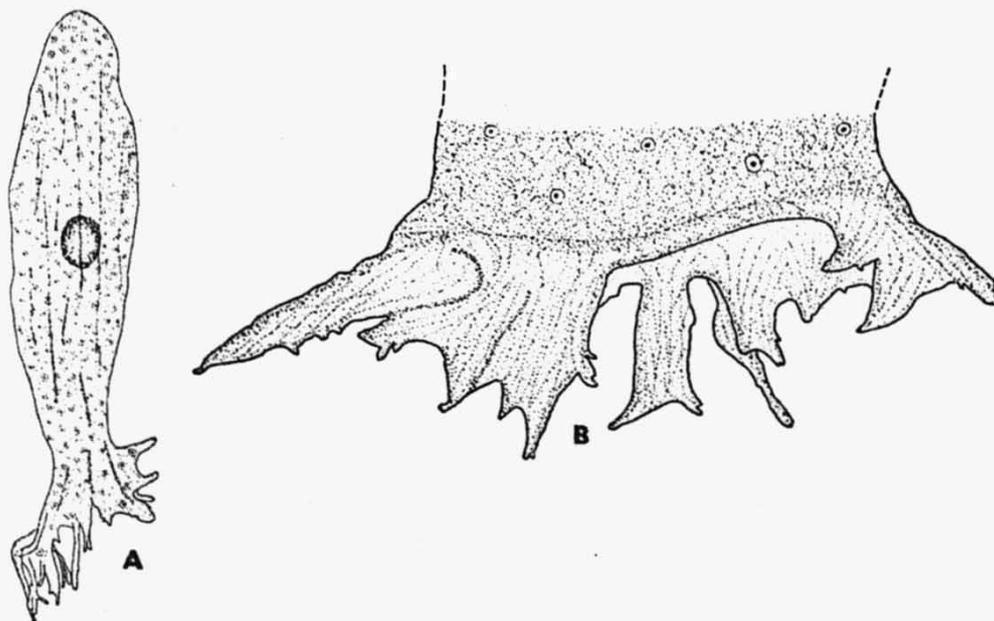


Fig. 3. Diagram of *Crepidoodinium cyprinodontum* (from Lom and Lawler 1973). A — general body shape of an attached trophont (host tissue not represented), B — holdfast organelle with projections, rhizoids, bearing finger-like tips.

Trophont is attached by its basal end flattened into a broad holdfast bearing projections ("rhizoids") with finger-like tips which closely adhere to the host cell membrane without penetrating inside the host cell (Fig. 3). No stomopode. Well developed chloroplasts. Theca without plates. An extremely spongy cytoplasm with a system of interlinked lacunae and vacuoles with starch grains, subthecally located mucocysts and acontobolocysts.

bolocysts. No digestive vacuoles. Nucleus without large interphasic chromosomes. Up to 670  $\mu\text{m}$  in length.

Division of the palmella (tomont) stage (Lawler, 1967 does not state whether it takes place in a common envelope or separately) produces up to 2048 gymnospires. Gymnospire without stigma.

Type species: *C. cyprinodontum* (Lawler, 1967) comb. n., by monotypy. (Syn. *Oodinium cyprinodontum* Lawler, 1967).

In the paper by Lom and Lawler (1973) there was no space to show other cell structures of *C. cyprinodontum* except the attachment organelles. Since the curiously spongy cytoplasm of this flagellate is markedly at variance with *Oodinium* and with other genera of fish invading dinoflagellates it is documented here on Plate III.

A comparison of characters of *Crepidoodinium* with those of *Oodinium* reveals differences substantiating the erection of the former as a new genus. The name *Crepidoodinium* has been derived from the Latin *crepida* for a sole. The need of this new genus was discussed with Dr. A. Lawler a long time ago, hence the joint authorship.

In contrast to *Amyloodinium* and *Piscinoodinium*, *Crepidoodinium* does not directly destroy host cells and thus appears to be a symphoriont rather than a parasite (Lom and Lawler 1973). To what extent a massive infestation can produce gill lesions (Needham and Wootten 1979) has to be clarified.

### Genus *Oodinioides* Reichenbach—Klinke, 1970

Ectoparasitic on the gills and skin of most various species of fishes; often penetrates below the epidermis and is also found in body organs such as liver and the intestine.

Trophont is spherical to pyriform, colourless and vesicle-like. There are no data on the mode of attachment or any other cell structure except refractile inclusions in the cytoplasm, 2–3 and 5–6  $\mu\text{m}$  in size, respectively, and a very fine theca (? = "Hülle"). Diameter up to 40  $\mu\text{m}$  (Fig. 4).

Formation of dinospores: refractile inclusions (which are brown and spherical) give rise — within the cell wall of the trophont — to small microspores or larger flagellated macrospores which become the actual gymnospires. Up to 256 spores (?) formed.

Reichenbach—Klinke (1970) states that the host range includes 37 genera of freshwater fishes belonging to 20 families and 12 genera of marine fishes of various families.

Type species: *O. vastator* Reichenbach—Klinke, 1970 (by monotypy).

Indiscriminate occurrence of this parasite — as far as site of infection and hosts are concerned — and lack of any convincing morphological documentation raises serious doubt about the identity of the observed structures with any kind of dinoflagellate parasites. The pictured gymnospire might be a concurrent contaminant. The spherical formation containing refractile inclusions and described as trophont are reminiscent of *Ichthyochytrium vulgare* Plehn, 1920. There is no positive evidence supporting the existence of *Oodinioides* as a real dinoflagellate genus. Contrary to its allegedly wide distribution, it has not been found since.

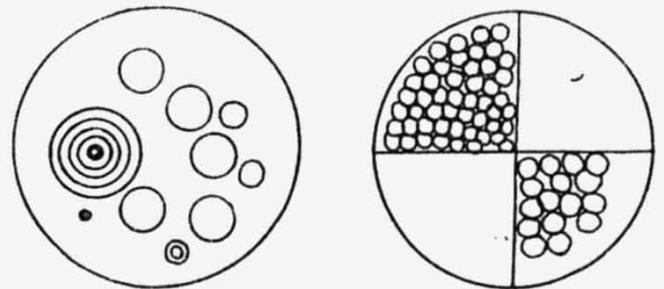


Fig 4. "Parasitic stage" of *Oodinioides vastator* Reichenbach—Klinke (from Reichenbach—Klinke 1970). To the left, beginnings of the spore formation; at right, "sporangium" with one sector of macrospores and the other of microspores.

Genus *Piscinoodinium* g. n.

Synonym: *Oodinium* Chatton, 1912, pro parte.

Ectoparasitic on gills and skin of freshwater fishes; rarely, subcutis (? — Reichenbach — Klinke 1956, Schubert 1959).

Trophont: From the attachment disc with a very short peduncle radiate numerous rod-like organelles, rhizocysts, which penetrate into and are firmly embedded in the epithelial cells of the host. There is no stomopode. There are well developed chloroplasts

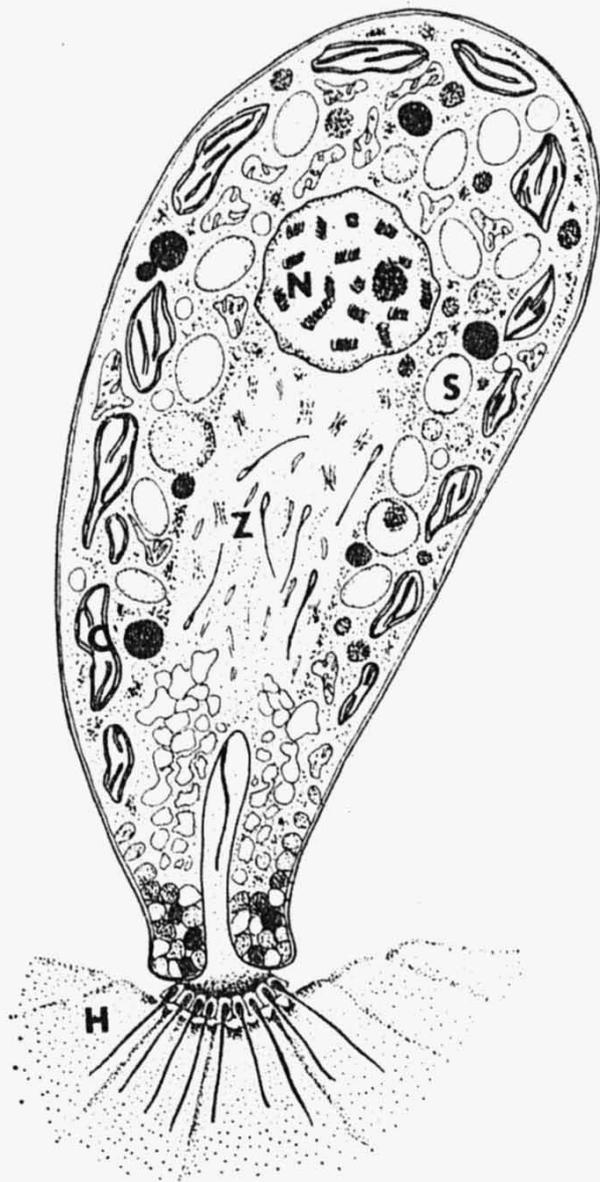


Fig. 5. A diagram of the cell organisation of a trophont of *Piscinoodinium pillulare* attached to host cells (H). The cytoplasm contains chloroplasts (C), starch grains (S), mitochondria and various other inclusions. The subnuclear zone of cytoplasm (Z) lacks many of the inclusions but contains rhizocysts (sperm-like structures). The bottom end of the cell bears the attachment disc with rhizocysts embedded into the host cells, N — nucleus.

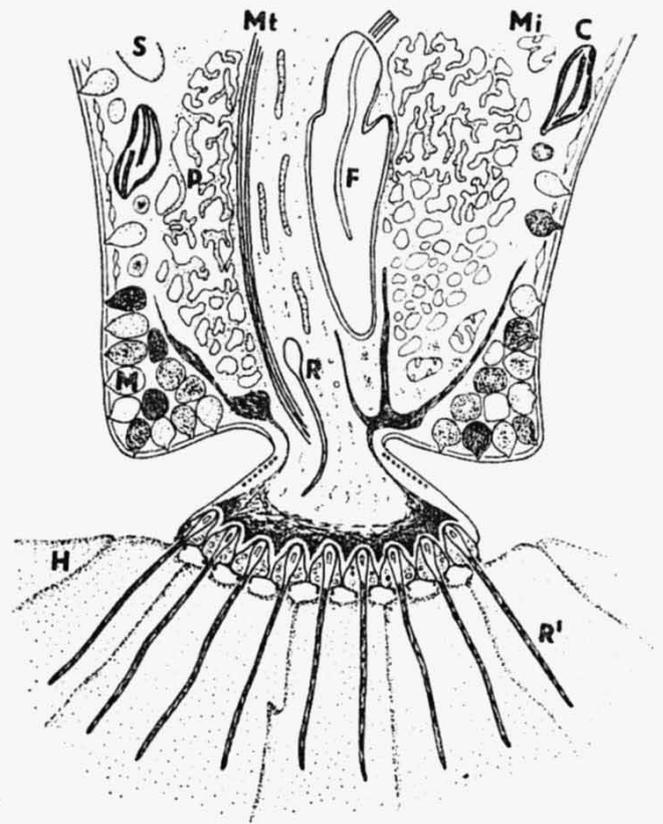


Fig. 6. A diagram of a longitudinal section through the attachment disc and adjacent body part of a fixed trophont of *Piscinoodinium pillulare*. C — chloroplasts, S — starch grains, Mi — mitochondrium, Mt — microtubular ribbon along the zone of special cytoplasm extending from nucleus into the attachment disc, R — migrating rhizocysts, R' — rhizocyst in situ, fixed in the attachment disc and embedded in the host cell (H). F — flagellum within the flagellar groove, P — pusular system, M — mucocyst.

and starch grains. Theca without plates. Cytoplasm contains rhizocysts, laminar inclusions; there are no digestive vacuoles. Subthecally, there are mucocysts. Nucleus with large interphasic chromosomes (Figs. 5, 6, Plate I, Fig. 3).

Division of the palmella (tomont) stage; without common envelope; produces up to 256 gymnospires. Gymnospires without stigma.

It is commonly found on most various freshwater aquarium fishes.  
 Type species: *Piscinoodinium pillulare* (Schläperclaus, 1954) comb. n. by posterior designation (syn. *Oodinium pillularis* Schäperclaus, 1954). With characters of the genus.

Schäperclaus (1951) found *P. pillulare* on free-living *Carassius carassius*. Geus (1960) reported a successful experimental infection of *Cyprinus carpio*, *Leucaspis delineatus*, *Tinca tinca*, but also of amphibians — larvae of *Amblystoma mexicanum* and tadpoles of *Rana temporaria* and *R. arvalis*.

Hirschmann and Partsch (1953) examining "oodinia" from aquarium fishes, reported the presence of a stigma in dinospores. Therefore Reichenbach—Klinke (1955) considered *P. pillulare* to be different from *P. limneticum* (Jacobs, 1946) comb. n., in which it was described as lacking. However, we failed to detect the stigma in gymno-spores reared from detached palmellas of *P. pillulare*; the identity of both species is therefore open to further study, as well as possible occurrence of more species on freshwater fishes in Europe.

The differences in the structure of trophont in *Amyloodinium* and *Piscinoodinium*, evident from the above paragraphs, fully warrant the separation of both genera. The derivation of the name in the latter (pisces, fishes) is obvious.

Summing up the differences between the genera of ectoparasitic dinoflagellates invading fishes, the following simple key for their determination can be devised (we do not include the controversial genus *Oodinioides*):

1. The pyriform trophont is attached to the host surface by structures extending from its tapered end and penetrating into the host cells . . . . . 2
- The trophont is sac-like, attached to the host's surface by a large, flat adhesive surface bearing projections just touching the host cells . . . . .
- . . . . . genus *Crepidoodinium* Lom et Lawler g.n.
2. There is a stomopode but no chloroplasts; invades marine fishes . . . . .
- . . . . . genus *Amyloodinium* Brown et Hovasse
- There is no stomopode, chloroplasts are present; invades freshwater hosts . . . . .
- . . . . . genus *Piscinoodinium* g.n.

**b) Endoparasitic genus**

***Ichthyodinium* Hollande et Cachon, 1953**

Endoparasitic in the vitelline sac of young fry of marine clupeoid fishes. Trophont is a seemingly structureless amoeba-shaped cell, growing from mono- to multinucleate plasmodium, giving rise, in two sequences of division (plasmotomy), to dinospores (Plate IV, Fig. 2). Dinospores are not of a *Gymnodinium* type. Mode of infection of the eggs is not known.

Type species: *I. chabelardi* Hollande et Cachon, 1953, by monotypy.

Host: *Sardina pilchardus* Walb. and *Maurolicus pennanti* Walb.

This species was found but once; in destroying fish fry it could be of considerable economic importance.

**CONCLUDING REMARK**

Besides the fact that they are serious pathogens in both freshwater and marine aquaria (Ghittino 1970, Hoffman and Meyer 1974, Jacobs 1946, Laird 1956, Needham and Wootten 1979, Nigrelli 1943, Schäperclaus 1954, Schubert 1978)

most of the questions concerning parasitic dinoflagellates of fish remain unanswered. It is evident that fish oodinia belong to genera proper to fish only and do not live on any other hosts. However, there may be many more genera and species than those presently known. Overstreet (1968) mentioned an "*Oodinium* sp." from the marine fish *Synodon foetus*, attached to the gill filaments which had no stomopode and lacked stigma in the dinospores. Thus it might be an organism different from *Amyloodinium*.

Their biology and exact relation to the host are uncompletely known, too. If the dinospores arise only from palmella stages detached from the host, why do we find *Piscinoodinium* (Plate I, Fig. 1) in distinct closely packed groups on the surface of the fish as if the flagellate would proliferate right there on the spot? Is it perhaps because there are some isolated spots on the hosts where the feeding is more easy or attractive? Or is it because the damaged cells release some substance acting as attractants? The way of nutrition is more clearly known only in *Amyloodinium* ingesting particulate food, although the exact mode of ingestion can only be speculated upon. In *Piscinoodinium* and *Crepidoodinium*, although the former inflicts heavy injury upon its host, the mode of nutrition remains to be determined by future studies. Such studies will contribute to the knowledge of very interesting adaptations to symbiotic way of life, and may reveal features important from the taxonomic point of view.

## ДИНОФЛАГЕЛЛАТЫ РЫБ: КРАТКИЙ ОБЗОР СУЩЕСТВУЮЩИХ И ВНОВЬ ПРЕДЛАГАЕМЫХ РОДОВ

И. Лом

**Резюме.** Дан обзор родов динофлагеллат, заражающих морские и пресноводные рыбы, приведены их диагностические признаки, показано отличие от жгутиковых рода *Oodinium* Chatton, 1912 — паразитов оболочника и приведены примечания по патогенности динофлагеллат. Род *Crepidoodinium* Lom et Lawler g. n. предполагается для *Oodinium cyprinodontum* Lawler, 1967 от морских ципринодонтидов и *Piscinoodinium* g. n. для пресноводных *Oodinium pillularis* Schäperclaus, 1954 и *O. limneticum* Jacobs, 1964. Самым важным диагностическим признаком является структура органеллы прикрепления, которая изображена вместе с другими морфологическими признаками.

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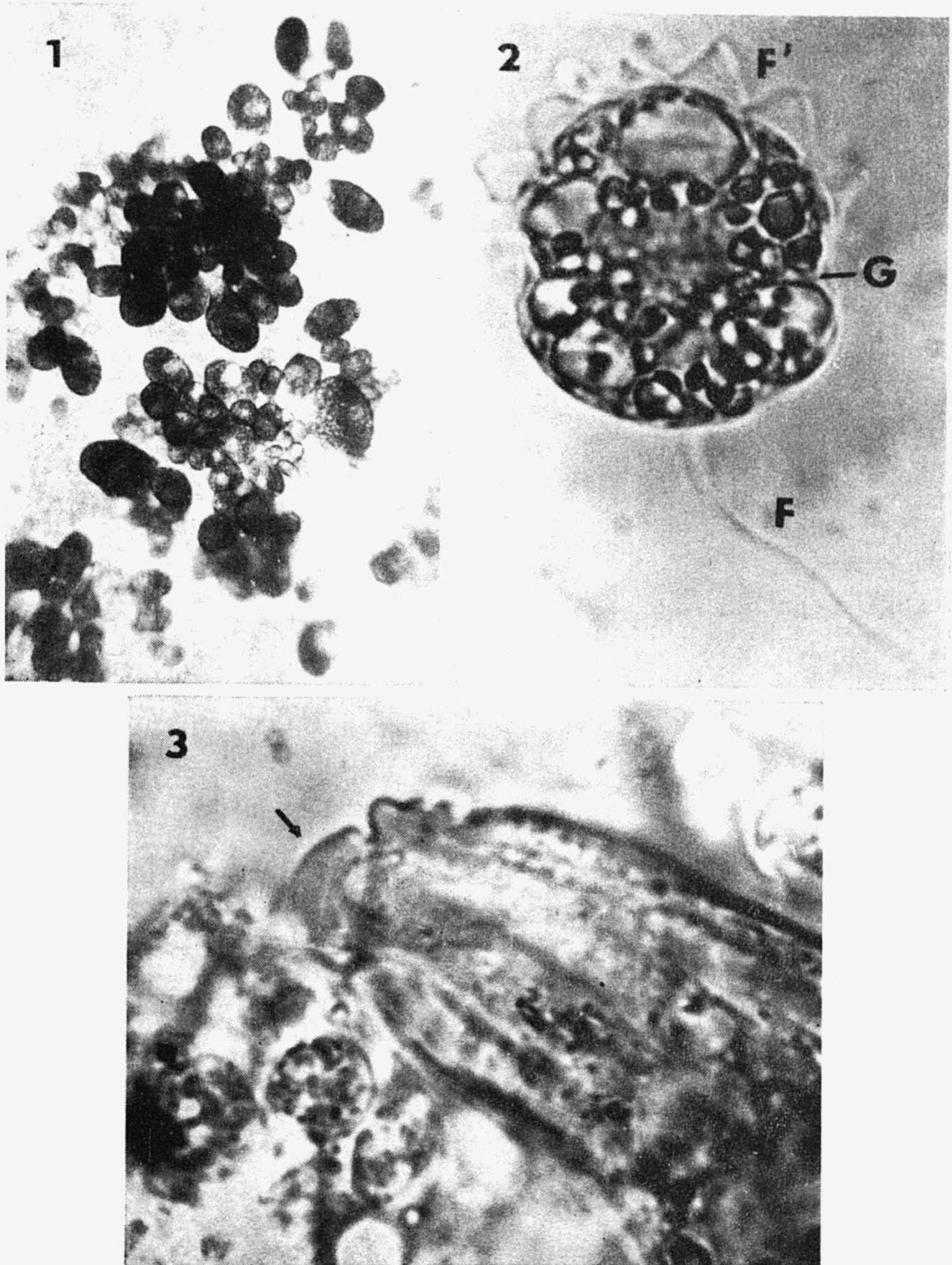
**W. Micherdziński: Eine taxonomische Analyse der Familie Macronyssidae Oudemans, 1936. I. Subfamilie Ornithonyssinae Lange, 1958 (Acarina, Mesostigmata).**

*Państw. Wyd. Naukowe, Warszawa—Krakow 1980, 264 pp., 132 Figs. Price 64. — Zl*

After the monographic treatment of mites of the family Parasitidae published in 1969, the author started to compile a similar monograph on mites of the family Macronyssidae of the world fauna. In the first volume of his work he deals with the subfamily Ornithonyssinae, which badly needed taxonomic classification due to the complexity of the whole group, the discrepancy of the authors' opinions on the taxonomy of the subfamily and due to its considerable medical importance.

In the introduction the author evaluates the existing taxonomic criteria from the viewpoint of individual, specific and generic variability. Briefly he mentions the specificity to the host, mainly the topic specificity, the geographic distribution and the medical importance of some species.

As most important characteristics the author considers functional adaptations to the parasitic way of life, particularly the change in the life cycle leading to gradual elimination of the



**Fig. 1.** Clusters of attached trophonts of *Piscinoodinium pillulare* on the fin of an invaded fish (*Puntius*). Note the largely different size of trophonts indicating continuous attractivity of certain predilected spots. ( $\times 180$ ). **Fig. 2.** A gymnosporangium of *P. pillulare*. Trailing flagellum (F) at the bottom; to visualize the transverse flagellum (F') it was shifted out of the equatorial groove (G). ( $\times 2,500$ ). **Fig. 3.** Basal part of the trophont with the attachment disc (arrow) partly detached from the host epithelial cells. ( $\times 2,700$ ).

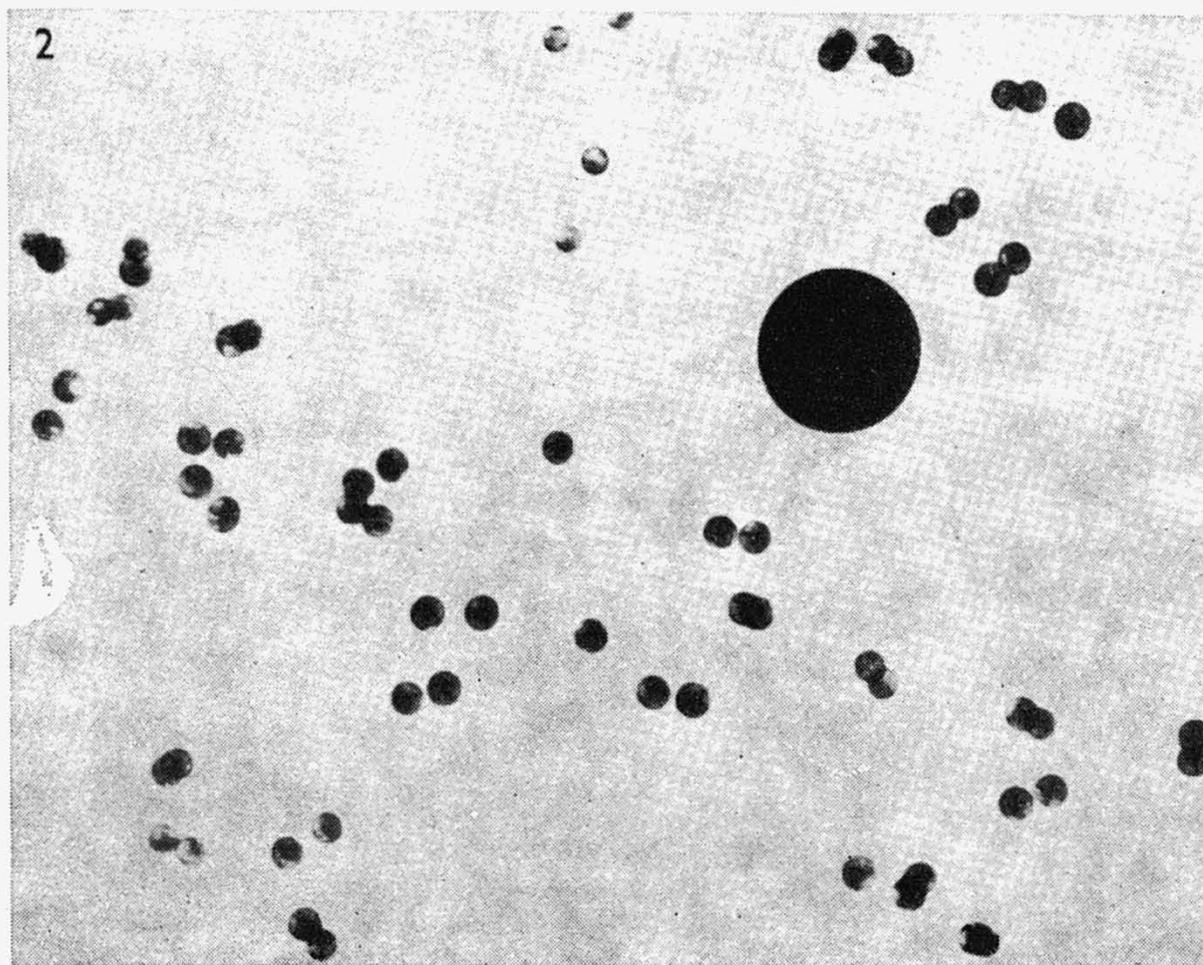
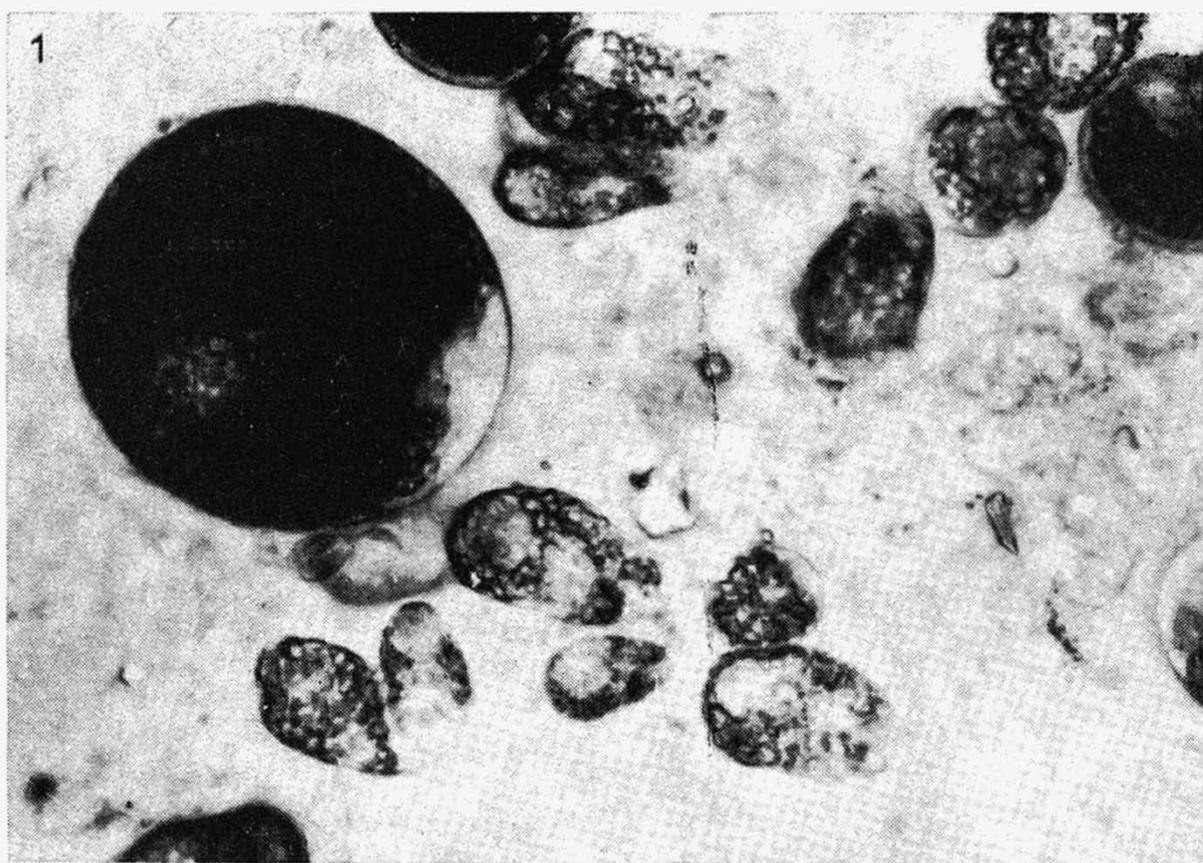
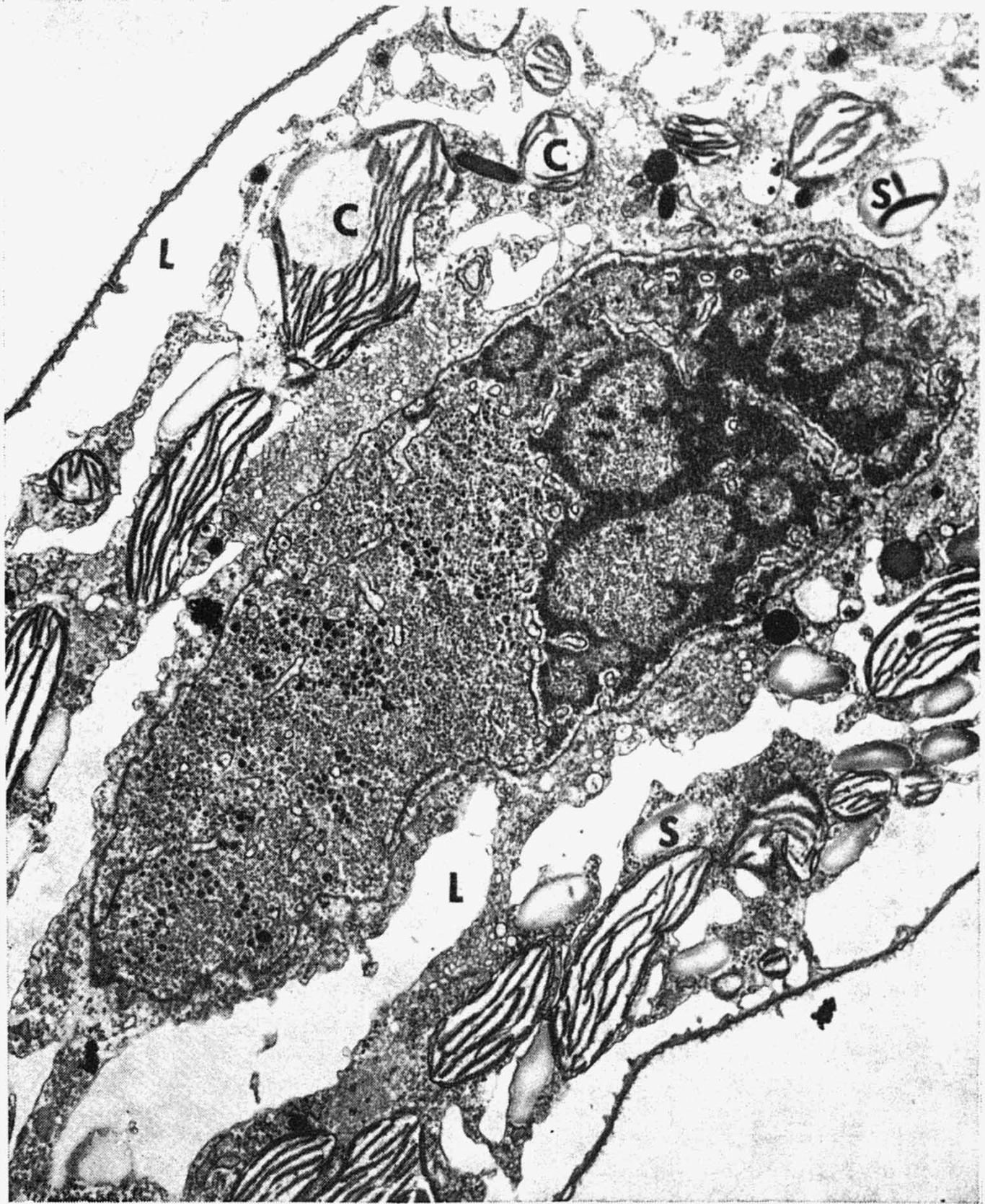


Fig. 1. A group of trophonts on the skin of the host (*Puntius*). Note the large globular one just prior to detachment off the host's surface. ( $\times 600$ ). Fig. 2. A large tomont preparing to divide in a group of small stages in various stages of division. The dividing process of them all is synchronized, although the division does not take place within a common envelope. ( $\times 110$ ).



**Fig. 1.** Electron micrograph of a longitudinal section through the mid body of a trophont of *Crepidodinium cyprinodontum*. Specimen preparation the same as described in Lom and Lawler (1973). Note the extent of interconnected cytoplasmic lacunae (L), numerous chloroplasts (C) and starch grains (S). Nucleus is characterized by numerous deep invaginations of nuclear membrane and by a conspicuous reticulated nucleolus. ( $\times 1,000$ ).

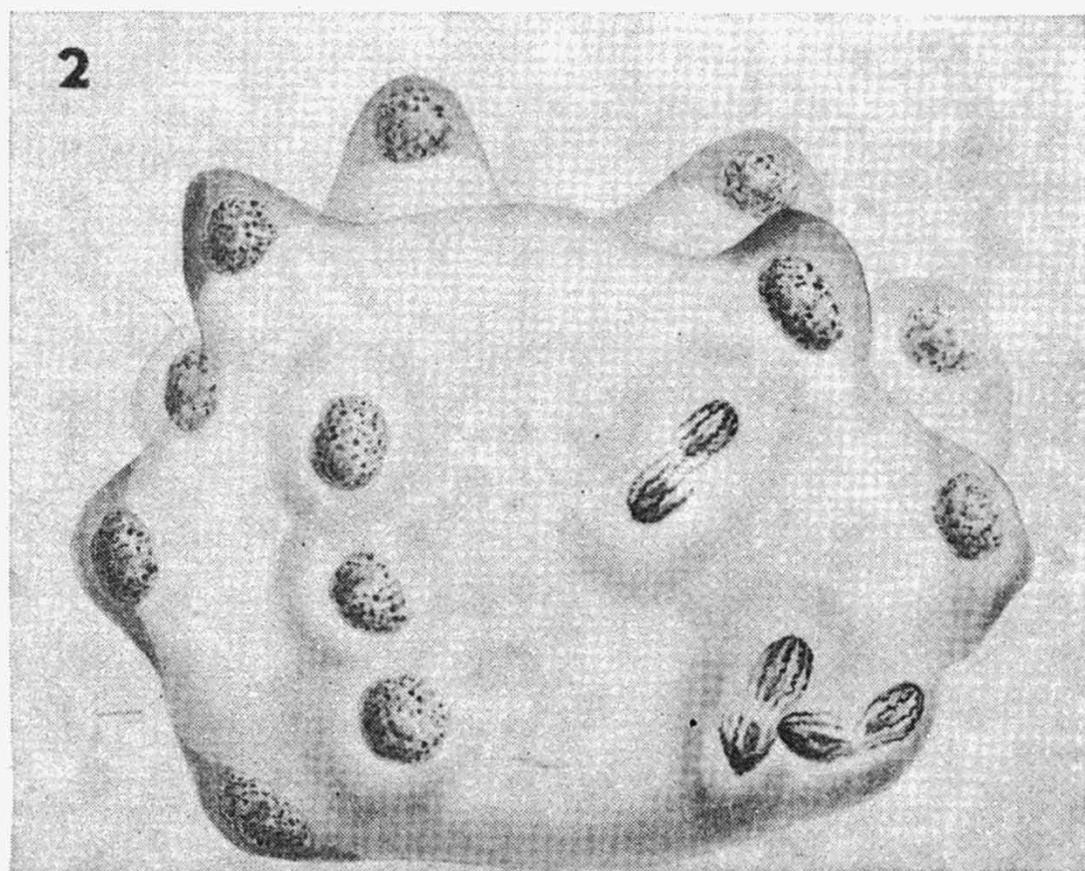
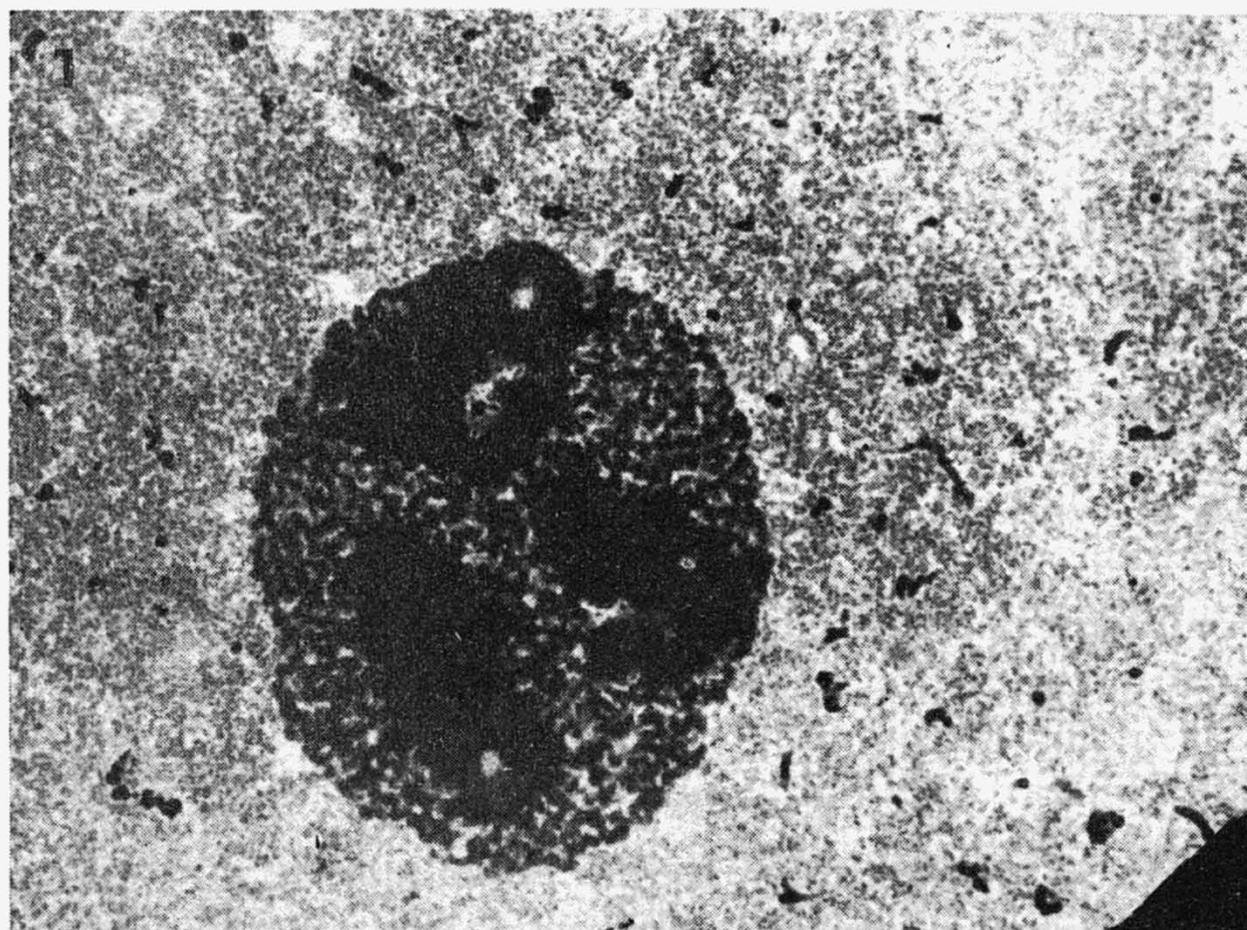


Fig. 1. Electron micrograph of a part of the nucleus of *Amyloodinium* sp. to show, in addition to a large nucleolus, vermiform structures in the nucleoplasm. ( $\times 10,000$ ). Fig. 2. *Ichthyodinium chabaudi* (from Hollande and Cachon 1953). A multinucleate trophic stage, a „primordial schizont“ ready to start division into schizonts. Vitelline sac of a newly hatched *Sardina pilchardus*-fry. ( $\times 1,200$ )