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CHAPTER 13
PARASITIC DINOFLAGELLATES

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1 INTRODUCTION

The dinoflagellate nature of many organisms parasitizing other protists, metazoans and even algae, was first recognized by Chatton (1910, 1912 . . . 1952). Despite great variety of morphology he pointed out particular features of the nuclear structures (dinokaryon) and mitosis (dinomitosis) which are common to both free-living and parasitic dinoflagellates. The parasites have special morphological features not present in free-living forms. However, life-history stages resembling free-living species (dinospores) occur and are responsible for the dispersal of the species. On this basis Chatton attributed several *incertae sedis* parasites to this class. He also described many new species and though he suspected that these were polyphyletic organisms, he grouped them into the single zoological tribe Blastodinida.

Chatton's original research on dinoflagellates concluded in 1937. In 1964, Jean Cachon gave more precise details of their cytology and life cycles and asserted their polyphyletic origin. He distinguished two tribes: Blastodinida and Duboscquodinida, differing in the morphology of their vegetative phase, their nuclear development and the structural and metabolic relations with their host. The first tribe is composed essentially of ectoparasites, the second of intracellular ones. The mechanisms of parasitism usually have major consequences for the morphology, physiology, reproduction and dispersal of the parasite. Loeblich (1976), using biochemical data as a basis, proposed that

Syndinium should be separated from the Duboscquodinida as an autonomous order (Syndiniales), to which he later (1983) transferred all those included in the Duboscquodinida here. He also recognized *Chytriodinium* and its relatives as a separate order (Chytriodiniales).

As a result of recent knowledge, including ultrastructural data, we shall distinguish primarily three zoological tribes, recognizing also the parasitic propensities of some of the Dinococcida (Dinococcales or Phytodiniales).

At present, the fungal-like Elliobiopsidae do not seem to belong among the parasitic dinoflagellates. Galt & Whistler (1970) and Hovasse (1974) have placed them there for the single reason that they possess flagella as dinospores, but other morphological and cytological features are unknown. Loeblich (1983) considers them to be a separate class.

This chapter concentrates on information recorded subsequent to the chapter by Chatton in Grassé's *Traité de Zoologie* (1952). The latter should be consulted for more general information.

2 DINOCOCCIDA (botanical order Dinococcales or Phytodiniales)

These organisms are characterized by the importance of a non-motile, vegetative, encysted stage. Some are planktonic, others are benthic, living epiphytically mainly in fresh water. Most possess chlorophyll, starch and a pyrenoid. They have long been considered to be strictly autotrophic. However, a great number are able to feed holozoically, perforating algal cell walls by means of a stalk and rapidly sucking out the cytoplasm. *Stylodinium sphaera*, *Cystodinedria inermis* (Pfiester & Popofsky 1979) and *Cystodinium bataviense* (Pfiester & Lynch 1980) form not only dinospores (naked or thecate, non-flagellated autospores), but also amoeboid forms bearing many thin straight pseudopods resembling axopodia. Autospores and amoebae are motile and attach themselves successively to cells of several algae (*Oedogonium*, *Spirogyra*, *Mougeotia*), finally emptying them. Using their pseudopodia these amoebae can also phagocytose small protists, e.g. algal zoospores, thus behaving as predators as well. Their apparent autotrophy needs re-examination. They possess chloroplasts, but the pigmentation varies from green to brown according to the life-history stage. The chloroplasts may result from feeding, disappearing when the cell contents are metabolized. These amoeboid forms can return to the typical dinococcal form by retracting their pseudopods and secreting an envelope. Dispersal is then by flagellated dinospores which behave either as zoospores with a direct development, or as gametes. The eventual development of zygotes is unknown.

Some previously described organisms could actually be stages of the complex life cycle of these parasites. For example, *Hypnodinium sphaericum* could be a part of the cycle of *Cystodinium*, and *Dinococcus* a part of the cycle of *Cystodinium bataviense* (Pfiester & Lynch 1980). *Dinamoebidium varians* of the monospecific

tribe Rhizodinida, some *Rhizochrysis* (chrysomonads) and *Vampyrella* (pseudoheliozoans) might also be stages of such Dinococcida. The genus *Paulsenella*, epiphytic and parasitic on marine pelagic diatoms, was considered by Chatton (1952) to be in the Apodinidae; but it is far from well studied and could also be a Dinococcidian, possessing a permanent cyst-like wall (according to Paulsen's description). On the other hand, *Dissodinium*, which has been placed in the Dinococcida (and is often mistaken for *Pyrocystis*, a free-living form) has to be considered as a member of the Blastodinida according to Drebes (1969, 1978, 1981) and Elbrächter & Drebes (1978).

In the Blastodinida, Duboscquodinida and Syndinida, the life cycle of the protist has two periods, the first corresponding to the vegetative phase (trophont stage), the other to a reproductive phase (sporont stage), which is responsible for new infections. Once attached to their host, spores develop *in situ*. As is nearly always the rule for parasites, reproduction is greatly developed: increased fertility and dispersal counterbalance the improbability of finding and infecting a new host. Table 13.1 lists the species of parasitic dinoflagellates which are currently recognized.

3 THE VEGETATIVE PHASE OF THE NON-DINOCOCCID PARASITES

Infective processes are known in only a few cases. The dinospore is biflagellated but loses its flagella as soon as it comes into contact with the host. It is then either passively swallowed by the host together with food, or it attaches itself by a posterior tentacle-like projection and eventually perforates the host membrane. This projection seems to be homologous to the peduncle, developed from the sulcus in some free-living dinoflagellates and used in phagocytosis (Chapter 6). The development of the parasite is defined at the very outset by the mode of attachment: extracellular (Blastodinida), or intracellular (Duboscquodinida, Syndinida). Comparisons between free-living and parasitic dinoflagellates are made more easily with the first group; the others are more deeply modified by parasitism. The cytology of the Blastodinida, Duboscquodinida and Syndinida will be successively described here.

3.1 Extracellular parasites

Blastodinida (botanical order Blastodiniales)

These organisms mainly parasitize marine protists and metazoans (copepods, siphonophores, appendicularians, jelly-fish, thaliaceans, annelids, fishes) a few algae, and diatoms. They show very clearly gradual modifications of morphology, constitution and physiology from free-living to parasitic dinoflagellates.

Table 13.1. Species of parasitic dinoflagellates currently recognized and their hosts

Tribe/Family	Genus	Species	Host
Dinococcida (semi-parasitic, semi-free)			
		Cystodinium bataviense	Siphonophones
		Stylodinium sphaera	,,
		S. gastrophilium Cachon *et al.*	,,
		Cystodinedria inermis	,,
I Blastodinida (entirely extra-cellular)			
Blastodinidae	*Blastodinium*	*B. apsteini* Sewell	Copepods
	13 spp.	*B. chattoni* Sewell	,,
		B. contortum Chatton	,,
		B. hyalinium Chatton	,,
Protoodinidae	*Protoodinium*	*P. chattoni* Hovasse	Hydromedusae
		P. hovassei Cachon & Cachon	Siphonophores
Apodinidae	*Apodinium*	*A. mycetoides* Cachon & Cachon	Appendicularia
		A. chattoni Cachon & Cachon	,,
		A. zygorhizum Cachon & Cachon	,,
		A. rhizophorum Cachon & Cachon	,,
Haplozoonidae	*Haplozoon*	*H. inerme* Cachon	,,
		H. axiothellae Siebert	Annelida
		H. armatum Dogiel	,,
Oodinidae	*Oodinium*	*O. poucheti* Chatton	,,
		O. dogieli Cachon & Cachon	Annelida
		O. acanthometrae Cachon	Acantharia
		O. fritillariae Cachon	Appendicularia
	Oodinioides	*O. vastator* Reichenback	Fish
	Amyloodinium	*A. ocellatum* Brown	,,
	Crepidoodinium	*C. cyprinodontum* Lawler	,,
	Piscinoodinium	*P. pillulare* Schläperclaus	,,
		P. limneticum Jacobs	,,
Diplomorphidae	*Cachonella*	*C. paradoxa* Cachon	Siphonophores
		C. echinaria Cachon	,,

Table 13.1. (continued)

Tribe/Family	Genus	Species	Host
Chytriodinidae	*Chytriodinium*	*C. affine* Dogiel	Crustacean eggs
		C. roseum Dogiel	,, ,,
		C. parasiticum Dogiel	,, ,,
	Myxodinium	*M. pipiens* Cachon *et al.*	*Halosphaera*
II Duboscquodinida (partly intra, partly extra-cellular)			
Amoebophryidae	*Amoebophrya*	*A. ceratii* Cachon (in Gymnodinians, Adinides, nuclei of Peridinians)	
		A. acanthometrae Borgert (in Acantharia)	
		A. sticholonchae Koeppen (in *Sticholonche*)	
		A. grassei Cachon (in *Oodinium poucheti* etc. *Oodinium acanthometrae*)	
		A. leptodisci Cachon (in *Pratjetella*)	
		A. rosei Cachon (in Ciliates, living in Siphonophores and *Sagitta*)	
		A. tintinni Cachon (in *Xystonella*)	
Duboscquellidae	*Duboscquella*	*D. anisospora* Grasse	
		D. aspida Cachon (in Tintinnids)	
		D. caryophaga Cachon	
		D. cnemata Cachon (in Tintinnids)	
		D. melo Cachon (in *Noctiluca*)	
		D. nucleocola Cachon	
	Duboscquodinium	*D. collini* Grasse	
		D. kofoidi Grasse	
	Keppenodinium (*Hollandella*)	*K. mycetoides* Cachon (*Spongosphaera* in Sphaerellaria)	
		K. lobata Cachon (in Sphaerellaria, *Plegmosphaera*)	
		K. piriformis Cachon (in Sphaerellaria, *Actinosphaera*)	
Sphaeriparidae	*Sphaeripara* (*Neresheimeria*)	*S. catenata* Loeblich (in *Fritillaria*)	
		S. paradoxa Loeblich (in Appendicularia)	
	Atlanticellodinium	*A. tregouboffi* Cachon & Cachon (in Radiolaria *Planktonetta*)	

Table 13.1. (continued)

Tribe/Family	Genus	Species	Host
III Syndinida (entirely intra-cellular)			
Syndinidae	*Syndinium* Chatton	*S. brandti* Hovasse	(in *Collozoum*)
		S. insidiosum Chatton	(in *Collozoum*)
		S. vernale Hovasse	(in *Collozoum*)
		S. mendax Chatton	(in *Myxosphaera*)
		S. dolosum Chatton	(in *Sphaerozoum*)
		S. chattoni Hovasse & Brown	(in *Sphaerozoum*)
		S. astutum Chatton	(in *Sphaerozoum*)
		S. breve Hovasse & Brown	(in *Sphaerozoum*)
		S. globiforme Hollande & Enjumet	(in *Collozoum*)
		S. belari Hollande & Enjumet	(in *Collozoum*)
		S. borgerti Hollande *et al*	(in *Aulacantha*)
		S. sp.	(in *Thalassophysa*, *Spongosphaera*, *Eucyrtidium*, *Cochlodinium*)
	Solenodinium	*S. fallax* Chatton	(in *Thalassicolla*)
		S. leptotaemia Hovasse & Brown	(in *Thalassicolla*)
		S. denseum Hovasse & Brown	(in *Thalassicolla*)
		S. sp. Hollande & Enjumet	(in *Sphaerellaria*)
	Synhemidinium Chatton		
	Ichthyodinium	*I. chabelardi* Hollande & Cachon	(in eggs of *Sardinia*)
	Cochlosyndinium Chatton		*Coryceus*
	Merodinium Chatton		Radiolarians
	Haematodinium Chatton & Poisson		Crabs
	Trypanodinium Chatton		Copepod eggs

Blastodinium, the type genus of this tribe, is not typical but it is the least modified for parasitism. Commonly observed in the gut of copepods, it is the only one which does not have a direct physical attachment to the host; all other Blastodinida are fixed by a posterior stalk. Nevertheless, it produces castration in its host.

A wall is observed in all Blastodinida. In *Blastodinium* (Fig. 13.1) the left-handed helical girdle and short sulcus are conspicuously lined by a cellulosic wall, and a row of small spines decorates one of the girdle edges, aiding perhaps in the anchorage of the organism. Though fixed by a stalk to the membrane of the umbrella of a jelly-fish or siphonophore, *Protoodinium* (Hovasse 1935; Cachon & Cachon 1971a) has a typical theca, with visible girdle and sulcus in which the transverse and longitudinal flagella undulate normally. The tabulation of the theca is still discernible by silver staining in some species of *Oodinium* (Hovasse 1935) but the girdle and sulcus are not lined by the wall. In all other Blastodinida (*Oodinium* pro parte, *Apodinium*, *Haplozoon*, etc.) the wall consists

Fig. 13.1. *Blastodinium spinulosum* Chatton. (a) Young trophont. The nucleus is figured at telophase. Its wall bears two helical girdles which are decorated with small spines; they are connected by a short sulcus(s). (b) This species can reproduce vegetatively while it is inside the copepod gut. (c) The parasite is undergoing palisporogenetic divisions within its original wall. Three generations of sporocysts may be seen: (I) the oldest sporocysts (stages 32–64), (II) the four sporocysts of the following stages, (III) one gonocyte and one trophocyte (IV) which are not yet separated.

of a thin continuous, resistant pellicular envelope, bearing no decoration. Beneath the cell membrane there is the usual layer of flat amphiesmal vesicles found in free-living dinoflagellates (Dodge & Crawford 1970, and see Chapter 3). Many of these organisms are able to shed their wall and build a new one, both during growth and sporogenesis.

Chloroplasts are highly modified in parasites. *Blastodinium* still possesses well developed chloroplasts, but Chatton noticed that the pigmentation of the chloroplasts progressively disappears during the vegetative phase, appearing again during sporogenesis (*B. spinulosum*, *B. pruvoti*, *B. contortum*). This pigmentation may be more intense in warm water species which have a rapid development than in those living in colder waters. *B. hyalinum* appears to have no chloroplasts. Thus, there are various intermediary stages between autotrophy and complete heterotrophy in this genus.

In *Protoodinium*, *Piscinoodium* and *Crepidoodinium*, chloroplasts are well developed and appear functional, although partial heterogeneity is probable: certainly something is sucked from the host through the stalk. The host attachment must be made before the parasite can continue its development. All other Blastodinida and most other parasitic dinoflagellates are heterotrophic and lack chlorophyll.

'Chromoplasts' responsible for dark pigmentation, have been described in *Oodinium*, but they have not been observed with electron microscopy. Pigmented lipid droplets are found scattered throughout the cytoplasm of *Oodinium*; they are food reserves. In other parasitic Blastodinida (*Amyloodinium*, *Crepidoodinium*) there are starch granules.

Trichocysts and mucocysts, which are so commonly observed in free-swimming and all other parasitic dinoflagellates, occur in *Protoodinium*, *Amyloodinium* and *Crepidoodinium*. In *Cachonella* they are numerous and grouped in three large bundles beneath the cell membrane. Their 'snap action' may be involved in the strange transformation of the protist at the beginning of sporogenesis (see below). The mitochondria of these marine aerobes do not appear to differ from the norm.

The most remarkable feature of the blastodinid trophont (excluding *Blastodinium*) is the stalk. It may be homologous to temporary pseudopodia which issue from the bottom of the sulcus of some phagotrophic dinoflagellates, e.g. *Podolampas* or *Protoperidinium* (G. Gaines & F. Taylor, pers. comm.), and the peduncle through which many organisms feed (*Gymnodinium*, *Gyrodinium*) (Chapter 6). It may also be homologous to the movable tentacle of forms like *Noctiluca*. This homology is clear in *Protoodinium* but in other organisms (*Oodinium*, *Haplozoon*, *Apodinium*) the hyposome is part of the stalk; the cell body of the latter group consists almost exclusively of the episome. In *Chytrodinium*, which must penetrate the thick chorion before reaching the egg of a crustacean, the hyposome is extraordinarily active and acts as a drill (Fig. 13.6a, b).

The ultrastructure of the stalk makes it clear that it can be an anchoring organelle as well as a feeding apparatus. It may remain totally or partially on the host cuticle, developing a system of ramified rhizoids. Or, the stalk may perforate the cuticle and penetrate the host cell. The parasite is then directly in contact with the host cytoplasm through its rhizoids; the host does not form any membrane around the parasite (parasitophorous membrane). This direct contact seems to be of the same type as in Gregarines, which are also extracellular.

Oodinium's stalk (Cachon & Cachon 1971b) (Fig. 13.2) is the simplest. With the light microscope it appears to be fibrous. It originates in the vicinity of the nucleus. It is globular in the median part but its extremity is flattened into a wide, sucking disc on the host surface. Its double function becomes evident with the electron microscope: the cell membrane of the stalk has deep, cylindrical, closely-packed invaginations which open on the host side producing a 'brush border' appearance. The invaginations reach the perinuclear cytoplasm of the dinoflagellate, where they appear as large, flattened and contorted bags. They appear to be empty but are clearly for exchange. The cell membrane of

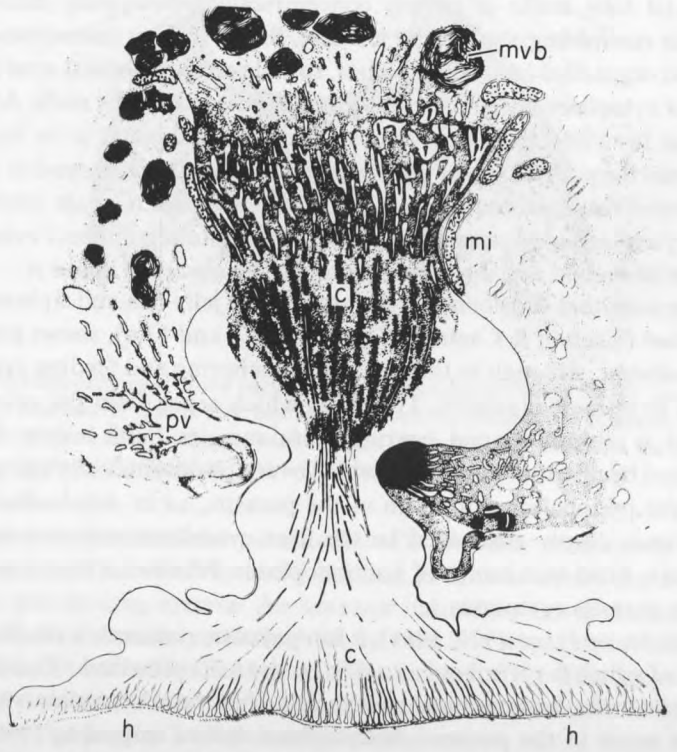

Fig. 13.2. The stalk of *Oodinium fritillariae* Chatton: the host (h), tubular invaginations of the cell membrane (c), pusule (pv), perinuclear mitochondria (mi), multivesicular bodies (mvb).

the stalk intimately adheres to the host surface between the invaginations; the areas of contact are not altered ultrastructurally.

In *Crepidoodinium* (Lom & Lawler 1973; Lom 1977, 1981), the anchoring disc has an irregular appearance. Its surface possesses a large number of small ramifications closely applied to the fish integument. The extremity of each ramification is conical and slightly inserted into the host cell. A bundle of tonofibrils similar to a desmose is developed. At the point of contact the host membrane appears fuzzy. Vesicles and microtubules perpendicular to the cell surface (transport?) are observed in the dinoflagellate but no particulate matter can be seen coming from the host.

The stalk apparatus is more complex in *Amyloodinium* (Fig. 13.3) (Lom 1973, 1981), and helps to explain that of *Protoodinium*. The stalk is essentially an anchoring organelle. A separate tentacle-like structure, the stomopod, is associated with a cytopharyngeal feeding apparatus. Rhizoids from the margin of the stalk disc radiate into long filiform projections which insert into the gill epithelial cells of fish and penetrate the cell membrane. The end of the rhizoids are ampulla-shaped and contain small vesicles which suggest an absorbtive function. A cylindrical, movable tentacle arises from the base of the stalk; it has an axial tube made of twenty concentrically overlapping microtubular sheets, thus resembling a suctorian tentacle. Small vesicles (membranous dark bodies) and organelles (clove-like bodies, spindle-shaped bodies) arise from the perinuclear cytoplasm of the parasite and are carried along the stalk. As no food vacuole has been observed here, lytic substances are thought to be injected by the stalk into the prey. If so, the stalk would resemble the stomopod or peduncle of some free-living gymnodinoids, e.g. *Erythropsidinium* (Greuet 1969). In the latter, a cytopharyngeal apparatus made of microtubular sheets exists at the base of the stomopod and many food vacuoles are observed above it.

The parasite that lives beneath the umbrella of jelly-fish and siphonophores, *Protoodinium* (Cachon & Cachon 1971a) (Fig. 6.1 and 13.4), shows similarities to *Amyloodinium*, although in this genus the anchoring and feeding systems are combined in a single organelle. The stalk, which arises from the sulcus at the girdle level, is tap-root shaped, bearing lateral radicles, but is hollow. Its wall is strengthened by microtubular sheets which overlap concentrically and penetrate as far as the perinuclear cytoplasm of the parasite, as in *Amyloodinium*. This stalk becomes deeply embedded in the host cytoplasm and acts as a large cytopharynx, filled with lumps of host cytoplasm. Numerous food vacuoles are seen in the parasite cytoplasm.

Piscinoodinium (Lom 1977, 1981), a fish parasite, possesses a short stalk, the extremity of which is spread out as a disc on the fish epithelium. This disc has a honeycombed sole, bearing numerous rod-like holdfast corpuscles (rhizocysts), which are made in the perinuclear cytoplasm before migrating to their final position in the disc. Microtubular sheets exist at the base of the stalk as in the previous organisms.

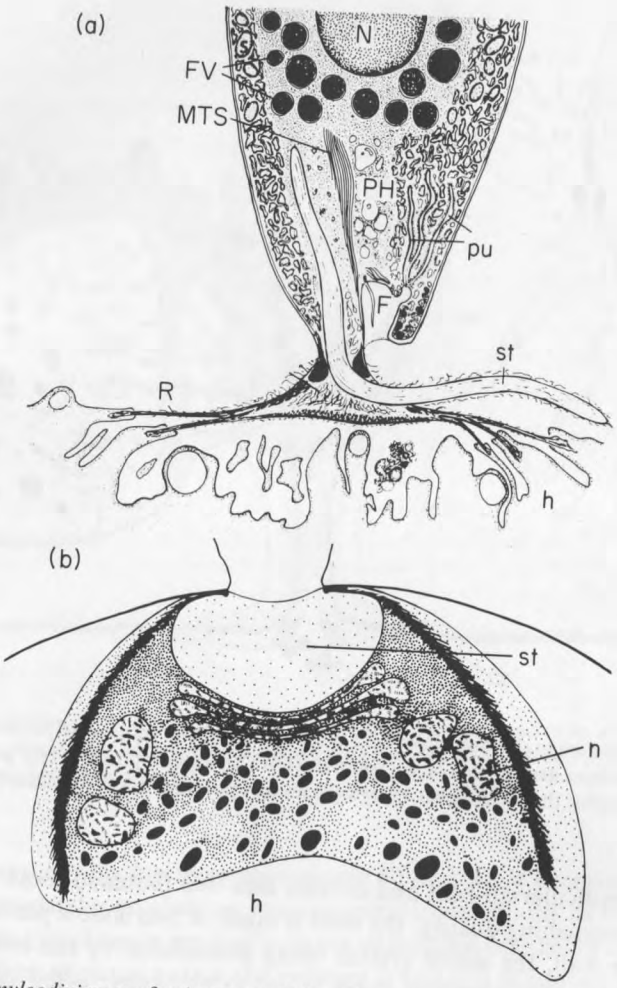

Fig. 13.3. (a) *Amyloodinium* sp: food vacuole (FV); microtubular ribbon (MTS); pusule (pu); rhizoids (R); flagellum (F); stalk (St); host (h); nucleus (N); phagocytic cytoplasm (PH). (b) *Chytriodinium roseum*. The basal portion of the stalk (st) is entirely included in the copepod egg (h), the cytoplasm of which has been sucked by the parasite; n = nucleus.

Haplozoon is a multicellular parasite found in annelids. Amphiesmal vesicles are present in each cell. Practically nothing is known about the *Haplozoon* anchoring and feeding system. An anterior individual has a suction disc in contact with the intestinal epithelium of the host and a movable 'stylet' which is thrust into the host cells (Shumway 1924; Siebert 1973). The 'stylet' may be similar to a stomopod. Nutrients must pass from the anterior individual to those behind it but this process has not been studied.

Apodinium (Fig. 13.5), a parasite of appendicularians, has a well developed stalk (Cachon & Cachon 1973). A long, cylindrical stem penetrates the cuticle

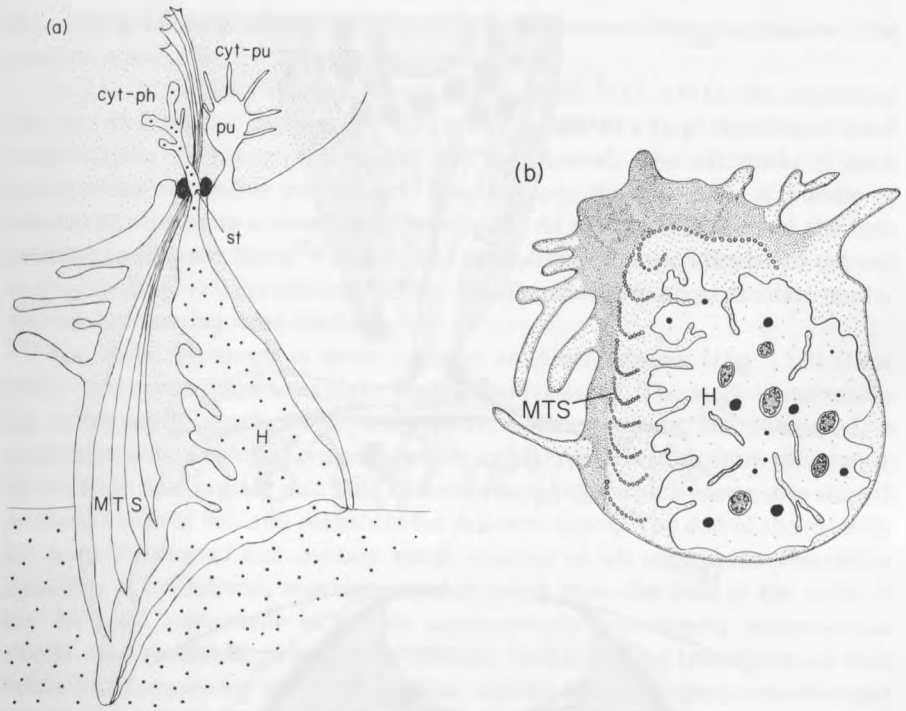

Fig. 13.4. *Protoodinium chattoni* Hovasse. Longitudinal (a) and transverse (b) sections of the stalk in which there are ribbons of microtubules (MTS), a stomopharynx (st), pharyngeal cytoplasm (cyt ph); the pusule (pu), its cytoplasm (cyt pu); and host cytoplasm (H).

of the appendicularian host and divides into two flattened roots. This system shows an astonishing duality: the stem is made of two hollow parts limited by a thick dense wall, the whole system being surrounded by the cell membrane. Between these two elements there is an axial cavity, often contorted and containing multimembranous vesicles. The elements continue as rhizoids running in opposite directions between the host muscles or along the urochord. These rhizoids are covered by a thick, tomentous wall, containing a thin granular material. Where the axial cavity ends at the base of the stalk, a great number of multimembranous vesicles can be seen. One of the elements is postero-dorsal, the other postero-ventral.

A well developed pusule opens into the axial cavity between the two stem elements. Differences in the stalk are used in the taxonomy of the genus (size, morphology, ultrastructural arrangements). *Amyloodinium*'s system is also made of two dorso-ventral elements (an attachment disc and a stomopod; Lom & Lawler 1973) which are associated with a pusule.

Chytriodinium (Cachon & Cachon 1968) (Fig. 13.3 and 13.6) uses its hyposome to drill through the thick chorion of the crustacean egg. It can

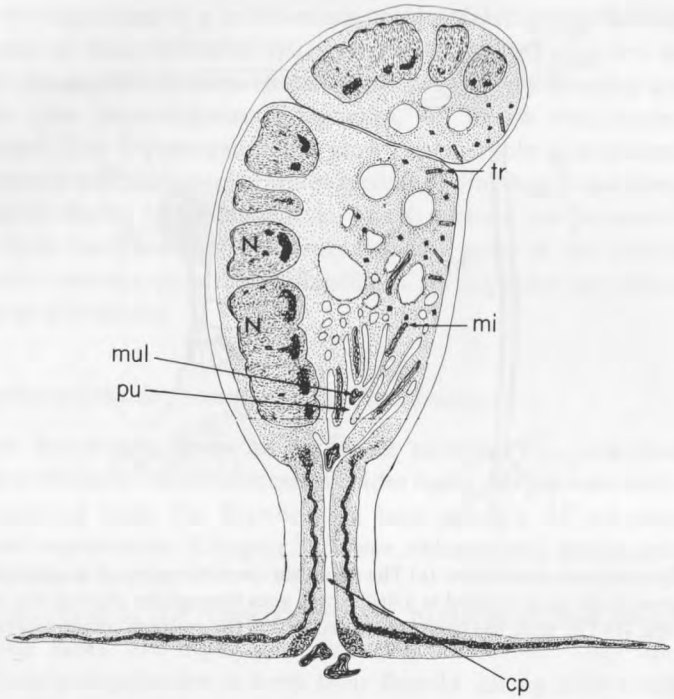

Fig. 13.5. *Apodinium* sp., showing the duality of the stalk structure and in its axis a canal (cp), related to the pusule (pu). Multilamellar bodies are observed (mul), as well as trichocysts (tr) and perinuclear mitochondria (mi).

lengthen considerably (up to approximately 50 μm) while becoming extremely thin. Unfortunately, no electron microscopical observations have been made. Once the egg cytoplasm is reached a crown of holdfast organelles develops. The hyposome then shortens so that the episome is brought in contact with the egg. The parasite seems to be rivetted onto the egg envelope. It feeds through the holdfast organelles, between which the ampulla (a vacuole, undoubtedly for absorbtion) appears. The host cytoplasm is progressively absorbed and drawn towards the ampulla where its nuclei, mitochondria and vitelligenous plates are gathered. The egg is emptied in 1–2 hours.

Dissodinium is also a parasite of crustacean eggs (copepods) and its behaviour is similar to the previous genus (Drebes 1978; Elbrächter & Drebes 1978). The infecting dinospores penetrate in a few minutes, using an anchoring and feeding stalk which issues from the hyposome.

In *Myxodinium* (Cachon *et al.* 1970), a pseudopodium issues from the sulcus of the spore. It comes in contact with the cellulosic wall of the phycoma of the prasinophycean alga, *Halosphaera*, and spreads out. In a few minutes the wall is perforated by two small holes (2 μm in diameter). Two small circular cups

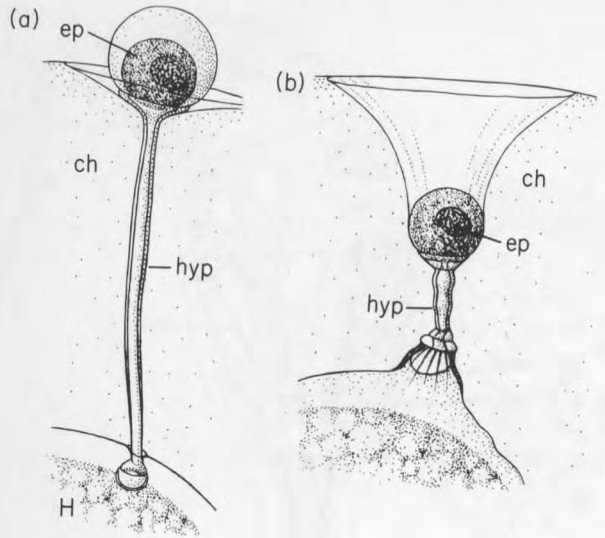

Fig. 13.6. *Chytriodinium parasiticum.* (a) The organism consists mainly of its episome (ep) while its hyposome (hyp) is reduced to a drill which goes through the chorion (ch) of the crustacean egg. (b) The stalk has been contracted so that the episome comes nearer to the egg.

develop in the stalk cytoplasm and the alga is rapidly sucked out through the two apertures until the shell is emptied. *Paulsenella*, an ectoparasite of diatoms (e.g. *Chaetoceros*) is imperfectly known: it also possesses a small peduncle used for sucking its host (Schnepf 1985).

Finally, the stalk of *Cachonella* seems to be similar to that of *Oodinium*, except that ramified rhizoids appear on the margin of the anchoring sole (Fig. 13.14a).

The pusule is generally well developed in members of the Blastodinida. For example, in *Oodinium* (Cachon *et al.* 1970; Cachon & Cachon 1971b) a system of lacunar vesicles makes up a 'spongiome' containing several types of vesicles. They are connected to a system of long collecting canals which finally flow into an ampulla (sometimes two). Around the ampulla are large ribbons of striated fibrils that may be responsible for its contractility. Multilamellar bodies are often observed within the vesicular system. They appear to be periodically ejected from the ampulla. The pusule is always positioned postero-ventrally and is associated with the stalk. In *Apodinium* the accumulation of multilamellar bodies in the vicinity of the rhizoids proves that these structures are excretory.

3.2 Intracellular parasites

These have been observed in a great variety of hosts, both protists (e.g. dinoflagellates, radiolarians, ciliates) and in the cytoplasm of tissues of

multicellular organisms (e.g. crustaceans, coelenterates, appendicularians). The mechanisms of their infection (passive, active, phagocytic) are usually not known. If the parasite is intracellular, the host reacts by forming a membrane around it (the parasitophorous vacuole), of which two types may be distinguished. The Duboscquodinida grow considerably as trophonts and lose all the external morphological features typical of dinoflagellates; these features then reappear during late sporogenesis. The Syndinida, on the other hand, lose not only their morphological features, but also some of the cytological and biochemical features typical of dinoflagellates. As trophonts they divide actively or form large plasmodia.

Duboscquodinida (botanical order Coccidiniales)

Except for *Sphaeripara* these all parasitize protists. They are always intracellular, sometimes even intranuclear. Besides being intracellular they can easily be distinguished from the Blastodinida because they do not have normal amphiesmal organization (Chapter 3). Theca, chloroplasts, pusule and generally mitochondria are absent.

The dinospores of the Amoebophryidae, parasites of both unicellular and multicellular hosts, are highly modified (Cachon 1964). They are the only dinoflagellate endoparasites to keep their flagella during their trophic phase, and they can proliferate extraordinarily. The girdle (or a depression homologous to a girdle) is helical. In the spore, it extends only half a turn. As the parasite grows, it becomes considerably lengthened at both ends, making several helical turns. At the same time, the episome progressively sinks into the hyposome. The *Amoebophrya* trophont appears as a round body in the host parasitophorous vacuole. A cavity, 'the mastigocoel' (Cachon 1964), becomes visible with the light microscope. It has a double system of helical structures, one parietal involving the hyposome, the other axial on the part corresponding to the episome (termed the 'columelle' by Chatton 1922). The edges of the hyposome expand and finally completely surround the episome with a small aperture at the apex of the parasite. The girdle may become extremely long and twisted so that its helical coils are not regular. The number of basal bodies and nuclei increases enormously; they form a long chain lying just beneath the girdle. There are as many flagella as basal bodies; the flagella remain motionless during the trophic phase. In some hosts, e.g. the dinoflagellates *Triadinium polyedricum* (Cachon 1964) or *Protogonyaulax catenella* (Taylor 1967), the nucleus of the host is rapidly digested.

Microtubular bundles run beneath the helical girdle, with others beneath the limiting membrane of the hyposome where they are arranged like the petals of a corolla (Cachon & Cachon 1969, 1970). Microfilaments are associated with these bundles (non-actin filaments, Cachon & Cachon 1984). A great number of trichocysts are present, mainly in the girdle. The cell membrane of the protist

makes contact with the parasite membranes through structures which resemble nuclear pores. No food vacuoles can be seen in the cytoplasm of the parasite.

The last intracellular phase involves great changes in organization and physiology. Suddenly, the flagella begin to beat. In less than 1 minute the protist goes through an eversion which is the inversion of its earlier development (Fig. 13.7). The episome pushes forwards through the aperture of the mastigocoel. The edges rapidly turn up and are thrown backwards so that they imprison a large portion of the host cytoplasm in a big trophic vacuole as the parasite

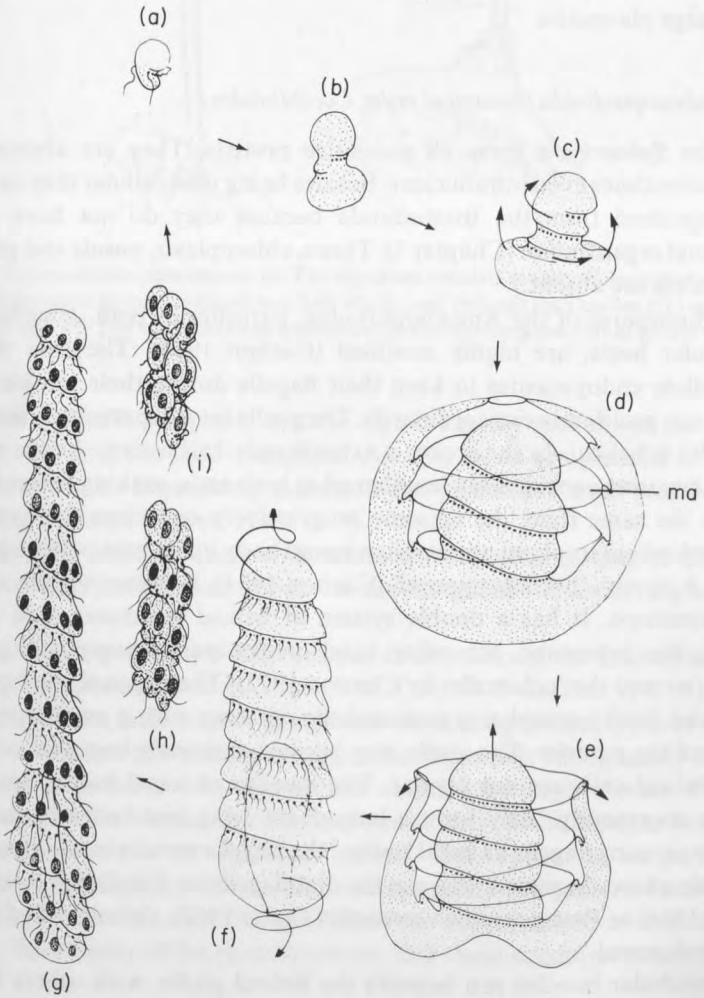

Fig. 13.7. Diagram of the life cycle of *Amoebophrya*: (a) dinospore; (b, c, d) invagination of the growing intracellular trophont (Ma = mastigocoel); (e, f) evagination of the trophont phagocytosis of the host and formation of a worm-shaped organism, the 'vermiform'; (g) lengthening of the vermiform; (i, h) formation of the swarmers.

leaves the host. The cell periphery is three layered, with a layer of flat vesicles and bears a great number of flagella. The parasite now appears worm-like (the vermiform stage) (Fig. 13.8b). It swims in a spiral manner with all its flagella

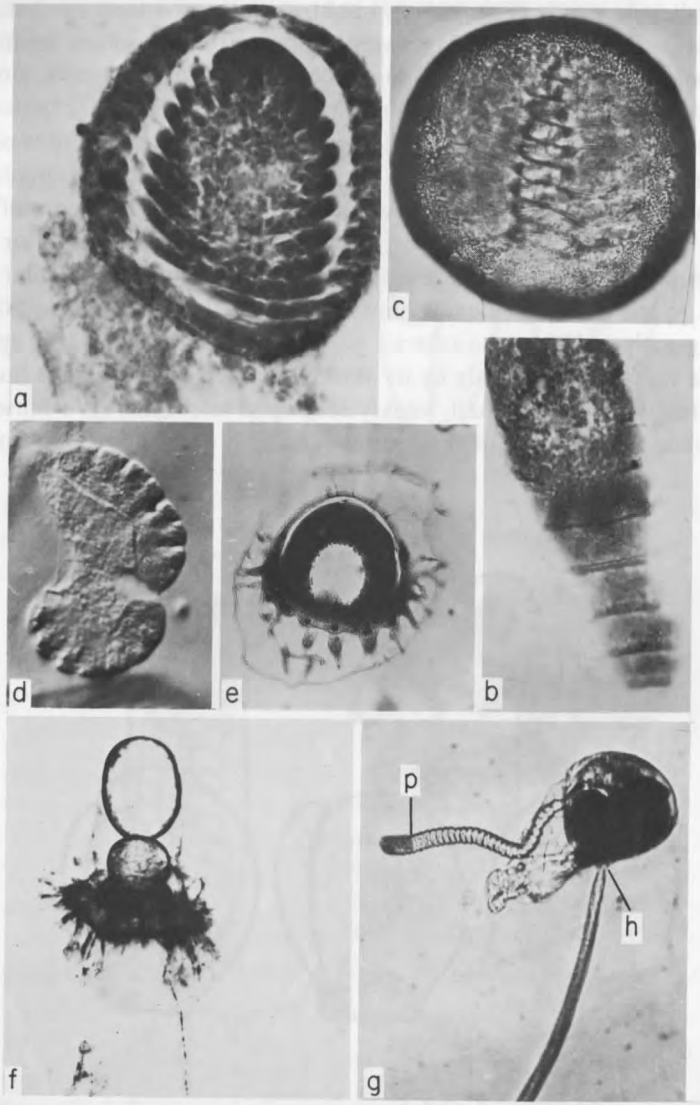

Fig. 13.8. All these micrographs are from living organisms. (a) *Amoebophrya sticholonchae* Koeppen, trophont. (b) *A. sticholonchae*, the vermiform. (c) *Amoebophrya grassei* Cachon which parasitizes *Oodinium*. (d) *Apodinium* sp. beginning its sporogenesis. (e, f) *Sphaeripara catenata*, a young trophont and an older one (g) *Haplozoon* sp. parasitizing *Appendicularia sicula* (h, host; p, parasite).

beating, its jerky movements resembling those of Orthonectids. The large, posterior digestive vacuole contents are progressively absorbed.

Duboscquella is also a parasite of protists (Cachon 1964). Although its trophont appears to be different from that of *Amoebophrya*, there are a number of common features in the development of the trophont and during sporogenesis. For example, *D. aspida* (Fig. 13.9) parasitizes tintinnids such as *Cyttarocylis*. The infection is caused by biflagellated spores with hyposomes smaller than their episomes. Inside the cytoplasm of the host the spore flagella, girdle and sulcus vanish (by phagocytosis?). The young trophont becomes spherical. Two distinct parts can be recognized in the nucleus: the anterior region is occupied by chromosomes, the other contains a cap-shaped nucleolus. A circular plate appears at the anterior pole of the cell; it is due to the development of fibrous elements beneath the cell membrane. This watch-glass shaped anterior plate is inserted into the cytoplasm and induces the formation of a circular groove around it. While growing (the trophont may reach 80 μm in diameter) the plate develops greatly and hides the anterior part (which corresponds to the episome). The girdle is recognizable only by its anterior (upper) edge which is lined with dense material. Beneath a small, weakly developed sulcus there is a dense helical ribbon made of a bundle of microtubules, which could be a non-functional

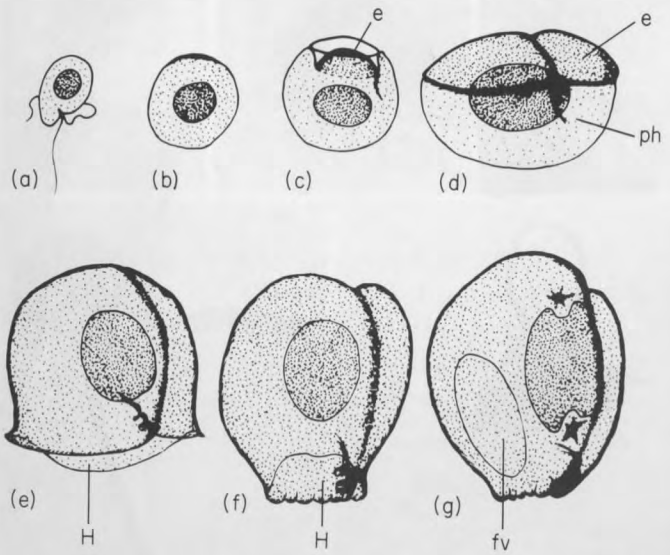

Fig. 13.9. Diagram of the life cycle of *Duboscquella aspida*: (a) spore; (b, c, d) growth of the trophont, formation of a fibrous cap at the anterior part (e = episome) in which there is a trace of a slight longitudinal groove; beneath this groove a ribbon of microtubules is observed (pharyngeal area, ph); (e, f) the hyposome (H) is pushed forward inside; (g) the episome which has incorporated a portion of the host in a large food vacuole (fv). The nucleus in (g) is beginning its first sporogenetic prophase.

cytopharynx and may indicate the ventral side. During its development the protist remains uninucleate (see Section 5 for further information of the development of synenergid nuclear structures). The cell membrane of the hyposome has considerable pinocytotic activity.

As in *Amoebophrya*, major structural rearrangements accompany the end of the feeding phase and the beginning of the reproductive one (Fig. 13.10). The

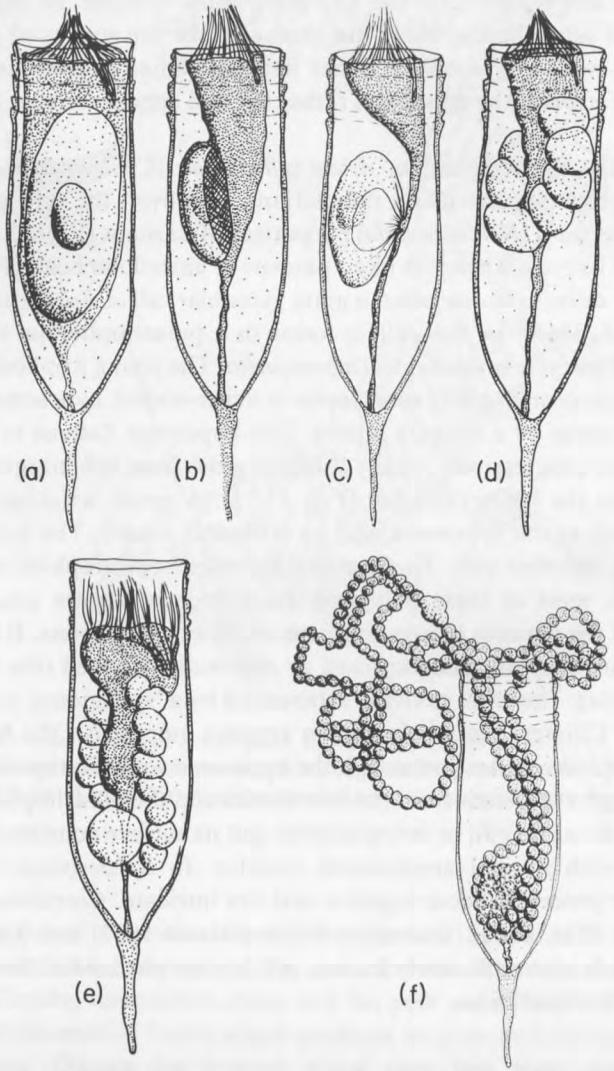

Fig. 13.10. Diagram of the sporogenetic processes of *Duboscquella aspida*. (a, b, c) The parasite escapes from its host, a portion of which has been taken along (by phagocytosis). (d, e) Large chains of sporocysts are formed, one of them being bigger because it still has the food vacuole. (f) The chain of sporocytes, moving with the aid of flagella, leaves the host lorica and soon will give rise to dinospores.

cap-shaped hyposome is suddenly pushed inwards, forming a large cavity at the posterior end of the cell. This cavity encloses a large part of the host cytoplasm in a food vacuole. The mechanisms are similar to those of *Amoebophrya*, although the microtubular cytoskeleton of *Duboscquella* is much less important than the microtubular ribbons of the corolla.

The differences between the various species of *Duboscquella* are solely in the construction and behaviour of the wall-plate of the episome. In *D. cnemata*, for example, the subpellicular fibrils are arranged like the spokes of a wheel and the episome, which is normally rather flat, has radial grooves. In *D. melo*, a parasite of *Noctiluca*, the episome is rather flat and appears to have longitudinal ribs.

Among the Sphaeriparidae, *Atlanticellodinium* (Cachon & Cachon 1965) parasitizes protists, particularly radiolarians. However, the type genus of this family, *Sphaeripara* (*Neresheimeria*) parasitizes Metazoans (Fig. 13.8e, f). At the beginning of its cycle it behaves like a parasite of unicellular hosts (Fig. 13.8e, f); it selectively infects the oikoplast, a giant glandular cell of *Fritillaria* (Cachon & Cachon 1964, 1966). In this cell, it forms in a parasitophorous vacuole. The beginning of its cycle is similar to *Duboscquella*. The young trophont, which has no girdle, sulcus or flagella, soon forms a dense-walled hyposome, separated from the episome by a circular groove. The hyposome flattens to form a disc which widens progressively; many rhizoids grow from the margin of the disc and sink into the host cytoplasm (Fig. 13.11). A small, axial cavity appears which extends to the hyposome wall by a fibrillar funnel. The hyposome wall forms highly ramified villi. The host cell becomes hypertrophied and contains many nuclei, most of these polyploid. Its mitochondria are attached to the hyposome of the parasite in invaginations of the cell membrane. It is difficult to know whether they are phagocytosed or externally digested (the latter seems more probable). The axial cavity is surrounded by a 'spongiome' made of small tubes, as in Ciliates; the whole system appears empty. All the host–parasite exchanges in *Sphaeripara* go through the hyposome wall. The episome does not act in feeding: it is distant from the host tissues and the parasitophorous vesicle membrane; it has no villi or invaginations and its surface consists only of a cell membrane with normal amphiesmal vesicles. In *Sphaeripara*, trophic and sporogenetic processes occur together and are intricate. *Coccidinium* (Chatton & Biecheler 1934, 1936), *Duboscquodinium* (Grasse 1952) and *Keppenodinium* (Cachon 1964) are insufficiently known. As they are plasmodial forms they may be closer to the Syndinida.

Syndinida (Botanical order Syndiniales)

These dinoflagellates can parasitize other protists, such as radiolarians and the curious organism *Sticholonche* (Fig. 13.13). In these they are intracellular (Fig. 13.12) and may even be intranuclear. Other syndinians parasitize Metazoans

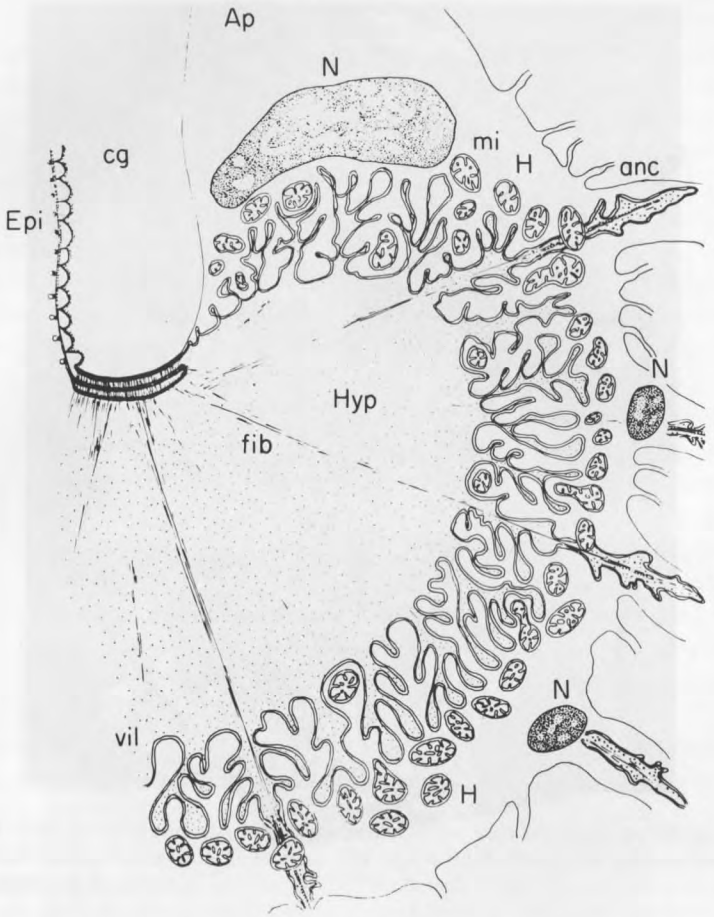

Fig. 13.11. Latero-basal portion of *Sphaeripara*. Episome (epi), hyposome (Hyp), cingulum (cg); host cell (H), nucleus (N) and mitochondria (mi) of the Appendicularium. Fibres (fib), anchoring rhizoids (anc) and villi (vil) of the membrane of the parasite hyposome.

and are mainly found in cavities (Soyer 1974; Chatton 1910; Manier *et al.* 1971), e.g. the gonocoele of hydrozoans, the hematocoele of crustaceans such as copepods and crabs, appendicularians and the yolk sac of fishes (Fig. 13.13). They occur as plasmodial forms which continue to grow and divide until they form swarmers. During the trophic phase they lose their dinoflagellate morphology: the girdle, sulcus and flagella disappear, although basal bodies remain and the amphiesma is normal. There is a thin polysaccharidic cell coat and amphiesmal vesicles without thecal plates. There are polysaccharidic and lipidic inclusions, mitochondria with poorly developed cristae and many

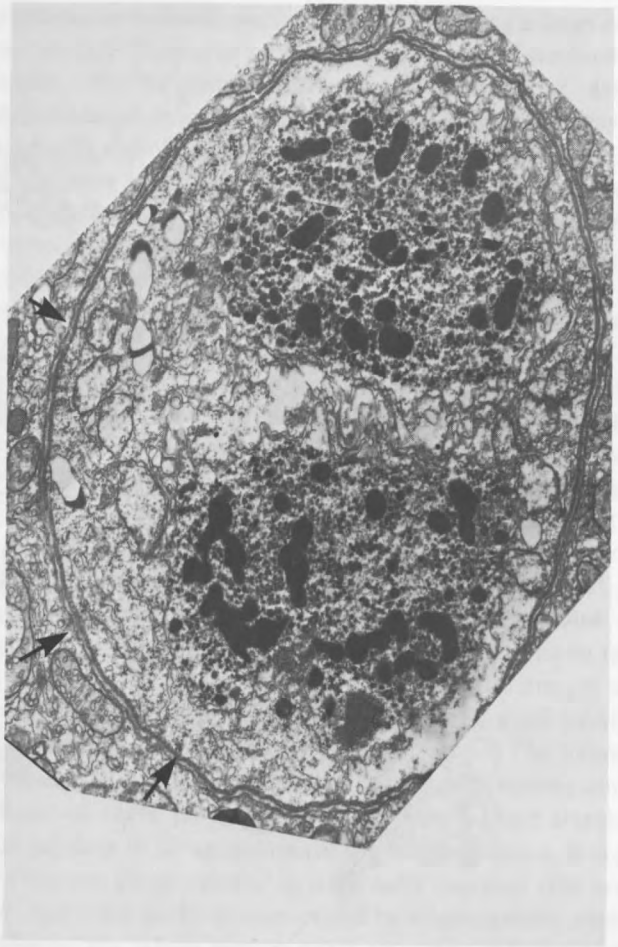

Fig. 13.12. Young trophont of *Syndinium borgerti* in the Phaeodarian *Aulacantha scolymantha*. This micrograph shows the parasitiphorous membrane of the host (arrows).

trichocysts. Chloroplasts are absent. Osmotrophy is the rule, although remnants of a cytopharyngeal funnel can sometimes be seen (*Syndinium* sp., Cachon 1964).

4 REPRODUCTIVE PROCESSES

Of all parasitic dinoflagellates, only some species of *Blastodinium* reproduce by simple binary fission. *B. spinulosum* divides in the same way as free-living forms, but in the intestine of a copepod (Chatton 1920); there may be as many as twenty in a single host. This endogenous multiplication may interfere with the

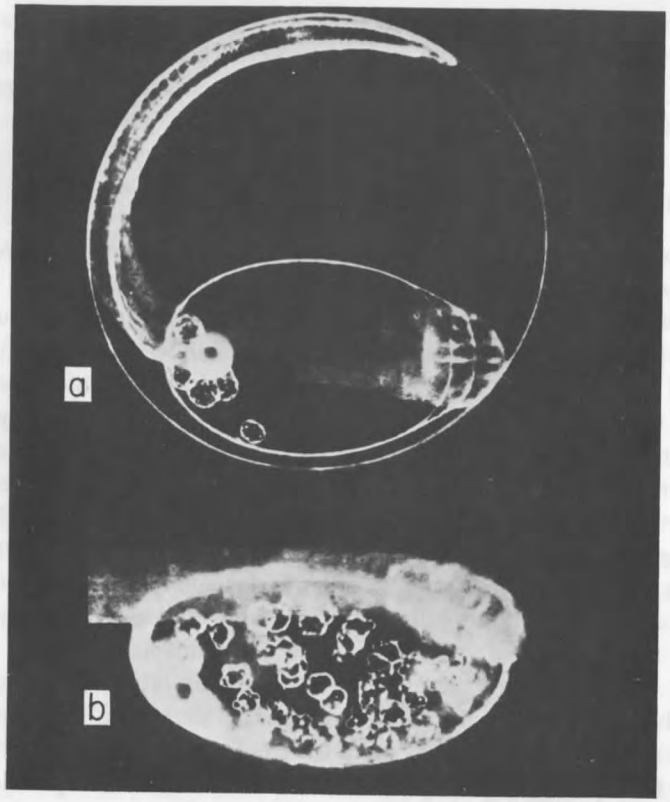

Fig. 13.13. *Ichthyodinium chabelardi* Hollande and Cachon. This syndinian parasitizes the vitelline vesicle of an embryo of the sardine. The vesicle finally bursts, the embryo dies and the dinospores are then free.

exogenous multiplication which produces swarmers and which is the only type of reproduction in most of the other parasites.

Sporogenesis may be by three different mechanisms.

1 The simplest is found in the Syndinida; the parasite multiplies its nuclei, plasmodia and cytoplasmic divisions until the last generation of sporocysts, when biflagellated dinospores are produced and liberated.

2 Alternatively, nuclear and cell divisions may not occur during the growth phase of the parasite, which remains uninucleate and may reach a large size. As soon as the parasitic stage is ended and maximum size is reached, nuclear and cytoplasmic divisions take place without interruption until swarmers are formed; Chatton (1938) termed this process 'palintomy'.

3 The parasite becomes multinucleate, after which one of two processes may occur: the cytokineses may occur (i) progressively throughout the parasitic phase, or (ii) only at the end of the parasitic phase with the organism producing

a great number of spores simultaneously. A single trophont can thus produce, through repeated reproductive phases, several generations of dinospores; Chatton (1906) termed this type of mechanism 'iterative sporogenesis' or 'palisporogenesis'.

4.1 Palintomic sporogenesis

This is commonly observed in *Oodinium*, *Cachonella*, *Dissodinium*, *Duboscquella*, *Amoebophrya* and *Chytriodinium*. It is easy to detach a sufficiently old *Oodinium* from its host. This induces mitosis and cytokinesis after 7–8 hours which proceed without interruption until progressively smaller sporocysts form, each enveloped by a cyst wall, later becoming liberated as flagellated spores. This triggering of sporogenesis is a good demonstration of the relationship between host and parasite and also shows that the parasites are extracellular. Under natural conditions, the rupture of the stalk always precedes sporogenesis.

Cachonella has a peculiar behaviour (Rose & Cachon 1951, 1952; Cachon 1953) (Fig. 13.14). It grows like *Oodinium*, while fixed to the wall of the swimming bell of a siphonophore. In order to develop it has to be swallowed by a gastrozoid of the siphonophore. Once in the presence of gastric juices, the cuticle is rapidly ejected, perhaps by the simultaneous extrusion of all its trichocyst batteries. Immediately after this, long digitations develop from the base to the top of the cell. These involve the stretching of a pre-existing membranous system. The cytoplasm of the trophont is filled with flattened and contorted membranous formations. Under the influence of the gastric juices of the host, a sudden increased turgidity of the cytoplasm causes the evagination of the membranous tubes, like the fingers of a glove turning inside out. The parasite is then ejected from the gastric cavity, these processes having taken only a few minutes. The cytoplasm in the digitations retracts and the empty digitations collapse. The cell leaves its envelope and the first sporogenetic divisions begin.

Dissodinium behaves in a similar way (Drebes 1978; Elbrachter & Drebes 1978). The parasite begins to divide only after it becomes detached from the egg by rupture of its stalk, even if the egg has been reduced to an empty shell. The sporogenetic processes of *Dissodinium* occurs in two stages. First, a spherical cyst wall is secreted within which the parasite divides to form eight to sixteen lunate or oval secondary cysts, which are then released. Next, inside each secondary cyst, eight dinospores are formed then released when the secondary cyst wall bursts. These directly infest new eggs. The primary and secondary cysts of the parasite and those of *Pyrocystis* (Dinococcales) are morphologically similar.

The end of feeding in *Amoebophrya* and *Duboscquella* triggers sporogenesis immediately after cell inversion. In *Duboscquella* the sporocysts remain connected end to end in long chains by a polysaccharide coat. The sporocyst

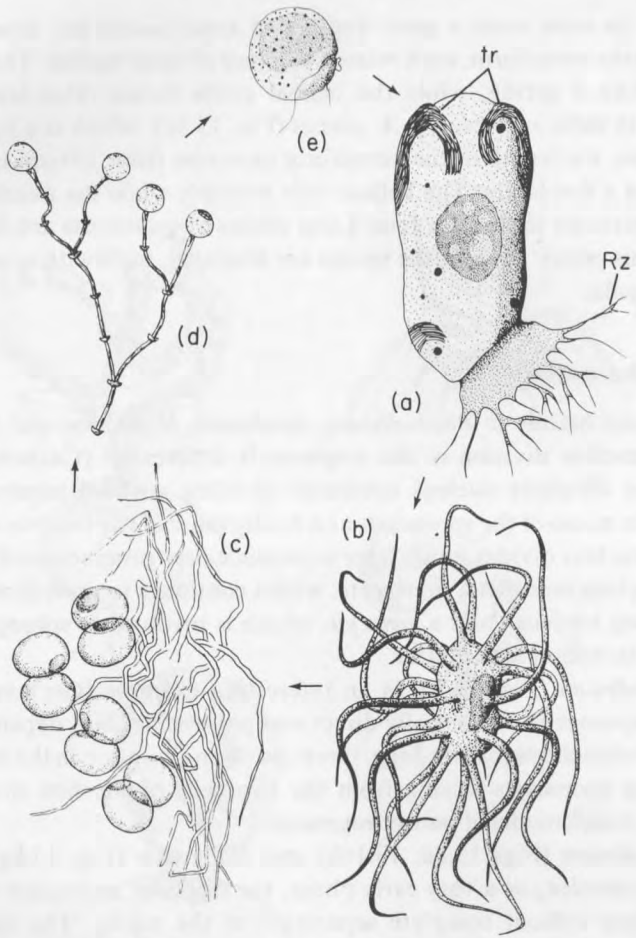

Fig. 13.14. *Cachonella paradoxa* Cachon and Rose. The trophont (a) is fixed on the cell membrane of the swimming bell of a siphonophore by a large stalk bearing many rhizoids (Rz). Three bundles of trichocysts (tr) are observed. At the end of the vegetative phase, the protist escapes (b) and once swallowed by the gastrozoid, long tubular digitations are developed. It is then ejected into the sea (c) and undergoes palintomic sporogenesis. Many cyst membranes are successively formed at each generation; they keep the sporocysts attached to each other (d). Finally, spherical biflagellated swarmers are formed (e).

inheriting the phagotrophic inclusion (which will be progressively absorbed) is larger than the others. In the final generation the sporocysts develop two flagella each and the chain moves. The individuals separate to become spores.

In *Amoebophrya*, the trophont either remains uninucleate during the first phase (e.g. *A. acanthometrae*), or it becomes multinucleate (e.g. *A. ceratii*), with the nuclei lying beneath the kinetosomes along the helical girdle. In the first case, the nuclear divisions begin only after the formation of the 'vermiform'

organism. In both cases a great number of small nuclei are observed in the multinucleate vermiform, each related to a pair of basal bodies. The vermiform stretches like a spring, while the helical girdle twists. This lengthening is fantastic: in some species, e.g. *A. grassei* (Fig. 13.8c), which is a hyperparasite of *Oodinium*, the length of the vermiform increases from 250 μm to more than 4000 μm in a few hours. The helical coils multiply while the number of nuclei per coil decreases to three or four. Long chains of sporocysts are formed, as in the previous genus. Finally, the spores are liberated, each with a nucleus and a pair of flagella.

4.2 Palisporogenesis

This is found mainly in *Blastodinium*, *Apodinium*, *Haplozoon* and *Sphaeripara*. The first nuclear division of the trophont is differential (Cachon & Cachon 1965). One daughter nucleus continues dividing without interruption, first forming the nuclei of the sporocysts and finally those of the swarmers. The other daughter nucleus divides much later to produce new generations of sporocysts. The distinction between a *trophocyte*, which continues to grow (containing the non-dividing nucleus), and a *gonocyte*, which is involved in sporogenesis, may be due to starvation of the latter.

Chytriodinium (Fig. 13.15) is an interesting example (Cachon & Cachon 1968). Its sporogenesis is usually direct and palintomic, but, depending on the food reserves in the parasitized egg, there can be an alteration in the development time of the sporocysts arising from the two cells of the first division. This provides a rough model of palisporogenesis.

In *Apodinium* (Figs 13.8d, 13.16b) and *Haplozoon* (Fig. 13.8g) palisporogenesis is complex; at a very early phase, the trophont undergoes two nuclear divisions but without complete separation of the nuclei. The nuclei of the sporocysts are tetrapolar and in final divisions the swarmer tetrads separate before becoming spores. In *Sphaeripara* the trophocyte nuclei divide actively throughout the trophic phase (Fig. 13.17). Palisporogenesis occurs by strobilation of the trophocyte; each strobilus is multinucleate. This development is reminiscent of *Amoebophrya*: the parasite lengthens while its diameter decreases; basal bodies and flagella appear but they are arranged in successive circles. The final processes are similar to those described above.

5 THE SWARMERS

All parasitic dinoflagellates produce swarmers which ensure dispersal of the species and are responsible for new host infection. They always have two dissimilar, laterally inserted, flagella, one trailing and the other transverse and undulating. The girdle and sulcus are often poorly developed and are associated with a striated root and a few microtubules, as in free-living dinoflagellates.

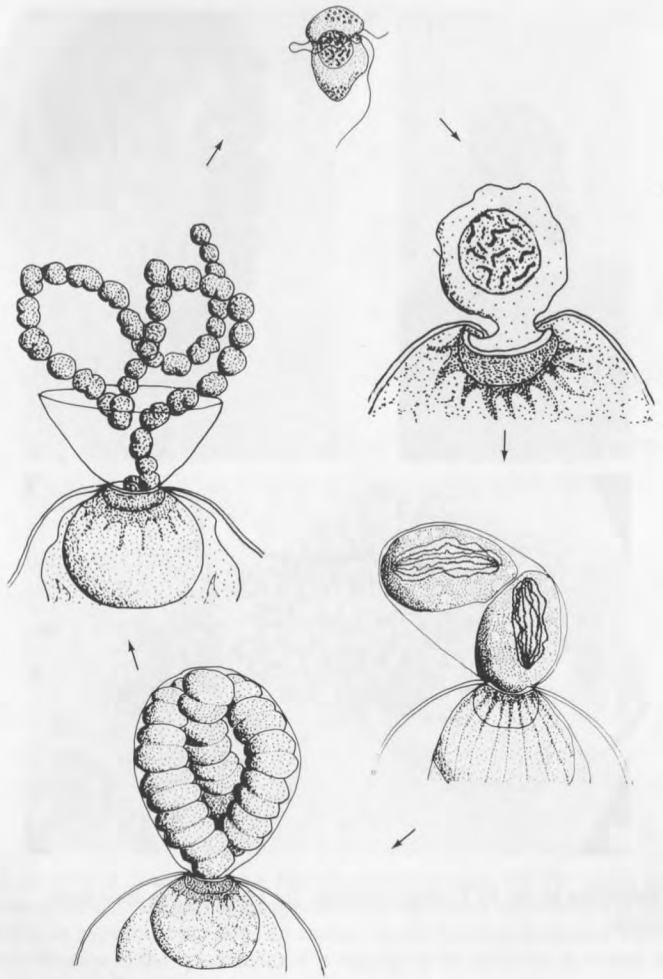

Fig. 13.15. Diagram of the life cycle of *Chytriodinium affine* Dogiel. The swarmer perforates the shell of the egg of a crustacean and a strong holdfast organelle develops. The palintomic sporogenetic divisions begin beneath the initial envelope of the trophont long before the egg is emptied. A chain of sporocysts is formed. The spores become free (64–128 cell stage) by the rupture of the trophont envelope.

Trichocysts and large refringent inclusions are often present. Chatton (1938) thought that swarmer morphology (gymnodiniform, gyrodiniform, cochlodiniform) could be important for the systematics of the parasitic taxa. However, our observations showed their morphology to be unstable. Thus, the spores do not seem to be sufficiently conservative to serve as the basis for the systematics of these species.

Some species may produce swarmers of two different sizes (macro- and microspores), which arise from different parent individuals. Sexual reproduction

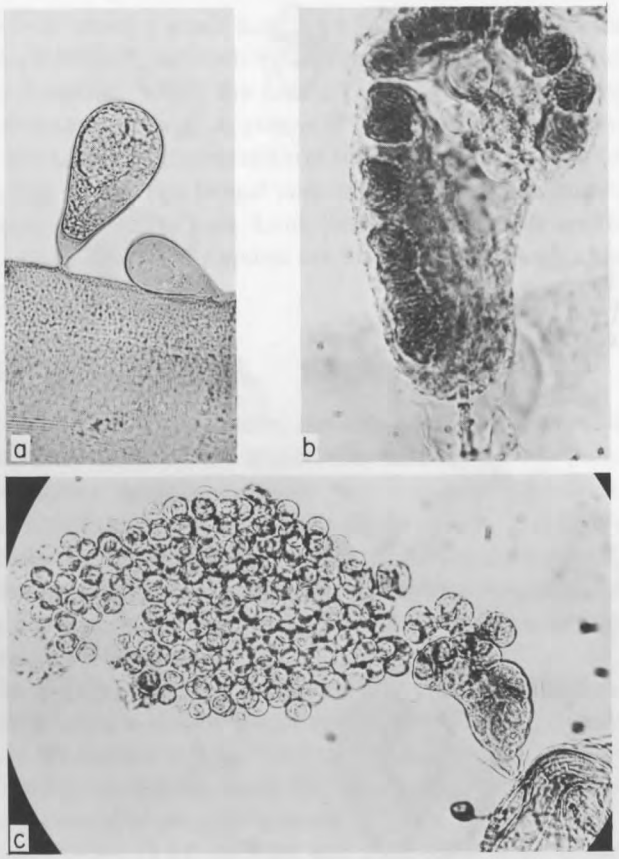

Fig. 13.16. *Apodinium* sp. (a, b) Young trophonts. (c) The parasite undergoes palisporogenesis.

comes to mind; syngamy has been observed only in *Duboscquella*, i.e. *D. tintinnicola* (isogamy) by Duboscq & Collin (1910), and *D. anisospora* (with micro- and macrogametes) by Grassé (1952), without knowledge of their further development. In *D. aspida*, infection of the tintinnid host can occur by macrospores without prior syngamy (Cachon 1964).

The spores of dinoflagellate fish parasites (*Amyloodinium*, *Crepidoodinium*, *Piscinoodinium*) and those of *Protoodinium* possess an attachment organelle, a small ventral pseudopod, by which they infect the host immediately.

6 PARASITE NUCLEAR STRUCTURE AND CYCLE

This aspect is difficult to resolve, even though it was the structure and development of the nucleus as well as the spore morphology which enabled

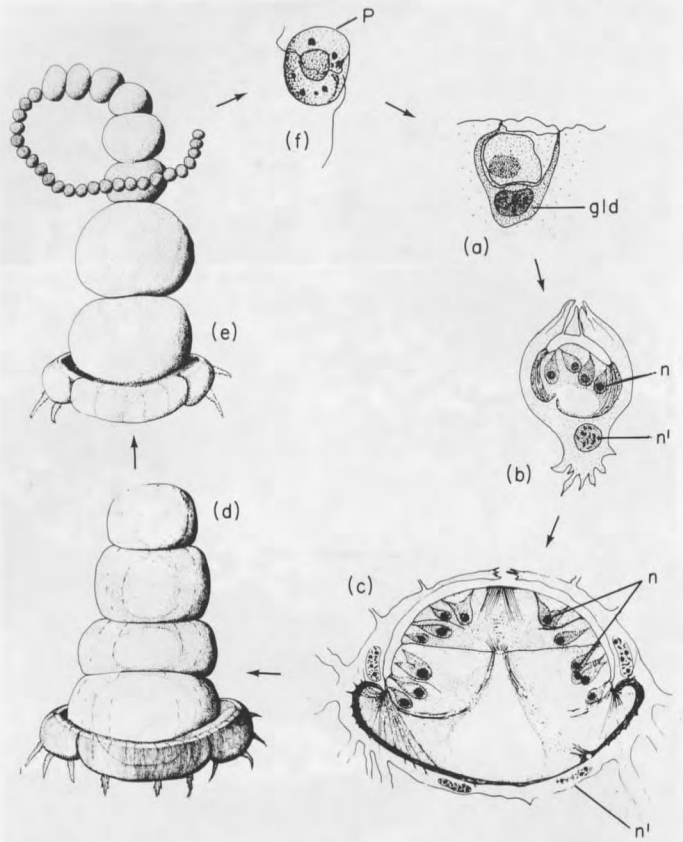

Fig. 13.17. Life cycle of *Sphaeripara* (= *Neresheimeria*) *catenata*. (a) The young parasite (p) is inserted in the glandula cell (gld) of an appendicularian which will eventually enclose it completely (b). Its hyposome develops an anchoring and feeding apparatus while there is much nuclear division in the episome (c). n = nucleus of the parasite, n′ = host nucleus. The episome becomes stabilized (d) and produces successive generations of multinucleated sporocysts by palisporogenesis (e). Each primary sporocyst produces a chain of secondary sporocysts which finally become dinospores (f).

Chatton to recognize the dinoflagellate nature of a great number of parasites. He thought that the simplest and most typical dinomitosis occurred in parasitic dinoflagellates (Fig. 13.18a, b) (syndinium mitosis), although they are now known to be anomalous in several ways. He also recognized the peculiar aspects of the nucleus of some trophonts which remain uninucleate during the growth phase. This large nucleus, which stops undergoing mitosis, progressively accumulates material which can later be used during the numerous nuclear divisions necessary to reach the final spore stage. He termed this type of nucleus 'synenergide', for it can store away a great potential for eventual activity.

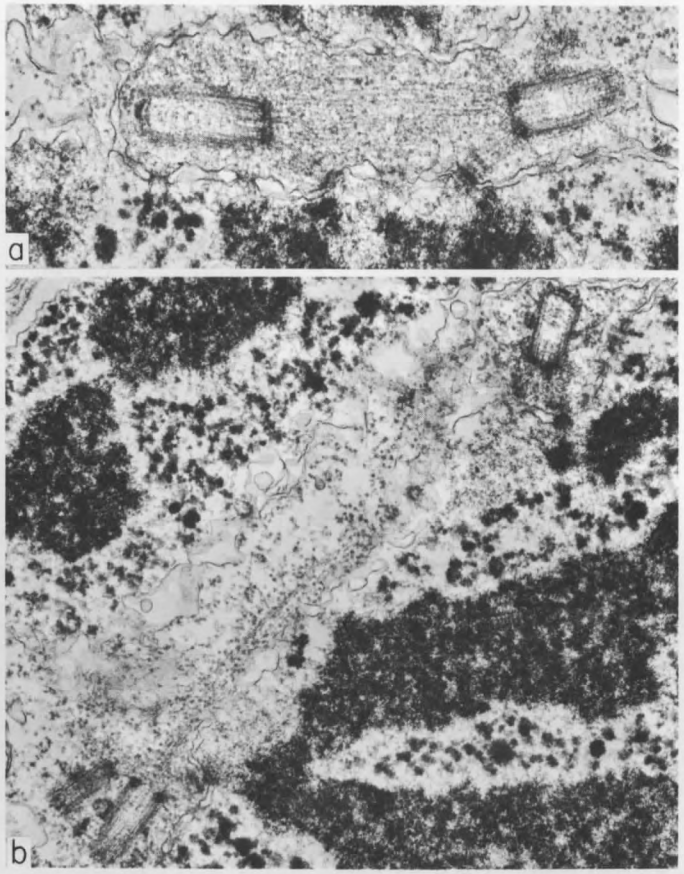

Fig. 13.18. Micrographs of syndinian mitosis seen by Ris & Kubai (a) and by Cachon & Cachon (b).

The data from electron microscopy and cytochemistry have confirmed the unusual structure and composition of the nucleus and mitosis in free-living dinoflagellates (see Chapter 3). However, most parasites do not have all these features. Most do not have condensed chromosomes throughout the whole cycle, and in some they do not condense at all. Furthermore, although the number of chromosomes is relatively high in Blastodinida, it is low in Duboscquodinida and Syndinida.

Oodinium (Cachon & Cachon 1974, 1977) is a typical example. The nucleus of the spore and of young trophonts (Fig. 13.19a–e) has typical rod-like dinoflagellate chromosomes. There are about thirty with arched fibrils, lacking histones. They stain strongly with Schiff reagent (DNA) but remain unstained with alkali fast green (for histones). As growth proceeds, the chromosomes lengthen and their first fibrils become irregularly arranged. The Schiff reaction disappears and nucleoli appear. Finally, in the adult trophont the chromosomes

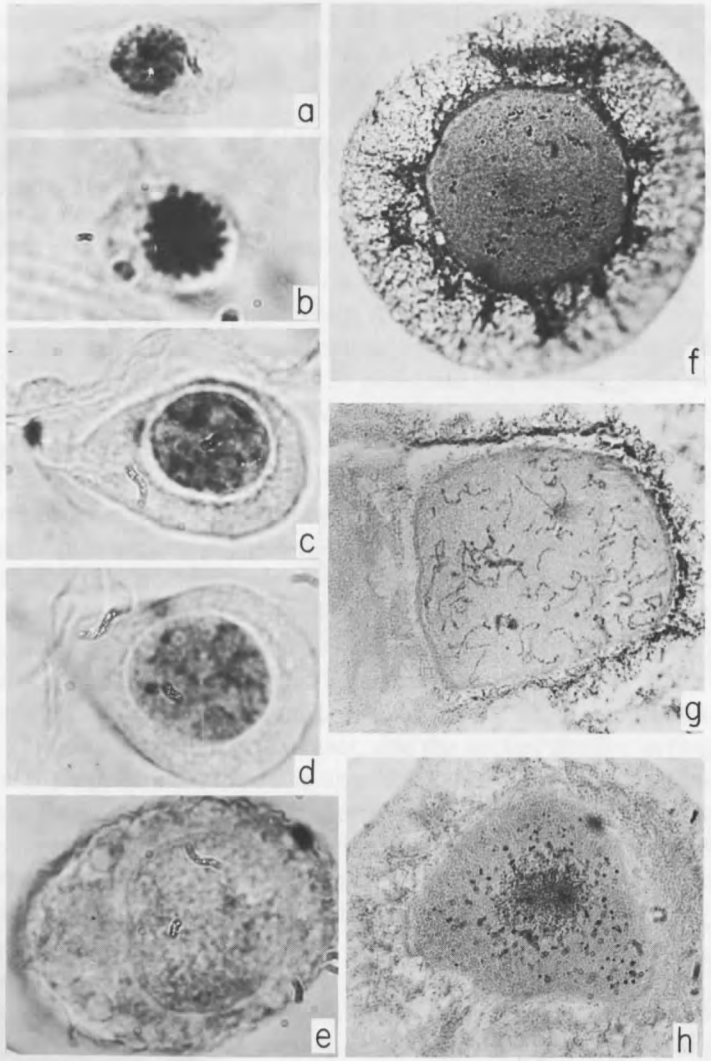

Fig. 13.19. Nuclear development in *Oodinium fritillariae* Chatton. (a, e) The Schiff reaction *in vivo* (× 800). The nucleus becomes progressively more homogeneous. The chromosomes which had normal dinoflagellate structure vanish. (f, g, h) (bi-acidic Mann staining). As soon as *Oodinium* becomes detached from the host, the nuclear substance disappears (f) while the chromosomes again become conspicuous (g) and are radially arranged (h). The first mitosis is then ready to begin.

become conspicuous; the Schiff reaction is negative and the fast green reaction is positive, diffuse except in the nuclei where it is intense. By the time sporogenesis begins, the protist is in a peculiar state, fundamentally different from that of a free-living dinoflagellate (Fig. 13.19f, g, h).

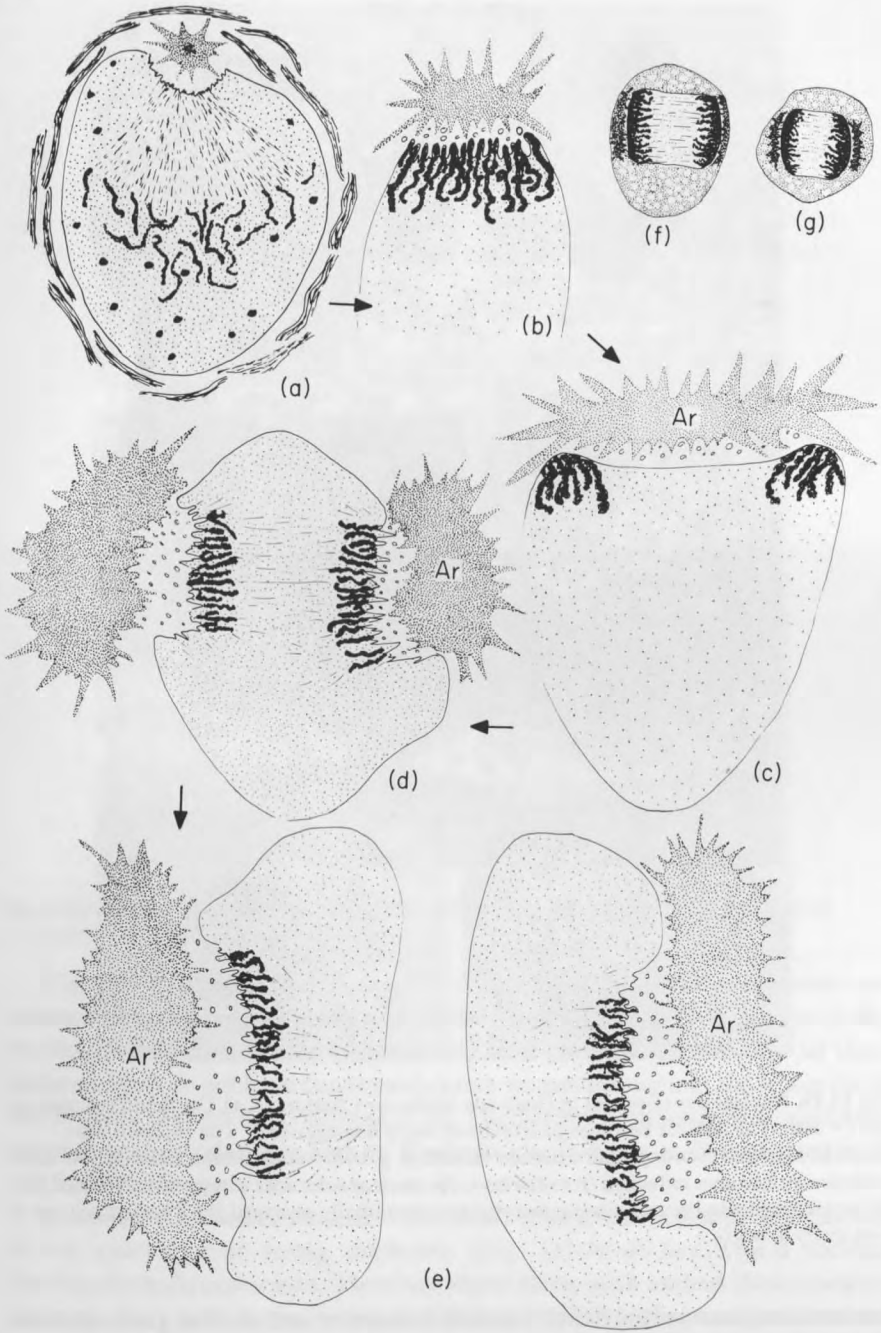

Fig. 13.20. *Oodinium fritillariae*. Diagram showing the first mitosis. (a) The chromosomes are pulled towards the archoplasmic area. (b, c) The beginning of the division. (d) Anaphase. (e) Telophase. (f, g) Late divisions of sporogenesis.

The beginning of sporogenesis (Fig. 13.20) is indicated by the development of an 'archoplasmic mass' (Boveri 1895), a dense cytoplasmic area consisting only of golgi vesicles and ribosomes and surrounded by dictyosomes. This 'archoplasm' is embedded in the anterior pole of the nucleus. Large chromosomes with dense axes and irregularly arranged fibrils reappear. They are stained only by fast green. They are pulled towards the archoplasmic area: one of their extremities becomes attached to the nuclear envelope (which does not break down during mitosis: 'closed' mitosis) (Jenkins 1967). The archoplasmic mass begins to stretch and soon after gives rise to two daughter archoplasmic masses (also known as 'archoplasmic spheres'). A spindle forms between them. The surface of the nucleus undergoes extensive changes: cytoplasmic strands containing spindle microtubules (MTS) penetrate the nucleus, some of which appear to originate from the spindle pole body and terminate at the attachment points of daughter chromosomes: each microtubule ends at a single nuclear pore in which an amorphous dense body (kinetochore?) can be observed.

This mitosis has several features which are typically dinoflagellate: closed mitosis, archoplasmic masses, pole-to-pole MTS, cytoplasmic channels, and the participation of the nuclear envelope in chromosome segregation. There are features peculiar to parasitic dinoflagellates, at least at the beginning of sporogenesis: a bundle of loosely arranged DNA fibrils with no arches, a weak Schiff reaction and a histone-like fast green reaction (see Chapter 4).

The sporogenic divisions proceed without pause. The chromosomes (Fig. 13.21, 13.22) become smaller and denser, and the arched fibrillar arrangement progressively reappears. At the same time, the Schiff reaction intensifies, while the Alfert and Gerschwind (fast green) test becomes negative. The kinetochore-like arrangements become less conspicuous. Finally, the chromosome attachments to the nuclear envelope become invisible. A pair of orthogonally arranged basal bodies appear *de novo* at the anterior pole of the nucleus. They act as centrioles during the final mitosis.

Oodinium-type chromosomes occur in all Blastodinida. However, in the Duboscquodinida and Syndinida the chromosomes are associated with basic proteins (judging by the fast green reaction) and the arched fibrillar arrangement never appears. They are sufficiently condensed to produce an intense, positive Schiff reaction.

Kinetochores have not been observed in Blastodinida or any of the Duboscquodinida. However, they are well developed in *Apodinium* (three-layered formations) (Cachon & Cachon 1979) and in the Syndinida (Hollande 1974; Ris & Kubai 1974).

Basal bodies, which appear in the final stages of sporogenesis in the Blastodinida and Duboscquodinida, seem to be superfluous in mitosis. This seems to be true in the Syndinida also, even though they are permanent in the latter.

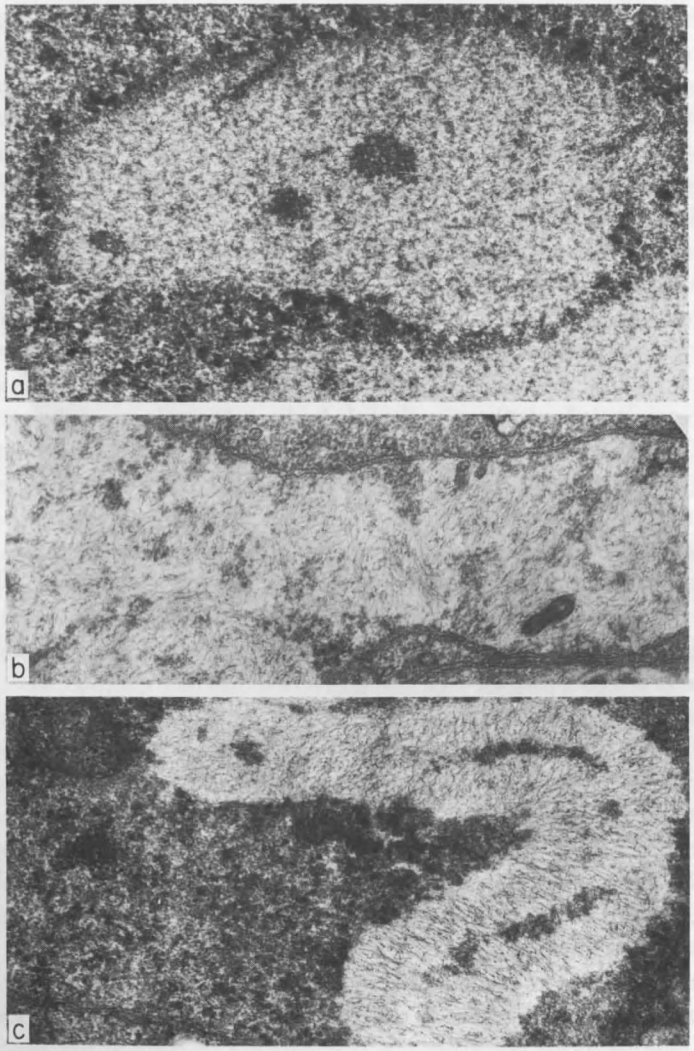

Fig. 13.21. *Oodinium fritillariae*. Development of the chromosome during the first sporogenetic prophase (× 40 000). The fibrous elements begin to appear in the axis of the chromosome (a, b); then they form a transverse array around this axis (c).

7 PRACTICAL ASPECTS

Parasitism in freshwater and marine organisms has both ecological and human economic repercussions. In marine plankton, for example, we often observe that there are sudden outbreaks of parasitism by particular dinoflagellates. In a very short time, a sudden fall in the density of the zooplankton population occurs. Syndinida causes rapid death of copepods, *Duboscquella* kills tintinnids,

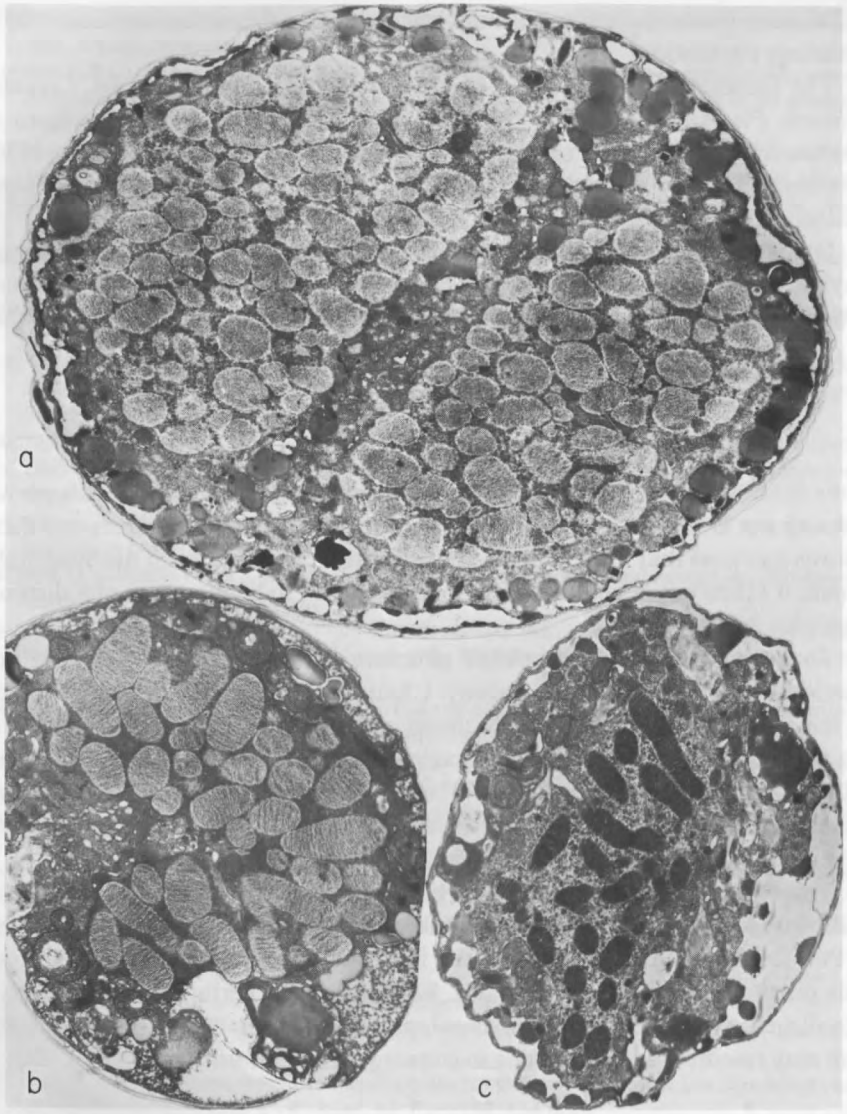

Fig. 13.22. *Oodinium fritillariae*. Development of chromosome ultrastructure during the last generation of sporocysts (a, b) and in the swarmer (c). The typical dinoflagellate structure has reappeared (× 15 000).

Chytriodinium empties the eggs of Euphausiacea, and *Sphaeripara* castrates *Fritillaria*. We have sometimes had great difficulty in collecting uninfected organisms for experimental studies.

In some cases there can be a more direct effect on resources. *Ichthyodinium chabelardi* (Hollande & Cachon 1952) infects and destroys the eggs of sardines

in 24 hours. Under certain conditions, still unknown, it can destroy nearly 100% of the egg population.

The Oodinidae which parasitize fish (*Oodinioides*, *Amyloodinium*, *Crepidoodinium*, *Piscinoodinium*) (Brown 1934; Geus 1960; Lom 1981; Needham & Wotten 1979; Nigrelli 1936, 1943; Reichenbac-Klinke 1955, 1956, 1970; Schubert 1978) cause great damage in aquaculture and require prophylactic measures.

Other parasitic dinoflagellates could be indirectly useful for human economy. Taylor (1968) observed that *Gonyaulax catenella*, one of the main producers of toxic red tides, is parasitized by *Amoebophrya ceratii*. The author suggested that *A. cerattii* might eventually be used as a biological control agent for that host.

8 CONCLUSION

Little is known about a great many parasitic dinoflagellates, e.g. *Amoebophrya*, *Sphaeripara*. Our knowledge of the development of their chromosomes and their mitosis confirms that these protists are truly dinoflagellates, even the Syndinida which, if taken out of context, could be considered to be members of a distinct class (Ris & Kubai 1974).

These comparisons of trophont structure and spore morphology do not provide a clear idea of their phylogeny. Chatton (1938) placed some importance on the morphology of the spore but this is questionable. With some exceptions, the morphology of the trophont is too peculiar to be compared to free-living cells. *Protoodinium* and *Blastodinium* have a structure and tabulation which are typical. *Dissodinium* has sporogenetic stages that have long been misidentified as being those of *Pyrocystis* (Dinococcales).

The Blastodinida have a wall which may have markings, whereas the Duboscquodinida and Syndinida are naked. Are the former more closely related to Peridinida or, conversely, could the two others, which are intracellular and thus more modified by parasitic life, have lost these features more recently? Dinoflagellate parasites may even be polyphyletic and the three tribes recognized here may resemble each other due to convergent evolution.

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CHAPTER 14
DINOFLAGELLATE REPRODUCTION

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1 INTRODUCTION

Early descriptions of both marine and freshwater dinoflagellates were based on living or preserved field samples. Only a small percentage of these organisms are even now available in culture. Thus, the older descriptions of their life cycles are only complete to the degree that the author was able to sample frequently and/or be fortuitous enough to have collected a population in all stages of its life history. Thus, researchers who are able to culture dinoflagellates and follow their life history in the laboratory are finding previously unknown vegetative and sexual stages not contained in original descriptions. In some instances these stages have been described as separate taxa.

2 VEGETATIVE REPRODUCTION

Bold & Wynne (1978) distinguish between vegetative or asexual cell division in which the products of cell division are either naked or surrounded completely by new cell walls that are not intimately related with the parental cell walls (*eleutheroschisis*) and that in which the development of the cell walls of the newly divided protoplast is initiated adjacent to, and continuous with, the

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