Protozoan Cysts and Spores

Secondary article

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Article Contents

Cysts are typically resting, dormant and/or resistant stages in the full life cycle of many protozoan species, sometimes playing a role in dispersal of the organism. Spores are a stage commonly associated with multiplication and propagation of a protozoan organism, sometimes having a resistant wall and often, in parasitic forms, serving as an obligate stage in the life cycle.

Introduction

The occurrence of cysts or spores in a stage of the life cycle of numerous free-living or parasitic Protozoa, fossil as well as contemporary, has been noted by many biologists over scores of years; yet its significance seems still generally to be underappreciated. In fact, however, these stages are indispensable for many species, and their importance warrants more attention from modern researchers. Most papers in the literature to date have been concerned with quite straightforward morphological descriptions of cysts and spores, or are limited to basic physiological studies on their resistance to physicochemical factors or on the phenomena of encystation and excystation.

This article is thus mainly limited to brief consideration of the known kinds of cysts and spores, the protozoan taxonomic groups in which they have been found, their role in the life cycles of species, and their general morphology and physiology.

Kinds of Cysts and Spores

The terms 'cyst' and 'spore' have sometimes been used with differing definitions by different authors, some of whom on occasion have even considered them as synonymous words. With respect to the protists, the following definitions (essentially after Corliss and Lom, 1985) are offered here.

A cyst (**Figures 1**, **2** and **3**) is typically a nonmotile, dehydrated, resistant, inactive, dormant cryptobiotic stage in the life cycle of many protists that is generally considered to serve a major role in either protection from unfavourable environmental conditions or dispersal of the species. (Paraphrasing Keilin (1959), cryptobiosis is the state of an organism during which no visible signs of life are exhibited and its metabolic activities are reduced to a barely measureable level.) It is often encased within a cyst wall of some complexity. But some cysts are of a temporary nature, are thin-walled, play other roles, for example in reproduction, reorganization, or even digestion, and may not be an obligate phase in the life cycle. In not a few cases, the two functions are combined: reproduction takes place before excystation of the organism from its resistant cyst. In certain ciliates (for a prime example, *Colpoda* (**Figure 3i,j**)) both kinds of cysts occur in separate stages of the cycle (Foissner, 1993). In the unusual tetrahymenid ciliate *Tetrahymena rostrata*, fissions may occur within a thin-walled reproductive cyst, as well as a regular binary fission of active trophozoites, while in the resting cyst the relatively rare sexual phenomenon of autogamy or self-fertilization always occurs.

A spore (**Figure 4**) is usually an infective and/or propagative stage in the life cycle of a species, sometimes provided with a resistant wall or shell when the organism is in a cryptobiotic state. For many protozoan groups, including biomedically important parasitic species, it is an obligate stage. Unfortunately, the term is used for likely nonhomologous stages known for some species of unrelated taxa. And sometimes 'spores' may really be cysts.

Without offering descriptions or definitions here, the following kinds of cyst have been mentioned in the literature: the very common vegetative, resting or protective; the quite common propagative, division or reproductive; the reorganization or reconstructive or 'rejuvenating'; the infective or invasive; the phoretic, the digestive and the 'postsex' cyst. Some additional specialized cysts, also sometimes called spores, characteristic of certain taxonomic groups include the ecdysal cyst, zygospore or hypnozygote, hystrichosphere and sporocyst of dinoflagellates; the stomatocyst or statospore of chrysomonads; the parthenospore of *Volvox*; the infective or gamontocyst and the resting or zygocyst of opalinids; the often resistant sporocyst, gametocyst, and/or oocyst of sporozoa/apicomplexans (but see below); the sporocyst and xenonoma of microsporidia; and the histozoic trophozoite of myxosporidia.

It should be noted that a number of specialized terms in protozoology using the suffix '-cyst' are not cysts at all but only organelles or specialized structures within the cytoplasm of protozoan bodies: for example, the trichocyst, mucocyst, clathrocyst, acmocyst, toxicyst, haptocyst, pigmentocyst and statocyst of certain ciliates; the rhabdocyst, trichocyst and nematocyst–taeniocyst complex of diverse dinoflagellates; the kinetocyst of some heterokont

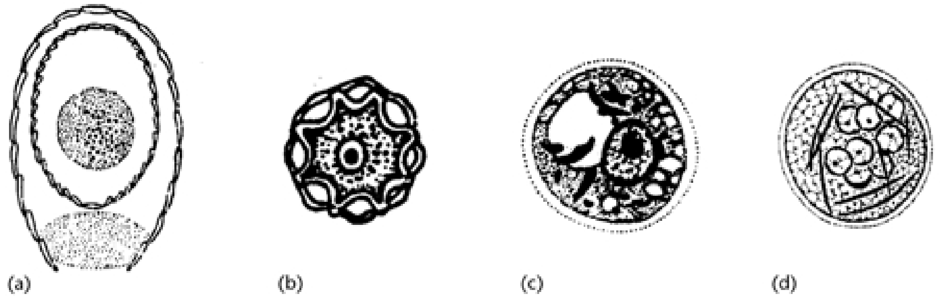

Figure 1 (a) Resistant cyst of *Euglypha*, a testaceous soil amoeba. Note two layers of siliceous scales and plugged aperture. (b) Resistant cyst of *Acanthamoeba*, a soil amoeba facultatively parasitic in humans. Note thick protective wall and stellate appearance of enclosed body. (c and d) Resistant cysts of *Entamoeba*, a parasite of the human digestive tract: (c) *histolytica* type, highly pathogenic; (d) *coli* type, less harmful commensal. (Note: the various cysts are not drawn to the same scale.)

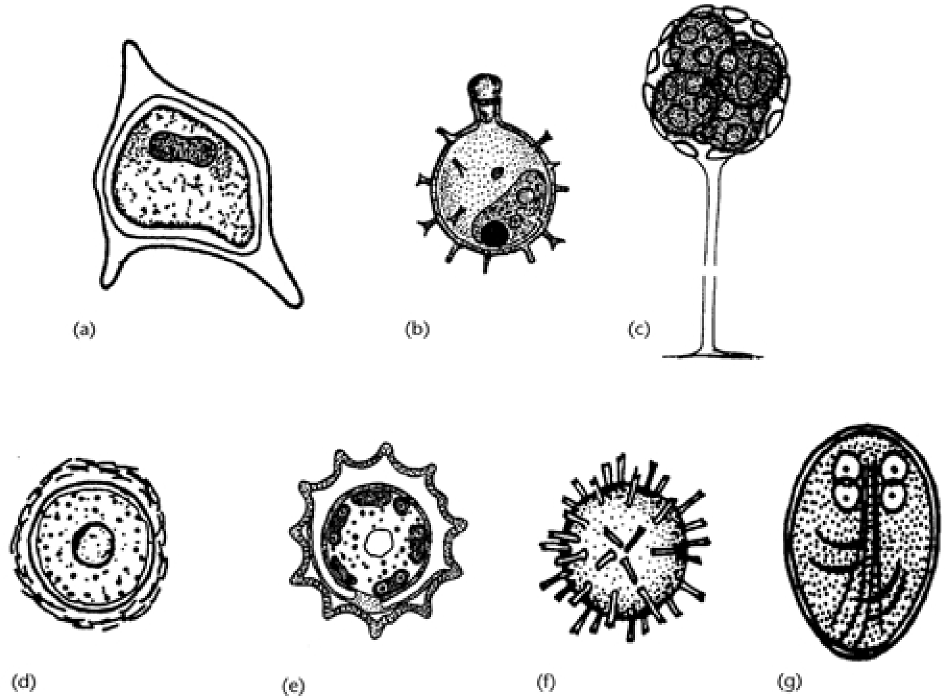

Figure 2 (a) Resting cyst of *Ceratium*, a dinoflagellate, with its own wall but also protected by the theca of the organism's vegetative stage, which encases it. (b) Protective cyst of *Ochromonas*, a chrysophyte heterokontic phytoflagellate: note outer spines and plugged emergence pore. (c) Resting cysts (four) of heliozoan 'actinopod' amoeba *Clathrulina*, within the perforated nonsiliceous single-piece test of stalked vegetative organism. (d) Resting cyst of another well-known heliozoan, *Actinophrys*, with outermost covering of siliceous scales. (e) Well-protected resting (seasonal) zygospore of *Volvox*, a chlorophytic colonial phytoflagellate. (f) A resting cyst of *Cosmarium*, a charophytic phytoflagellate. Note the externally projecting spines. (g) A resistant cyst of *Giardia*, a zooflagellate which is a harmful intestinal parasite of humans. (Note: the zygospore and the various cysts are not drawn to the same scale.)

algae and heliozoa; and the nematocyst of the myxosporidia.

The following kinds of spore have been described: the propagative spore, which is universal in free-living mycetozoan protists and many 'higher' fungal and plant groups; the similar sorocyst of the remarkable ciliate *Sorogena*; the cystospore of the pseudofungal oomycetes; the gametocyst–oocyst–sporozoite complex of the spor-

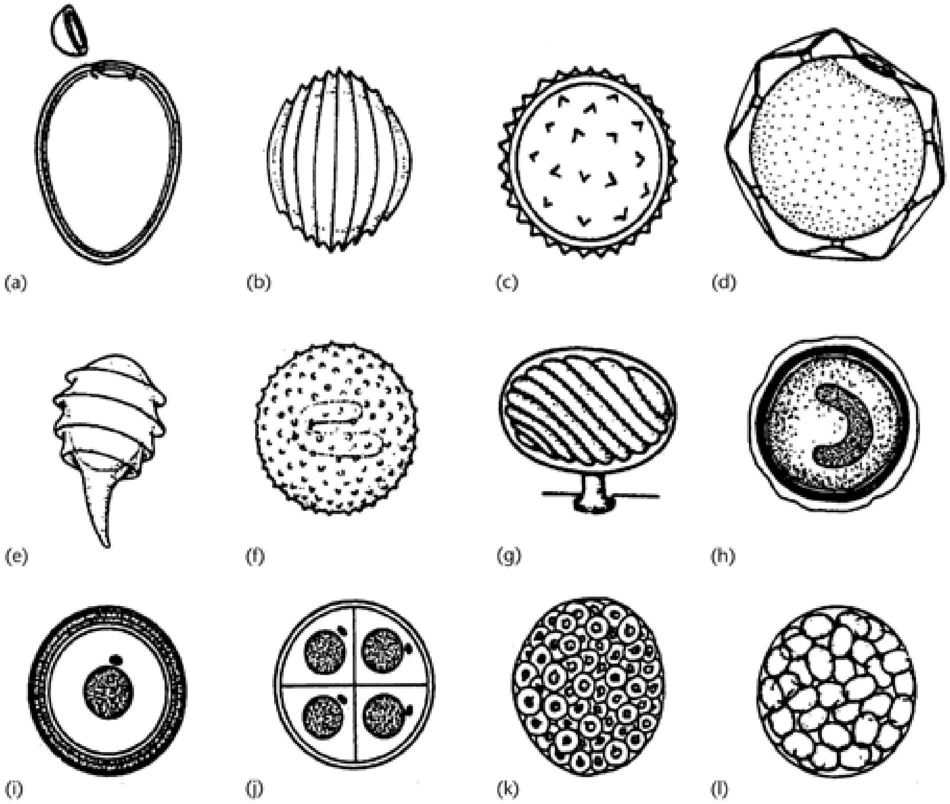

Figure 3 (a) Resting or protective cyst (empty) of *Nyctotherus*, a parasitic heterotrichous ciliate whose cyst has a heavy lid over its apical aperture. (b) Cyst of the hypotrichous ciliate *Euplotes*, emphasizing the ridged or grooved outer cyst wall. (c) Cyst of another hypotrich, *Oxytricha*, showing its heavily spiked/spined outer wall, one of several cystic membranes or walls. (d) Large cyst of the colpodean genus *Bursaria*, with an angular inner wall and a smooth outermost wall; also note the aperture or exit pore. (e) Unusually shaped resting cyst of a species of the suctorian genus *Podophrya*. (f) Resting cyst of the well known peritrich *Vorticella*. Note numerous 'warts' covering the surface of external wall. (g) Phoretic cyst of the apostome *Spirophrya*, showing the mode of attachment to the carapace of the crustacean host carrying it around. (h) Protective cyst of the haptorian gymnostome (or litostome) *Didinium*, whose complex triple-walled covering has been studied in detail by electron microscopy. (i, j) Cysts of the much-studied genus *Colpoda*, a common soil ciliate easily maintained under experimental laboratory conditions: (i) resting cyst, showing heavy cyst walls for protection from unfavourable environmental conditions; (j) reproductive cyst, showing the result of two fissions of an originally encysted organism: note the much thinner wall of this temporary cystic stage. (k) Reproductive cyst of the hymenostome *Ichthyophthirius*, a common tropical fish parasite. Note the numerous tomites inside, result of a series of very rapid fissions. (l) Reproductive cyst of the hymenostome *Ophryoglena* (related to *Ichthyophthirius*), free-living but a tissue-feeder of a scavenger-type. The number of tomites produced within a cyst is multiple but fewer than found in *Ichthyophthirius*. (Note: the various cysts are not drawn to the same scale.)

ozoa; the quite different resistant and infective spore of the myxosporidia, a group now considered to be animals not protozoa, and of the microsporidia, now considered taxonomically to be fungi; the motile dinospore of dinoflagellates; and even, according to some authors, the motile sporozoite ('naked' in the case of malarial species) of sporozoa.

Major Taxonomic Groups Involved

Practically all phyla of the kingdom Protozoa *sensu lato* (Corliss, 1994, 1998) contain a considerable number of species exhibiting cyst or spore formation in some part of their life cycles. Using vernacular names, and recognizing that some of the taxa may be better assigned today to other eukaryotic kingdoms, the following groups are mentioned here: the rhizopod amoebae, the actinopod amoebae, the foraminiferans, the mycetozoa, the zoosporic and plasmodial 'lower' fungi, the 'higher' zooflagellates, the dinoflagellates and some of the other so-called phytoflagellates, the opalinids, the ciliates, the totally parasitic sporozoa/apicomplexans (gregarines, coccidians, haematozoa), the microsporidia, and the myxosporidia. The last two parasitic groups of protists are now preferably called the microsporans and the myxozoa, but the older and much better known vernacular names will be used for them throughout this article.

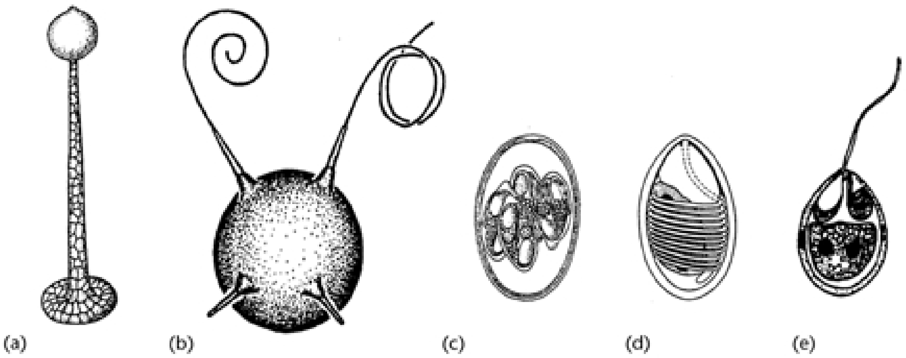

Figure 4 (a) Multicellular spore-containing sorocarp (atop stalked sporophore) of *Dictyostelium*, a mycetozoan cellular slime mould. Spores (not shown) dispersed on rupture of the sorocarp. (b) The huge gametocystic stage in the life cycle of *Gregarina*, a sporozoan gregarine parasitic in insects. Outside the host's body, it houses developing oocysts, known as spores (each containing eight sporozoites); the latter will eventually be expelled through everted radial tubes or sporoducts (two fully extended ones depicted), eventually to be taken up from soil by fresh hosts. (c) A mature oocyst (outside the host) of the widespread coccidian sporozoan genus *Eimeria*, whose species are destructively parasitic in practically all vertebrates except humans, simplified to emphasize thick outer walls, with micropyle at apex, and the contained sporocysts, each with pair of sporozoites. See text for further comments. (d) Minute spore of *Thelohania*, microsporidian protist with fungal affinities, showing particularly the coiled extrusible filament through which the single contained sporoplasm will be transferred to a fresh host (often an insect). (e) Spore of *Myxobolus*, myxosporidian protist with invertebrate animal affinities, showing a binucleated sporoplasm and two cnidoblasts (polar capsules), one with extruded filament for attachment in a fresh host (often commercially important fish species). (Note: the various structures are not drawn to the same scale.)

Perhaps most studied among the Protozoa, especially from biochemical and ultrastructural approaches, have been cysts of species of the ciliates, outstandingly of *Colpoda* (**Figure 3i,j**), members of the large phylum Ciliophora; but the spores (oocysts) of such very important parasites as those found among the Sporozoa have also been intensely investigated in recent years, as have the cysts of such harmful rhizopod amoebae as *Entamoeba* (**Figure 1c,d**) and *Acanthamoeba* (**Figure 1b**), and of such zooflagellates as the intestinal parasite *Giardia* (**Figure 2g**).

Roles in Life Cycles

Whatever part cysts and/or spores serve in the lives of protists, it is obviously related to survival of the species concerned. Not surprisingly, then, means of protection against unfavourable conditions of the surrounding environment, methods of dispersal of the organism to fresh locations, and rapid increase of a population are the most common usages of such stages in the life cycle, whether they are of an obligate or facultative nature.

Depending on the species and the local circumstances, protective or resistant cysts, more or less elaborate, occur as a dormant phase in the life cycle of protozoa of practically all major taxonomic groups. Such cysts, in well-studied cases (e.g. in *Colpoda* and certain other ciliates; see van Wagtendonk, 1955; Corliss and Esser, 1974; Bradbury, 1987; Gutiérrez *et al.*, 1998a), are more tolerant of various physicochemical changes in the environment than is the trophozoite or trophont – the common feeding stage in the life cycle; but, being incapable of independent locomotion, they are generally at the mercy of their local environment for movement, unless they are equipped with attachment structures or are buried in the soil. However, in both of the latter cases, they may be picked up by active organisms in the area and thus become passively dispersed, or they may be carried elsewhere by currents of water, wind, etc. In the case of some spores, malarial sporozoa for example, vectors may be involved, with direct inoculation into the next obligate host in the full cycle of the parasite. In a broad sense, the microbial ecology of cyst- and spore-producing protists, and fungi and bacteria, demands further attention than it has received to date.

Reproductive cysts, known by a variety of names, serve the obvious function of increasing the population size of a given species, although the great majority of protists also quite regularly undergo the process of simple binary fission – free from any cyst – in their 'normal' life cycles. Reproductive cysts are not usually surrounded by thick or resistant walls or membranes; their advantage lies in rapid production of multiple tomites or ciliospores, a so-called palintomic stage which is quickly transformed back into the typical trophont or vegetative stage by rapid feeding when the tomites emerge from the cyst. Outstanding examples of this process are seen in the histophagous ophryoglenid hymenostome ciliates (**Figures 3k,l**), the parasitic apostome ciliates, and the curious flagellate *Stephanopogon*, a protist originally described as an 'eociliate'. Analogous examples may be found in the sporogony of the sporozoa, in which tomitogenesis becomes a kind of schizogony. One or more environmental factors, although often unknown with precision, trigger the occurrence of rapid multiple fissions within cysts or spores in all groups of protists in which the phenomenon has been observed.

In some of the opalinid flagellates, an infective cyst, produced following palintomic divisions of the trophic organism (also called a gamontocyst) leaves its anuran host with faecal material, becomes ingested by a tadpole host, and produces anisogametes; these fuse to form zygotes, each of which, in turn, encysts as a zygocyst, from which a freshly emerging flagellated trophozoite eventually emerges within the gut of its new host. Gamontocysts have also been described from gregarine sporozoa and actinopod amoebae (heliozoa and radiolarians).

In the hymenostome ciliate *Lambornella* a cuticular cyst is formed on the outside of treehole-breeding mosquito larvae and the single organism within it emerges to bore through the cuticle, entering the coelom, where it starts to multiply, eventually bringing about the death of the host. Some free-living dinoflagellates have a temporary vegetative stage, or ecdysal cyst, that occurs under certain environmental stress conditions which cause the thecal plates and the flagella to be shed for a time. A so-called digestive cyst is formed in certain litostome/pleurostome ciliates, dinoflagellates, foraminiferans and filosean rhizopod amoebae after the trophozoite has gorged itself on prey organisms; it is thin-walled and a short-lived stage in the life cycle. A stomatocyst or statospore is a unique resting or resistant cyst of chrysomonad phytoflagellates formed by a complex process and possessing a strongly silicified outer wall or membrane, with a prominent emergence pore plugged until time of excystation (**Figure 2b**). The large multinucleated amoeboid-like stage of myxosporidian parasites of fish tissue, a temporary body in the life cycle, is known as a pseudocyst. The phoretic cyst is best exemplified by certain apostome ciliates (**Figure 3g**). It is a stage in the life cycle in which the organism in question has encysted on the carapace of some crustacean, thus getting carried about by this host. The 'postsex' cyst occurs in several groups of protists: effectively, it is any cyst or spore housing a zygote which, just before excystation occurs, divides to produce a few to many cells that carry on with the life cycle.

With respect to spores, major roles in the life cycle are also generally very straightforward: to increase the number of individual cells by rapid fissions, to disperse those filial products widely, and in some instances to protect the organism from an unfavourable environment. In the formerly called 'lower' fungal groups involving plasmodial stages, a complex transformation results in production of numerous uninucleate single-organism spores in a sporangium generally found atop a stalk, the sporophore (**Figure 4a**). On being freed by rupture, typically the spores are disseminated and, by subsequent germination, start new life cycles elsewhere. In most of the sporozoa, the process is basically similar; but, since the species are all internal parasites, no stalks are involved, and transfer to or infection of fresh hosts is eventually by contamination, ingestion, inhalation or inoculation, depending on the taxonomic group of species and the particular hosts involved. In many dinoflagellates, especially members of major parasitic taxa, the diploid fission products of a zygote, sometimes encased in a resistant zygospore equipped with an apical aperture called the archeopyle, emerge as dinospores, tiny biflagellated free-swimming forms able to invade fresh hosts.

Morphological and Cytological Data

As a general statement it may be said that both cysts and spores are spherical-to-ovoid in shape, and of a size, for most cysts, not exceeding that of the diameter of the trophozoite/trophont stage, or, for most spores, considerably smaller than that of the vegetative stage in the life cycle. There are, however, a number of significant exceptions throughout the diverse protozoan taxa; some are mentioned below, and various examples are illustrated in the accompanying figures. Many studies have been carried out at both light- and electronmicroscopic levels, yielding details far too numerous to be mentioned in this brief overview.

With respect to cytoplasmic inclusions in encysted or sporic bodies, it may generally be stated that essential organelles, such as nuclei, mitochondria, plastids, dictyostomes (Golgi apparatus) etc., are retained, although sometimes in condensed or otherwise altered form. Along with frequent loss of water by dehydration, food vacuoles, functional mouths, and locomotory organelles are typically lost, or absorbed, as well. Also, especially in parasitic species, special organelles or bodies may appear as new: for example, glycogen vacuoles and chromatoid bodies in encysted parasitic amoebae; residual and refractile bodies in sporozoan oocysts; coiled or polar filaments (not homologous structures) in microsporidia and myxosporidia. Cysts and spores are basically colourless, although inclusions may make them appear brown or grey or, especially in the case of algal protists, green from retained chloroplasts.

The enveloping walls or membranes may vary considerably from group to group, or even within groups. Some are smooth or slightly wrinkled, thin and unadorned, but many have become highly distinctive in their shape, their thickness and their ornamentation. For example, multiple layers, known as ecto-, meso- and endocystic membranes, occur in such ciliates as *Bursaria*, *Didinium* and *Colpoda* (**Figure 3d,h–j**); the multivalved myxosporidian spore contains 1–6 polar capsules or cnidoblasts (**Figure 4e**); micropylar openings or exitpores, plugged or capped, appear apically in cysts and spores of diverse taxa (**Figures 1a**, **2b**, **3a,d** and **4c–e**). The main macromolecular components are proteins, glycoproteins and carbohydrates. The outermost walls may be chitinous, pseudochitinous, siliceous, calcareous, cellulosic, occasionally tectinous or gelatinous, and sometimes simply membranous, with or without an external mucoid coating (Preisig *et al.*, 1994).

Worthy of brief mention here is the existence of containing or supporting structures associated with cysts or spores of eukaryotic microorganisms. With the notable exception of many fungal and some algal groups, however, such accessories are generally conspicuous by their absence among other protists. The stalks of the mycetozoa, some heliozoa and a few ciliates might qualify for that label, and the long attachment filaments associated with various taxa of parasitic forms might also be considered as a kind of 'supporting' structure (**Figures 2c**, **3e,g** and **4a,b,d,e**).

Shapes of cysts and spores may vary from spherical to ovoid to pyriform to ellipsoid to lunate to crescentic to 'horned' to spindle-like. Distortions are sometimes linkable to outer surface ornamentation, which in many dormant/resistant cysts may vary from grooves, knobs, warts, spurs, spines or scales to more elaborate or more lengthy processes, filaments, tubes, horns or 'tails' extending some distance from the central body of the cyst or spore (**Figures 1a**, **2a,b,d–f**, **3b,c,f** and **4b**). A striking anchor-like shape is attained by some of the triple-valved spores of myxosporidia. The so-called gametocyst of some gregarine sporozoa extends several radial tubes or sporoducts, sometimes thousands of micrometres in length, out from its spherical surface (**Figure 4b**). Through these are discharged long chains of oocysts (spores), each of which contains eight sporozoites, the infective stage when ingested by a fresh host, for example the grasshopper.

Sizes vary enormously, depending mostly, of course, on what array of protozoan forms are being considered. For a given species within a particular taxonomic group, the dimensions can sometimes be of genuine diagnostic value. Overall, ranges in diameter extend from about 5–15 μm for the cysts or spores of certain soil and parasitic amoebae, some free-living phyto- and zooflagellates, sporozoan sporozoites ('naked' spores), and all microsporidian species (in fact, 3–6 μm is the total range here) to frequent averages of 15–50 μm for most ciliates, many rhizopod amoebae, dinoflagellates, opalinids and many myxosporidia, not including cyst-wall extensions. Many thin-walled cysts, for example digestive, ecdysal and certain reproductive cysts, have a diameter greater than 50 μm; and the resting cysts of the pelobiontid rhizopod or archezoan *Pelomyxa* may reach 150–250 μm. The spore (gametocyst) of some gregarine sporozoa can measure 500 μm in diameter, exclusive of its projections. The tissue spore (pseudocyst) of some myxosporidia can show a width of 1000 μm, even reaching 30 000 μm or more in certain species.

Physiological and Molecular Data

Cysts and spores, being nonfeeding states, have been subjected to a barrage of tests, especially those to determine specific reactions to physicochemical parameters of their environments. Ranges of tolerance have been established in a number of cases, and a search for the particular factors thought to be involved in triggering both encystation and excystation has been a continuing activity of biochemists and others in several research laboratories. In recent years, some molecular data have started to accumulate (Bradbury, 1987; Gutiérrez *et al.*, 1998a): for example, it has become clear that a major characteristic of any cryptobiotic form is its transcriptionally inactive state.

Physiological/biochemical and other conditions explored have included these sometimes overlapping factors or stimuli: pH, temperature, oxygen concentration, desiccation, barometric and osmotic pressure, light intensity and photoperiod, ultraviolet and X-irradiation, toxic chemicals, enzyme activities, and the concentration of diverse ions or organic materials, including depletion of specific growth factors and accumulation of metabolic waste products in the medium. Also studied have been such broader general ecological considerations as pollution, starvation, autophagy (cannibalism), overfeeding, body size, population density (including crowding), dispersal abilities, occurrence of sexual phenomena, seasonality or other kinds of periodicity (including tidal rhythms), and, for parasitic protists, changing external and internal conditions of hosts and of host cells and tissues.

A combination of factors may often be involved in causing encystation or excystation, greatly complicating the effort to identify the responsible triggering mechanisms. Another frustrating roadblock to progress in the area has been the widespread inability of researchers to establish axenic cultures of the great majority of protozoan species investigated, and to obtain large synchronized populations for analysis from all stages in the process. Nevertheless, definite advances in our knowledge of protozoan life cycles have been made.

Some general conclusions that may be drawn are that 'resting' protozoan cysts and spores can withstand greater environmental extremes, at either end of the spectrum, than can the relatively unprotected feeding or dividing forms in the cycle. Their walls/membranes, and often their cytoplasmic contents, are able to make survival possible for varying lengths of time, sometimes measurable in scores of years, because they possess properties different in kind or degree from those known for the more vulnerable stages. Speed in multiplying cells is the main characteristic of the typical reproductive cyst or spore, and this often requires quite different ecological, morphological and physiological properties or activities than those characteristic of the encysted state. And conditions causing/allowing excystation are also unique.

Review or overview papers of value, although relatively few in number and mostly dated or restricted to specialized subtopics, include van Wagtendonk (1955), Corliss and Esser (1974), Bradbury (1987), Gutiérrez *et al.* (1998a, 1998b, 1990). As stages in life cycles of both free-living and parasitic protists, cysts and spores receive some mention in standard textbooks of protozoology, phycology and mycology; and the reader is referred to the appropriate chapters in the works by Lee *et al.*, Margulis *et al.*, and Harrison and Corliss, which may all be found in the Further Reading.

Encystation and Excystation

The specific phenomena of forming cysts and spores and of the subsequent exiting of individuals from such structures (germination or sporulation) have long been of interest to biologists engaged in both basic and applied research. Interestingly enough, greater emphasis has been placed on encystation than on excystation. Why or how these processes occur in nature are questions posed, if not wholly answered, on preceding pages. The numerous factors or stimuli involved, or presumably involved, have been listed above, along with mention of major difficulties in carrying out such researches. Only very recently have molecular/genetic approaches become feasible; much more remains to be done in such a precise and promising area.

To recapitulate briefly here, in general terms, the principal causes of encystation, at least of free-living protists, in nature as well as under laboratory conditions have long been, and still are, thought to be depletion of essential nutrients in the medium, desiccation, crowding, lack of oxygen, and changes in temperature and pH; and of excystation, changes in osmotic pressure, restoration of high food and oxygen concentration, abundant supply of moisture, and the triggered enzymatic dissolution of cystic membranes or walls. Some of the same factors apply to parasitic protists, although the picture is complicated because of the presence, often, of obligate hosts in the full life cycle. The hosts are a vital part of the parasites' environment: we are obviously no longer dealing with a relatively simple aqueous or terrestrial medium.

An attractive generalized model of encystation has recently been hypothesized for ciliates by Gutiérrez *et al.* (1990). It is primarily based on numerous structural and physiological studies published before 1990, many carried out by Gutiérrez and various colleagues on species of *Colpoda* and several hypotrich genera. The following points are emphasized by these workers:

- The most important exogenous 'inducer' of cryptobiosis is considered to be starvation, possibly simply a deficiency in an essential nutrient, which acts as the first 'trigger' for the whole differentiation process.
- A 'switch on' of encystation genes causes the appearance of several newly synthesized transcripts containing information on structural and/or enzymatic proteins.
- Cell autophagy and protein turnover provide material for synthesis of new cystic proteins.
- Dehydration plays a significant role throughout – the loss of intracellular water shutting down many of the cell's usual metabolic activities.
- Distinctive cystic walls or envelopes, often derived from different cytoplasmic precursors, for example the rough endoplasmic reticulum or the Golgi apparatus, are formed and serve to isolate/protect the resting organism, in its new stable state, from the hostile external environment.

Eventually, occurrence of appropriate internal and external 'inducer' conditions will stimulate or permit return of the organism, via activation of 'vegetative genes' in the process termed excystation, to its former equally stable trophic and reproductive state of existence.

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