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COCCOMYXA PARASITICA SP. NOV. (COCCOMYXACEAE, CHLOROCOCCALES), A PARASITE OF GIANT SCALLOPS IN NEWFOUNDLAND

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Coccomyxa parasitica sp. nov. (Coccomyxaceae; Chlorococcales) is described as a parasite of the marine giant scallop, *Placopecten magellanicus* Gmelin, from Newfoundland, Canada. Cells occur in colonies distributed through various host organs, but especially in the mantle fold. Cell morphology is highly variable, although characterised by the possession of a distinct hyaline tip which is reduced or absent in culture. Pyrenoids are lacking, 1–3 parietal chloroplasts occur and the cell wall lacks cellulose. Reproduction is by 2, 4 or 8 autospores in the host, and by 2, 4, 8 or 16 autospores in culture. Sexual reproduction is lacking. Pigment analysis reveals the predominance of chlorophyll *a*, with chlorophyll *b*, α- and β-carotene and neoxanthin also present. The parasitism is regarded as at best facultative, although free-living *C. parasitica* is at present not known.

The giant scallop, *Placopecten magellanicus* Gmelin, is well known as an important commercial species in Newfoundland (Squires, 1962). Naidu (1971) discovered the presence of conspicuous colonies of unicellular algae in the scallops, the algae having first been reported as zoochlorellae (Naidu & South, 1970). Naidu (1971) considered the algae to be parasitic, causing considerable harm to the host when it is heavily infected. Stevenson (1972) has conducted a detailed in vivo and in vitro study of the algae, accumulating evidence to indicate that they exhibit the generic characteristics of the genus *Coccomyxa* Schmidle (1901) (Coccomyxaceae; Chlorococcales).

Coccomyxa spp. are largely known as freshwater algae, or epiphytes and phycobionts of lichens (Jaag, 1933; Bourrelly, 1966; Ahmadjian, 1967). Of the few marine species described, two are reportedly parasitic in invertebrates: *C. ophiurae* Rosenvinge (Mortensen & Rosenvinge, 1910), parasitic in *Ophiura texturata* Lamarck; *C. astericola* Rosenvinge (Mortensen & Rosenvinge, 1933), parasitic in *Hippasteria phrygiana* Parel. From Rosenvinge's brief descriptions, it is difficult to make detailed comparisons with our material. Sufficient information exists, however, to show that our *Coccomyxa* represents a new species: we propose the designation *C. parasitica* sp. nov. This would appear to be the first report of an occurrence of *Coccomyxa* in N. American marine invertebrates.

COCCOMYXA PARASITICA sp. nov.

DIAGNOSIS

Plantae unicellulares, parasiticae, in globosis, irregularibus vel coalitis coloniis, in mantello, in musculo, in gonade, in lamellis vel in interiore concha *Placopectinis magellanici* Gmelin. Cellulae 1–11 μm longae, in forma valde variantes, vel sphaericae vel ellipticae vel oblongae vel falcatae; saepe apice attenuato hyalino ornatae. Chloroplastus unicus, vel ad 2–3 adsunt, parietalis, saepe cyathiformis. Pyrenoides deficientes; nucleus parvus, unicus; cellulae paries cellulosae destitutus, rigidus, inornatus.

Reproductio ab 2, 4, 8 (16) autosporis, divisionibus primis oblique longitudinali cellulae

maternae axi factis. Reproductio sexualis abest. In cultura formans massam nitidam, laevem, primo chlorinam, deinde viridem.

Typus speciei in Figs 2 et 3 depictus.

Locus typi: Port au Port Bay, Newfoundland, Canada. In *Placopectine magellanico* Gmelin.

Plants unicellular, parasitic, in globular, irregular or coalesced colonies in the mantle, muscle, gonad, gills or inner shell of *Placopecten magellanicus* Gmelin. Cells 1–11 μm long, very variable in shape from spherical to elliptical, oblong or sickle-shaped, frequently with an attenuated hyaline tip. Chloroplast usually single, or up to three present, parietal, often cup-shaped. Pyrenoids absent, nucleus small, single; cell wall lacking cellulose, rigid, unornamented.

Reproduction by formation of 2, 4, 8 (16) autospores, the initial divisions oblique to the longitudinal axis of the mother cell. Sexual reproduction not known. In culture forming an initially lime-green, later brilliant green, shiny cell mass.

Figs 2–3 have been taken as the type of the species.

Type locality: Port au Port Bay, Newfoundland, Canada. In *Placopecten magellanicus* Gmelin.

MATERIALS AND METHODS

Studies were based on parasitised scallops obtained from St Joseph's, Salmonier, St Mary's Bay, and the Boswarlos bed, Port au Port Bay, Newfoundland. Isolates included those originally obtained in 1968 (Naidu & South, 1970) and others obtained later in 1969 and 1970. Algae were examined in smear preparations. By extracting samples from the exposed mantle edge of live scallops, using a finely drawn-out pipette, repeated sampling could be made from the same animal. Samples from the gills, gonads and adductor muscle were taken when heavily infected scallops were destroyed and the valves removed.

Cultures were incubated under a variety of conditions. Media were Erdschreiber, or a modified Erdschreiber (Naidu & South, 1970), *Symbiodinium microadriaticum* Freudenthal medium (McLaughlin & Zahl, 1966) and U.R. II medium as employed by Hanic (1965).

Liquid and agar slope cultures were incubated in screw-cap test tubes. Biphasic cultures, consisting of 50 ml agar medium under 25–50 ml liquid medium, were maintained in 125 ml Erlenmeyer flasks. Most cultures were incubated at 15 ± 0·5°C, at light intensities of 1,400 or 3,500 lx, using cool-white flourescent tubes (Westinghouse, F24T12/CW/HO). Under all conditions an 18–6 h light-dark photoregime was maintained.

Pigments were extracted in 25% chloroform in methanol (V/V) and paper chromatography was carried out using Whatman No. 3 Mn chromatography paper. The solvent was 25% chloroform in light petroleum (60–80°C). Absorption spectra of pigment fractions were measured with a Beckman Ratio Recording Spectrophotometer, Model DK-A. Combined fractions from three separate extractions were required for each series of readings.

OBSERVATIONS

THE ALGAE IN VIVO

Naidu (1971) described the principal areas of infection within scallops as the left (upper) and right (lower) mantle folds, the distal end of the gonad, and the base of the adductor muscle between the muscle and the left valve, with sloughed-off colonies on the inner surface of the shell margin. Additional sites were found during the present study, colonies occurring in the gill filaments, deeply embedded in the adductor muscle (posterior and anterior), on the anus, and in amoebocytes in smears from the stomach and blood fluid. An analysis of the sites of infection of 96 scallops is shown in Table I. The regions most heavily infected are the left and right mantles, particularly the mantle edges. An example of a heavily infected scallop is shown in Fig. 1. Colonies are most numerous in this mid-line mantle region, especially of the left mantle. The shell fold, which lies in direct contact with the inner shell surface, is the site of the highest concentration of infection.

Examination of a large number of infected scallops showed that colony size and frequency decrease from the mantle edge inwards. Colonies of algae may occur at various depths in the host tissues. In the mantle and gill filaments they

TABLE I. Analysis of sites of infection of 96 scallops by *C. parasitica* sp. nov. in Newfoundland

Anatomical area	No. scallops infected
Right (lower) mantle	
(a) Anterior	72
(b) Mid-mantle	81
(c) Posterior	79
Left (upper) mantle	
(a) Anterior	84
(b) Mid-mantle	96
(c) Posterior	87
Anus	3
Adductor muscle	12
Gill filaments	3
Shell	10
Amoebocytes in stomach	2*
Leucocytes in blood	2*

* Single *C. parasitica* cells only

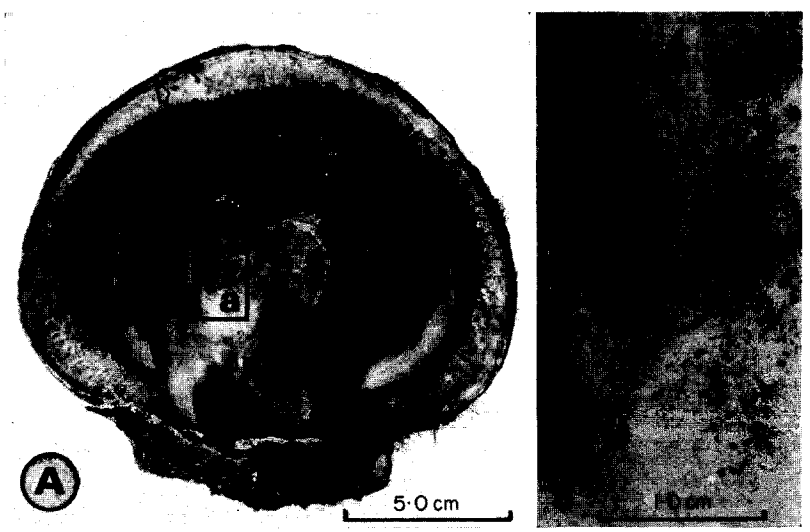

FIG. 1. Newfoundland specimen of *P. magellanicus* (A) with left (dorsal) valve removed to show a heavy infection of *C. parasitica* sp. nov. The enlargement (a) of the adductor muscle region shows the degree of concentration of *C. parasitica* colonies. An individual colony is indicated (dark arrow).

mostly occur just below the epithelium, where they may easily be removed with a capillary pipette. In the thicker mantle edge their occurrence may be one to several mm below the surface. Colonies may be found at any depth in the adductor muscle, while on the gonads and anus they are restricted to the surface layers. The colonies are spherical, elliptical, irregular or anastamosed. In lightly infected hosts they are discrete; in heavily infected scallops they may form a more or less continuous algal mass, especially in the mantle, imparting a dark green colouration to the tissues. The colony surface is frequently irregular, with numerous algal cells protruding into the surrounding animal tissue; in some colonies,

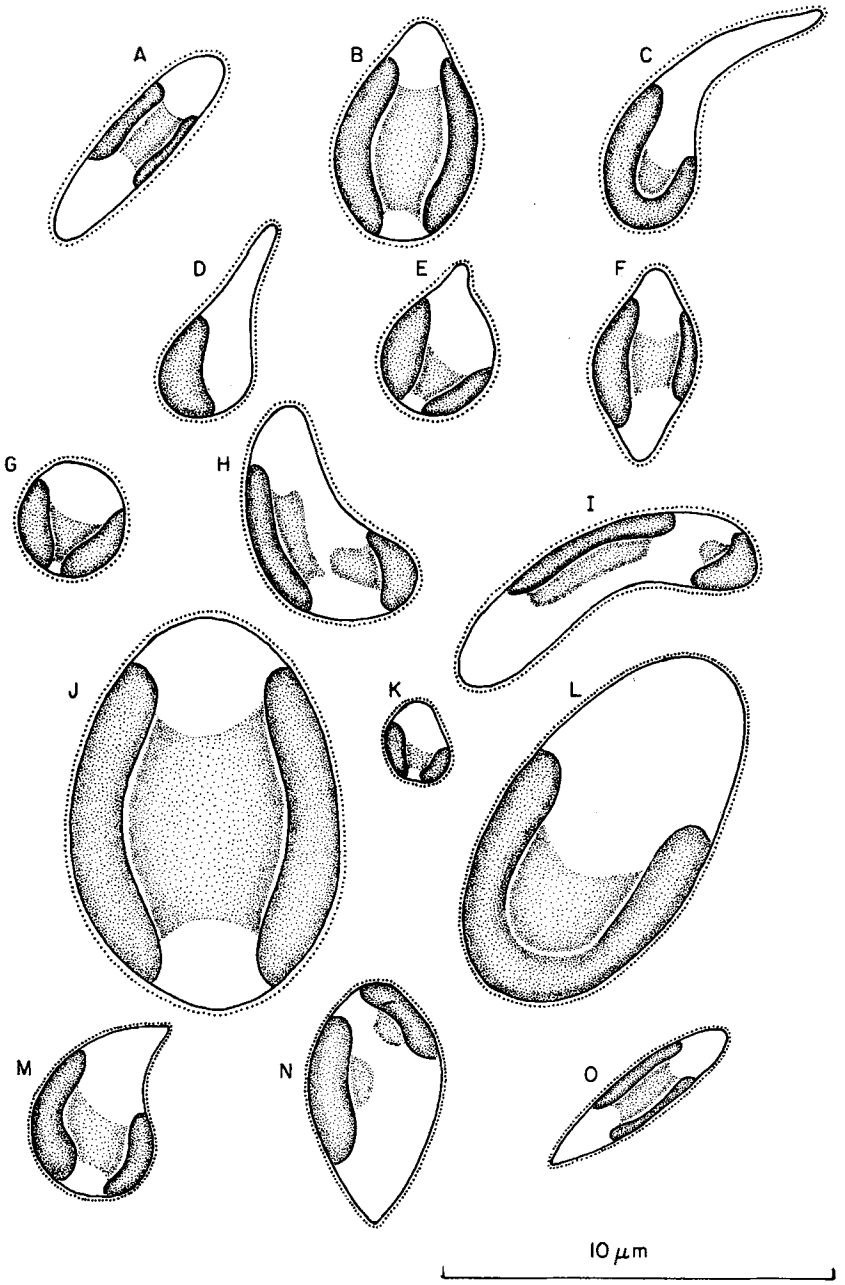

FIG. 2. *C. parasitica* sp. nov. from Newfoundland *P. magellanicus*, showing a selection of morphologically variable cells from a single host; for detailed explanation see text.

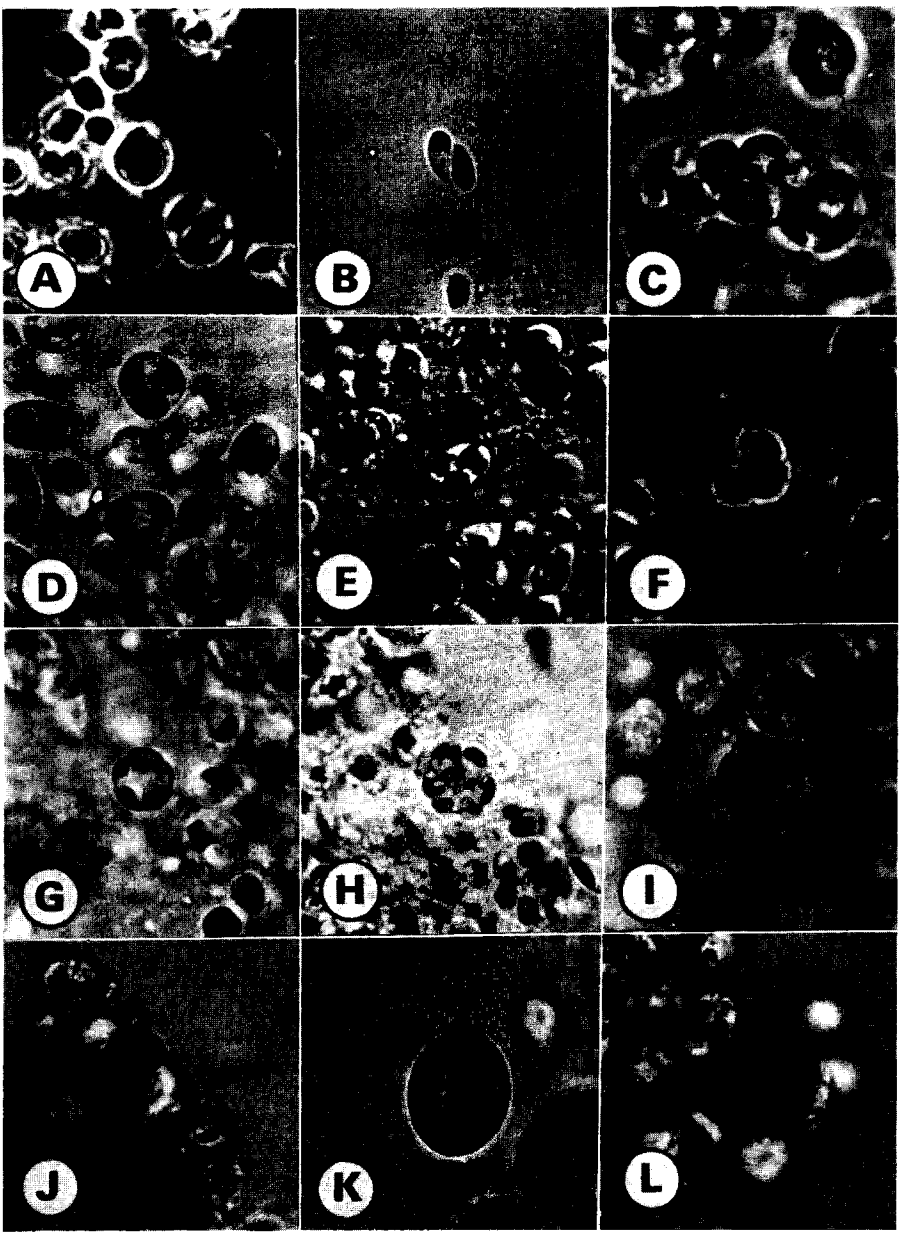

FIG. 3. Formation and release of autospores in *C. parasitica* sp. nov. in vivo (A–J) and in culture (K, L). A. Formation of division plate (central cell). B. 2-celled autosporangium. C. Polar view of 4-celled autosporangium. D. Completed division in 4-celled autosporangium from the polar (solid arrow) and lateral (open arrow) views; note the compact arrangement of the spores in the latter. E. Reorientation of the four spores, when they appear to be loosely arranged. F. Rupture of the sporangium wall and release of spores from a 4-celled autosporangium. G. Initial divisions in formation of an 8-celled autosporangium. H, I. 8-celled autosporangia. J. Rupture of the sporangium wall and release of spores from an 8-celled autosporangium. K. Formation of a 16-celled autosporangium. L. Mature 16-celled autosporangium. A, F phase contrast; B, C, D, G–L, bright field; E phase interference microscopy.

animal tissue extends towards the centre of the algal mass. The tissue reaction of the scallops to infection, described by Naidu (1969, 1971), results in a form of encapsulation.

Naidu & South (1970) briefly described the cell morphology of *C. parasitica* (as "zoochlorella"). The following account is based on standard, phase contrast and interference phase light microscopy.

Cell shape and size are highly variable; a range of representative forms from a single scallop is shown in Fig. 2. Cells may be rod-shaped, oval, sausage-shaped, spherical or sickle-shaped. Many have smooth, symmetrical tips (Fig. 2 J), or rather accentuated hyaline tips (Fig. 2 C, D, M). Two (Fig. 2 H, I, N) or occasionally three chloroplasts may occur in some cells, although a single parietal band-shaped chloroplast is more usual. Cells from a fresh smear range in size from 1–11 μm. Peaks in cell size frequency occur at 3–4 μm and 7–8 μm. The mean dimensions of 50 cells from a total of ten smears from ten randomly selected scallops were 5·5 × 3·0 μm.

Some standard chemical tests were made on the cell wall and cell contents. The I_2-KI-H_2SO_4 and chlor-zinc-iodide tests for cellulose gave negative results. Meyer's starch test was also negative, and no pyrenoids were observed. Refractile cytoplasmic inclusions are clearly visible, and vacuoles may occur. The cell wall is highly resistant to chemical penetration, cells remaining intact for as long as 10 min in 75% H_2SO_4.

Cells fixed in 3 : 1 alcohol : acetic acid for 12 h were stained with aceto-carmine and aceto-orcein. The latter stain demonstrated the presence of a single, small, centrally positioned nucleus.

PIGMENTATION

The typical one-dimensional paper chromatogram revealed the presence of neoxanthin, chlorophyll *a*, chlorophyll *b*, and α- and β-carotene, the last two imperfectly separated. Absorption spectrophotometry permitted confirmation of the identification of the pigment fractions. The total extract showed absorption maxima at 430 and 665 nm (Table II), indicating a predominance of chlorophyll *a*.

REPRODUCTION IN VIVO

Reproduction is entirely by means of autospores. Two-, four- and eight-celled autosporangia were observed, and a series of examples of stages in their formation are shown in Figs 3 and 4. The first division is oblique to the longitudinal axis of the cell (Fig. 3 B, Fig. 4 A). Ultimate formation and release of the autospores results from a re-orientation of the spores within the mother cell capsule

TABLE II. Summary of pigment analysis, *Coccomyxa parasitica* sp. nov.

Fraction	Rf value	Absorption maxima (nm)			Colour	Identification
1	0·97	420	445	473	yellow	α-carotene
2	0·95	420	450	473	pale orange	β-carotene
3	0·78	409	430	663	blue-green	chlorophyll *a*
4	0·65	424	453	644	yellow-green	chlorophyll *b*
5	0·41	415	439	465	bright yellow	neoxanthin

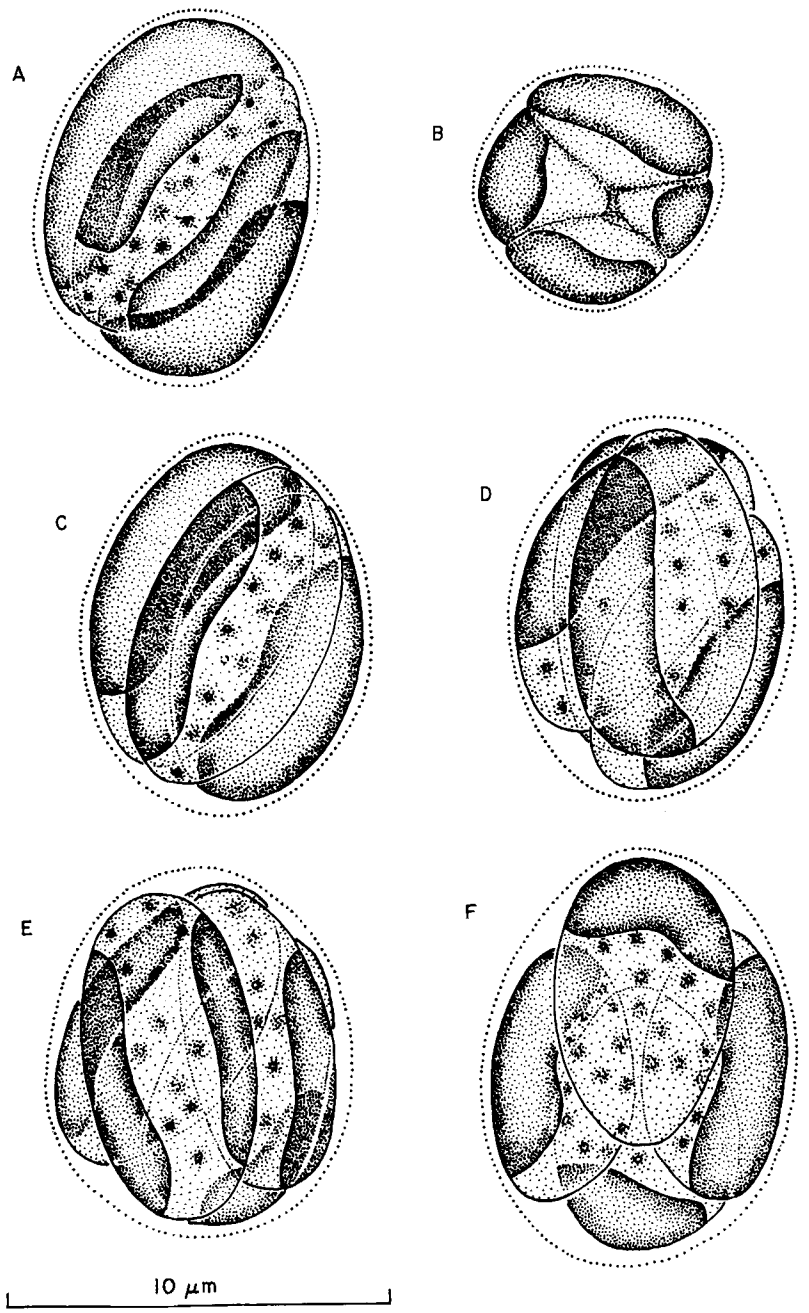

FIG. 4. Formation of 4-celled autosporangium in *C. parasitica* sp. nov. (A–D) and reorientation (E, F) of the spores within the capsule.

(Fig. 3 D, E, Fig. 4 D–F) and a rupturing of the mother-cell wall (Fig. 3 F, J). Autosporangia range in length from 5–11 μm, with a peak at 7–8 μm. Two-celled autosporangia predominate, and eight-celled examples are uncommon. Following release the individual autospores range in size from 2–5 μm (products of eight-celled autosporangia) to 5–7 μm (products of two-celled autosporangia).

THE ALGAE IN VITRO

On agar the algae form smooth, often shiny colonies and in clonal cultures these are initially circular, eventually becoming irregular. The colour is lime-green at first, and finally becomes bright green on maturation. Penetration of the agar readily occurs in older cultures, to several mm below the surface. Stab cultures were successful, and in many instances growth reached the agar surface and spread beyond the site of inoculation. Several weeks' growth on agar usually results in an even spread of cells.

In liquid culture, both in test tubes and in biphasic cultures, growth is initially along the bottom of the vessel if left undisturbed, later spreading to the side of the vessel furthest away from the light source.

Bacteria-free cultures were not obtained; bacilli were commonly attached to the algal cell walls, and repeated washings were insufficient to remove them.

Cell morphology and size vary considerably with differences in culture medium, age and the number of subculturings. In general, however, the tendency in culture is towards greater uniformity in shape and smaller size than in vitro. In young liquid and agar cultures the cell morphology differs little from that in the scallop. The parietal chloroplasts are well defined, usually single and band- or cup-shaped, with occasionally two, rarely three chloroplasts present. Cell size in young cultures ranges from 1–(4·5)–10 × 1–(4·0)–6 μm.

Changes with culture age consist principally in reduction in cell size, a tendency for most cells to become spherical, an increased incidence of cell vacuolation, a thickening of the cell wall, development of coarse refractile cell inclusions, reduction in chloroplast size, formation of oil-like storage products and a reduction in the rate of autospore formation. The tendency for spherical cells is most marked in agar cultures, while the vacuolation and formation of cytoplasmic inclusions is more characteristic of old liquid cultures.

Cultures left for long periods without replenishment of nutrients show a general degeneration. The chloroplast becomes a minute body, large vacuoles develop and conspicuous oil bodies form. Cells become spherical, with a thickened wall, and are comparable to a resting phase. Subculturing results in a rapid reinstatement of the more "normal" culture form.

By a cycle of isolation from the scallop, culturing, subculturing and then re-inoculation of cultured cells into a scallop, it has been shown that the above changes associated with isolation and culture are reversible on re-infection.

REPRODUCTION IN VITRO

Reproduction in vitro is the same as in vivo. In addition to two-, four- and eight-celled autosporangia, sixteen-celled autosporangia occurred in some young (14 day) agar slope cultures. Since elliptical cells are less common in culture than in the scallop host, oblique division of the autospore mother cells was not observed. On some rare occasions in culture, certain autosporangia produce three autospores.

All attempts to produce possible motility of the spores failed, and reproduction thus appears to be entirely by autospores both in the scallop and in culture. Rapid rates of division are characteristic of young cultures or new subcultures, two-celled autosporangia being the most frequent under all conditions.

DISCUSSION

Table III shows a comparison between *C. parasitica* and the two previously described *Coccomyxa* species known from marine invertebrates. Cells of both *C. ophiurae* and *C. astericola* fall within the size range of *C. parasitica*, and there are few reasons for separation of the species on reproductive grounds. The number of autospores produced in *C. parasitica* may exceed recorded levels for the other two species. Breakdown of skeletal calcium carbonate by *C. ophiurae* has not been demonstrated for either *C. astericola* or *C. parasitica*, and *C. parasitica*, possibly with *C. ophiurae*, lacks cell-wall cellulose.

TABLE III. Comparison between *Coccomyxa parasitica* sp. nov. and previously described parasitic, marine *Coccomyxa* species

Species	Size range of cells (μm)	Cell-wall cellulose	Pyrenoid	$CaCO_3$ digestion	Reproduction
C. parasitica	1·0–(5·5)–11·0	—	—	—	2, 4, 8 (16) autospores
*C. ophiurae**	7·0	(—)	—	+	2,4 autospores
C. astericola†	4·0–5·5	+	—	—	2,4 autospores

* Mortensen & Rosenvinge (1910).
† Mortensen & Rosenvinge (1933).

Coccomyxa is included in the family Coccomyxaceae which Herndon (1958) placed in his new order Chlorosphaerales. An assessment of the Chlorosphaerales is given by Groover & Bold (1969), who advocate that the order should be renamed the Chlorosarcinales on the grounds of the illegitimacy of *Chlorosphaera*, the basis of Herndon's (1958) order. It is apparent from Groover & Bold (1969) that the Chlorosarcinales represent a distinct taxonomic group which should be retained at the ordinal level. The order includes those zoosporic unicellular and colonial genera which divide vegetatively. The problem of interpretation of vegetative division in unicellular algae, long a source of confusion, is fully defined by Groover & Bold (1969). Bourrelly (1966) did not recognise a comparable order, but included the packet-forming members in a separate family, the Chlorosarcinaceae of the Chaetophorales. He placed the Coccomyxaceae in the Chlorococcales.

Groover & Bold's (1969) concepts have, however, been perpetuated (Bold, 1970; Round, 1971). As suggested by Groover & Bold's definitions, the Coccomyxaceae, which are azoosporic, must be excluded from the Chlorosarcinales. They further indicate the lack of intensive studies in culture of coccomyxacean algae, despite the admirable early work of Jaag (1933). In general, these algae bear insufficient resemblance to typical chlorosarcinalean algae sensu Groover & Bold (1969), Bold (1970) and Round (1971); Bourrelly's (1966) placement of the

Coccomyxaceae in the Chlorococcales thus seems acceptable at the present time.

It is apparent that of the morphological changes which occur in *C. parasitica* in vitro, compared with in vivo, those of cell shape and size are the most important. Changes in cell wall thickness are less apparent. Taylor (1971) has pointed out that direct contact with the host cells, or an "intracellular phase", may play a major role in morphological changes in the symbiont *Amphidinium*. Such an intracellular phase may occur in *C. parasitica*, especially during the phagocytosis process reported elsewhere (Stevenson, 1972). The time of exposure to the intracellular environment may be the most important determining factor. Experimentation during the present study revealed the reversibility of the morphological changes, and serves to confirm the relationship between the isolated cultures and the original material. The artificial infection procedure, although not as refined as the experiments of Provasoli, Yamasu & Manton (1968), illustrates a practical method by which more detailed comparisons between cultured and parasitic *C. parasitica* could be made. The existence of the morphological changes does permit speculation on the relationship. Taylor (1971) suggested that in symbiotic partnerships, the failure of the algal partner to undergo morphological adaptation may be indicative of a recently formed association. By this reasoning, the relationship between *C. parasitica* and *P. magellanicus* is not recent.

There are few examples of algal parasitism of marine or terrestrial animals documented. In addition to *Coccomyxa* species, a *Chlorella* has been reported as cysts within the eye orbits of bluegills, *Lepomis* sp. (Hoffman, Prescott & Thompson, 1965). Dr R. E. Norris (personal communication) has encountered unicellular green algae within the epidermis of several starfish species in the Friday Harbor area. The algae eventually caused the death of the starfish.

Davies, Spencer & Wakelin (1964) isolated and named the colourless alga *Prototheca segbwema* from cutaneous lesions of a man in Sierra Leone, and also demonstrated that spread of algae to lymph nodes occurred. The algae were considered potentially dangerous since they were resistant to commercial antibiotics and antifungal agents. Other *Prototheca* infections of humans have been noted from North Carolina (Klintworth, Fetter & Nielsen, 1968) and South Africa (Dr R. E. Lee, personal communication).

Parasitic algal infections so far reported all involve unicellular Chlorophyceae. Only in *Prototheca* have the algae apparently become obligate parasites. Naidu (1971) suggested that the adverse effects of *C. parasitica* are sufficiently serious to consider the relationship parasitic. That the causal algae may be isolated and readily grown on inorganic media, however, is proof that the parasitism is at best facultative. Although free-living *C. parasitica* is not known, and was not discovered despite careful searching during the present investigation, there seems little reason to doubt that it may occur. At present, the free-living marine *C. littoralis* (Haug) Wille, known from Europe, is not included in the N. American marine flora; the possible discovery of a similar taxon in Newfoundland could throw light on the origins of *C. parasitica*.

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