Acta Bot. Neerl. 30 (5/6), November 1981, p. 353–431.

TAXONOMIC STUDIES ON UROSPORA (ACROSIPHONIALES, CHLOROPHYCEAE) IN WESTERN EUROPE

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CONTENTS

SUMMARY

In this report on the taxonomic studies on the genus *Urospora* Areschoug in Western-Europe, a reclassification of the species is proposed. Comparative studies were made on natural collections, uni-algal cultures, herbarium collections and sections prepared for electron microscopy. These studies confirm the recognition of four species, viz. *Urospora wormskioldii* (Mertens in Hornemann) Rosenvinge, *U. bangioides* (Harvey) Holmes & Batters, *U. penicilliformis* (Roth) Areschoug and *U. neglecta* (Kornmann) nov. comb. The morphology of the gametophytic filament and the uni-celled sporophytic (*Codiolum*-)phase, the life-history, the nomenclature and historical aspects, and details of the ultrastructure of the vegetative thallus and the zoospores (in particular the flagellar apparatus) are discussed. Reliable, diagnostic characters for these species are shown to be the degree of rhizoidal development in the most basal cell and its neighbouring cells, the shape of mature vegetative cells in the filaments and their cell diameter, the dimensions of zoospores and gametes, and the presence of dwarf plants in the life cycle. The shape and size of the developing *Codiolum*-plants are shown to vary with external conditions. The *Codiolum*-plants in culture are clearly shorter than their natural counterparts. Moreover, differently shaped *Codiolum*-plants, collected from various natural populations, proved to belong to the life-history of the same *Urospora* species. A brief discussion is given to the taxonomic status of the genus *Codiolum* Braun. No species-distinguishing ultrastructural features were found among these four species. The micro-anatomy of the pyrenoid and the unique flagellar apparatus proved to be similar for all *Urospora* species. At the fine structural level, *Urospora* forms a clear-cut taxonomic unit.

1. INTRODUCTION

The genus *Urospora* includes a group of multinucleate, unbranched, uniseriate,

filamentous green algae. The algae have a parietal reticulate chloroplast and a rhizoidal holdfast arising from one or more differentiated basal cells. The genus was erected by ARESCHOUG in 1866. There has been much confusion in the past between this genus and the genus *Hormiscia* which FRIES described in 1835. In his presentation of *Urospora* in 1866, ARESCHOUG left *H. penicilliformis* intact while defining the new genus and species *Urospora mirabilis*. In 1874, ARESCHOUG realised that the *Hormiscia penicilliformis* and *U. mirabilis* he had studied in 1866 were, in fact, the same species. He discovered that *H. penicilliformis* was the sexual phase and *U. mirabilis*, the zoospore-producing phase of the same alga. Areschoug decided at that time to preserve the genus name *Urospora*. He reasoned that *Urospora* had been described on the basis of its characteristically posteriorly pointed zoospores. Based on the proposal of Cotton (in BRIQUET 1935) the genus *Urospora* is conserved over the older generic name *Hormiscia*. Although this decision was erroneous in our opinion and has led to many difficulties, the common usage of the name *Urospora* has dictated its acceptance. In 1933, JORDE united *Urospora* with the one-celled genus *Codiolum* when she showed that the *Codiolum*-plants were sporophytes in the life cycle of *Urospora*.

The taxonomy of the *Urospora-Codiolum* complex is still in a confused and changing state. To resolve this confusion, it seemed necessary to make a detailed study of the vegetative characteristics, the life histories, and the ultrastructural features of the *Urospora* representatives in Western Europe. Four species were studied: *U. wormskioldii*, *U. bangioides*, *U. penicilliformis*, and *U. neglecta*.

2. HISTORICAL PERSPECTIVES OF THE GENUS

The *Urospora* species presented here have, in the past, been placed in various genera and families by various authors. This further illustrates the taxonomic chaos that has troubled the systematics of green algae. The same algae alternately received the generic names *Hormiscia*, *Hormotrichum*, *Urospora*, *Ulothrix* and *Conferva*. The problem is confounded by the fact that more than one species were later found to be included in Areschoug's *U. penicilliformis*.

Urospora penicilliformis was first described by ROTH in 1806 under the name *Conferva*. In 1835, FRIES defined the two species *Hormiscia penicilliformis* and *H. wormskioldii* in the family Ulvaceae. RABENHORST (1847) employed *Hormiscia* in its restricted sense. In 1845, KÜTZING used the name *Hormotrichum* instead of *Hormiscia*. In 1849, he had added several other species to *Hormotrichum*. In doing so, he combined species which are now known as *Urospora* and *Ulothrix*. HARVEY (1857, 1860) continued to use the name *Hormotrichum*. Some of his species were also shown later to be species of *Ulothrix*. Both Kützing and Harvey placed *Hormotrichum* in the Confervaceae. In 1868, RABENHORST separated *Hormiscia* from *Ulothrix*. However, his *Hormiscia* included, in addition to *Urospora* species, a number of thick-walled species which are now known to be *Ulothrix* (LOKHORST 1974, 1978). In 1874, ARESCHOUG reduced the *U. mirabilis* he had presented in 1866 and *H. penicilliformis* to one species, *Urospora penicilliformis*. He added *Conferva flacca* and *C. speciosa* as synonyms to this new

combination. These latter species are actually *Ulothrix* species (LOKHORST 1978).

The genus *Urospora* was again confused with *Ulothrix* when LE JOLIS (1880) used the name *Ulothrix isogona* for forms earlier given the names *Conferva isogona*, *C. youngana* and *Hormotrichum isogonum*. FARLOW (1881) continued in this trend by giving the synonyms for *Ulothrix isogona* as *C. youngana*, *Lyngbya speciosa*, *Hormotrichum younganum* and *Urospora penicilliformis*. DE-TONI (1889) joined all existing *Ulothrix* in *Hormiscia*, whereas he reported only *U. penicilliformis* under *Urospora*. He classified *Urospora wormskioldii* in the genus *Chaetomorpha*. On account of the multinucleate character of the vegetative cells WILLE (1890) placed *U. penicilliformis* in the Cladophoraceae. FOSLIE (1890), on the other hand, placed *U. penicilliformis* in the Confervaceae, with a reference to earlier published figures of *Conferva youngana*, *Hormotrichum penicilliforme*, *H. younganum*, *H. vermiculare*, *H. isogonum* and *Lyngbya speciosa*. ROSENVINGE (1893, 1898) followed WILLE's classification (1890) of *Urospora* in the Cladophoraceae and preferred the name *Urospora mirabilis* to *U. penicilliformis*. He found that ROTH's original description (1806) of *U. penicilliformis* gave too little information on its identity. HAZEN (1902) felt that the name *Hormiscia* should be revived in its original sense. She listed *Hormiscia penicilliformis*, *H. wormskioldii* and *H. collabens* and grouped *Hormiscia* in the Cladophoraceae. COLLINS (1909) continued to use the name *Hormiscia* and listed and described six species from North America. In 1918 he amended the generic description of *Hormiscia* by adding details on its reproduction. JÓNSSON (1903, 1912) returned to the use of the name *Urospora*. FRYE & ZELLER (1915) described a new *Urospora* species under the name *Hormiscia tetraciliata*. SETCHELL & GARDNER (1920) classified *Hormiscia* in the Siphonocladiales and divided the genus into three sections based on chloroplast structure, mode of attachment and cell dimensions. GAIN (1922) observed two growth forms of *Urospora penicilliformis* from Antarctica. We believe one of the two to be a young *Urospora wormskioldii*. *Urospora penicilliformis* was reported from The Netherlands in 1920 by VAN GOOR and was placed in the Ulotrichaceae. PRINTZ (1926, 1932) agreed with ROSENVINGE (1893) and continued to use the name *U. mirabilis* instead of *U. penicilliformis* and placed the genus in the Cladophoraceae.

In 1933 JORDE brought the two genera *Codiolum* Braun (1855) and *Urospora* Areschoug (1866) together. She found that *Codiolum gregarium* belonged to the life-history of *Urospora mirabilis*, thereby demonstrating the occurrence of a heteromorphic life-history in *Urospora*. The genus *Codiolum* comprises small free living, unicellular plants with a basal stalk and a parietal chloroplast containing several pyrenoids. Reproduction is by means of quadriflagellate zoospores. Jorde's observations on the life history of *Urospora* will be more comprehensively described later in this paper. Even after her findings were reported, the genus was frequently described in algal floras without reference to the *Codiolum*-sporophyte (LUND 1934, HOCKE HOOGENBOOM 1937, SMITH 1944, TAYLOR 1957). These authors placed the genus in the Cladophoraceae. Despite this, it appeared that the difficulties with the taxonomy of these algae might be resolved with the possibility to add information about the life cycle to the species

descriptions. For example, from her life cycle experiments, Jorde concluded that *U. elongata* was not a distinct species but merely a form of *U. mirabilis*. Similar one-celled *Codiolum*-like sporophytes have since been reported from life histories of *Ulothrix* (KORNMANN 1963, 1964a; LOKHORST 1974, 1978), *Spongomorpha* (HOLLENBERG 1957, 1958; FAN 1959; JÓNSSON 1959b, 1962; KORNMANN 1961a), *Acrosiphonia* (JÓNSSON 1959a, 1962, 1963, 1964a, b), *Monostroma* and *Gomontia* (KORNMANN 1962, 1963, 1964b) and *Cladophora* (ARCHER & BURROWS 1960, VAN DEN HOEK 1963). JÓNSSON (1959b, 1962) created the Acrosiphoniaceae to include *Urospora*, *Spongomorpha* and *Acrosiphonia*. Members of this family had a common life history with filamentous gametophytes, biflagellate iso- and anisogametes and uninucleate unicellular sporophytes with quadriflagellate zoospores. The genus *Cladophora* which resembles the growth habit of *Spongomorpha* and *Acrosiphonia* was excluded from this family, probably because this genus possesses different cell wall chemicals (NICOLAI & PRESTON 1952, 1959). On the other hand, KORNMANN (1963) rejected the Acrosiphoniaceae sensu Jónsson and redefined the old order, Ulotrichales, to include *Ulothrix*, *Urospora*, *Monostroma*, and *Gomontia* but to exclude *Spongomorpha* and *Acrosiphonia*.

SILVA (1957) relied entirely on the priority rule in the nomenclature code to make the new combination *Codiolum penicilliforme*. DEN HARTOG followed this lead in 1959, and recombined *U. wormskioldii* to *Codiolum wormskioldii* and *U. hartzii* to *Codiolum hartzii*. The dimorphic life history prompted Den Hartog to create a new family, the Codiolaceae, for the genus *Codiolum*.

KORNMANN has written several papers on his studies of *Urospora* at Heligoland. In each paper, a different relationship between *Codiolum* and *Urospora* forms is described. In 1961 (b, c), he contended that *C. gregarium* fits into the life history of *U. wormskioldii*, which is asexual and has a temperature dependent development into either dwarf plants or filaments. In 1966 (b), he introduced the generic name *Hormiscia* for those species which show an anisogamous sexual reproduction and which are filamentous when cultivated at either 15° or 5°C. The name *Urospora* was applied to species that are without gametes and are filamentous at low temperatures but form dwarf plants at 15°C. He erected the new species *Hormiscia neglecta* and at this time listed *C. gregarium* as its sporophyte. In 1977, KORNMANN & SAHLING retained the species reported in KORNMANN's earlier paper (1966b). *Hormiscia neglecta* and *H. penicilliformis* (KORNMANN 1966b) were reported to have identical life histories but to differ in the development of the basal holdfast, the size of the gametes, and the shape of the *Codiolum*-sporophytes.

HANIC (1965) studied the life history of several British Columbian forms of *Urospora* and *Codiolum* in culture. He concluded his study by recognizing five species. In his culture, *U. wormskioldii* did reproduce sexually, which is in contrast with the earlier findings (KORNMANN, 1961c). Hanic was not completely convinced of the separate status of *U. penicilliformis* since he had never observed sexual plants in nature. NAGATA (1971) studied the life history of *U. mirabilis*. Whether he used *U. penicilliformis* or *U. neglecta* is not entirely clear.

In 1973, KORNMANN gave the *Codiolum* form the central role by creating the

new class, the Codiolophyceae. In this way, the Chlorophyta were divided into the Zygnemaphyceae, Oedogoniophyceae, Bryopsidophyceae, Chlorophyceae and Codiolophyceae. Although the gametophyte stages of the members differ greatly, all Codiolophyceans have a heteromorphic life history with a one-celled sporophyte. The early differentiation of the germinating zygote into the basal disk, stalk and club of the sporophyte is similar in all four orders: Ulotrichales (unbranched filaments with a parietal band-shaped chloroplast), Monostromatales (plate-like thallus), Codiolales (unbranched filaments with reticulate chloroplast, zoospores pointed posteriorly) and Acrosiphoniales (branched filaments with apical growth). All members of the class are also what Kornmann termed eclipsiophytes with gametophyte development in the spring and sporophyte maturity in the winter. To the characteristics of a heteromorphic life history and anisogamy which DEN HARTOG (1959) gave for the Codiolaceae, Kornmann added intercalary growth and the peculiar nuclear behaviour at division. Studies on *U. wormskioldii* and *U. penicilliformis* have shown that at cell division, only some of the nuclei line up in the equatorial plane. The rest are scattered throughout the cell. All nuclei divide synchronously with cell division. In order for the number of nuclei to remain constant, mitosis without cell division occurs (KORNMANN 1966a, 1970).

In 1974, STEWART still classified *Codiolum* in the Chlorococcales and *Urospora* in the Acrosiphoniales. By 1976, PARKE & DIXON had removed *Codiolum* from their list of British algae and placed *U. wormskioldii*, *U. penicilliformis* and *U. bangioides* in the Ulotrichaceae (Ulotrichales).

Recently, VAN DEN HOEK (1978) classified *Urospora* in the Acrosiphoniales, based on the growth habit, the shape of the chloroplast, the presence of a *Codiolum*-hypnozygote in the haplont life history and the possession of cellulose II in contrast to cellulose I fibrils.

Most recently, BERGER-PERROT (1980) discovered new species of Chlorophyceae on the Brittany coast in France having characteristics of both *Ulothrix* and *Urospora*. She attributed the species to *Urospora*. By this choice, the species were tentatively classified in the Acrosiphoniales.

3. MATERIAL AND METHODS

Samples of the species were scraped off hard substrates such as stones and wooden pilings in the middle-upper eulittoral or in the splash zone. In some cases, bits of stone were chipped off for further inspection in the laboratory. Collections were made in a large number of brackish water and marine areas along the Dutch coast, the West German coast (Kieler Bucht and Deutsche Bucht), the western coast of Jylland (Denmark) and in the vicinity of Drøbak, Larvik and Bergen in Norway. Several localities in The Netherlands were inspected regularly over a two year period.

Clean filaments or pieces of filaments from these samples were brought into sterile glass petri dishes containing nutrient-enriched sea water ($16‰$ Cl^-, after PROVASOLI 1968). The temperature and photoperiod could be varied and care-

fully controlled. SD indicates short day conditions (8h light, 16 h dark) and LD indicates long day conditions (16 h light, 8 h dark). Techniques used for the isolation of the algae brought into unialgal cultures, the maintenance of stock cultures, the observation of the development of zoospores, germlings and sporophytic stages and the use of diurnal photoperiods have been described earlier (LOKHORST & VROMAN 1972, 1974; LOKHORST 1978). In order to better observe gametes, gamete-producing filaments from the field were kept at 4°C at the laboratory. Filaments were transferred to a slide and were directly placed on the microscope stage. The produced warmth or the relatively high light intensity usually caused the release of the gametes if they were present. After several weeks at 8°C/SD, the growth in the dishes was inspected. From these cultures, forms were chosen which most closely fit species descriptions from the literature. These cultures served as starting material for further investigations.

Selected uni-algal cultures of *U. penicilliformis* and *U. neglecta* were tested under a series of 27 different culture conditions, which are summarized in *table 1*. In general, the reasoning behind the selection of the experimental conditions was, on the one hand, to create in culture the conditions which, in nature, might

Table 1. Experimental conditions.

1. Temperature and day length variation: 4°C/SD, 8°C/LD, 8°C/SD, 12°C/LD, 16°C/LD, 20°C/LD.
2. Temperature and day length shifts: 12°C/LD to 4°C/SD and 4°C/SD to 12°C/LD.
3. Temperature shock: 8°C/LD to 3 × 4 h/day 4°C; and 3 × 4 h/day 16°C.
4. Salinity variation: 2, 8 and 16‰ Cl^-, 8°C/SD and 2, 8 and 16‰ Cl^-, 8°C/LD.
5. Shift in salinity: 2‰ to 16‰ Cl^-, 8°C/SD and 8°C/LD; 8‰ to 16‰ Cl^-, 8°C/SD and LD.
6. Aeration: +/− 8°, C/SD; +/− 8°, C/LD.
7. Shift in aeration: + to −, 8°C/SD and LD; − to +, 8°C/SD and LD.
8. Tide simulating machine.
9. Growth on agar plates: 8°C/LD, 8°C/SD, +/− medium layer.
10. Nitrogen and phosphate deficiencies in culture medium: Synthetic sea water, sea water +/− Provasoli's enriched sea water (Prov.); 12°C/LD, 8°C/SD and 8°C/LD.
11. Shift in medium: Synthetic sea water to Prov., Prov. to synth. sea water; sea water − Prov. to + Prov., 12°C/LD, 8°C/SD and 8°C/LD.
12. Medium exhaustion.
13. Desiccation I: 8°C/SD to 5 days dry at 20°C/LD, return to 8°C/SD.
14. Desiccation II: 8°C/LD to 1 × 4 h dry at 16°, return to 8°C/LD.
15. Desiccation III: 8°C/SD to 5 × 4 h/dry at 16°, return to 8°C/SD.
16. Freezing: 8°C/SD to 1 × 4 h/day in freezer, return to 8°C/SD.
17. Light regime I: Extra short day 6/18, 12°C.
18. Light regime II: 8 days 6/18, shift to 14/10, 12°C.
19. Light regime III: Continuous light, 12°C.
20. Light regime IV: 4 cycles continuous light, shift to 14/10, 12°C.
21. Light regime V: 4 cycles continuous light, shift to 8 cycles 14/10, return to continuous light, 12°C.
22. Light regime VI: Dark for one cycle.
23. Light regime VII: Dark/light shocks: 8°C/LD to 3 × 4 h/day dark or high light intensity, return to 8°C/LD.
24. Variation in light intensity: 8°C/LD.
25. Light quality I: UV shock: 3 × 1 h/day UV irradiation, 12°C/LD.
26. Light quality II: Red/blue light shock: 4 × 3 h/day red/blue light, 12°C/LD.
27. Light quality III: Red/blue continuous light, 12°C/LD.

induce sexuality. In many cases, this involved exposure of the algae to shocks or shifts in an environmental parameter. Those conditions reported to induce sexuality in other algae (COLEMAN 1962; DRING 1974) were also tested. On the other hand, ranges of various environmental parameters were used to test the variability of the vegetative characteristics of these species. Medium was periodically refreshed except where stated otherwise.

Duplicate or triplet cultures of each of the collected forms were used in each experiment. Cultures were checked weekly for evidence of sexual reproduction and the general habit of the filaments was observed. Both algae growing at the bottom of the culture vessel and that growing at the air-water-glass interface were checked. HANIC (1965) had reported a concentration of *Codiolum*-forms at the latter site.

Various methods were tested for preparing *Urospora* for ultrastructural studies. Vegetative cells in filaments, the *Codiolum*-form and released zoospores and those still inside the mother cell were studied. Filaments were prepared during stages of active growth so that accumulation of starch in the chloroplasts was at a minimum. In some cases, filaments present in fresh collections from natural environments were used. The techniques for the preparation of filaments for electron microscopy have been described previously (LOKHORST 1978). Released zoospores were isolated using a capillary and were fixed for about two hours in a solution of 1% glutaraldehyde in 0.1 M cacodylate buffer. The osmolality of the fixing solution was adjusted to approximately that of sea water with the addition of 0.7 M NaCl. The cells were then centrifuged and were embedded in 2% agar. Then they were washed for ten minutes in 0.1 M cacodylate buffer with stepwise decreases in osmolality by adding 3.5%, 2.6%, 1.9%, 0.7% and then, 0% NaCl. The pH of each buffer was 7.5. The zoospores were postfixed in 1% OsO_4 in 0.1 M cacodylate buffer for one hour at 4°C. After washing in distilled water for 15 minutes, they were dehydrated in a graded series of ethanol and embedded in Epon. Polymerisation lasted 48 h at 60°C. Sections were cut with a LKB Optical Ultramicrotome and were in some cases poststained with uranyl acetate and lead citrate. Preparations were viewed with a Philips EM-300 electron microscope.

In order to quantify the colour difference between *U. penicilliformis* and *U. neglecta*, the absorption spectra of these two algae was measured. Details on this method used and the obtained results will be presented in the section on morphology, reproduction and life-history of *Urospora neglecta*.

Herbaria, from which specimens were examined are listed below. Abbreviations are according to the Index Herbariorum (HOLMGREN & KEUKEN 1974). BG – Universitetets Botaniske Museum, Bergen; C – Botanical Museum and Herbarium, Copenhagen; TCD – School of Botany, Trinity College, Dublin; E – Royal Botanic Garden, Edinburgh; GB – Botanical Museum, Göteborg; HBG – Institut für Allgemeine Botanik, Hamburg; KIEL – Botanisches Institut der Universität, Kiel; L – Rijksherbarium, Leiden; BM – British Museum (Natural History), London; LD – Botanical Museum, Lund; O – Botanical Museum, Oslo; PC – Muséum National d'Histoire Naturelle, Laboratoire de Crypto-

gamie, Paris; S – Section for Botany, Swedish Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm; UPSV – Växtbiologiska Institutionen, Uppsala Universitat, Uppsala. Some herbarium specimens from the private collection of Dr. Kornmann were studied and are identified as HELGOLAND. The herbarium specimens were treated with a synthetic detergent before microscopical observation (LOKHORST 1978).

4. KEY TO THE SPECIES

1a. Mature filaments with a basal holdfast consisting of only one rhizoid from the most basal cell (in culture commonly 1–2 rhizoids observable as a result of rhizoidal development of the vegetative cell lying above the basal cell in the filament) . . . . . 4. *Urospora neglecta* (Kornmann) comb. nov.

b. Mature filaments with a basal holdfast consisting of, in addition to the rhizoid arising from the most basal cell, several (long) extramatrical rhizoidal outgrowths descending from cells above the basal cell towards the base of the filament 2

2a. Mature cells in the filaments distinctly barrel-shaped or spherical with constricted transverse cell walls. Diameter of the vegetative cells (9–) 18–1510 (–1900) μm . . . . . 1. *Urospora wormskioldii* (Mertens in Hornemann) Rosenvinge

b. Mature cells in the filaments principally cylindrical and at most with rounded ends. Diameter of the vegetative cells less than 180 μm 3

3a. Diameter of vegetative cells in the filaments (6–) 14–130 (–180) μm, zoospores relatively slender, 15–25 (–29) μm by 5–9 μm. Mature zoosporangia usually dark olive-green. Cells in broad filaments frequently ± square or longer than wide. . . 2. *Urospora bangioides* (Harvey) Holmes and Batters

b. Diameter of vegetative cells in the filaments (4–) 9–90 (–101) μm, zoospores relatively robust, 18–36 μm by 5–11 μm. Mature zoosporangia green to dark green. Cells in broad filaments frequently flattened. . . . . 3. *Urospora penicilliformis* (Roth) Areschoug

1. *Urospora wormskioldii* (Mertens in Hornemann) Rosenvinge – *Figs. 3–4; Plates 1–2.*

Conferva wormskioldii Mertens in HORNEMANN (1816) Tab. 1547; AGARDH (1817) 85; LYNGBYE (1819) 158; AGARDH (1824) 121. – *Hormiscia wormskjoldii* (Mertens in Hornemann) FRIES (1835) 328; HAZEN (1902) 147. – *Hormotrichum wormskioldii* (Mertens in Hornemann) KÜTZING (1845) 205; KÜTZING (1849) 383; KÜTZING (1853) 21, Tab. 66, fig. II. – *Chaetomorpha wormskioldii* (Mertens in Hornemann) KJELLMAN (1883) 384; DE-TONI (1889) 277. – *Urospora wormskioldii* (Mertens in Hornemann) ROSENVINGE (1892) 57; (1893) 920; (1898) 106; BØRGESEN (1902) 502; JÓNSSON (1903) 364; HAGEM (1908) 296; HYLMÖ (1916) 38; PRINTZ (1926) 253; LAKOWITZ (1929) 170; HAMEL (1930) 126; LEVRING (1940) 10; KYLIN (1949) 47; SUNDENE (1953) 145;? FELDMANN (1954) 18; STARMACH (1972) 223; VON WACHENFELDT (1975) 256; KORNMANN & SAHLING (1977) 22; RUENESS (1977) 233. – *Codiolum wormskioldii* (Mertens in Hornemann) DEN HARTOG (1959) 111. – Lectotype: Greenland, Godthaab, as *Conferva ovalis*, Wormskiold (C), isotype in the Agardh herbarium (LD) No. 7431 and in the Areschoug herbarium (S).

Codiolum wormskioldii (Mertens in Hornemann) Den Hartog var. *biflagellatum* KORNMANN (1961c) 42. – *Urospora wormskioldii* (Mertens in Hornemann) Rosenvinge var. *biflagellatum* (Kornmann) KORNMANN (1963) 64 – *Codiolum wormskioldii* (Mertens in Hornemann) Den Hartog var. *caudatum* KORNMANN (1961c) 44. – *Urospora wormskioldii* (Mertens in Hornemann) Rosenvinge var. *biflagellatum* (Kornmann) KORNMANN (1963) 64. Type not seen.

Conferva collabens auct. non Agardh: KÜTZING (1845) 205, pro. syn. – *Hormotrichum collabens* KÜTZING (1849) 383; (1853) Tab. 66, fig. 1.

Urospora incrassata KJELLMAN (1897) 7. Type not seen, but drawings are evident, Figs. 6–13.

Urospora claviculata KJELLMAN (1906) 4. Type not seen, but drawings are evident, Tab. 3, Figs. 1–3.

Urospora grandis KYLIN (1907) 18. – Lectotype: Sweden, Bohuslän, Kristineberg (Stångholmen), 7/4/1906, Kylin (S, holo; UPSV).

Marine filamentous plants, up to 11 cm long, green to dark green. Thalli rather stiff and glossy. Filaments solitary or gregarious, often tuft-like, at times forming rope-like bundles, straight when young, later more bent and sometimes irregularly whirled, uni-seriate and unbranched. Sometimes with bulges. Cell wall usually firm and thin, with increasing age sometimes soon (slightly) thickened and sometimes somewhat lamellated and rough, occasionally studded with fouling organisms and/or with micro-particles. Transverse cell walls often alternately tunicated with a continuous ring, clothed with an adhesive layer in which micro-particles and bacteria may anchor.

Cells when young usually cylindrical, their polar ends closely appressed to one another, soon becoming slightly swollen or distinctly barrel-shaped or spherical with constricted transverse cell walls, apical cells always cylindrical. Cell diameter 18–360 μm (in culture), up to 1510(–1900) μm (in nature), height 9–450 μm. Young filaments, in which zoosporogenesis rarely occurs, 9–18 μm wide. Cell width and cell height usually gradually diminishing towards the apex of the filament.

Chloroplast parietal and varying in shape with age and environmental conditions. In young cells, always a pronounced open continuous girdle, lobed to unlobed along its longitudinal margin, occasionally delicately constricted, usually covering about 3/4 of the cell circumference; not always approaching cell length. In mature cells, the chloroplast reticulate and clothing the entire inner cell wall, the cross wall inclusive; usually finely reticulate with small perforations, in the basal and more distal cells often more coarsely perforated. Sometimes throughout the filament the chloroplast only forming delicate connected strands with large perforations between them, infrequently containing assimilates and oil-droplets. Occasionally cells with a chloroplast consisting of unconnected bands arranged in a helical or parallel fashion. In aged cells, sometimes withdrawn to the middle of the cell lumen, forming an almost continuous, dark green belt. Upon disintegration, distorted by storage products, which are also abundantly present in the cell lumen.

In germlings, cells with one nucleus, soon becoming multinucleate. Pyrenoids 1–2(–3) in cells of germlings, in mature cells up to several hundreds, almost globose, sometimes slightly compressed or slightly tapering towards one end, 2–6 μm in diameter, not always distinct by a coarse development of starch.

Basal cell in germlings generally differentiated into a simple conspicuously

lengthened rhizoidal cell, up to 160 μm long, slightly dilated at irregular intervals and usually narrowing towards its distal end, incidently terminating inflated. Mature basal cells lengthened up to 690 μm, rarely ending in a point but usually blunted, cell wall showing an increase apically, relative short basal cell sometimes terminating with proliferations.

Cells above the basal cells, up to 4–42, developing rhizoidal outgrowths, sometimes sparsely branched, often showing (widened) ends with short divaricate runners, serving for a firm grip on the substratum. Cells with protruding rhizoidal outgrowths smaller and containing chloroplastic material less developed than other cells in filament.

Chloroplast in germling rhizoidal cells an open band, usually completely occupying the cell length, upon lengthening of the basal cell extending in the cell length axis and producing more pyrenoids; in mature rhizoidal cells the chloroplast becoming broken up into large pieces, which withdraw in aged cells and sometimes disappear.

Apical cell usually rounded, exceptionally capped, upon contacting hard substrates producing a gelatinous layer, clothing the upper part of the apical cell. Asexual reproduction in the filaments by zoospores and aplanospores, initiated in all ordinary cells, including the apical cells, but not in differentiated basal cells and usually not in those from which secondary projections protrude. Generally, first occurrence of zoosporogenesis in the upper part of the filament progressing into the basal part. Mature *zoosporangia* light to dark (olive) green, cylindrical to inflated, in culture 9–360 μm wide, 22–569 μm long, in nature to about 1.5 mm in diameter. The cell length/width ratio of especially the smaller zoosporangia often markedly greater than in vegetative cells with comparable cell width.

Zoospores usually arranged parallel to the surface of the cell, in long cells often in star-shaped clusters. Zoosporangia not always completely filled, then in smaller cells zoospores only present along one inner side of the longitudinal cell wall, in larger cells zoospores arranged in connected bands or strands, enclosing large vacuolar lumina. Zoospores usually released in a stream through a single (two), sometimes protruding discharge pore(s), formed by gelatinization of the wall, randomly located. Zoospores (4–)8– hundreds per cell, (23–) 25–37 μm by (5–)9–11 (–14) μm, quadriflagellate, usually pyriform-obovoid, usually extending into a thin long projection below, sometimes short and generally tapering, a flattened papilla occupying the zoospore apex. In cross-section, quadrate with four ridges, extending from the points of insertion up to the posterior end. Chloroplast parietal, cup-shaped, sometimes with anterior projections, with 1–2 pyrenoids embedded in the posterior part. Uninucleate and with anteriorly-positioned vacuolar droplets.

Zoospores non-phototactic, locomotion slow, but usually rapidly vibrating, prior to settlement quadrate and ultimately becoming globose, followed by abscission of the flagella. Germination of the zoospore bipolar, beginning with enlargement, followed by repeated partioning of the cells, ultimately leading to filaments several cms long.

Aplanospores, up to hundreds per cell, often in slightly inflated sporangial

cells. Aplanospores spherical, 8–16 μm, able to germinate in the parent cell.

Occasionally, development of the zoospore into dwarf plants. In that case, germination of the attached zoospore various, either by bipolar cell division, giving rise to a 2–6-celled filament with a differentiated basal cell, later on in the upper cells mainly cell division in random planes, leading to the formation of irregular multiseriate filaments, sometimes pseudoparenchymatic dwarf plants, or frequently the zoospore upon germination after one cell division, the daughter cells independently developing uniseriate filaments with rhizoidal basal cells (twin-filaments), later in the upper cells sometimes cell division in several directions occurring, or the attached zoospore upon germination promptly dividing in random planes leading to the formation of compact dwarf plants with one to several rhizoidal basal cells. Chloroplast of dwarf plants, parietal, continuous, band-shaped, with lobed and unlobed margins, clothing the cross and longitudinal cell wall, later on becoming finely-reticulate. Filamentous dwarf plants up to 540 μm long, pseudoparenchymatic dwarf plants up to 390 μm in diameter. Asexual reproduction in dwarf plants by zoospores and aplanospores, often restricted to the upper inflated cells, up to 57 μm in cell diameter. Upon ripening, sporangial cell wall smooth-rough, in older plants brownish. Quadriflagellate zoospores 8–16 per cell, sometimes about the same cell dimensions as zoospores initiated in filaments, but zoospores usually smaller in size, 10–13 μm by 2–4 μm. Zoospores and aplanospores from dwarf plants germinating to give rise to dwarf plants.

In nature, *sporophytes* (*Codiolum*-plants) forming dense, dull, (dark-)green velvety-like cushions, up to 1.24 mm in height. The stipe of the individual plant up to 0.97 mm long and up to 27 μm wide, hyaline, in a young stage smooth, later on becoming rough, wall often undulating and grooved, in the apical part the incisions conspicuous, giving the impression that the stalk is constructed of joined rings. Basal end often nodded and inflated or terminating in a flattened end. Transition between the clava and the stipe abrupt to gradual. When gradual, the inner cell wall of the clava forming a saccate fold towards the apical part of the stalk. Clava mostly (more or less) (sub-)cylindrical, sometimes narrowing in the middle, sometimes more or less oblong to obovoid to ovoid. Cell wall usually smooth and relatively thin. Chloroplast parietal, often dense granular, rarely reticulate and vacuolate, containing several pyrenoids and many (up to 95) in larger cells. Clava up to 270 mm long, up to 72 μm wide. Zoospores up to hundreds in the sporophyte, (16–) 20–30 μm by (5–) 7–11 μm, identical in morphology, in behaviour, in mode of attachment, and in germination to those from filaments. Initiation of growth of aplanospores mostly inside the sporophyte cell wall.

ICELAND. Brimnes, Jónsson, 1/6/1898, ex Plantae islandicae 41 (C); Borgarnes, Jónsson, 13/6/1898, ex Plantae islandicae 103 (C); Hvalfjördur, Jensen, 9/5/1890, (C); Reykjavik, Jónsson, 31/3/1897, ex Plantae islandicae 31 (LD); Akurey, Jónsson, 17/4/1897 (C); Vestmannaeyjar, as *Urospora hartzii*, Jónsson, 21/5/1897, ex Plantae islandicae 382 (C).

DENMARK. Greenland. Merkuitsok (Skinderhvalen), Rosenvinge, 25/5/1888, ex Plantae Groenlandicae 515 (C); Holsteinborg, as *Conferva wormskioldii*, 5/1832 (C); Godthaab, Vahl, 5/1831 (C, S,

O, UPSV); Lassen, 5/1890 (C); sine loco in Greenland, as *Conferva wormskjoldii*, Hornemann (O); as *Conferva wormskioldii*, ex herb. Møreh (C); as *Conferva monile*, Wormskiold (C); as *Conferva wormskjoldii*, ex herb. Drejer (C); as *Conferva wormskjoldii*, Rosenvinge 3/1902, ex herb. Schübeler (O). Faerøerne, Thorshavn, mixed with *Urospora penicilliformis*, Børgesen 927, 24/4/1898, ex Algae Marinae Faeroensis (O).

U.S.S.R. Murmansk, Afanas'jeva, 14/4/1964 (L).

NORWAY. Spitsbergen, Magdalene Bay, Vahl, ex herb. Schübeler (O); Drøbak, near Biological Station, Hagem, 1/4/1907 (BG, O, S); as *Urospora wormskjoldii*, Wille, 1/4/1912, ex Kryptogamae exsiccatae 2149 (LD, S, UPSV); as *Urospora elongata*, Hylmö, 14/4/1912 (LD, S, UPSV); Sjöstedt, 11/4/1917 (LD).

SWEDEN. Varberg, Hylmö, 31/1/1913 (O, UPSV); Lillesand, as *Conferva bangioides*, 4/1846, ex herb. Schübeler (O).

GERMANY. Norderney, as *Hormotrichum younganum*, ex herb. Kützing (L sheet 939.67-711); Nordsee, as *Hormotrichum collabens*, ex herb. Kützing (L sheet 939.26-274).

GREAT BRITAIN. Cumbrae, as *Urospora collabens*, Robertson, 5/1894, ex Holmes, Algae Britannicae Rariores Exsiccatae Fasc. VII 174 (KIEL, TCD).

Nomenclature and historical aspects

Mertens' original description was merely: "filis precatoriis" (filaments forming garland of roses). The filaments were found at Godthaab in Greenland. Interestingly enough, there already existed a name for this species, namely *C. ovalis*, which had been proposed by Wormskiold himself. This name is not legitimate because it is found in Wormskiold's handwriting on the label of herbarium specimen no. 7431 in the Agardh herbarium. Also handwritten is an accompanying species description, separetely labelled as no. 7427, describing the macroscopic thallus structure, the cell form, the colour of the plants and the basis of the filaments. Wormskiold also reported how this species differs from *Conferva melagonia* in filament length, cell wall structure and the transparency of the cell contents. Wormskiold's text was essentially adopted by AGARDH (1817) and LYNGBYE (1819) for the name *Conferva (= Urospora) wormskioldii*. The common names in Greenland for this algae, "sapangaursak" and "uncrassib sarpangei" are also reported. The latter name was also reported by Wormskiold next to the name *C. ovalis* on the afore-mentioned herbarium label. It is still a puzzle why, in the original species description of *Urospora wormskioldii*, Mertens did not use the available data from Wormskiold's description of *C. ovalis*. In a biography of Wormskiold by WARMING (1890), the botanical journal of his visit to Greenland in 1813 was cited. There he reported that on May 1, 1813, *C. ovalis* was collected from the beach. However, "30 april" is written on the herbarium label. Wormskiold apparently had some difficulty with the choice of a name for this alga. This is evident from the fact that he gives collections of *U. wormskioldii* the just as unacceptable name of *Conferva monile*. This name refers to the barrel-shape of the cells in the filaments which is observable with the naked eye. Wormskiold's specimen, marked "*Conferva ovalis*, Godthaab", preserved in C (isotype in LD and S), is hereby designated the lectotype. Its general habit and the anchored diatoms on its surface fit well with Mertens' drawings in HORNEMANN (1816). No zoosporangia were drawn in these illustrations. However, these reproductive cells could be detected in the lectotype specimen.

During the nineteenth century, the systematic position of the species changed frequently, due to the uncertain taxonomy of various green algae genera. Authors disagreed on whether this alga was branched or not. LYNGBYE (1819), for example, placed this alga with *Conferva* (= *Cladophora*) *rupestris* in the group of branched marine algae because of what he thought were branched basal portions on the filaments. It is understandable that a lack of knowledge about the ontogeny of the rhizoidal holdfast on the filaments could lead to this misinterpretation. In 1883 and in 1889, KJELLMAN and DE-TONI, respectively, placed this species in the genus *Chaetomorpha* probably because of the inflated cells. Shortly thereafter, in 1892 and 1893, ROSENVINGE corrected this error. He was the first to describe the zoospores and placed the species in the genus *Urospora* because of their shape. He also stated that because of the structure of the cell wall and the extremely developed holdfast, this species should not be placed in the *Chaetomorpha*. Even so, in a few herbaria, *U. wormskioldii* specimens are still stored under the genus name *Chaetomorpha*. The large cell diameter variation and the presence of characteristically swollen cells sets this species apart from the other three *Urospora* species discussed here. This fact caused Mertens to consider creating a new genus for this species (in HORNEMANN 1837).

In the 19th century, there were no reports of collections of this species outside of Greenland and Iceland. This is probably because the name *Hormotrichum collabens* was in use for this alga in the rest of Western Europe. An example of this alga is in the Kützing herbarium (L sheet 939.26-274). Illustrations of *Hormotrichum collabens* in KÜTZING's Tab. Phycol. 66, fig. 1 (1853) actually depict young *Urospora wormskioldii* filaments. However, the lectotype of *Conferva collabens*, found in the Agardh herbarium (LD, no. 7423 and 7424), partially consisting of original material of Dillwyn's *Conferva aerea* (Yarmouth, april 1808), appears to belong to the genus *Chaetomorpha*.

Species have been described from North America which strongly resemble *U. wormskioldii*. These are, for example, *Hormiscia* (= *Urospora*) *tetraciliata* Frye and Zeller (1915) and *Hormiscia vancouveriana* (Tilden) Setchell and Gardner (1920). In our opinion, based on herbarium studies (the isotype of *H. tetraciliata* is in UPSV) and the degree of cell diameter variation, is that the last mentioned species should be included in the *Urospora wormskioldii* complex. It was not possible to give a definite judgment on the existence of the closely related *Urospora vancouveriana*. HANIC (1965) found this species to be very similar to Kornmann's *U. wormskioldii* var. *biflagellatum* (1961c) described from Heligoland. This similarity extended to the temperature requirements for the production of the biflagellate zoospores. Hanic (l.c.) reported that the main difference in the two species was in the fertile zoosporangia in dwarf plants which produce biflagellate zoospores. They are warty at the apex in *Urospora wormskioldii* var. *biflagellatum*, but smooth in *U. vancouveriana*. This characteristic is arbitrary. Zoosporangia in dwarf plants of *U. wormskioldii*, which produce quadriflagellate zoospores, had both warty and smooth apexes in this study.

Morphology, reproduction and life history

The life cycle of *Urospora wormskioldii*, as determined from our experiments and observations is as follows. Zoospores produced in *Codiolum*-plants can give rise to either dwarf plants or filaments. Zoospores produced by these dwarf plants give rise to dwarf plants again. Zoospores produced in filaments can give rise to either dwarf plants or filaments depending on culture conditions. The form which gives rise again to the *Codiolum*-form and where it is produced has not been established in culture.

To follow the life cycle, cultures were started from developing zoospores which had matured in *Codiolum*-plants collected in the field. The development of zoospores either into filaments or into dwarf plants could be correlated to environmental factors such as temperature and light regime. Under SD conditions at 4°C or 8°C, the majority of the zoospores formed filaments. At 12°C, both dwarf plants and filaments were found, while at 16°C, only dwarf plants developed from the zoospores. The proportion of dwarf plants formed at 8° and 12°C could be increased by lengthening the photoperiod.

The general habit of the filaments in culture was identical to that found in rehydrated herbarium specimens from the field. The cells in germlings are cylindrical; later they become inflated.

In culture, the cells in the filaments usually have smooth cell walls. In later growth phases, the cell walls sometimes become slightly rough. In the field, they appear to be somewhat sticky considering the number of microparticles and microorganisms which are found on the outer surface.

The cell dimensions of field material can vary greatly. This variation has led to misinterpretations in the past. *U. wormskioldii* plants with smaller dimensions were described under various names: *Urospora incrassata* Kjellman (cell diameter up to 135 μm), and *Urospora grandis* Kylin (cell diameter up to 200 μm). Material from Godthaab, Greenland, had cell diameters up to 1510(–1900) μm. Plants from Drøbak (Oslofjord) had cell diameters only as large as 518 μm. The maximum cell diameter observed by us in culture was 360 μm. Changing the photoperiod regime or the temperature did not affect the dimensions of the cells significantly. Germlings have relatively short cells, while adult plants have a higher length/width ratio.

The form of the chloroplast is related to the age of the filaments. At a young stage, the chloroplast forms an almost closed, parietal band. This band covers the whole longitudinal cell wall and sometimes also a portion of the transverse cell wall. In this growth stage, the chloroplast can become somewhat reticulate. The chloroplast in adult filaments is usually finely to coarsely reticulate. However, in some cases, the chloroplast is observed in strands running parallel to the cell wall. The pyrenoids are embedded in the strands at regular intervals similar to the arrangement found in the single chloroplast of the freshwater genus *Mougeotia*. The number of pyrenoids is correlated with the age of the cell. There are few (up to 3) in cells of young filaments, while there are hundreds in cells of mature filaments.

The germination of the zoospores which develop into filaments is bipolar. It

starts with enlargement and is soon followed by transverse cell division into two cells. The lower cell produces the rhizoid which can already be quite long in a 2- to 3-celled germling. With time, the cells above the most basal cell develop secondary projections for attachment. Many more cells are involved in the holdfast in culture than are in natural habitats. The characteristic divaricate end growths on the rhizoidal projections have not (yet) been observed in natural specimens. Often the transition between cells which do and those which do not form secondary rhizoid projections is abrupt. In the development of the outgrowths, the cell diameter does not significantly increase.

The *Codiolum*-phase in *U. wormskioldii's* life cycle could only be studied on plants from natural populations. The *Codiolum*-plants were found on hard substrates, often in exposed places and usually at the border between the high littoral and the supralittoral. There, they form dark green velvety mats, often about 0.5–1.0 mm thick and sometimes to a diameter of ± 15 cm. Zoospore formation starts usually within 7–14 days after bringing the *Codiolum*-plants into culture at 4°C and 8°C, SD. Sporophytes which were kept at these temperatures for four weeks produced only aplanospores.

There has been considerable discussion in the literature about the naming and the habit of this sporophyte. Probably JORDE (1933) studied the sporophyte of *U. wormskioldii* (there reported to be *Urospora mirabilis*) under the name *C. gregarium*. KORNMANN contended in 1961 that *Codiolum gregarium* fitted into the life history of *U. wormskioldii*. In 1966(b) his views had changed. He introduced the new sexual species, *Hormiscia* (*Urospora*) *neglecta*, for which he claimed *C. gregarium* as sporophyte. In 1977, KORNMANN and SAHLING reported that the sporophytic stage of *U. wormskioldii* could be distinguished from that of *U. neglecta* by the former's clavately-shaped club which shows an abrupt transition into the stipe. Their pictures show the *Codiolum*-phase of *Urospora neglecta* to have a gradual transition between its stipe and club. However, some earlier published photographs of the sporophytic stage of *U. neglecta* (KORNMANN 1966b) show a sharp transition between the stipe and the club. HANIC (1965) illustrates a sporophyte under the name *C. gregarium* which differs completely from that described by KORNMANN (1966b) under the same name.

In the past, there have been many species described in the genus *Codiolum*. Species characteristics used were the size of the plant, the form of the club and the ratio of the length of the club to the stipe. A summary of a selection of these species is given in *table 2*. Those species which most probably are a phase in the life cycle of a *Urospora* species are listed. Some of these forms could qua habitus also fit into the life cycle of, for example, *Monostroma undulatum* (KORNMANN 1962) or *Ulothrix implexa* (LOKHORST 1978).

Characteristics of *Codiolum*-plants which we studied from field populations are summarized in *table 3*. These *Codiolum*-plants all gave rise to zoospores in culture which developed into the filamentous phase of *U. wormskioldii*. The degree of variation in the form of this sporophyte is evident.

Attempts have been made in the past to separate the genus *Codiolum* into "species". That this approach is incorrect is shown by the following. Plants from

Table 2. Survey of the characteristics of *Codiolum*-species reported in literature.

Name	Total length of the plant up to	Shape of the club	Ratio of stipe to club	Transition between stipe and club
Codiolum pusilla (Lyngbye) Foslie. Lyngbye (1819) 79. Lectotype: Faerøerne, Qvalboë Suderöe, as Vaucheria pusilla, 12/7/1817 (C).	1.3 mm	cylindrical	stipe longer than club	gradual
Codiolum gregarium Braun (1855) 20. Lectotype: Heligoland, Braun, 8/1853 (L sheet 937.351-187)	1.5 mm	oblong	stipe 1.5–3 times longer than club	slightly abrupt, but usually gradual
Codiolum nordenskiöldianum Kjellman (1877) 56. Lectotype: Norway, Måsö, Kjellman, 13/8/1876 (L sheet 938.7-15)	0.6 mm	subcylindrical or elongate-obovate	stipe usually shorter than club	gradual
Codiolum longipes Foslie (1881) 11. Lectotype: Norway, Gjesvär, Foslie, 2/9/1880, ex Wittrock & Nordstedt, Algae exsiccatae 458 (L sheet 910.185-406)	1.2 mm	elongate-obovate	stipe 2–3 times longer than club	gradual
Codiolum cylindraceum f. major Foslie (1887) 189. Lectotype: Norway, Gjesvär, Foslie, 31/8/1880, ex Wittrock & Nordstedt, Algae exsiccatae 457 (L sheet 910.185-433)	2.7 mm	(sub-) cylindrical	stipe 1/3–2/3 times length club	gradual
Codiolum intermedium Foslie (1887) 193. Lectotype: Norway, Vardö, Foslie, 12/8/1887, ex Wittrock & Nordstedt, Algae exsiccatae 954 (L sheet 910.185-407)	0.6 mm	elongate-obovate, obovate or roundish	stipe usually longer than club	in case of globose club, abrupt
Codiolum brevipes Foslie (1890) 152. Lectotype: Norway, Vardö, Foslie, 12/8/1887, ex Wittrock & Nordstedt, Algae exsiccatae 955 (L sheet 938.7-3)	1 mm	subcylindrical, elongate-obovate	stipe usually shorter than club	gradual

populations collected at Glückstadthavn, Thyborøn, and West Terschelling could be determined to *Codiolum intermedium*, *C. gregarium* and *C. brevipes*, respectively, based on the literature information (Compare *tables 2* and *3*). All these plants gave rise to *U. wormskioldii* filaments. Environmental conditions appear to be determining factors for the form of the *Codiolum*-plants. For example, the plant is very developed in exposed sites such as those found at Thyborøn, Denmark.

Table 3. Survey of the characteristics of *Codiolum*-plants collected in various natural populations, all giving rise to *U. wormskioldii* filaments.

Locality	Total length of plant up to	Shape of the club	Ratio between length of stipe and club	Transition between the stipe and club
Thyborøn (Denmark)	1 mm (–1.24) mm	oblong	stipe 2–4 times longer than club	abrupt
Venø Sund (Denmark)	0.6 (–0.75) mm	subcylindrical-elongate-obovate-ovate	stipe usually longer than club	abrupt-gradual
Hvide Sande (Denmark)	0.63 mm	oblong-elongate-obovate	stipe 1–2 times longer than club	abrupt-gradual
Bogense (Denmark)	0.55 (–0.72) mm	subcylindrical-oblong	stipe 1–2 times longer than club	gradual
Glückstadthavn (Germany)	0.55 mm	(sub-) cylindrical-elongate-obovate	stipe 1–2 times longer than club	gradual
Kiel-Stohl (Germany)	0.72 (–0.98) mm	subcylindrical-elongate-obovate	stipe up to 2 times longer than club	gradual
West-Terschelling (The Netherlands)	0.4 mm	subcylindrical-obovate-ovate	stipe 1/3–1 times length of club	abrupt-gradual
Breezanddijk (The Netherlands)	0.5 (–0.6) mm	subcylindrical-elongate-obovate	stipe 1–2 times longer than club	abrupt-gradual

As stated previously, zoospores develop into dwarf plants at 12°C or above. The pattern of zoospore germination into dwarf plants, either via bipolar germlings, twin filaments or direct cell division in random planes, was independent of culture conditions. Why only some dwarf plants developed rhizoids could not be established. HANIC (1965) found plants without rhizoids only at high salt concentrations (at c. $50‰ Cl^-$).

KORNMANN (1961c) distinguished two different variations of *U. wormskioldii*, var. *biflagellatum* and var. *caudatum*. Dwarf plants of the former variety formed biflagellate oval swarmers at temperatures above 13°C. These swarmers developed predominantly into *Codiolum*-plants and into some dwarf plants. Mature dwarf plants of the var. *caudatum* produced quadriflagellate swarmers which developed at the same temperatures predominantly into dwarf plants and into only a few *Codiolum*-plants in the second or third generation. HANIC (1965) found sexual *U. wormskioldii*-filaments in cultures originating from the British Columbian coast. In his cultures, the *Codiolum*-form was produced from zygotes or parthenogenetically from female gametes. In all our cultures, dwarf plants of *U. wormskioldii* produced only quadriflagellate zoospores. These germinated and developed only into a new generation of dwarf plants. Zoospores produced in filaments germinate to give rise to another generation of filaments or dwarf plants.

We have not been able to observe any gametogenesis or any sexual process in the *U. wormskioldii* life cycle. The form which can give rise to the *Codiolum*-plant could not be established from our cultural experiments.

Origin of material in culture

Uni-algal cultures were started from plants collected in the following localities. DENMARK: Thyborøn, on boulders, exposed, in the splash zone; Hvide Sande, on an exposed jetty, around the boundary line of the littoral and supra-littoral zones; Limfjorden near Venø Sund, on a sheet-piling, near the waterlevel, in rather turbulent waters; Bogense, near the harbour, on wood and stones, around the waterlevel, fairly exposed. GERMANY: Glückstadthavn, on stones in heavily polluted water, growing together with blue-green algae crusts; Kiel-Stohl, near navy barracks, on the north side of a breakwater, on the vertical side of stones. THE NETHERLANDS: On the Wadden Island Terschelling, on a head of a jetty, in the mid-high littoral, growing together with *Urospora penicilliformis*, *Prasiola stipitata* and *Ulothrix flacca*; Breezanddijk, in the inner harbour, on basalt blocks in the high littoral.

2. *Urospora bangioides* (Harvey) Holmes & Batters – *Fig. 5, Plates 3–4.*

Conferva bangioides HARVEY (1841) 130; (1849) 210; (1851) Tab. 258; ARESCHOUG (1850) 204. – *Hormotrichum bangioides* (Harvey) KÜTZING (1849) 383; (1853) 20, Tab. 65, Fig. III; DE-TONI (1889) 233 (pro. syn.). – *Aplonema bangioides* (Harvey) HASSALL (1852) 224. – *Urospora bangioides* (Harvey) HOLMES & BATTERS (1891) 73; BATTERS (1902) 14; NEWTON (1931) 95; ? PARKE (1953) 500; ? KORNMANN (1961c) 44. – Lectotype: Great Britain, Plymouth, Blatch, 18/4/1833 (TCD, holo).

Urospora hartzii ROSENVINGE (1893) 922; (1898) 106; JÓNSSON (1903) 362. – *Codiolum hartzii* (Rosenvinge) DEN HARTOG (1959) 111. Lectotype: Greenland, Frederikshaab, Hartz, 9/7/1889 (C, holo).

Filamentous plants, mainly from marine waters, up to 8 cm long, mostly dark green. The upper, smaller cells often lighter green. Mature thalli relatively stiff and glossy upon moistening. Filaments solitary or regularly united in tufts or crowded and entangled to form dense patches; straight when young, later slightly undulating, strictly unbranched and uniseriate.

Cell wall firm and relatively thin, with increasing age often thickened and occasionally delicately rough, occasionally locally studded with mucilaginous droplets and/or microparticles and fouling organisms such as bacteria. Transverse cell walls frequently tunicated by H-shaped remnants of parent cell walls.

Cells cylindrical, at times slightly inflated with somewhat rounded ends. In young filaments, cells often arranged in pairs or in groups of several cells. Cell diameter 14–130 μm, in nature up to 180 μm, length 9–220 μm, predominantly isodiametric. In young filaments where zoosporogenesis rarely occurs, cells 6–14 μm wide. Cell width and length markedly diminishing towards apex of the filament.

Chloroplast parietal, variously shaped according to age and environmental conditions. In young cells, regularly shaped, usually extending over more than half of the cell circumference, lobed to unlobed along its margins. In long cells, not always extending over the whole length. In mature cells, the chloroplast becoming reticulate and covering the entire inner cell wall, the cross wall inclusive; under optimal conditions, fine to coarse reticulate with perforations of

varying size. In the smaller distal cells, often coarsely perforated. Under less favourable conditions, the chloroplast often finely granular with concomitantly fewer conspicuous pyrenoids and with (heavy) accumulation of assimilates, sometimes bleached and withdrawn into corner of cell or against both cross walls.

In germlings, cells with one nucleus, soon becoming multinucleate. *Pyrenoids* 1–2(–4) per cell in young plants and up to approximately 150 in mature cells, approximately globose or slightly compressed, or rarely ovoid, 3–7 μm in diameter, not always pronounced by a coarse development of the starch shell.

In germlings, the *basal cell* usually differentiated into a simple lengthened rhizoid, up to 176 μm long, sometimes hardly lengthened and for firm attachment with proliferations at its distal end, cell wall sometimes undulating or inflated at irregular intervals. Mature basal cells lengthened to up to 623 μm, usually with slightly swollen ends, exceptionally pointed and sometimes terminating with divaricate rhizoidal ends. The apex often with a locally thickened wall. Cell wall of the basal cell locally or continuously covered with a thin gelatinous layer.

Cells above the basal cells, 2–49, developing rhizoidal outgrowths, sometimes sparsely branched (1–3 times), sometimes terminating with a swollen end and showing (widened) ends with short divaricate runners, serving for a firm grip on the substratum.

Chloroplast in germling rhizoidal cells an open band; in nature chloroplast often becoming densely granular, often evenly filling the cell; cells sometimes clear with local concentrations of the chloroplast, chloroplast sometimes disappearing. Rarely formation of interstitial rhizoids.

Apical cells usually rounded, upon contacting hard substrates producing a gelatinous layer, covering the upper part of the apical cell.

Asexual reproduction in the filaments by zoospores and aplanospores, initiated in all ordinary vegetative cells, including the apical cell. Generally, first occurrence of reproductive activity in the upper part of the filament. Mature *zoosporangia* usually dark olive green, characteristically cylindrical, sometimes slightly inflated, 12–164 μm wide, 18–176 μm long. Cell length/width ratio of especially the smaller zoosporangia often markedly greater than in vegetative cells with comparable cell width.

Zoospores usually arranged parallel to the surface of the cell, occasionally in star-shaped clusters. Zoosporangia usually completely filled; if not, the zoospores present only along one inner side of the longitudinal and/or transverse cell wall of the zoosporangium. Zoospores usually slowly released in a stream through a single, sometimes slightly protruding discharge pore, formed by gelatinization of the cell wall, randomly located. Zoospores 4-hundreds per cell, 15–25 (–29) μm by 5–9 μm, quadriflagellate, usually pyriform – obovoid, extending into a thin tiny long projection below, relatively fast in locomotion, a flattened hyaline papilla occupying the zoospore apex. In cross-section, quadrate with four ridges, extending from the apical up to the posterior end. Chloroplast parietal, cup-shaped, sometimes with extending strands or seemingly completely clothing the

inner zoospore wall, with 1–(2) pyrenoids embedded close together in the posterior part. Uni-nucleate and possessing anteriorly-positioned vacuolar droplets.

Zoospores non-phototactic, exhibiting various movements after release from the zoosporangium, some of them making fast jerking movements over a short distance, sometimes alternated with (gyrating) movements tracing a small circle. Others, immediately after release, contacting the substrate with their apical pole and exhibiting violent jerking movements, caused by rapid vibrations over the whole length of the flagella. This trembling phenomenon is sometimes restricted to the flagellum furthest from the substrate. After some time, with trembling flagellar movements, some of the zoospores crawling. Prior to attachment, becoming quadrate and ultimately becoming globose, followed by concurrent abscission of the flagella. Subsequent germination of the zoospores bipolar, beginning with enlargement, followed by the differentiation of the original apical pole of the zoospore into the basal cell of the developing germling, later repeated division of the cells, leading to the formation of filaments several cms long.

Aplanospores, up to hundreds per cell, often in slightly rigid sporangial cells, spherical, 7–10 μm in diameter, able to germinate inside the parent cell wall.

Sexual reproduction through gametes could not be confirmed. Young sporophytic (*Codiolum*-) plants have only been found in nature, light green and tubiform, approximately 50 μm long. Chloroplast reticulate to stringy, containing one to three pyrenoids. In culture, mature plants relatively small, up to 150 μm long, club oval to ovoid, 2.2 times length of stipe. Zoospores with approximately the same dimensions as those found for zoospores produced in filaments.

Cells may form thick-walled akinetes.

SWEDEN. Kristineberg, as *Urospora incrassata*, Kylin, 11/4/1906 (UPSV); Mölle, as *Urospora wormskioldii*, Levring, 17/3/1934 (LD); Helsingborg, as *Conferva hormoides*, 7/1823, ex herb. Agardh 7367–7374 (LD).

THE NETHERLANDS. Den Helder, sea dike on stones, as *Urospora wormskioldii*, Den Hartog 2297, 23/4/1955 (L sheet 956.313–725); Vlissingen, on pontoon, as *Urospora wormskioldii*, Mulder, 16/4/1954 (L sheet 956.182–315).

GREAT BRITAIN. Torquay, as *Hormotrichum bangioides*, ex herb. Kützing (L sheet 939.67–708).

Nomenclature and historical aspects

HARVEY (1841) referred to material collected at three sites: Plymouth (leg. Blatch), Torquay (leg. Griffiths) and Port Ballantrae (leg. Moore). All three of these syntypes are still present in the Harvey herbarium in Dublin (TCD). The specimen marked "Breakwater, *Conferva bangioides*, ap/18/1833" is hereby designated the lectotype. Filaments of *Urospora penicilliformis* could also be detected in this type specimen. The other herbarium specimens contain primarily *Ulothrix speciosa* (Torquay) and what are probably young *Urospora wormskioldii* filaments.

Because of the meagre description this species was given, the understanding of it and its taxonomy have been difficult. It is still a puzzle why HASSALL (1852)

placed this marine species under the genus *Aplonema* in his freshwater flora. KÜTZING was the first, in 1849, to report more reliable cell dimensions for this species. KÜTZING's illustrations (1853, Tab. 65, fig. III) also give a more realistic representation of the characteristics of the species than did HARVEY's illustrations in Phycologia Britannica (1851, Tab. 258). The characteristically square profile of the cells is clearly evident in Kützing's illustrations. From Harvey's comments, it is obvious that no one was aware of the mode of reproduction at that time. He reported that, in an advanced stage of growth, the endochrome contracts and condenses into a dark coloured oblong spore, which remains in the center of the articulation. In our opinion, Harvey was describing the atrophication of the chloroplast of vegetative cells, a phenomenon which takes place under unfavourable growth conditions. HARVEY (1851) also described this alga as being rare. Initially, it was thought that this species was found only in Great Britain.

In 1891, the systematic place of this species in the genus *Urospora* was confirmed by HOLMES & BATTERS. They observed the characteristic tailed zoospores.

Until recently, the identity of this species has remained unclear. In 1961(c) for example, KORNMANN reported the presence of *U. bangioides* in Heligoland. In 1966(b) however, he asserted that *U. bangioides* was merely a growth variant of *U. penicilliformis*.

Morphology, reproduction and life history

The general characteristics of the individual plants of *U. bangioides* in nature are similar to those observed in culture. Clones were started in culture with developing zoospores. These had matured in filaments collected in the field. Under every culture condition used, the zoospores developed into filamentous germlings. Approximately two to three weeks after the dissemination of zoospores in cultures, simple germlings, each arisen from one zoospore, appeared at the glass bottom of the culture vessel. The plants quickly reached a length of c. 8 cm. The development of the zoospores was clearly slower at 4°C. The filaments became wound around each other in older cultures.

In aging filaments, the cell wall sometimes becomes slightly roughened and coated with adhering microparticles or studded with micro-organisms. The cell wall of older cells may become lamellated. Cells in the filaments are closely appressed to one another.

In two cases, fragmentation of the filaments could be observed. In one exceptional case, one cell became geniculate and swollen. At this point, the filament bent.

In some cases, only one filament of *U. bangioides* is found in well developed populations of *U. penicilliformis* or *U. neglecta*. This species is recognizable by its typical cell form, by the more intense green colour of its cells, and by the size of its cells (average cell diameter 90 to 120 μm).

The presence of isodiametric and long rectangular cells in fully mature filaments is characteristic for this species. This characteristic is most pronounced under laboratory conditions. In contrast, the cell length of *U. penicilliformis*, the

most closely related species, is shorter when the cell diameter increases.

Variation of the photoperiod or temperature did not significantly change the dimensions of the cells. However, the development of the cell diameter at 4°C was slower than at higher temperatures.

The morphology of the vegetative filament of *U. bangioides* changes in a medium of low salinity. Filaments grown in a medium containing only 2‰ Cl^- are broken in several places and contain cells which are inflated. Growth is irregular and secondary rhizoid formation is stimulated. At the same time, the frequency of zoosporogenesis decreases, the cell diameter is reduced and the chloroplast becomes stringy and lighter green in colour.

The diameter of the cells in filaments may vary in different natural populations. It appears that plants which grow in sites more exposed to wave action have a larger cell diameter than plants grown at calmer sites.

In addition to the characteristic cell form described above, the finely reticulate chloroplast is also characteristic for this species. The longitudinal and transverse cell walls of *U. bangioides* are usually evenly covered with chloroplast material. In some cases, the accumulation of chloroplast material is so high that, at low powers, the cells look similar to the freshwater genus *Microspora*. When filaments are grown under suboptimal conditions, the chloroplast becomes coarse and its contours more vague. Many relatively small pyrenoids are regularly distributed in the chloroplast stroma. The number of pyrenoids increases with an increase in the cell size.

The differentiation of the basal portion of the filament usually takes place in the germling stage. After the attachment of the apical portion of the zoospore to the substrate, rounding-up and growth through elongations occurs. The original apical pole of the zoospore becomes narrowed in the two-celled stage. This pole then develops into the rhizoid. In exceptional cases, this differentiation does not occur until the four-to-ten-celled germling stage. In some cases, the top cell in the one-to-two-celled germling is pointed. This is probably the result of insufficient rounding of the pointed tail of the zoospore. The vegetative filament, exclusive of the basal cell, will develop from this portion. The formation of rhizoid-like outgrowths in the cells above the basal cell is much more pronounced in cultural material than in natural material.

Very little is known about the life cycle of *U. bangioides*. Zoosporogenesis takes place immediately after transferring vegetative filaments into fresh medium. This process usually begins in the apical region of the filament. No differences in the frequency of zoosporogenesis was detected among the various clones from different locations (under different conditions). With maturation, the zoospores exhibit a colour change to olive green. Even before the maturation of the zoospores, the cell wall shows a local thickening at the place where the zoospores will eventually be released. The zoospores are usually released in a stream, although, in some cases, the zoospores are released together in a hyaline vesicle. The zoospores are smaller and their swimming motions faster than those of the other *Urospora* species studied. The zoospores shed their flagella singly after attachment. Unfavourable conditions may induce aplanosporogenesis.

The *Codiolum*-phase has only been found in the field (Breezanddijk, The Netherlands) and only in a young stage. As was found for the other *Urospora* species, the young sporophytes do not mature in culture to the form and size of the same plant grown under natural conditions. They do, however, produce zoospores in culture. Sexual filaments were not found. However, the existence of sexual filaments of *U. bangioides* can be deduced from the absence of dwarf plants and the presence of *Codiolum*-plants in the life cycle.

Origin of material in culture

Uni-algal cultures were initiated from plants collected from the following localities. THE NETHERLANDS: Harlingen, near the harbour, on wooden piles, in the high littoral, exposed; Huisduinen, on blocks, exposed, solitary filaments in an abundant growth of *Urospora penicilliformis* plants; IJmuiden, on a jetty covered with bitumen, in the high littoral, solitary filaments in mats of *Urospora penicilliformis*; Cadzand, on a wooden pile in the high littoral.

3. *Urospora penicilliformis* (Roth) Areschoug – *Figs. 6–7, Plate 5.*

Conferva penicilliformis ROTH (1806) 271. – *Hormiscia penicilliformis* (Roth) FRIES (1835) 327; ÖRSTED (1844) 42; RABENHORST (1847) 115; (1868) 364; ARESCHOUG (1866) 12; KORNMANN (1966b) 409; KORNMANN & SAHLING (1977) 20. – *Hormotrichum penicilliforme* (Roth) KÜTZING (1845) 204; (1849) 382; (1853) 21, Tab. 64, fig. IV. – *Ulothrix penicilliformis* (Roth) BRAUN (1855) 21. – *Urospora penicilliformis* (Roth) ARESCHOUG (1874) 4; KJELLMAN (1877a) 56; (1877b) 55; (1883) 386 (ex parte); TRAILL (1885) 16; DE-TONI (1889) 232; FOSLIE (1890) 145; BATTERS (1891) 7; REINBOLD (1891) 128; KYLIN (1907) 18; LAKOWITZ (1907) 60; ? HARIOT (1912) 14; VAN GOOR (1923) 107; LAKOWITZ (1929) 169; NEWTON (1931) 95 (pro syn.); LEVRING (1937) 30; (1940) 9; KYLIN (1949) 46; SUNDENE (1953) 145; ? BREIVIK (1958) 35; LUND (1959) 30; KORNMANN (1961b) 45; JAASUND (1965) 22; PANKOW (1971) 122; STARMACH (1972) 233; LAVERACK & BLACKLER (1974) 276; von WACHENFELDT (1975) 255; RUENESS (1977) 233. – *Codiolum penicilliforme* (Roth) SILVA (1957) 142; DEN HARTOG (1959) 111. – Lectotype: Eckwarden, as *Conferva penicilliformis*, Trentepohl, ex herb. Agardh (LD, no 7417 holo; C).

Conferva isogona SMITH & SOWERBY (1808) Pl. 1930; AGARDH (1824) 102. – *Hormotrichum isogonum* (Smith & Sowerby) KÜTZING (1845) 204; (1849) 382; (1853) Tab. 65, fig. 1. – *Ulothrix isogona* (Smith & Sowerby) Thuret in LE JOLIS (1880) 57. – *Urospora isogona* (Smith & Sowerby) BATTERS (1902) 14; NEWTON (1931) 95. – Type not seen, but drawings are evident.

Conferva youngana DILLWYN (1809) 53, Tab. 102; JÜRGENS (1819) no. 9; AGARDH (1824) 101; HARVEY in HOOKER (1833) 354; (1841) 131; (1849) 210; (1851) Pl. 328; JOHNSTONE & CROALL (1860) 99; BATTERS (1902) 14 (pro syn.); NEWTON (1931) 95 (pro syn.). – *Hormotrichum youngianum* (Dillwyn) KÜTZING (1845) 204; (1849) 382. – *Hormiscia penicilliformis* (Roth) Fries var. *youngiana* (Dillwyn) RABENHORST (1847) 115. – *Aplonema younganum* (Dillwyn) HASSALL (1852) 224. – Lectotype: Yarmouth, on jetty, as *Conferva youngana*, 3/1808, ex herb. Dillwyn (BM, holo; iso, from Cromer, BM).

Conferva hormoides LYNGBYE (1819) 145, Tab. 49; AGARDH (1824) 101; ARESCHOUG (1850) 205. – Lectotype: Copenhagen, as *Conferva hormoides*, 5/7/1818, ex herb. Lyngbye 20 (C, holo; iso, Trekroner, ex herb. Agardh no. 7352, LD).

Hormiscia assimilis ORSTED (1844) 42. – Lectotype: Helsingør Trekroner, ex herb. Schübeler (O, holo).

Hormotrichum globiferum KÜTZING (1849) 382. – Lectotype: "Holländische Küste", ex herb. Kützing (L sheet 938.174–373).

Urospora mirabilis ARESCHOUG (1866) 16; ROSENVINGE (1893) 918; JÓNSSON (1903) 360; BØRGESEN (1902) 500; HAGEM (1908) 294; HYLMÖ (1916) 39; PRINTZ (1926) 254; HAMEL (1930) 128; PRINTZ (1932) 276; VAN DEN HOEK (1958) 194. – Lectotype: In mari Bahusiae, as *Conferva hormoides*, june, ex Areschoug's Alg. Scand. exs. no. 186 (S, holo).

Urospora mirabilis Areschoug var. *elongata* ROSENVINGE (1893) 918; JÓNSSON (1903) 360. – ? *Urospora elongata* (Rosenvinge) HAGEM (1908) 296; PRINTZ (1926) 254. – Lectotype: Greenland, Holstensborg, on *Ptilota pectinata*, Hartz, 6/1889, ex Plantae groenlandicae (C, holo).

Marine gametophytic filamentous plants, uniseriate and unbranched up to 5–6 cm long. Thallus stiff and glossy, green to dark green. Filaments solitary or gregarious, usually concentrated in tufts, attached firmly to substrate by an extensive basal holdfast consisting of (long) rhizoidal outgrowths from the basal cells.

Cell wall firm and thin, in older stages slightly lamellated, becoming thicker under adverse conditions, maximally 10–12 μm thick. Often studded with epiphytes and/or microparticles, particularly in the basal regions. Transverse cell walls thinner than lateral cell walls.

Cells cylindrical, not constricted at nodes, their polar ends closely appressed to one another; rarely in basal portions of mature filaments becoming somewhat swollen and nodally constricted. Cell dimensions varying considerably, in culture mature cells 9–80 μm in diameter, in nature 9–90 (–101) μm. Young filaments, in which zoosporogenesis rarely occurs, 4–9 μm wide. Filament distinctly tapering to apex, especially evident in young filaments (40–50 cells). Cells ranging from shorter than wide to isodiametric to longer than wide (width/length ratio 0.5–4.0, average 1.0). Width/length ratio range same for smaller, apically located cells as for larger basal cells, but basal cells generally shorter than wide.

Chloroplast parietal and varying in shape with age. Chloroplast in young cells an open continuous girdle, lobed to unlobed along longitudinal margin, usually covering 3/4 of cell circumference, soon becoming granular and globular filling entire cell. In mature cells, chloroplast opaque and thick, covering entire inner cell wall, including cross walls, appearing folded back upon itself in dense, thickened masses or lobes around a central lumen. Finely reticulate with many perforations which, through denseness of chloroplast, are not visible as clear holes. In aged cells, chloroplast shrunken to a centrally located body. Density of chloroplast increased by presence of many (to hundreds in mature cells) small free starch granules. Chloroplast dull to dark green, yellow in aged cultures.

In germlings, cells with one nucleus, soon becoming multinucleate. Pyrenoids difficult to discern in mature cells due to dense chloroplast and starch granules. Pyrenoids 1–2 in cells of germlings, (1–)5–15(–80) in mature cells, spherical and surrounded by irregularly shaped starch plates, hyaline interior often containing several small clear inclusions. Pyrenoids average 4.5 μm in diameter, range 2–10 μm.

Basal cell in germlings differentiated into a simple lengthened rhizoid, 85–700 μm long, slightly dilated at irregular intervals and narrowing toward its distal end, ending roundly, lobed or slightly branched at tip for better attachment to substrate. Cell wall in rhizoid usually thicker than in rest of filament. In mature filaments, cells above the basal cell also contributing to basal holdfast with (long) extramatrical rhizoidal outgrowths, extending from posterior portion of side walls and growing towards base of filament, usually unbranched, narrowing to a

blunt tip distally, 320–1250 μm long. In natural specimens, holdfast normally consisting of 3–5 rhizoids. In culture, most commonly with approximately 10 rhizoids from as many basal cells. Sometimes, holdfast reduced to 6–8 rhizoidal cells or developed to a maximum of 20–25 long rhizoids from as many basal cells. Dense chloroplastic material extending into rhizoidal outgrowths, becoming densely granular, often whole rhizoid filled evenly with granular chloroplastic material, sometimes clear with concentration of chloroplast at tip. Rarely formation of interstitial rhizoids. In basal cells of mature filaments, chloroplast compressed into centrally located irregularly shaped bodies. Apical cell usually rounded with clear rounded tip.

Asexual reproduction in the filaments by zoospores and aplanospores, initiated in all ordinary cells including the apical cells, but not in differentiated basal cells and usually not in those from which secondary projections arise. Mature *zoosporangia* green to dark green, cylindrical or only slightly swollen, outer cell wall not usually constricted at nodes, normally 15–80 (–130) μm wide and 20–140 μm long. *Zoospores* usually arranged radially with pointed posterior ends directed toward center or infrequently parallel to surface. In very large zoosporangia, sometimes in several star-shaped clusters. Zoosporangia only rarely incompletely filled. Zoospores usually quickly released in a stream through a single lateral discharge pore, sometimes at the site of a swelling in the cell wall, randomly located. Zoospores approximately 8 to about hundreds per cell, 18–36 μm long by approximately 5–11 μm, quadriflagellate, usually pyriform-obovoid extending acutely into a thin long projection below (rarely ovoid without posterior projection, then with posterior spinelike extension) as seen from side view. Quadrate in cross-section of anterior end, corners of square at ends of ridges converging at apex. Chloroplast parietal, cup-shaped, sometimes with anterior projection, 1–2 pyrenoids surrounded by thin starch plates or no starch plates, centrally to posteriorly located. Anterior end with many secretory vesicles, uninucleate.

Zoospores non-phototactic, locomotion slow in any given direction but rapidly vibrating. Germination after attachment to substrate at anterior (flagella-carrying) end, then retraction of posterior projection becoming globose followed by abscission of flagella. Rhizoid differentiation of basal cell occurring in 2-celled germlings. Repeated division of cells leading to filaments of several cms long. Often germination within sporangium. Under unfavourable conditions, *aplanospores*, spherical in aplanosporangial cells.

Filaments with *male gametangia* straight, in exceptional case slightly bended. Ripe male gametangia yellow-olive green, their cell wall sometimes slightly lamellated, cells up to 44 μm wide and up to 41 μm long. Male gametes, up to hundreds per cell, released simultaneously through an irregular shaped pore in the lateral cell wall, 7–9 μm by 2–5 μm, biflagellate, with conspicuously long flagella, up to 23 μm long, ovoid to spindle-shaped. Sometimes bluntly pointed posteriorly, occasionally slightly asymmetric in shape, normally rather fast in locomotion, becoming spherical at the moment of immobility, followed by abscission of the flagella. Their chloroplast less developed, irregularly cup-shaped,

sometimes only some chloroplast material present in their posterior part, a stigma possibly present. Ripe *female gametangia* yellow-green, in wide filaments slightly inflated, cells up to 57 μm wide and up to 91 μm long. Filaments with female gametangia straight. Gametes, up to many (–64?) per cell, released simultaneously enclosed in a hyaline mucilaginous vesicle. Gametes 8–15 μm by 4–6 μm, biflagellate, with an apical papilla, ovoid-elliptical, sometimes slightly asymmetric or showing an inflated apical part and an irregularly narrowed posterior part, often bluntly pointed posteriorly, rather slow in locomotion, soon after release becoming spherical, followed by the loss of flagella. Chloroplast cup-shaped with irregular ridges, sometimes its edge deeply fissured, with one pyrenoid and one distinct median-posterior stigma. Gamete fusion anisogamous, dioecious. Both male and female able to develop parthenogenetically. Upon germination, male gamete differentiating into a thick-set *Codiolum*-plant with a short, broad stalk and an oblong-cylindric club, up to 50 μm long, with a well developed chloroplast containing 1–7 pyrenoids. Female gamete, at germination, growing into globose sporophyte, up to 35 μm in diameter, unstalked, with a parietal chloroplast, containing up to 5 pyrenoids. Upon maturation its contents dividing into 8–16 aplanospores which, upon germination, develop into filaments.

Mature *Codiolum*-plants, from natural environments, up to 0.72 mm long, length of the stipe up to twice the club. Stipe frequently lamellated near the club and showing an undulating outline, its basal end usually swollen, rough. Club sub-cylindrical-elongate-obovate with a gradual transition into the stipe.

Senescent cells may form characteristic thick-walled akinetes.

U.S.S.R. Novaja Zemlya, Matochkin Shar, Kjellman, 12/7/1875 (S).

NORWAY. Spitsbergen, on stones, as *Conferva hormoides*, Berggren, 8/1868, ex herb. Agardh 7189 (LD); Måsö, Kjellman, 8/1876, ex Wittrock & Nordstedt – Algae exsiccatae 417a, (L sheet 939.26–73); Bergen, as *Urospora mirabilis*, Hylmö, 17/7/1913 (LD); Drøbak, as *Urospora mirabilis*, Hylmö, 14/4/1912 (BG).

ICELAND. Vattarnes, as *Urospora mirabilis*, Jónsson, 13/4/1898, ex Plantae islandicae 333 (C); Reykjavik, as *Urospora hartzii*, Jónsson, 27/4/1897, ex Plantae islandicae 203 (C).

DENMARK. Greenland, Frederiksdal, as *Conferva hormoides*, Vahl, 9/1829, ex herb. Lyngbye (C); Godthaab, as *Urospora mirabilis*, Rosenvinge, 21/5/1886 (C, KIEL). Faerøerne, Thorshavn, intermingled with *Urospora wormskioldii*, as *Urospora mirabilis*, Børgesen 927, 24/4/1898, ex Algae marinae Faeroensis (O, UPSV). Jylland, Fredericia, as *Conferva hormoides*, Hofmann Bang, 8/1847 (C). Sjaelland, Helsingör, Børgesen, 1/5/1892, ex herb. Mortensen (C); Copenhagen, Rosenvinge, 18/4/1880, ex herb. Rasch and Wittrock & Nordstedt – Algae exsiccatae 417c (C, S). Moën, as *Urospora mirabilis*, Ingerslev, 15/5/1904 (UPSV).

SWEDEN. Bohuslån, Torslanda, Varholmen, Åkermark, 7/1863 (LD, S); Fiskebäckskil, Kylin, 16/4/1906 (S); Kristineberg, Bondhålet, Kylin, 9/4/1906 (LD); Göteborg, as *Conferva hormoides*, Areschoug 133, september (S); Varberg, as *Urospora mirabilis*, Hylmö, 2/5/1925 (LD); as *Urospora mirabilis*, Hylmö, 13/3/1927 (S); Kullen, as *Conferva hormoides*, 16/8/1833, ex herb. Agardh 7347–7348 (LD); Hallands Väderö, as *Urospora mirabilis*, Sjöstedt, 6/1919 (L); Mölle, as *Urospora mirabilis*, Hylmö, 20/3/1921 (LD); Barsebäck, as *Urospora mirabilis*, Sjöstedt, 29/11/1927 (L); Barsebäckshamn, as *Urospora mirabilis*, Hylmö, 11/6/1917 (LD); Malmö, as *Ulothrix isogona*, Simmons, 3/8/1896 (LD); Malmö, Limhamn, as *Urospora mirabilis*, Hylmö, 3/11/1912 (O); Löderup, Käseberga, as *Urospora mirabilis* f. *juvenilis*, Sjöstedt, 12/6/1927 (LD); Kivik, as *Urospora mirabilis*, Sjöstedt, 27/6/1917 (LD, O); Stenshuvud, Sjöstedt, 12/6/1927 (LD); Blekinge, Levring, 26/6/1936

(GB); Visby, Wittrock, 13/7/1879, ex Wittrock & Nordstedt – Algae exsiccatae 417b (L); Dalarö, as *Urospora mirabilis*, ex Areschoug exsiccatae 340 (S, O).

GERMANY. Flensburg, as *Hormotrichum penicilliformis*, Weidemann, 10/5/1879 (L sheet 939.26–77); Kiel, as *Urospora mirabilis*, Reinbold, 4/1887 (L sheet 939.26–82); Kieler Föhrde, Ellerbeck, Reinbold, ex Hauck & Richter, Phycotheca universalis 380 (BG, L sheet 920.13–334); Warnemünde, as *Ulothrix isogona*, Heiden, 15/4/1888 (L sheet 939.25–61).

GREAT BRITAIN. Firth of Forth, ex herb. Merrifield (BM); Yorkshire, as *Conferva collabens*, beginning summer 1858, ex herb. Cocks (BM); Filey, as *Conferva youngana*, 1852, ex herb. Merrifield (BM); Cromer, as *Conferva youngana* (E); Teignmouth, as *Conferva youngana*, on limestone, Cresswell, 11/1855 (E); Budleigh Salterton, as *Conferva youngana*, Cutler, ex herb. Harvey (BM); Yarmouth, piles of jetty, as *Conferva youngana*, 25/3/1868, ex herb. Hook (BM).

THE NETHERLANDS. West-Terschelling, Kom, on stones, as *Ulothrix flacca*, Den Hartog 1772, 2/9/1954 (L sheet 956.313–512); Den Helder, harbour, as *Hormiscia penicilliformis*, Swennen 84, 25/7/1949 (L sheet 951.101–588); Den Helder, sea dike, as *Urospora isogona*, Den Hartog 152, 29/3/1951 (L sheet 956.313–550); Camperduin, on basalt block, Koster 6132, 10/5/1957 (L sheet 957.142–230); Hondsbosse Zeewering, on wooden pile, as *Urospora isogona*, Den Hartog 760, 14/4/1950 (L sheet 956.313–554); Hoek van Holland, as *Urospora isogona*, Van den Hoek 386, 15/3/1953 (L sheet 956.314–062); Schouwen Duiveland, Rengerskerke, Koster 4374, 23/4/1954 (L sheet 954.125–110); Walcheren, West-Kapelle, as *Codiolum penicilliforme*, Mulder, 16/4/1954 (L sheet 958.045–717).

FRANCE. Brest, as *Hormotrichum isogonum*, De Brébisson, ex herb. Suringar (L sheet 939.26–68); Côtes de Bretagne, as *Conferva isogona*, De Brébisson (L sheet 910.200–464).

Nomenclature and historical aspects

Despite the relative lack of knowledge about algae at that time, ROTH (1806) gave a relatively detailed description of this species. The filament morphology, the form of the cells and the cell length/width ratio were all reported. As is the case with the majority of the unbranched filamentous algae, "*penicilliformis*" was placed in various genera by various phycologists (FRIES 1835; KÜTZING 1845; BRAUN 1855, etc.). It was not until 1874 that this species was placed in the genus *Urospora* by Areschoug. On the mainland of Europe, the name *U. penicilliformis* is now generally accepted. Even so, KORNMANN (1966b) recently brought this species again under the genus *Hormiscia*. The rules of nomenclature do not allow this since *Urospora* was conserved against the older genus *Hormiscia*. ROTH's description (1806) was based on material collected by Trentepohl in Eckwarden, Germany. Roth's herbarium was destroyed in the second world war. Luckily, a few poorly conserved filaments from Eckwarden were found in the Agardh herbarium in Lund. Apart from a few filaments of *U. penicilliformis* dried on mica, the remainder of the material consists primarily of *Prasiola*-species. This specimen, located at the Agardh herbarium under no. 7417 and marked "*Conferva penicilliformis* dedit Roth" is, nevertheless, named as the lectotype.

U. penicilliformis is very similar in cell diameter to *U. neglecta* but their identification is made possible by the degree of differentiation of the basal portion of the filaments. Because the few lectotype filaments were badly conserved, the identification as one of these two species is quite arbitrary. It should be noted that for the identification of material made available by various herbaria, only that material was chosen which had been carefully collected and still possessed basal cells. In addition, one should regard the summarized literature citations as highly probably referring to *U. penicilliformis*. It was not always

possible to determine from the literature descriptions the degree of basal cell differentiation.

In the past, a number of different names were associated with material which is now recognized as *U. penicilliformis*. DILLWYN, for example, described this species under the name *Conferva youngana* (1809). This name comes back repeatedly in the English literature. Later, this name was suggested as a synonym for *Urospora isogona* (Smith and Sowerby) BATTERS (1902). This is also most probably *U. penicilliformis*. Although the type material was not available, the illustration of *Conferva isogona* in SMITH & SOWERBY's English Botany (1808, Pl. 1930) strongly resembles *U. penicilliformis*. The name *Urospora isogona* was still used in NEWTON's British algae flora (1931). In 1866, ARESCHOUG described *Urospora mirabilis*. Shortly thereafter, in 1874, this species was given as a synonym for *Urospora penicilliformis*. The name *Urospora mirabilis*, however, remained in use in the Scandinavian literature until far into this century.

Morphology, reproduction and life history

The general morphology of filaments collected in various natural habitats is largely similar to that observed under culture conditions. However, the attached plants usually attain a length of up to 6 cm in nature, while filaments in culture grew to a length of only 3 cm. Two to three weeks after the release of zoospores from filaments and their settlement, a dense green flexible carpet of filaments arises at the bottom of the culture vessel. The developing germlings were arranged on the bottom of the culture disk with their length axes in the direction of the illumination. This alga could also grow on and into agar coatings.

The cell wall is firm and normally 2 to 3 μm thick in mature filaments. It becomes thicker (to a maximum of 10 to 12 μm) under dry conditions such as in the desiccation experiments, in the tide simulating apparatus and on agar. The cell wall surface in both young and mature filaments is smooth; in older cells, it may become slightly lamellated. It is often studded with epiphytes and/or microparticles, particularly in the basal regions of the filaments. It may sometimes vary in thickness in one cell, appearing slightly wavy.

Cells are normally cylindrical. However, in two localities in nature (Stavern, Norway, and Kuiershoek, The Netherlands) barrel-shaped cells were found. These had thick walls and contained disordered chloroplasts. After one week in culture, the cells assumed their normal growth habit. Normally the cells are closely appressed to one another. Once, in a clone showing suboptimal growth from the Veerse Meer (The Netherlands), the cell division orientation was aberrant, resulting in irregular multiseriate filaments.

Variations in photoperiod length (SD or LD) or in moderate temperatures (8° and 12°C) did not significantly affect the absolute range of the cell diameter. However, at 4°C/SD, *Urospora penicilliformis* grew suboptimally. Growth at 16°C/LD was slow and the filaments became yellowed. Although the zoospores germinated at this temperature, they did not grow well into long filaments. The clones died after three weeks at 20°C/LD. The salinity of the culture medium (2,8 and 16‰ Cl^-) did not significantly affect cell dimensions. In this respect,

NIENHUIS (1976) reported that *U. penicilliformis* could be found in the province Zeeland, The Netherlands, in areas with salinities ranging from 1 to 15‰ Cl^-. Growth under aeration and in the tide simulating apparatus was suboptimal and germlings did not develop into healthy plants. At high light intensities (5500 lux), filaments of *U. penicilliformis* show swollen cells and so-called "ball" formations at the ends of short cell rows. These give a zig-zag appearance to the filaments. Under normal culture conditions, the filament tapers in diameter apically. This is most noticeable in young filaments.

The chloroplast of *U. penicilliformis* is thick and opaque. It appears to be folded back and forth upon itself into thickened, dense masses. However, there is still a central vacuole. The chloroplast may line the transverse cell wall to the same degree as it does the lateral wall, giving rise to a *Microspora*-like growth habit. The colour of the chloroplast is usually a dark green (see under *U. neglecta* for a further discussion of chloroplast colour). However, in material from unfavourable natural environments, the chloroplast may become yellow-brown. This is caused by the heavy accumulation of assimilate granules. Such cells resemble cells which contain male gametes. Under unfavourable culture conditions, the chloroplast may seemingly shrink away from the cell wall and withdraw itself to the center of the cell. It may become concentrated in two central clumps, similar to the healthy chloroplast of the freshwater genus *Zygnema*.

The pyrenoids are often difficult to discern in the dense chloroplast without the help of the staining reagent IKI. Young cells generally contain one or two fairly large pyrenoids. Up to c. 80 pyrenoids have been observed in mature cells. The pyrenoids of *Urospora penicilliformis* are, on the average, 1 μm smaller than those of *Urospora neglecta*. The pyrenoids were measured at their longest diameter, the starch plates included. This difference of 1 μm may represent a difference in the thickness of the starch plates or a difference in the diameter of the pyrenoid itself. Because these measurements were made on filaments grown under different cultural conditions (see *table 1*) it is doubtful that the difference in size due to a difference in growth milieu.

The holdfast of *U. penicilliformis* can be described as extensive. At maximum development, in culture, there are 20 to 25 long, large rhizoids growing from as many basal cells. In its most reduced form, cultured, for instance, at 8 °C/LD or under high light intensities, it consists of rhizoids arising from 6 to 8 basal cells. In nature the holdfast normally consists of 3–5 rhizoids. The rhizoids from field material are usually shorter than from culture material and the basal part of the basal cell is often inflated. Filaments grown on agar or under high light intensities may develop short secondary projections for attachment at points higher up in the filament. These are similar to the rhizoids which HANIC (1965) found on filaments of *Urospora vancouveriana* at sharp bends or at tips that reached the air/water surface. SETCHELL & GARDNER (1920) also found short or rhizoidal branches, sometimes in pairs and sometimes long, as a result of injuries or disturbances. These were rare in normal development. PRINTZ (1932) reported the formation of lateral branches with acute ends and thick membranes, in

material collected in July from the Oslofjord.

Perhaps because of the widespread occurrence of *U. penicilliformis* along the coasts of Western Europe, most aspects of its reproduction and life history have been studied intensively in the past. Under the name *U. mirabilis*, ARESCHOUG (1866) described the asexual reproduction by quadriflagellate (mega-)zoospores with acutely pointed ends. Considering his pictures (1866, Tab. III, fig. 6), it might also be possible that he studied the zoosporogenesis and germination of the closely related *U. neglecta*. The illustrated germlings did not develop rhizoidal basal cells which normally occurs in *U. penicilliformis*. Sexual reproduction was also described by ARESCHOUG in 1866 under the name *Hormiscia penicilliformis*. Only in 1874 did ARESCHOUG realise that *Hormiscia penicilliformis* was the sexual individual of the same species whose zoospore-carrying individuals he had called *U. mirabilis*. It is doubtful whether he really drew the sexual products of *U. penicilliformis*. The large range in the sizes of the illustrated gametes includes the size range of *U. neglecta's* gametes. Without being aware of it, ARESCHOUG depicted the start of parthenogenetic development of sexual cells into the *Codiolum*-phase (1866, Tab. 1, figs. 9 and 10). PRINTZ (1932) has stated that Areschoug undoubtedly confused several different species under the name *U. penicilliformis*. The opinion is reinforced by the fact that ARESCHOUG (1874) pictured the fusion of two isogametes for *U. penicilliformis* similar to that seen in marine species of *Ulothrix* (LOKHORST 1978). This is not, though, true for *Urospora* where sexual reproduction is definitely anisogamous. WOLTKE (1887) gave additional information on zoospore germination.

PRINTZ (1932) was the first to report valid, comprehensive details about the reproduction of *Urospora penicilliformis*. He described the morphology of the zoosporangia, the zoospores and the male and female gametes in detail. He did not complete the life cycle of this species; however, JORDE succeeded in doing so in 1933. She united the life cycle of *Codiolum gregarium* with that of what she called *Urospora mirabilis*. It is questioned whether the *U. mirabilis* sensu Jorde is identical to the true *U. penicilliformis*. We agree with KORNMANN (1961c) who believed that Jorde had studied a mixture of *Urospora* species. This could have been caused by the fact that she worked with various algal samples collected in the field and subsequently brought into the laboratory and placed near a north-facing window. The heterogeneity of her starting material is demonstrated by the fact that zoospores developed under similar conditions into different products. Moreover, zoospores which ripened in *Codiolum*-plants collected in natural environments also germinated into different growth forms. As argued before, it is not possible to distinguish *Codiolum*-plants at the species level. Jorde also observed several types of gametes which differed in size and form. It can be assumed that the pictured gametes belong to *U. penicilliformis* (fig. 3a in JORDE 1933) and to *U. neglecta* (fig. 3c, loc. cit.).

KORNMANN (1961c, 1966b) studied the life history of *Urospora penicilliformis* with filaments collected in the field and with filaments grown in uni-algal cultures. The fusion products of *U. penicilliformis* gametes were observed to germinate in culture into small *Codiolum*-like plants. These small plants were not

found by Kornmann in nature. Zoospores from these *Codiolum*-plants developed into filaments. This germination process was not dependent on temperature and no dwarf forms could be found. Additional information was given on the morphology of the gametes and the gametangia.

Our data on the reproduction and life history of *U. penicilliformis* concur in general with the characteristics summarized by PRINTZ (1932) and KORNMANN (1961c, 1966b). More detailed information is given here on the shape and dimensions of zoospores and zoosporangia, the mode of zoospore germination, the shape and dimensions of the gametes and gametangia and the parthenogenetic development of both types of gametes. Filaments in nature and in culture generally reproduce only by means of zoospores. Zoospores are formed within five days after transferring vegetative plants into fresh medium. Zoosporogenesis did take place in filaments grown on agar plates, but the zoospores were not released from the mother plant. This resulted in a mat of young filaments growing from the original filament. Cultures of *U. penicilliformis* which had been fully frozen for four hours showed strong recovery through zoospore release 4 days after thawing. Normally, zoospores shed their flagella singly after settling to the substrate. The acuminate tail is retracted as the zoospore rounds up. After germination of the zoospore, a rhizoid is formed in as early as the two-celled germling stage. This pattern is the same at all moderate temperatures and normal photoperiods. However, under extra short day conditions (6 hours light), under continuous light conditions and at 16°C/LD, the germlings remained small. The rhizoid of the filament is formed from the former anterior end of the zoospore. JORDE (1933) reported, incorrectly, that the tail became the rhizoid.

The zoospores are arranged radially in the zoosporangia. The narrow posterior pole is usually pointed inwards and the wider anterior pole lies against the cell wall. In contrast to the findings of earlier workers who described spherical zoosporangia, the zoosporangia observed in this study are rectangular or only slightly swollen and rarely, if ever, spherical. Zoospores are released through a lateral pore at the site of a swelling in the cell wall. In one case, filaments showed the beginning of a fragmentation process in the apical portion.

None of the experimental conditions listed in *table 1* caused the induction of gametogenesis in *U. penicilliformis*. In only two cases were gametangia observed in culture. Male filaments were found in a neglected culture originating from Huisduinen (The Netherlands) which had been kept under short day conditions at 8°C. Female filaments arose in a healthy culture from Verdens Ende (Norway) which had been kept under long day conditions at 8°C. Unfortunately, the production of male and female gametes in these cultures did not happen at the same time. The factors responsible for the induction of gametogenesis are still unknown. Presumably, the special spectrum of conditions in nature which are required for sexuality are difficult to simulate in culture.

Male gametes of *U. penicilliformis* are characterized by two very long flagella. They move in a characteristically whirling motion. Just before coming to a complete stop, they assume a definitive position while their flagella continue to oscillate. These vibrations end abruptly. Shortly after the flagella are shed, the

gametes round up but do not attach firmly to the substrate. The presence of a stigma and of a pyrenoid in the male gametes could not be demonstrated. At strong magnifications and illuminations using the light microscope, however, there appears to be a small red eyespot near the edge of the chloroplast in the middle of the gamete. KORNMANN (1961c) was also not convinced of the presence of a stigma in male gametes. PRINTZ (1932), in contrast, reported that the red stigma in the male gamete was so distinctive that it imparted a reddish-brown colour to the gametangium. We have observed parthenogenetic development of male gametes into the stalked *Codiolum*-plant. KORNMANN (1966b) reported this possibility, but stated that this phenomenon had not been sufficiently proved in his experiments. The wall of the male gametangia is locally indistinctly lamellated.

Female gametes of *U. penicilliformis* are characterized by the presence of a distinct stigma. Gamete-producing cells are easily distinguishable from zoosporangia by their yellow-green colour, the presence of the stigmas and the non-radial arrangement of the gametes. When comparing KORNMANN's fig. 3A (1961c) with our pictured gametangia (*fig. 6c*), it should be noted that the gametangia in this study contain a countable number of gametes and that gametes still inside the mother cell are larger than those shown by Kornmann. The female gamete moves relatively slowly. KORNMANN (1966b) observed a change in the gamete shape after a swimming period of 8 hours. This phenomenon could not be confirmed in this study. In our hands, female gametes developed parthenogenetically into globose sporophytic plants, some of which were provided with a gelatinous attachment disc. After a month under short day conditions at 8°C, the contents of the sporophyte divided into aplanospores which were able to germinate inside the mother cell wall. Germlings developed into *U. penicilliformis* filaments. It appears that the male and female gametes may produce differently shaped sporophytes through parthenogenesis. Due to the low number of observations made, that possibility could not be confirmed conclusively. KORNMANN (1966b) found that zygotes could develop into either globose or short stalked elongate ovoid *Codiolum*-sporophytes.

Codiolum-plants of any given species can vary greatly in morphology under varying external conditions. *Codiolum*-plants collected from Vlissingen (23/8/1978) and Gorishoek (22/9/1978) in The Netherlands were brought into culture. These *Codiolum*-plants resembled the plants pictured by KORNMANN (1966b) as the sporophyte of *U. neglecta*. However, these *Codiolum*-plants gave rise to zoospores which germinated into *U. penicilliformis* filaments. In culture, the sporophytic stage of *U. penicilliformis* is globose, ovoid or thick-set, with short stalk and is of microscopic size. In contrast, plants grown in nature are slender with a total length of up to 720 μm and have a stipe up to twice the length of the club.

Origin of material in culture

Uni-algal cultures were started from plants collected from the following localities. NORWAY: Nevlunghavn, on stones, rather exposed; Stavern, growing together with *Acrosiphonia* species, forming

dense tufts in the high littoral which was further inhabited by red algae such as *Porphyra linearis;* Verdens Ende, exposed, in the high littoral, forming small algal carpets. THE NETHERLANDS: Harlingen, on wooden pilings, exposed; Huisduinen, on an iron pile, exposed, intermingled with *Urospora neglecta;* Gorishoek (as *Codiolum*-plant), on a tile-shedding in the high littoral, growing among *Blidingia* and *Prasiola*-plants; Sas van Goes, on lime stone, intermingled with *Ulothrix speciosa*; Veerse Meer, an inland salt lake, in the splash-zone, intermingled with *Ulothrix implexa;* Vlissingen (as *Codiolum*), on the vertical side of blocks, growing together with *Prasiola* species and Cyanophyta; Kuiershoek, exposed, on a jetty.

4. *Urospora neglecta* (Kornmann) nov. comb. – *Fig. 8, Plates 6–7.*

Hormiscia neglecta KORNMANN (1966b) 417; KORNMANN & SAHLING (1977) 20. – Type: Heligoland, on stairs, Kornmann, 11/7/1966, on a slide in the private collection of Dr. Kornmann (HELGOLAND).

Urospora speciosa (auct. non Carmichael ex Harvey in Hooker) Leblond ex HAMEL (1930) 129; KORNMANN (1961c) 47.

?Urospora kornmannii BERGER-PERROT (1980) 143, type not available.

Marine gametophytic plants, uniseriate and unbranched filaments, up to 7 cm long. Thallus soft and flexible, glossy, green to light green. Filaments solitary or gregarious, usually concentrated in tufts, sometimes entwined in rope-like strands.

Cell wall firm and thin, becoming thicker under adverse conditions to a maximum of 3–5 μm, in older stages indistinctly lamellated, occasionally fouled with epiphytic algae or microparticles in basal portions. Transverse cell walls thinner than side walls.

Cells usually cylindrical, not constricted at the nodes, sometimes in mature filaments slightly swollen, particularly in basal portions. Cell dimensions varying considerably, in culture mature cells 15–90 μm in diameter, 15–50 μm in nature. Young filaments in which zoosporogenesis rarely occurs, 10–15 μm wide. Mature cells ranging from shorter than wide to isodiametric to longer than wide (width/length ratio 0.5–1.5). Cell diameter gradually decreasing towards apex of filament. Range of width/length ratio about the same for apical, middle, and basal portions.

Chloroplast parietal and varying in shape with age and conditions. Chloroplast in young cells an open continuous girdle, lobed to unlobed along longitudinal margin, usually covering 3/4 of cell circumference, with few, if any, large perforations. In mature cells, chloroplast a thin parietal sheet, covering entire inner cell wall, appearing fairly translucent, made coarsely reticulate with few large perforations, appearing darker along the walls. Occasionally, throughout filament, chloroplast forming a network of thin, flat connected strands, with large perforations. In aged cells, chloroplast sometimes shrunken to the middle of cell lumen. Chloroplast light, bright, yellowish green to green, whitish green in depleted cultures, yellow in aged filaments.

In germlings, cells with one nucleus, soon becoming multinucleate. Pyrenoids distinct, 1–2 per cell of germlings, in mature cells ranging from 1–10 (–40) per cell, spherical, surrounded by irregularly shaped starch plates, average 5 μm in diameter, range 2–10 μm, hyaline interior often containing small clear inclusions.

Basal cell in germlings, differentiated into rhizoid, appearing longer in younger filaments than in older, tapering slightly to distal end and ending roundly, sometimes branched at tip into brush-like tufts. Basal holdfast of mature natural specimens consisting of only 1 rhizoid from the most basal cell. In culture, most commonly 1–2 short rhizoids, ranging from 150–400 μm long, usually approximately 250 μm Not infrequently, cultural specimens with rhizoidal outgrowths from more apically located cells (separated from basal holdfast by many cells without rhizoids), usually short, 177–257 μm long, sometimes up to 564–1040 μm long, extending laterally from cell, point of protrusion from cell constricted, number of these interstitial rhizoids increasing with unfavourable conditions, sometimes rounded into a spherical bulb, containing parietal chloroplastic mass in open network.

Chloroplast in basal cell a very open parietal network extending into rhizoid, often a concentration of chloroplast in distal tip of rhizoid, connected by open network with chloroplastic mass in basal cell. Chloroplast in other cells with rhizoids extending a short distance into the rhizoidal outgrowths, then extending as open parietal network into entire rhizoid. Rhizoid for the most part clear, studded on surface with contaminating organisms. Cell directly above basal cell, often hemispherically rounded on basal side.

Asexual reproduction in the filaments by zoospores and aplanospores, initiated in all ordinary cells including the apical cells, but not in differentiated basal cells and usually not in those from which secondary projections arise. Mature *zoosporangia* light green to green. Cylindrical or slightly inflated, sometimes constricted at nodes, rarely if ever spherical, normally 15–80 (–190) μm wide and 55–130 μm long. *Zoospores* usually arranged radially with pointed posterior ends directed toward center or parallel to surface. In very large zoosporangia, sometimes in several star-shaped clusters. Zoosporangia not always completely filled, then in larger cells zoospores arranged in connected bands, separated by open spaces or appressed at one end of cell. Zoospores usually quickly released in a stream through a single lateral discharge pore, sometimes at the site of a swelling in the cell wall, randomly located. Zoospores approximately 8 to about 100 per cell, (21–) 30–40 (–54) by approximately 10–13 μm, quadriflagellate, usually pyriform-obovoid extending acutely into a thin long projection below (rarely ovoid without posterior projection, then with posterior spinelike extension) as seen from side view. Quadrate in cross-section of anterior end, corners of square at ends of ridges converging at apex. Chloroplast parietal, cup-shaped, sometimes with anterior projection, 1–2 pyrenoids surrounded by thin starch plates or no starch plates, centrally to posteriorly located. Anterior end with many secretory vesicles, uninucleate.

Zoospores non-phototactic, locomotion slow in any given direction but rapidly vibrating. Germination after attachment to substrate at anterior (flagella-carrying) end, retraction of posterior projection becoming globose, and abscission of flagella. Rhizoid differentiation of basal cell occurring in 2-celled germlings. Repeated division of cells leading to filaments of several cms long. Often germination within sporangium. Under unfavourable conditions, spheri-

cal aplanospores in zoosporangial cells. Germination inside the mother cell wall.

Sexual reproduction through biflagellate anisogametes. *Male gametangia* very pale gold to green with contents divided into small bead-like bodies, generally swollen and constricted at transverse cell wall. Male gametes moving agitatedly in gametangia before release. Release of all gametes from gametangia simultaneously. Dispersal of cluster of gametes after few seconds. Locomotion of male gametes rapid and jerking. Male gamete, pyriform to spherical, 4–6 μm long and 3–4 μm wide, biflagellate, flagella long, 9–14 μm, chloroplast parietal, cup-shaped and positioned against posterior wall, no pyrenoid. *Female gametangia* similar in colour to zoosporangia but usually more swollen, and gametes arranged randomly in gametangia. Release of female gametes singly, locomotion very slow with spiral gliding motion. Female gamete 16–30 μm long, and 4–7 μm wide, variable in shape, obovoid to pyriform to bean-shaped, mostly with red stigma, one pyrenoid, chloroplast parietal, cup-shaped and posteriorly placed, biflagellate, flagella up to 20 μm long.

Sporophytic plants (*Codiolum*-plants) formed from zygote or parthenogenetically from female gametes. In nature, *Codiolum*-plants gregarious, forming dense, dull, dark green velvety-like cushions, 330–500 μm in total length. Stipe clear, hyaline, 150–300 μm long, in a young stage smooth, later becoming rough, wall often grooved in most apical portion, giving the impression of growth rings, tapering from junction with clava to base, ending rounded or with small bulb-like inflation. Transition between stipe and clava gradual. Clava elongate-ovoid with parallel sides, to slightly swollen at apex, pyriform to sub-cylindrical, approximately 300 μm long, 0.8–1.5 times length of stipe, 4–5 times longer than wide. Cell wall usually smooth and relatively thin. Chloroplast parietal, often dense granular, containing several to many pyrenoids. In culture, clava of *Codiolum*-plants becoming wider and shorter, ovoid approximately, 125–161 μm long by 60–90 μm wide, inflated at apex, cell walls becoming thicker. *Codiolum*-plants grown from zygotes and parthenogenetically from female gametes in culture reduced and short, with constricted sharp distinction to stipe, then with clava globose to obovoid, up to 115 μm by 50 wide, and stipe very short, straight or curved and blunt, up to 60 μm long by 25 μm wide; or with no distinction into clava and stipe, then elongate, oblong, irregularly inflated, one end usually more bulbous, variously shaped body, 125 μm long, entirely filled with zoospores. Zoospores produced in clava of all above *Codiolum*-forms identical in morphology, behaviour, mode of locomotion, and in germination to those from filaments.

U.S.S.R. Novaja Zemlya, Matochkin Shar, Kjellman, 12/7/1875 (UPSV).

ICELAND. Skálholtsvik, as *Urospora mirabilis*, Jónsson, 6/9/1897, ex Plantae Islandicae 983 (C); Videy, as *Urospora mirabilis*, Oskenfeld Hansen, 21/6/1896, ex Plantae Islandicae 84 (C); Vestmannaeyjar, as *Urospora mirabilis*, Jónsson, 15/5/1897, ex Plantae Islandicae 305 (C).

SWEDEN. Varberg, as *Urospora incrassata*, Hylmö, 21/5/1917 (O); Hälsingborg, as *Conferva implexa*, ex herb. Agardh no. 7375–7415 (LD); Malmö, Limhamn, as *Conferva mirabilis*, Hylmö, 13/4/1914 (O); as *Urospora wormskioldii*, Hylmö, 25/3/1914 (LD); Visby, as *Urospora penicilliformis*, Wennersten, 6/1893 (UPSV); Dalarö, as *Hormotrichum youngeanum*, Strömfelt, 7/1887 (S).

DENMARK. Helsingör, as *Urospora penicilliformis*, Børgesen, 1/5/1892 (S); Korsör, as *Conferva hormoides*, Hoffman Bang, 6/1844 (C); Koster, as *Conferva flacca*, 20/7/1835, ex herb. Agardh no. 7366 (LD).

GERMANY. Heligoland, as *Hormotrichum penicilliformis*, ex herb. Kützing (L sheet 939.67–712 & sheet 939.67–776).

GREAT BRITAIN. Aberdeen, as *Conferva youngana*, 1843, ex herb. Dickie (BM); Fife, 21/5/1891, ex herb. Merrifield (BM).

IRELAND. Clare Island, as *Urospora mirabilis*, Cotton, 4/1911 (BM).

THE NETHERLANDS. Zeeland, as *Hormotrichum isogonum*, Hoffmann Bang, ex herb. Kützing (L sheet 938.174–374).

FRANCE. Le Havre, as *Ulothrix isogona*, Dupray, 10/1897, ex Mougeot, Roumeguere & Dupray, Algues des eaux douces 1266 (BM); Batz, as *Conferva youngana*, 4/1847, ex Algues de l'Ouest de la France 217 (P).

Nomenclature and historical aspects

This species was described as late as 1966. This is probably due to the fact that the filaments of this species are morphologically very similar to those of *U. penicilliformis*. These two species are often found together in mixed populations. An important difference between the two species is the degree of attachment to the substrate. This characteristic is most pronounced in cultures although it is also apparent in field material. Because not every author gave a description of the basal holdfast, it is difficult to separate literature references for this species from those for *U. penicilliformis*.

It is our opinion that *Urospora speciosa* (auct. non Carmichael ex Harvey in Hooker) Leblond ex HAMEL (1930) falls within the species limits of *U. neglecta*. It appears to be a specific growth form of *U. neglecta* observable under optimal culture conditions. This form is characterized by a smooth cell wall and flat thin cells with an *Ulothrix*-type chloroplast containing few pyrenoids. There have been earlier doubts about the identity of the above-mentioned *Urospora speciosa* (LOKHORST 1978). At that time, it was not sufficiently proved that *Ulothrix*-like filaments with a life cycle and zoospores and gametes similar to the genus *Urospora* exist. Without the availability of asexual zoospores, it is still possible to identify this material. *Ulothrix* species always have one nucleus while mature specimens of the *Ulothrix*-like form of *Urospora neglecta* contain multiple nuclei. A second aid to identification is the addition of 1% iodine solution in 5% lactophenol to the filaments. This results in an inflation of the cell wall of the true *Ulothrix speciosa* (LOKHORST 1978) while the cell wall of the *U. neglecta* growth form shows no changes.

Morphology, reproduction and life history

The general habit of the filaments in the field is similar to that observed in cultures. Zoospores released from either filament or *Codiolum*-plants develop into filaments. In culture, this led to a dense algal carpet at the bottom of the culture dish. The filaments are solitary or gregarious, but are usually concentrated in tufts, and are sometimes entwined in rope-like strands. The filaments could grow well on and into agar coatings. Filaments grew spirally into the agar medium.

The filaments of *U. neglecta* are somewhat more flexible and softer than those of *U. penicilliformis*. The cell wall is usually firm, but is more mucous than that of *U. penicilliformis*. The cell wall is generally thin (average 1 μm), but under desiccative conditions, it becomes thicker to a maximum of 3–5 μm. In both young and mature cultured filaments, the surface of the cell wall is smooth. However, the basal part of filaments collected from natural environments is often studded with epiphytic algae and microparticles, giving the cell wall a rough appearance. Old cell walls are indistinctly lamellar.

The cells are normally cylindrical. The filaments of *U. neglecta* taper more gradually apically than those of *U. penicilliformis*. In an exceptional case of aged filaments from the field, cells were slightly swollen with a thickened cell wall. Cells are sometimes grouped in pairs or in fours in the filaments. One cell in a cell row may individually be inflated. Normally, the cells are closely adherent to one another. In one case of an uniseriate filament, a short double cell row enclosed in a common cell wall was observed.

In culture, variations in temperature (4°, 8° and 16°C), in photoperiod (SD and LD) and in the salinity of the culture medium (2, 8 and 16‰ Cl^-) did not significantly affect the range of the cell dimensions. At 16°C/LD the growth was suboptimal and at 20°C/LD, the clones died in three weeks. Growth in aeration flasks was suboptimal. In contrast to *U. penicilliformis*, the growth of *U. neglecta* was very good in the tide simulating apparatus. Filaments of *U. neglecta* showed a higher frequency of the aberrant "ball" formations, swollen cells at the ends of short cell rows, under high light intensities (5500 lux) than did *U. penicilliformis* filaments.

The chloroplast of *U. neglecta* is thinner and less dense than the chloroplast of *U. penicilliformis*. The chloroplast is a thin reticulate sheet with large perforations. Moreover, there is a difference in the colour of the chloroplasts of these two species. The chloroplasts of *U. neglecta* are light, bright yellowish-green to green. We studied whether this colour difference was the result of an ultrastructural difference in the chloroplasts, such as in thylakoid spacing, or the result of differences in the pigment composition of the chloroplasts. Electron micrographs of the chloroplasts of *U. neglecta* and *U. penicilliformis* showed the number of thylakoids in the lamellae in both species to vary from 2 to 9. In *U. neglecta* chloroplasts, the lamellae are often spaced further apart than in *U. penicilliformis*. On the average, however, the lamellar distance was the same in both species.

An analysis of the chloroplastic pigments, however, proved fruitful in the quantification of the colour difference. In order to quantify this colour difference, the absorption spectra of these two algae were measured. The colour of plant cells is determined by the relative amounts of various light absorbing pigments in the chloroplast. Each of these pigments has a characteristic absorption spectrum. The absorption spectrum of a given plant cell is a composite of the individual absorption spectra of the pigments found in that cell.

The spectra were measured on a Beckman JA 25 Spectrophotometer. Absorption was measured in the visible region from 800 nm, where absorption by algae

is virtually absent, to 400 nm. Clumps of filaments were placed in a 1.0 cm cuvette at the level of the light beam. Reference cuvettes contained only growth medium. Whole filaments will scatter light leading to an error in the absorption measurements. Correction was made for this phenomenon by placing the frosted, matt sides of the cuvettes in the light beam. Additional light scatter caused by the algae in the sample cuvette is negligible compared to that caused by the cuvette itself.

In this method, the number of cells through which the light passes can vary from one trial to the next. Therefore, a comparison of absolute absorption is meaningless. However, the relative absorption at different wavelengths should be constant for a given species grown under constant conditions. The absorption spectra shown here have been normalized. The value of 100 % is assigned to the peak of chlorophyll *a* absorption at 675 nm. Average absorption intensities at 475, 550, 600, 650, 675 and 800 nm were obtained for each species from measured spectra, normalized and replotted. These points were connected to simulate the actual absorption spectra.

Fig. 1 shows the normalized absorption spectra ± S.E. of *U. penicilliformis* and *U. neglecta*. This figure is the result of measurements on 15 different *U.*

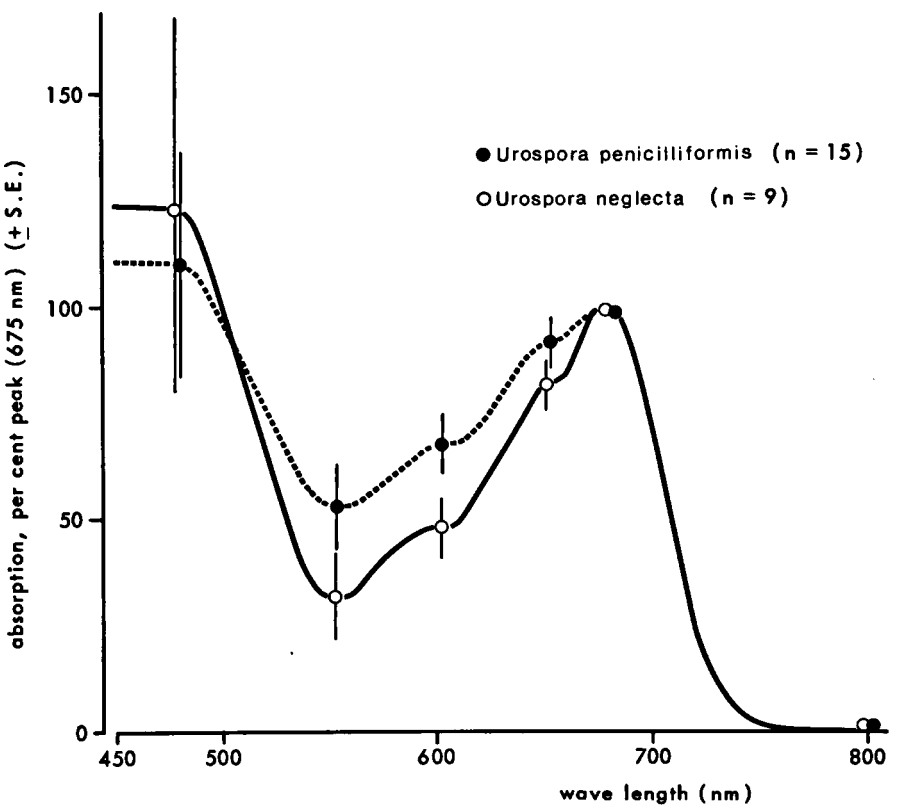

Fig. 1. Absorption spectra of whole filaments of *Urospora penicilliformis* and *U. neglecta*.

penicilliformis cultures and 9 different *U. neglecta* cultures. The spectra of these two species are significantly different. Significant differences in the absorption spectra of these two species are observed with this technique even when the filaments are obtained from varied cultural conditions (data here are average measurements). The differences are especially evident in the wavelength range from 550 to 600 nm. This may indicate a higher concentration of accessory pigments, such as carotenoids, in the filaments of *Urospora penicilliformis* than in *U. neglecta*. The carotenoids have an absorption maximum near 480 nm. A comparison of the absorption spectra of *U. neglecta* and *U. penicilliformis* is, therefore, useful as an additional, quantifiable parameter to discriminate these two species.

The chloroplast of *U. neglecta* is granular and yellow-green in filaments from the field. This may indicate a less favourable environment there. The chloroplast is often contracted away from the longitudinal inner cell walls and may not always completely coat the transverse cell wall in young filaments. In mature cells, the parietal chloroplast is equally distributed over the inner cell wall giving a *Microspora*-like growth habit.

The pyrenoids appear very distinctly due to the thinness and the light colour of the chloroplast. They are, on the average, 1 μm larger than those of *U. penicilliformis*. In addition, mature cells of *U. neglecta* contain fewer pyrenoids than *U. penicilliformis* cells.

Both in nature and in culture, the filaments of *U. neglecta* are attached to the substrate by a reduced basal holdfast. In its smallest and most common form, the holdfast consists of only one or two short rhizoids coming from the most basal cell(s). The holdfast can consist of 3 to 5 rhizoids under certain conditions. *U. neglecta* clones collected from sheltered localities were tested under aeration to simulate the agitation undergone by the filaments with wave action. However, the basal cell remained reduced under these turbulent conditions. In nature, the rhizoidal basal cell is usually short, up to 3 to 5 times its width. The cell wall often has hyaline thickenings posteriorly, possibly to ensure a firm(er) attachment to the substrate. In culture, the tips of the rhizoids may form finger-like protuberances. The basal holdfast in most cultures of *U. neglecta* in this research were smaller than those pictured by KORNMANN (1966b) when he described the species. Basal cell development into a rhizoid in 1–7-celled germlings is often later than in *U. penicilliformis*. The undifferentiated cell normally adheres to the substrate by an inconspicuous hyaline disc. However, in one case, bipolar rhizoid development was observed in a 2-celled germling. In general, the development of the rhizoid proceeds slowly. Vegetative cells adjacent to empty zoosporangia may develop rhizoids which grow into the lumen of these empty neighbour cells. As observed for *U. penicilliformis*, *U. neglecta* may develop interstitial rhizoids which arise from vegetative cells higher up in the filament.

Because many earlier authors did not recognise the separate status of the closely related species, *U. penicilliformis* and *U. neglecta*, some aspects of the reproduction of the latter have been described for the former (ARESCHOUG 1866; JORDE 1933). It was KORNMANN (1966b) who completed the life history of

Urospora neglecta for the first. Additional features are given here.

Reproduction is generally by means of zoospore production. A high zoospore production normally takes place within five days after refreshing the liquid culture medium. Zoosporogenesis usually starts in the apical part of the filaments and proceeds downwards. Sometimes, however, zoosporogenesis begins in the middle of the filament. In the tide simulating apparatus, zoospore production was exceptionally high. Under continuous light conditions for 8 weeks, high zoospore production was also observed. However, the germlings remained small for the duration of this experiment. Cultures of *U. neglecta* in which the filaments were almost dead after freezing showed a strong recovery through zoospore release. In experiments in which the filaments were exposed to ultraviolet illumination at room temperature once per day for three consecutive days, zoospore production was defective. Zoospores were 1/4 to 1/2 their normal size and had misformed, thick flagella.

In completely filled zoosporangia, the zoospores are arranged radially. In longer zoosporangia, the zoospores cover only the transverse cell walls. The zoospores are released through a lateral pore opened at the site of a swelling in the cell wall. The zoospores of *U. neglecta* are significantly larger than those of *U. penicilliformis*. The average ($\pm$ S.E.) zoospore length of *U. neglecta* was 35.4 $\pm$ 5.6 μm versus 25.3 $\pm$ 5.2 μm for *U. penicilliformis*. The zoospores vary in width resulting in some zoospores which are slender and others which are robust.

Unfortunately, except in one case no sexual reproduction was induced under any of the experimental conditions listed in *table 1*. In that particular case, female gametes were produced in a culture 6–7 weeks after exposing that culture to high intensity light shocks lasting three hours on three consecutive days. It is doubtful whether the gamete production was directly caused by the light shock treatment since it occurred so long after the treatment and only one of the three *U. neglecta* cultures receiving this treatment responded in this way. The produced gametes in this culture were atypically small (13 μm by 4 μm). Gamete producing cells were observed in natural material collected at Vlissingen (26/5/1979) and West-Kapelle (22/5/1978) (Zeeland, The Netherlands). These were kept in the laboratory at 4°C. Gametes appear to be released in the first few hours of the light phase. Male gametangia can easily be recognized by their colour, a very pale golden green, and the division of the contents into small bead-like bodies. In general, the male gametangia are more swollen than their vegetative neighbours. Male gametes move agitatedly in the gametangia before release. They are released simultaneously in a hyaline vesicle. After a moment, this ball of male gametes explodes as all the gametes move rapidly and jerkingly away. The male gametes in this study were similar in size and shape to those described for *U. neglecta* by KORNMANN (1966b). The chloroplast is parietal and usually positioned against the posterior cell body membrane.

The female gametangia are difficult to distinguish from zoosporangia. While still enclosed inside the mother cell, the female gametes are approximately the same size as zoospores and have the same colour. They are, however, arranged more randomly in the cell than the radially arranged zoospores. In addition, the

eyespots of the individual gametes are normally visible in the female gametangia. The female gametes are released singly from the gametangia. They move slowly with a spiral gliding movement using their flagella. The size and shape of the gametes corresponds to the reported findings of KORNMANN (1966b). The red stigma is usually positioned medianly in the chloroplast. The chloroplast is parietal and irregularly covers about 2/3 of the cell membrane. There is one pyrenoid.

Fusion is conspicuously anisogamous and is followed by the rounding-up process and subsequent attachment. When brought under 8°C/SD conditions, the zygotes developed into small globose and obovoid *Codiolum*-plants with or without a very short stipe. The total length of these sporophytes was up to 165 μm and the width up to 50 μm. This type of *Codiolum*-plant corresponds with the sporophyte which KORNMANN (1966b) described for *U. penicilliformis*. As stated earlier, the morphology and the shape of the *Codiolum*-phase in *Urospora* is affected by external parameters. KORNMANN (1966b) described the sporophytes of *U. neglecta* as clearly differentiated into a club and a stipe and with a total length of more than 1 mm. In this study, *Codiolum*-plants of *U. neglecta* were found in nature (Vlissingen, The Netherlands) which approximately corresponded to the size and shape reported for Heligoland material by Kornmann. The effect of environmental conditions is further illustrated by the fact that female gametes, ripened in natural filaments from Vlissingen, developed parthenogenetically into completely different sporophytes than zygotes did. Only a few sporophytes with short stalks could actually be described as *Codiolum*. The vast majority of the sporophytes were curved, elongate plants. One end was often more swollen than the rest in some cases, but there was never a stipe present.

In a clone from West-Kapelle, The Netherlands, akinete formation was observed. These reproductive cells were serially arranged and globose. Each was thick-walled whereas the mother cell wall of the filaments was very thin and seemingly soft.

Origin of material in culture

Uni-algal cultures were initiated from plants collected from the following localities. DENMARK: Venø Sund, Limfjorden, on a wooden piling in the splashzone. THE NETHERLANDS: Termunten, in a fairly sheltered point on granite blocks; Grevelingen, an inland salt lake, on wooden pilings in the splash zone; Gorishoek, on dead *Salix*-branches, which acted as a buoy, in the high littoral; West-Kapelle, on the northwestern side, on wooden pilings of a jetty, intermingled with *Rhizoclonium riparium* and *Pilayella litoralis* (collected as filaments and as *Codiolum*-plants); Vlissingen, in the high littoral on the vertical side of a thick cement block, in the company of blue-green algae (collected as filaments and as *Codiolum*-plants).

5. ULTRASTRUCTURE – *Plates 8–13*

The study of the ultrastructure of the *Urospora* species treated in this report did not reveal any characteristics by which the species could be discriminated. Therefore, the ultrastructural features summarized here should be regarded to be representative of the entire genus *Urospora*. The ultrastructure of the filamen-

tous thallus, the *Codiolum*-plants and the zoospores will be discussed.

Cell division. From light microscopical observations, KORNMANN (1966a) described details of the cell cleavage process in *U. wormskioldii* and *U. penicilliformis*. Before the formation of what KORNMANN (1966a) called the cell plate, some nuclei arrange themselves in a line at the equatorial plane. After synchronous mitosis has taken place, the developing cell wall is differentiated from uniting phragmoplasts of neighbouring spindles.

Our electron microscopical observations of *U. neglecta* reveal that the formation of daughter transverse cell walls occurs through furrowing. The initiated septum extends into the cell lumen as an ingrowth from the existing lateral wall, thereby dividing the chloroplast. No longitudinally or transversely oriented microtubules are involved with the developing septum. The furrow is surrounded by highly active cytoplasm with numerous mitochondria, ribosomes and vesicles probably containing precursory cell wall material. It seems that the cytokinesis in *Urospora* is fundamentally similar to that observed in *Klebsormidium* (FLOYD et al. 1972; PICKETT-HEAPS 1972), *Ulva* (LØVLIE & BRÅTEN 1970), *Stichococcus* (PICKETT-HEAPS 1974) and *Ulothrix* (LOKHORST 1978). The starting point for the cleavage process of the chloroplast in *Urospora* is comparable to that in the brackish-water and marine species *Ulothrix implexa* and *U. flacca* (LOKHORST 1978). The daughter nuclei remain together during cytokinesis in *Urospora* whereas they reside near the ends of the cell until the cleavage is completed in *Klebsormidium* (l.c.). This difference may be due to the difference in cell lengths in these genera.

Cell wall. Electron microscopical observations on the cell wall of the filamentous phase confirm previous findings with light microscopy. The cell wall is bordered on the outside by a continuous smooth envelope. This apparently consists of a double membrane. It may be covered by a thin, amorphous, gelatinous layer in which bacteria and microparticles are anchored. Depending on the environment, the cell wall can become quite rough with these particles. In culture, the cell wall is normally smooth and sparsely overgrown with bacteria. In contrast, filaments of natural material can be so coated with embedded particles so as to obscure the outer membranes of the cell wall. At irregular intervals, the cell wall may show local swellings. Two main layers can be seen in the lateral cell walls beneath the outer membranes. The outermost layer is electron-dense and consists of microfibrils which in longitudinal section seemingly run parallel to each other. The inner layer varies in thickness, consists of 2 to 3 sublayers and is mostly fairly electron-lucent. It contains microfibrils running parallel to the cell contents. The innermost sublayers also contribute to the formation of the transverse cell wall. The inside of the cell wall is often undulating, frayed or fringed toward the cell contents. The cell wall of the club of the *Codiolum*-plants is bordered by two coarse, parallel membranes and it consists of two main layers. The inner layer of the cell wall is more electron-lucent than the outer layer. However, strands of more electron-dense material are sometimes present here. A thin gelatinous sticky substance is present on the cell wall surface. Considerable numbers of bacteria and blue-green algae are often embedded in

this substance. In the transition area between club and stipe, the outer surface of the cell wall is deeply fissured. The inner layer is distinctly stratified in this area by concentric, electron-dense rings which run parallel to the contents of the club.

Chloroplast. Electron microscopical data on chloroplast structure support the observations made with light microscopy. In adult cells, the reticulate chloroplast covers both the transverse and lateral cell walls completely, but is separated from the wall by a thin layer of cytoplasm and the undulating plasmalemma. In sections, the chloroplast may extend as a more or less continuous mass, but it is usually present in separate finger-like extensions, lobes or thick strands. These protrusions extend inwards towards the cell lumen. The openings in the chloroplast are usually filled with cytoplasm. The space between the double chloroplast membrane is of variable thickness. In some cases, the membrane has a wavy appearance.

In the (finger-like) lobed areas of the chloroplast, the thylakoids lie almost parallel to the length axis of the chloroplast. They end abruptly just before reaching the chloroplast membrane. The thylakoid may be single, but there are usually several (up to ten) thylakoids in straight or undulating lamellae. One or two thylakoids may leave one lamella and pass into another, creating a reticulate appearance. In some longitudinal sections, thylakoids are seemingly associated in conspicuously short lamellae. This arrangement resembles the thylakoid arrangement in granal and intergranal regions found in *Ulothrix implexa* and *U. subflaccida* (LOKHORST 1978). The two membranes of an individual thylakoid are usually not parallel. Furthermore, the individual thylakoid may terminate somewhat dilated.

The chloroplast stroma contains ribosomes. There are osmiophilic plastoglobuli in varying numbers between the chloroplast lamellae. They lie separately, in groups or are arranged in one or two parallel series. The latter arrangement is seen predominantly in one-celled germlings. These plastoglobuli resemble rudimentary eyespots. The plasmoglobuli vary in size and are circular-ellipsoid. Elongated (sometimes spherical) starch grains are usually distributed in the chloroplast. The margin of each starch grain usually appears denser than the inner area. Most starch in the cell is present in the segmental grains, up to 12 per section, in the monolayer of starch surrounding the pyrenoid. Some sections, however, contained pyrenoids which were (partially) without starch grains. In other cases, starch grains could be found irregularly piled up around the starch shell of the pyrenoid. This accumulation of extra starch obscures the contours and the matrix of the pyrenoid for the light microscopist.

The *pyrenoid* is positioned between the lamellae of the chloroplast. The pyrenoid normally protrudes from the chloroplast into the cell lumen, but is still bordered by some chloroplast stroma and its envelope. The finely granular pyrenoid matrix is penetrated by tubular chloroplast invaginations on all sides. The invaginations branch repeatedly in the matrix so as to appear reticulate. The frequency of branching and the dimensions of the branched strands differ from section to section. In some sections, only two coarse strands were seen; in others, the branched intrapyrenoidal chloroplast lamellae were present in only half of

the sectioned matrix. Bundles of thylakoids, up to six in number, succeed in invading the starch shell through gaps between the starch grains. The thylakoids normally terminate abruptly partway across the gaps or at or just below the surface of the pyrenoid. Only the chloroplast stroma continues into the matrix. However, in one section, remnants of a thylakoid membrane seemed to be present in a branched intrapyrenoidal tubule. Another exceptional situation was observed where the chloroplast invagination, containing a bundle of 6–8 thylakoids, did not enter the pyrenoid after passing the intergranular gap, but continued in the space between the starch layer and pyrenoid. The continuous bundle left this area through the nearest gap.

The increase in the number of pyrenoids in maturing or dividing daughter cells takes place through cleavage of existing pyrenoids. During this process, the pyrenoids elongate considerably and are bisected by the inward growth of 1 to 3 chloroplast strands containing about five thylakoids. The continuous starch shell breaks up during this separation. The production of the starch grains needed to complete the interrupted starch shell apparently begins after the daughter pyrenoids are separated a distance from each other.

The reticulate nature of the *Urospora* pyrenoid matrix is similar to that reported for the chlorophycean algae *Oedogonium* (HOFFMAN 1968), *Bulbochaete* (RETALLACK & BUTLER 1970), *Ankyra* (SWALE & BELCHER 1971), *Oedocladium* (MARKOWITZ & HOFFMAN 1974), and *Hafniomonas* (ETTL & MOESTRUP 1980). In these genera, however, the starch shell and the pyrenoid matrix are invaded by invaginations coming from the cytoplasm and not from the chloroplast as in *Urospora*. These invaginations pass a considerable distance through the chloroplast before reaching the pyrenoid. The lumen of each intrapyrenoidal cytoplasmic tubule consists of a dense core lined by two membranes from the chloroplast envelope. Hypotheses on the phylogenetic relationship of these pyrenoids would be premature. Nevertheless, we are inclined to consider the pyrenoid with intrapyrenoidal cytoplasmic invaginations to be more primitive than the pyrenoid found in *Urospora*. Perhaps the pyrenoid functions more independently of the cytoplasm in starch production in *Urospora* than in these other genera.

Nucleus. Several nuclei could be observed in each cell in longitudinal sections of *Urospora* filaments. Normally, the nuclei are approximately circular in section. One side of the nucleus is usually adjacent to the chloroplast and is separated from it by a small strand of cytoplasm. In what appear to be metabolically active cells, the nucleus is surrounded by a complex network of mitochondria, dictyosomes and accompanying vesicles. The single nucleolus is usually circular in shape and usually lies in the central part of the nucleus. The nucleus matrix contains two types of chromatin. The inner membrane of the nuclear envelope is smooth; the outer membrane seems to be ribosome-studded and is continuous with the cytoplasmic endoplasmic reticulum. The two membranes undulate independently in some areas. The nuclear membrane is perforated at irregular intervals.

Mitochondria. The number of mitochondria may vary among sections. They lie randomly in the cytoplasm, even in the thin strand of cytoplasm between the

chloroplast and the cell wall. The mitochondria are predominantly oval or circular in cross-section, but are occasionally (curved) elongate. The individual cristae in the mitochondria may be arranged parallel to one another in a section, but in most cases they are irregularly oriented. In some cases, the base of the crista is slightly constricted. As in *Ulothrix* (LOKHORST 1978) all mitochondria are of the same type. The type can be described as the narrow cristate form with a relatively electron-dense matrix. In one particular case, a mitochondrial profile was found with a swollen appearance. The cristae were still irregularly implanted along the inner periphery of the mitochondria. The center of the mitochondria was filled with vesicular and membraneous structures. This rare case may be the result of a lytic process.

Golgi apparatus. The Golgi apparatus is usually located near (new) cell walls and in the vicinity of nuclei. It is usually made up of an array of several dictyosomes. The individual dictyosomes consist of a stack of up to twelve cisternae. There is a gradual change in the diameter of the individual cisternae from one pole to the other. Vesicles containing small, electrondense granules are found as buds on the lateral ends of the individual cisternae. Small multivesicular bodies are also found in the immediate vicinity of the Golgi apparatus. These bodies contain small vesicles arisen apparently from the edges of the Golgi cisternae and subsequently aggregated.

Cytoplasmic inclusions. Osmiophilic fat droplets are occasionally found in the cytoplasm of *Urospora* cells. They are usually single, are variable in size and are spherical, (sinuous) elongate or ovoid. Peroxisomes are found in cytoplasmic strands that are pinched between chloroplast lobes containing pyrenoids.

Membranous inclusions like those observed in *Ulothrix speciosa* (LOKHORST 1978) were also found in *Urospora* cells. Their function is unknown. These inclusions consist of an irregular membrane system, varying from a single, simple ring of membranes to complexly organized whorls of concentric lamellar rings. In some cases, the inclusions seem to be continuous with endoplasmic reticulum strands. In *Urospora wormskioldii*, remnants of these inclusions were encountered in vacuolar vesicles. These vesicles may represent pieces of degraded endoplasmic reticulum which will eventually be transferred to the cell vacuole to be broken down.

Elongate, flat structures were observed in cultured clones of *U. wormskioldii* collected from Hvide Sande, Denmark. They were made up of hexagonal structures. These may represent a virus-like inclusion. A peculiar sort of inclusion consisting of irregularly packed vesicular subunits was found in other sections. The possibility that this inclusion is an artifact of the preparation procedure can not be ruled out.

Vacuoles. Cells in one- and two-celled germlings generally already contain one single large central vacuole. Smaller and variously shaped vacuolar vesicles are found in the cytoplasm surrounding the cell lumen. Depending on the rate of metabolic activity in the cell, the electron density of the vacuolar matrix can vary.

Zoospores. KRISTIANSEN (1974) published the first ultrastructural information about on the zoospores of *Urospora penicilliformis*. To better study the phylo-

geny and taxonomy of the green algae, the ultramorphology of the zoospore's flagellar apparatus was studied in further detail by SLUIMAN et al. (in press). In most respects the results of Sluiman et al. confirm the description given by Kristiansen. However, details were added which helped in placing *Urospora* in the overall classification of green algae. The question remained from these studies whether the same flagellar apparatus was found in all *Urospora* species. The present study shows that the ultrastructure of the zoospores of *U. wormskioldii*, *U. bangioides* and *U. neglecta* is fundamentally similar to that of *U. penicilliformis*. The majority of the data presented here was obtained from longitudinal and transverse sections of the zoospores of *U. bangioides*.

The flagellar apparatus is diagrammed in *fig. 2*. The four flagella emerge from cavity-like niches in the cruciform papillae, i.e. from between the four papillar ridges or lobes. The flagella, which are rather stiff, bear two keels. Each flagellum has 4 or 5 longitudinal parallel wings which project from the single peripheral microtubules in the flagellar axoneme. Distally, the wings gradually shorten. Each wing becomes curved and they depart from their parallel orientation. The wings disappear in the most distal part of the flagella. In longitudinal sections, the outline of the flagellum is wavy. In the transition region between the basal bodies in the cruciform papilla and the keel bearing area, the flagella are narrowed. Near the basal bodies are approximately ten electron-dense parallel lamellae which lie close to one another. These lamellae lie perpendicular to the longitudinal axis of the flagellum.

By analysing serial transverse and longitudinal sections of the papilla, five different types of (striated) elements have been found in the flagellar root system.

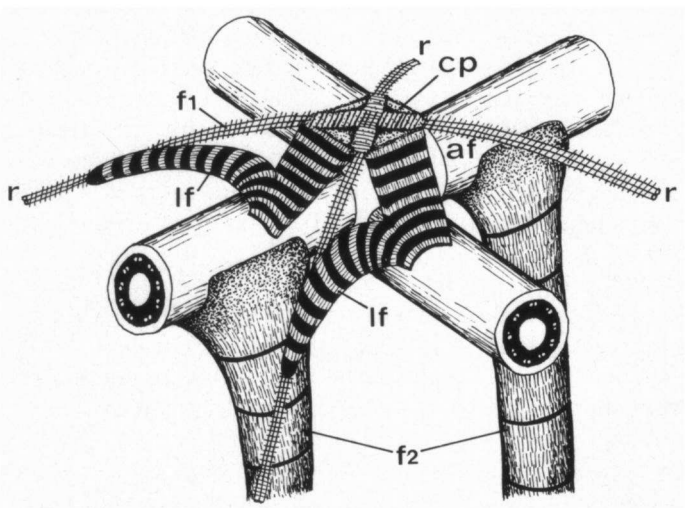

Fig. 2. Diagrammatic representation of the flagellar apparatus of the zoospore of *Urospora* in which most of its structural components are depicted: ascending fiber (af), lateral fiber (lf), microtubular roots with associated system I striations (r, f_1); system II striated fiber (f_2), capping plate (cp), and internal structure of wingbearing portion of flagellar axoneme. This figure is from the paper of SLUIMAN et al. (in press).

One of these is composed of microtubular roots which are associated with an electron-dense plate-like structure in the center of the papilla. This structure will be referred to as capping plate (cp). The remaining four are associated with the basal bodies. The microtubular roots run via the longitudinal lateral ridges in the direction of the posterior end of the zoospores. The ridges are visible with light microscopy as four fine hyaline projections ornamenting the periphery of the zoospore. Because of these ridges, the zoospore is more or less quadrangular in profile when sectioned transversely. The number of microtubules can vary from about four in the papilla to about seven distally. The microtubular roots seem to be held together by the two parallel electron-dense layers. In longitudinal sections, both layers show a striation pattern composed of alternatingly thin and relatively thick electron-dense lines. MELKONIAN (1980) defined this type of root system as the system I striation pattern. The system I striations of opposing roots clearly continue into the papilla; they run through the capping plate area. The microtubules terminate near the plate region. In *Urospora neglecta*, there appear to be two parallel capping plates, each cleaved by one of the striated, electron-dense layers. A small electron-lucent space is discernable between the parallel plates. The microtubules of the root terminate near this space.

The first of the striated structures associated with each basal body is an ascending striated fiber (af). This fiber links the basal body to the capping plate associated with the flagellar root. It is composed of transverse dark striations and longitudinal fibrillar subunits. The second striated fiber (lf) appears to link each basal body to an adjacent microtubular root. It can be thought of as a side branch of the ascending fiber. The micro-anatomy of the lf is fundamentally the same as that of the af. The number of dark striations is higher in the lf, however. The third type of striated element is made up of four fibrous elements which bridge the adjacent basal bodies(ce). They are composed of a few dark striations and longitudinal fibrillar subunits. In transverse sections of the papilla, these elements are easily recognised by their electron-lucent X-configuration which appears to be embedded in the opaque matrix of the basal body. The same sections reveal that the flagella are not inserted precisely symmetrically into the papilla. Probably for that reason, the basal bodies are not arranged precisely in a line. The fourth type of striated structure is one that is associated with two opposing basal bodies. This structure descends into the cell lumen of the zoospore, passing closely along the nucleus and terminating near the chloroplast. This striated structure is known as the rhizoplast or the system II striation fiber (MELKONIAN 1980). In some cases, the rhizoplast appears to leave the attachment structure as three barely-separated subunits. The rhizoplast is approximately reniform in cross-section. The fibers are divided into zones by transverse dark striations. Near the basal body, these striations are more frequent, resulting in an irregular periodicity. The longitudinal fibrillar subunits of the rhizoplast are distinct.

Superficial cytoskeletal microtubules have occasionally been seen in longitudinal sections in areas between the papillar ridges. In well-prepared transverse sections, these microtubules are also found just beneath the outer membrane

along the entire periphery of the zoospore. They descend separately to the posterior portion of the zoospore. The cytoskeletal microtubules do not appear to be associated with the basal bodies, in as much as they can be found in sections of the most apical area of the papilla. It is possible that they run from one side of the zoospore to the other and that they are continuous in the papilla. In this way, these microtubules together form an umbrella-like skeleton. The microtubules terminate before reaching the tip of the tail of the zoospore. It is plausible that the higher number of microtubules in the root at the longitudinal ridges is the result of a fusion of cytoskeletal microtubules with the microtubular root bundle. Some photographs suggest this fusion process by showing an individual microtubule which approaches the bundle closely. The distance between the remaining cytoskeletal microtubules is constant. However, this hypothesis is weakened by observation of the longitudinal ridge in transverse sections. One or two separate microtubules are also observed in addition to the descending root. They are situated beneath the surface of the ridge and above the dorsal system I striated fiber, which coats the bundle of root microtubules.

The remaining ultrastructural aspects of the *Urospora* zoospore are similar to those adequately discussed by KRISTIANSEN (1974) and SLUIMAN et al. (in press). However, the presence of peculiar globose microbodies in the papillar lobes near the implantings of the flagella should be mentioned. The central matrix of these microbodies is moderately electron-dense and is encircled by an electron-lucent ring. These microbodies are bounded by a characteristically crenated outer membrane. The membrane appears to be spliced from two pieces over a short distance.

Despite its cup-shaped appearance under the light microscope, the chloroplast of the zoospore is frequently separated into pieces when viewed in transverse section. These pieces extend as separate lobes along the inner periphery of the zoospore. There is always a small strand of cytoplasm, usually containing vesicles and mitochondria, between the lobes and the zoospore cell membrane.

Extracellular mucilaginous appendages can be seen on the surface of the papilla. The presence of wart-like protrusions on all four longitudinal ridges of the released zoospore (SLUIMAN et al., in press) could not be detected in zoospores which are still inside the zoosporangium cell wall. These protrusions probably have a function in the crawling movement of zoospores and are, therefore, only connected with the free-living swarmers.

6. DISCUSSION AND CONCLUSIONS

This study has revealed the existence of four *Urospora* species in Western Europe, namely, *Urospora wormskioldii*, *U. bangioides*, *U. penicilliformis* and *U. neglecta*. It is not necessary to adopt KORNMANN's (1963) suggestion to conserve the later erected name *Urospora* ARESCHOUG (1866) against the name *Codiolum* Braun (1855). *Codiolum* represents merely a form genus and must therefore be indicated as a legitimate synonym to the genus *Urospora*. SILVA's (1957) new combination *Codiolum penicilliforme* and those of DEN HARTOG (1959) are therefore rejected.

The controversial name *Urospora bangioides* is maintained. In 1966b, KORNMANN recognised this species as a growth habit of *U. penicilliformis*. However, we found it to be a distinct and separate entity.

The species delimitation of the largest species, *U. wormskioldii*, is relatively easy to establish. *U. wormskioldii* is distinguishable from the remaining *Urospora* species by the development of zoospores into dwarf plants at temperatures at or above 8°C. The distinctly barrel-shaped or spherical vegetative cells in mature filaments, the large cell size (individual cells can be observed with the naked eye), the shape of the zoosporangia and the arrangement of the zoospores inside the mother cell all contribute to an unequivocal distinction of this species.

The above features give *U. wormskioldii* a rather isolated position in the genus *Urospora*. The remaining three species form a taxonomic group of closely related forms. The range in the cell diameters of these three species are wide and overlapping. All three have basically cylindrical cells. These characteristics are, therefore, inadequate for the identification of these species. Additional species distinguishing characteristics have been found in the study of the basal holdfast, the colour, the zoospore development and the reproduction and life history of these three species. Unfortunately, all features necessary for an accurate species identification are not always available in filaments from natural environments, particularly when the material is scarce. In that case, algal cultures must be employed for an accurate identification.

The two species, *U. penicilliformis* and *U. bangioides*, are distinguishable from *U. neglecta* by their extensive holdfast development which is most pronounced in cultures. The basal holdfast of *U. neglecta* is reduced to a single rhizoid in the field and to normally 2 rhizoids in culture. Holdfasts on natural filaments of *U. penicilliformis* consist of 3 to 5 rhizoids. In cultures, there are normally at least 10 rhizoids arising from as many basal cells (maximally 20 to 25). We can report little on the holdfast of *Urospora bangioides* in nature. However, in culture, up to 49 rhizoids develop from the most basal cells in this species. In culture, 1- to 2-celled germlings of both *U. penicilliformis* and *U. bangioides* show the development of rhizoidal outgrowths. This rhizoidal development occurs usually later in the germlings of *U. neglecta*. Although the differences in the holdfast development are smaller in nature, the holdfast form still remains a useful identification criterium for carefully collected *Urospora* species. To lessen the risk of breaking the rhizoids off with collection, we advise collecting the filaments of these algae along with the substrate on which they are growing. Careful analysis of the basal part of the filament can be made with a stereomicroscope in the laboratory. Even with these precautionary measures, the holdfast may be obscured by molds, bacteria and blue-green algae.

In the past, the presence of intramatrical and extramatrical rhizoids which develop from the basal part of the filaments has served as a taxonomic criterium. *Urospora mirabilis* (here synonymous to *U. penicilliformis*), for example, was separated from *U. wormskioldii* with BØRGESEN's observations (1902) that the former had both intra- and extramatrical rhizoids whereas *U. wormskioldii* showed only extramatrical ones. PRINTZ (1932) felt that the rhizoids of *U.*

wormskioldii are originally intramatrical but break out of the cell wall to become extracellular. This phenomenon was also observed in this study for *U. penicilliformis* collected from Huisduinen (The Netherlands). HANIC (1965) reported that the rhizoids of cultural filaments of *U. wormskioldii* are always extramatrical unlike their natural counterparts. This could be explained by the suggestion that in natural environments strongly exposed to wave action, the developing rhizoids are prevented from growing through the thick cell wall. They are then first forced to develop themselves inside the cell wall. This, however, was not born out under experimental conditions using aeration flasks to simulate wave action. The intramatrical rhizoid growth may, in fact, be an optical illusion. The basal portions of natural filaments are often heavily overgrown with micro-organisms and studded with microparticles, thereby obscuring the true nature of the holdfast. An incorrect diagnosis of extracellular rhizoid development may also be made when short sticky rhizoids, springing laterally from the basal part of the filament, lie between the outline of the lateral walls during observation. In our opinion, BØRGESEN (1902) may have made this optical mistake when comparing intra- and extramatrical rhizoids.

The two species, *U. penicilliformis* and *U. bangioides*, are not easily distinguishable at the germling stage. At maturity, the typical cell shape of *U. bangioides* appears, especially in culture. The cells are isodiametric or, when longer than wide, rectangular. The chloroplast of *U. bangioides* shows a slight colour change to dark green or olive green with maturity and the cell wall becomes thicker. Nevertheless, cells in the filaments of *U. bangioides* may also become flattened lengthwise as observed for *U. penicilliformis*. In that case, other features must be used for species identification. If many filaments are collected, the absolute range in cell diameters can be useful. If filamentous material contains fully developed zoosporangia, these may provide helpful characteristics. Zoosporangia in mature filaments of *U. bangioides* contain hundreds of zoospores, their contents are frequently olive-green and the zoospores usually lie parallel to the surface of the cell or occasionally in star-shaped clusters. The zoosporangia of *U. penicilliformis* contain fewer zoospores, are always dark green and the zoospores are normally arranged radially. Moreover, the individual zoospores of *Urospora bangioides* are, on the average, smaller and faster in locomotion than those of *U. penicilliformis*. These features are more easily recognizable in cultured material.

In addition to the degree of holdfast development between the two species, *U. penicilliformis* and *U. neglecta* can further be delineated by differences in the colour and density of the chloroplasts, the absorption spectra, the size and number of pyrenoids per cell, the size of the zoospores and the shape and size of the female gametes. The measurement of absorption spectra may prove to be a rapid means of distinguishing algae species (TRASK et al., in press). Although the holdfast development and the colour and form of the chloroplast are the most reliable characteristics, it is necessary to use all these characteristics collectively in order to make an accurate species identification. For example, in cultures at 8°C/LD, the basal holdfast of *U. penicilliformis* is reduced while that

of *U. neglecta* is more developed. In these cultures, species discrimination could be based on chloroplast colour and form. The size of the zoospore is a useful characteristic only when many zoospores can be measured. In that way, an accurate range in dimensions and an average size can be calculated for each form. Even though the zoospore size distributions of the two species are nicely separated, measurements on only a few individual zoospores may lie in the area of overlap. Cell size and the number and size of pyrenoids are the least useful of the species characteristics. The distributions of these parameters overlap considerably. These measurements should only be used to supplement the more predictable characteristics in the repertoire.

In unfavourable growing conditions, a distinction between *U. bangioides*, *U. penicilliformis* and *U. neglecta* is difficult to make. The colour of the filaments becomes yellow, zoosporogenesis is defective, cell diameter development is retarded, the number of interstitial rhizoids increases and the chloroplast is broken into large pieces in all three species. However, when these ailing plants are reinoculated into fresh medium, they develop the specific species characteristics noted above.

It was not possible to induce sexuality in cultured filaments. Although an increase in oxygen concentration was found to stimulate gamete production in the freshwater genus *Chlamydomonas* (COLEMAN 1962), it did not do so in *Urospora*. Deficiencies in nitrogen and phosphate in the culture medium, reported to induce sexuality in some algae (DRING 1974), did not affect *Urospora* filaments. Presumably, combinations of conditions similar to those in nature must be carefully timed and coordinated in order to induce sexuality in cultures. It is difficult to reproduce the natural situation completely *in vitro*, and that is what appears to be required by *Urospora* for sexual reproduction. The data on gametes and sporophytes were obtained from natural material, from natural material brought into culture, and from the few unexplained cases where gametogenesis occurred in culture. By combining data from cultural and natural material, the life histories of *U. penicilliformis* and *U. neglecta* could be completed. This was not the case for *U. wormskioldii* and *U. bangioides*. In these species, sexual plants were not encountered. The presence of the *Codiolum*-phase in their life cycles, however, has been proved in these studies.

It can be concluded from this study that the description of the life histories of *Urospora* species cannot be based solely on cultural material. *Codiolum*-plants in culture are smaller and their shape different from their natural counterparts. The findings that *Codiolum*-plants of a given *Urospora* species may assume different growth habits in nature is reinforced by the analysis of several *Urospora wormskioldii* populations. Because the shape of filaments in culture is reasonably similar to the shape of filaments in nature, the change in the form of the *Codiolum*-plant upon culturing is surprising. Necessary trace nutrients or daily drying with high temperature may be missing from the cultural conditions. An analysis of cell wall substances in the *Codiolum*-plants may explain this form change. While slicing *Codiolum*-plants for electron microscopy, scratches in the sections appeared. This may indicate that the cell wall of the *Codiolum*-plants

contains a very hard substance similar to the silicates present in the cell walls of brown algae and diatoms. It is most probable that *U. wormskioldii* does not produce sexual plants in Western Europe. No sexual plants of this species were found in nature or under any experimental condition used in this study. It can also be concluded from herbarium studies that *U. wormskioldii* from Western Europe does not reproduce sexually. No gametangia could be found in the relatively large quantities of dried specimens available. Zoosporangia were, on the other hand, abundantly present. Instead, *U. wormskioldii* produces dwarf plants which germinate from zoospores matured in filaments. From our data from cultural experiments, one can hypothesize that zoospores in filaments present in winter and early spring in nature (as evident from the literature) produce dwarf plants when the temperature rises. Reproductive cells in the dwarf plants develop into *Codiolum*-plants in autumn. Indeed, many *Codiolum*-plants were encountered in the late autumn along the coasts of Western Germany, Denmark and The Netherlands. HANIC (1965), however, found sexual plants of *U. wormskioldii* from early spring to late September in a coastal region in southern British Columbia. From a phytogeographical point of view, this is interesting. If one assumes that *U. wormskioldii* is a taxonomic complex having a world-wide distribution, there may be populations which have developed or reduced their reproductive mechanisms.

In contrast to *U. wormskioldii*, gametes and zygotes from cultural and natural filaments of both *U. penicilliformis* and *U. neglecta* developed in culture to adult *Codiolum*-plants. In culture, these *Codiolum*-plants were smaller than their counterparts found in the field. The *Codiolum*-plants of all species show large variations in size and shape. Therefore, the genus *Codiolum* can only be considered to be a form genus which cannot be subdivided into species.

More studies on *Urospora bangioides* are necessary to clarify the role of sexuality in its life history. It is expected that there will be sexual plants found because *Codiolum*-plants are found in the field and no zoospores were observed to develop into a dwarf plant generation.

The morphology of the chloroplast has been extensively described. It is clear that its shape can be considered a generic characteristic, but within a species its form is age-specific. In germlings, it is girdle-shaped. Therefore, young *Urospora*-plants may be mistaken for *Ulothrix subflaccida* and *U. implexa*. There are, however, minute differences. The chloroplast of the *Urospora* germling is darker green; it is more irregular with point-like projections; and, it usually coats the transverse cell wall as well as the longitudinal wall. The reticulate chloroplast may be variably shaped in mature cells. It can vary from finely to coarsely perforated. In some cases, the chloroplast forms delicately connected strands spaced by large perforations as in *U. neglecta*. In some cases, it appears to be folded back upon itself in dense, thickened masses or lobes around a central lumen as in *U. penicilliformis*. In aged cells, the chloroplast may shrink into a centrally located body.

In contrast to the results for *Ulothrix* (LOKHORST 1978, LOKHORST & STAR 1980), ultrastructural studies here do not provide obvious differences in the

species of the genus *Urospora*. Ultrastructural differences among the species in cell wall surface, cell wall stratification, microfibril orientation in the sublayers of the cell wall, pyrenoids, chloroplast stroma and thylakoid arrangement, and zoospores including their flagellar apparatus were too small to consider them as diagnostic characteristics within the genus *Urospora*.

Despite the fact that we have not encountered *U. wormskioldii* or *U. bangioides* in large numbers in nature, we believe them to be pure euryhaline marine algae which occupy the middle and upper zone of the intertidal belt of open and naturally or artificially rocky shores. Information obtained from herbarium sheets confirms this assessment. Though *U. penicilliformis* and *U. neglecta* may invade brackish waters, they grow especially luxuriantly in the upper littoral of open coastal waters. Their tolerance for lower salinities has been confirmed in culture and they are presently considered to be euryhaline marine.

ACKNOWLEDGEMENTS

The authors are highly indebted to Professor Dr. C. Kalkman for the critical reading of the manuscript, to Drs. H. J. Sluiman (Free University, Amsterdam) and to Dr. J. S. Craigie, editor of the Journal of Phycology, for their permission to use figure 2 in the present paper, to Mr. W. Star for his expert technical assistance in electron microscopy and his great enthusiasm, to Dr. G. J. van den Engh (Radiologisch Instituut/TNO, Rijswijk) for making the spectrophotometer available for absorption measurements, to Mr. J. H. van Os and Mr. C. L. Marks for preparing the drawings and photographs for publication, and to Miss J. M. de Wolf for typing the manuscript. We are also grateful to the Directors and Curators of various herbaria and institutes mentioned elsewhere, for lending herbarium specimens.

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EXPLANATION OF FIGURES AND PLATES

For all plates the following abbreviations are used: af = ascending fiber; b = bacterium; c = chloroplast; cb = club; ce = basal body connecting fibrous element; cf = cleavage furrow; cg = plastoglobule; ci = tubular chloroplast invagination; cp = capping plate; cs = chloroplast strand containing thylakoids; f = flagellum; fl = system I striated root component; f2 = system II striated fiber (rhizoplast); g = Golgi-body or dictyosome; gv = vesicle derived from the Golgi apparatus; l = lipid droplet in the cytoplasm; lf = lateral fiber; mb = microbody; mvb = multivesicular body; p = peroxisome; py = pyrenoid; r = flagellar root; t = thylakoid; st = starch; stp = stipe; w = cell wall; wa = adhesive (mucilaginous i.e. micropartical) layer on the surface of the cell wall; wm = cell wall membrane.
In the figures the bar drawn represents a length of 20 μm.

FIGURES

Fig. 1. on p. 390.
Fig. 2. on p. 398.
Fig. 3. *Urospora wormskioldii.* – a. *Codiolum*-plants, collected from Thyborøn; b. their club in detail; c. *Codiolum*-plants, collected from Venø Sund; d. ditto, collected from Bogense; e. ditto, collected from Kiel-Stohl; f. ditto, collected from Hvide Sande; g. ditto, collected from Breezanddijk; h. ditto, collected from Glückstadthavn.
Fig. 4. *Urospora wormskioldii.* – a. zoospores ripened in *Codiolum*-plants, collected from Hvide Sande; b. zoospores, ripened in cultural filaments, originally collected from Vlissingen; c. bipolar germination of the attached zoospore; d. dwarf plant, not producing rhizoids. Note the presence of two less distinct zoosporangia; e. dwarf plants, producing rhizoids.
Fig. 5. *Urospora bangioides.* – a. zoospores, ripened in filaments; b. bipolar germination of the attached zoospore; c. portions of vegetative filaments, showing the variability in the growth habit of the individual vegetative cells.
Fig. 6. *Urospora penicilliformis.* – a. zoospores; b. bipolar germination of the attached zoospore; c. akinete formation in a filament; d. small filaments, showing a *Ulothrix*-like chloroplast; e. zoosporangia in a young filament. Note their high length/width ratio; f. filament with a swollen cell wall; g. filament with a *Microspora*-like growth habit; h. extensively developed holdfasts in natural filaments, collected from Venø Sund.
Fig. 7. *Urospora penicilliformis.* – a. filament with male gametangia; b. male gametes; c. filaments with female gametangia; d. female gametes; e. parthenogenetic development of the male gamete into stalked *Codiolum*-plants; f. parthenogenetic development of the female gamete into globose plants which, upon ripening, produce aplanospores; g. *Codiolum*-plants, collected from Vlissingen; h. detail of the attaching disc of the stalk of a natural *Codiolum*-plant. Note its rough appearance, caused by the coating of micro-particles.
Fig. 8. *Urospora neglecta.* – a. filament with male gametes and zoospores. Note the radial arrangement of the zoospores; b. filament with female gametangia. Note the non-radial arrangement of the gametes and the distinct eye-spot; c. zoospores; d. bipolar germination of the attached zoospore; e. bipolar rhizoid-formation in a germling; f. filaments with reduced holdfast consisting of one differentiated (basal) cell; g. female gametes; h. male gametes; i. zygotes; j. *Codiolum*-plant, ripened from a zygote in the laboratory.

PLATES

Plate 1. *Urospora wormskioldii.* – 1. spherical zoosporangia with zoospores arranged in star-shaped clusters, × 118; – 2. zoosporangia in a relatively thin filament, × 290; – 3. zoosporangia with releasing zoospores, × 147; – 4. zoosporangia. The left filament contains zoosporangia which are not completely filled with zoospores. They are arranged in connected strands enclosing large vacuolar lumina, × 210; – 5. swollen basal ends of the stalk of *Codiolum*-plants (arrows) which are

anchored in a dense mass of micro-organisms (molds, unicellular algae), × 572. Collected from Thyborøn (Denmark).

Plate 2. *Urospora wormskioldii.* – 1. vegetative cell showing the finely reticulate appearance of the chloroplast, containing a large number of pyrenoids, × 210; – 2. & 3. mature, barrelshaped vegetative cells, focused at different levels in cell, × 210; – 4. basal part of a vegetative filament, showing abrupt transition between the rhizoid-producing and non-rhizoid-producing cells, × 210; – 5. mature, nearly ripened *Codiolum*-plants, collected from Thyborøn, × 210; – 6. detail of the clava of the *Codiolum*-plant. Majority of zoospores are arranged parallel to the cell wall, × 572.

Plate 3. *Urospora bangioides.* – 1, 2 and 4. mature, vegetative filaments showing the characteristic isodiametric or long rectangular cells which possess a strongly reticulate chloroplast in which a relatively high number of pyrenoids is embedded, × 147 and 118; – 3. detail of the filament depicted in 1 & 2, × 290; – 5. cultured, nearly mature *Codiolum*-plants which were collected from Breezanddijk at a very young stage, × 572; – 6. akinete formation in a filament. Note the thick-walled envelope, still enclosed in the original mother cell wall, × 572.

Plate 4. *Urospora bangioides.* – 1 and 2. a zoosporangium focused at different levels in cell. Note the protruding pore through which zoospores will leave the mother-cell wall, × 572; – 3. zoosporangia in which zoospores are relatively loosely arranged, × 290; – 4. and 5. subsequent stages in the liberation of zoospores. Note that zoospores leave the mother cell in a stream, × 147.

Plate 5. *Urospora penicilliformis.* – 1 and 2. vegetative filaments focused at different levels in cell. Note the luxuriant chloroplast development which obscures the visibility of the pyrenoids, × 275; – 3. small filament with its characteristic girdle-shaped chloroplast, × 595; – 4. filament with zoosporangia in which the zoospores are radially arranged, × 595; – 5 and 6. filaments filled with female gametangia, focused at different levels, × 364; – 7. ditto. Note the eye-spots (arrows), × 572.

Plate 6. *Urospora neglecta.* – 1 and 2. mature, vegetative filaments, focused at different levels in cell. Note the transitional stage of the chloroplast, between the girdle-shaped stage and the pronounced reticulate stage, × 441; – 3. twisted, vegetative filaments in general view. Note the clear delineation of the pyrenoids, × 110; – 4. vegetative filament with short cells which resemble *Ulothrix speciosa* in growth habit, × 572; – 5. nearly completely ripened, strongly reduced, sporophytic plant which developed parthenogenetically from a female gamete, × 1100; – 6. a lengthened zoosporangium. Its inner cell wall is locally coated by zoospores, × 817.

Plate 7. *Urospora neglecta.* – 1 and 2. filaments with zoosporangia, focused at different levels in cell, × 441; – 3. clustered young filaments. Note the *Ulothrix*-like chloroplast, × 110; – 4 and 5. vegetative filaments with relatively extensive chloroplast development focused at different levels in cell. Note that in spite of this development, the pyrenoids are still easy to detect, × 441; – 6. germination of aplanospores inside the mother cell wall, × 275; – 7. detail of the holdfast which consists of only the rhizoidal outgrowth of the most basal cell, × 275; – 8. an interstitial rhizoid, × 275.

Plate 8. – 1. *Urospora wormskioldii.* A dictyosome with a lateral bud, presumably containing precursory cell wall material, × 39,150; – 2. *U. neglecta.* Vesicular profiles which are presumably produced by dictyosomes. They will most probably be utilised in the adjacent transverse cell wall, × 39,150; – 3. *U. neglecta.* Cell division by furrowing. The outer surface of this filament, collected from a natural habitat near Vlissingen (The Netherlands), is densely studded with a continuous layer of microparticles in which bacteria are embedded, × 4,785; – 4. *U. neglecta.* Detail of the beginning of the ingrowth of the septum. Note the high metabolic activity in the surrounding cytoplasm, × 9,860; – 5. *U. wormskioldii.* Parallel rows of osmiophilic lipid globules situated in the chloroplast of a one-celled germling. Whether a rudimentary eye-spot is pictured here is still in question, × 47,850; – 6. *U. neglecta.* A peroxisome which is pinched between two chloroplast lobes, × 39,150.

Plate 9. – 1. *Urospora bangioides.* Pyrenoid with invaginating chloroplast strands, × 18,125; – 2. *U. bangioides.* Detail of the chloroplast invagination in the pyrenoid matrix. Note that only the chloroplast stroma penetrates the pyrenoid matrix and continues in the form of tubules, × 39,150; – 3. *U. penicilliformis.* Ditto. Note the very unusual behaviour of the thylakoids traversing the shell and subsequently continuing their way between the adjoining starch grain and the pyrenoid matrix, × 39,150.

Plate 10. – 1. *Urospora penicilliformis.* Cleavage of the pyrenoid in two. Note that the production of starch remains behind, × 9, 860; – 2. Detail of the previous photograph. The separation of the

daughter pyrenoid is achieved by the annular ingrowth of several chloroplast strands, each containing a different number of thylakoids, × 39,150; – 3. *U. wormskioldii.* Longitudinal section of a part of two parallel chloroplast lobes. Note that the arrangement of thylakoids in short lamellae looks like that in higher plants (arrows), × 18,125; – 4. *U. wormskioldii.* Longitudinal section of the transitional region of the stipe and the club of the *Codiolum*-plant. Note the strongly waving outline of the stipe, visible as annular rings in light microsopical observations, × 4, 785; – 5. *U. wormskioldii.* Longitudinal section of part of the cell wall of the club of the *Codiolum*-plant. The outer membrane seems to consist of two firm, parallel membranes. Their surface is covered with a mucilaginous layer, in which a micro-organism is embedded, × 29,000.

Plate 11. – 1, 2 and 3. *Urospora bangioides.* Serial oblique-longitudinal sections through the papilla showing basal bodies with electron dense material, the flagellar roots with capping system I fibers, the ascending and lateral fiber complex, and the rhizoplast, × 47,850; – 4 and 5. *U. bangioides.* Ditto, however, here the papilla is apparently more longitudinally sectioned than in the previous series. The basal body interconnecting fibrous elements are better depicted here, × 47,850.

Plate 12. – 1–5. *Urospora bangioides.* Serial transverse sections of the cruciform papilla, commencing in the apical part and showing the opposite basal bodies, the lamellated transition region (arrow in *fig. 1*) between the basal body and the beginning of the keel-bearing flagellar axoneme region, four fibrous striated elements that bridge adjacent basal bodies (ce in *fig. 2*, arrows in *figs. 3* and *4*), flagellar roots, system I striated root component and lateral fibers. In *fig. 5*, the point where the rhizoplast attaches to the basal body is indicated by arrows, × 47,850.

Plate 13. – 1. *Urospora neglecta.* Longitudinal section through the papilla. Both system I striated fibers are continuous in opposite flagellar roots. It seems that the dorsal fiber runs through the capping plate. It is assumed that the ventral fiber also passes through its own capping plate. Both plates are separated from each other by a space. It seems that the microtubular roots terminate at approaching this space (arrow), × 39,150; – 2. *U. wormskioldii.* Transverse section of the zoospore beneath the papillar region showing the papillar ridge containing the flagellar root which consists of six microtubules and the coating parallel system I striated fibers. The superficial cytoskeletal microtubules are situated just beneath the zoospore outer membrane at (ir-)regular intervals (arrows), × 47,850; – 3. *U. bangioides.* Longitudinal section through the papilla, showing cytoskeletal microtubules in an irregular arrangement (arrows), × 60,900; – 4. *U. bangioides.* Detail of a longitudinal section near the papillar region, showing three descending superficial cytoskeletal microtubules (arrows) and the peculiar microbody with warty outer membrane, × 47,850.

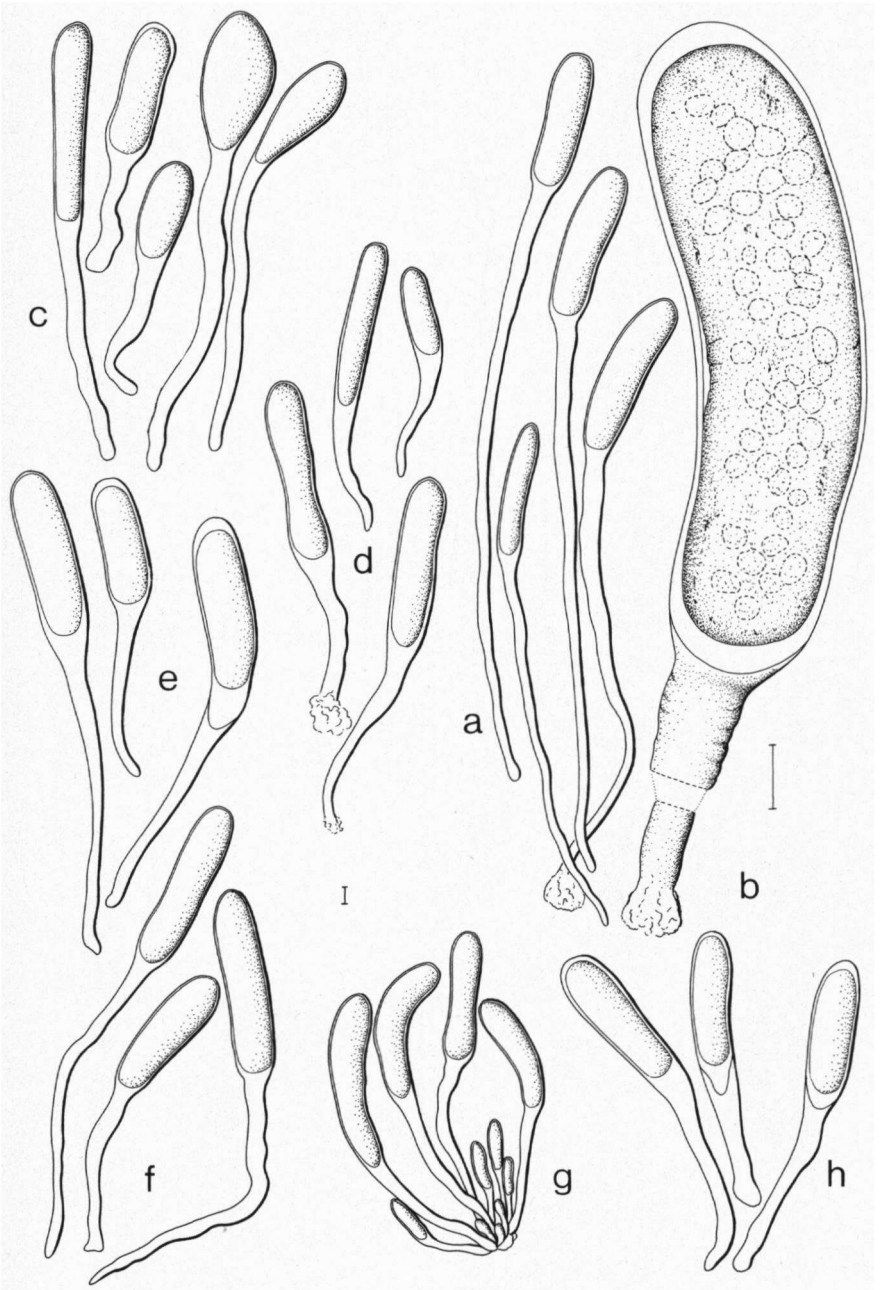
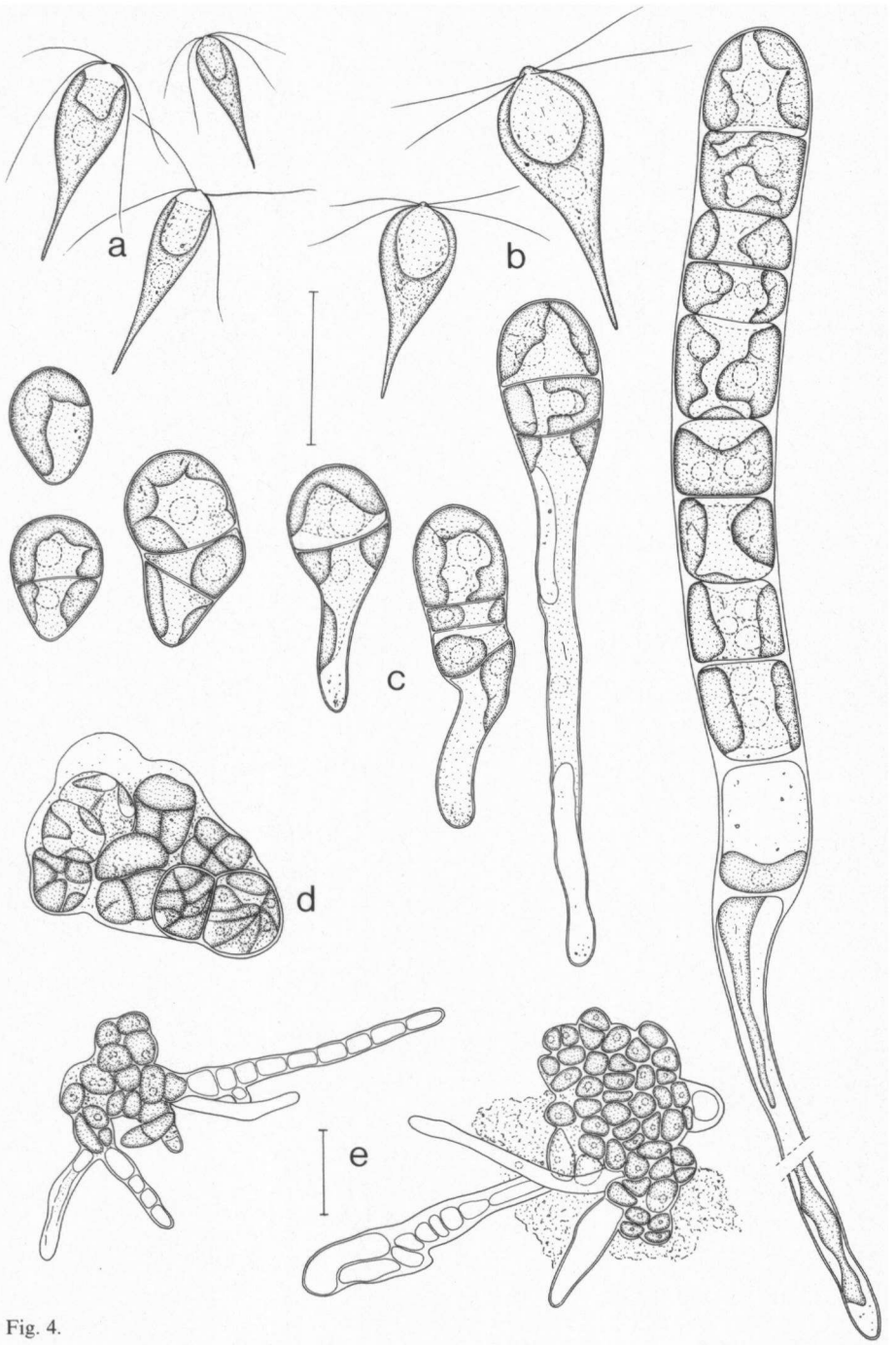


Fig. 3.



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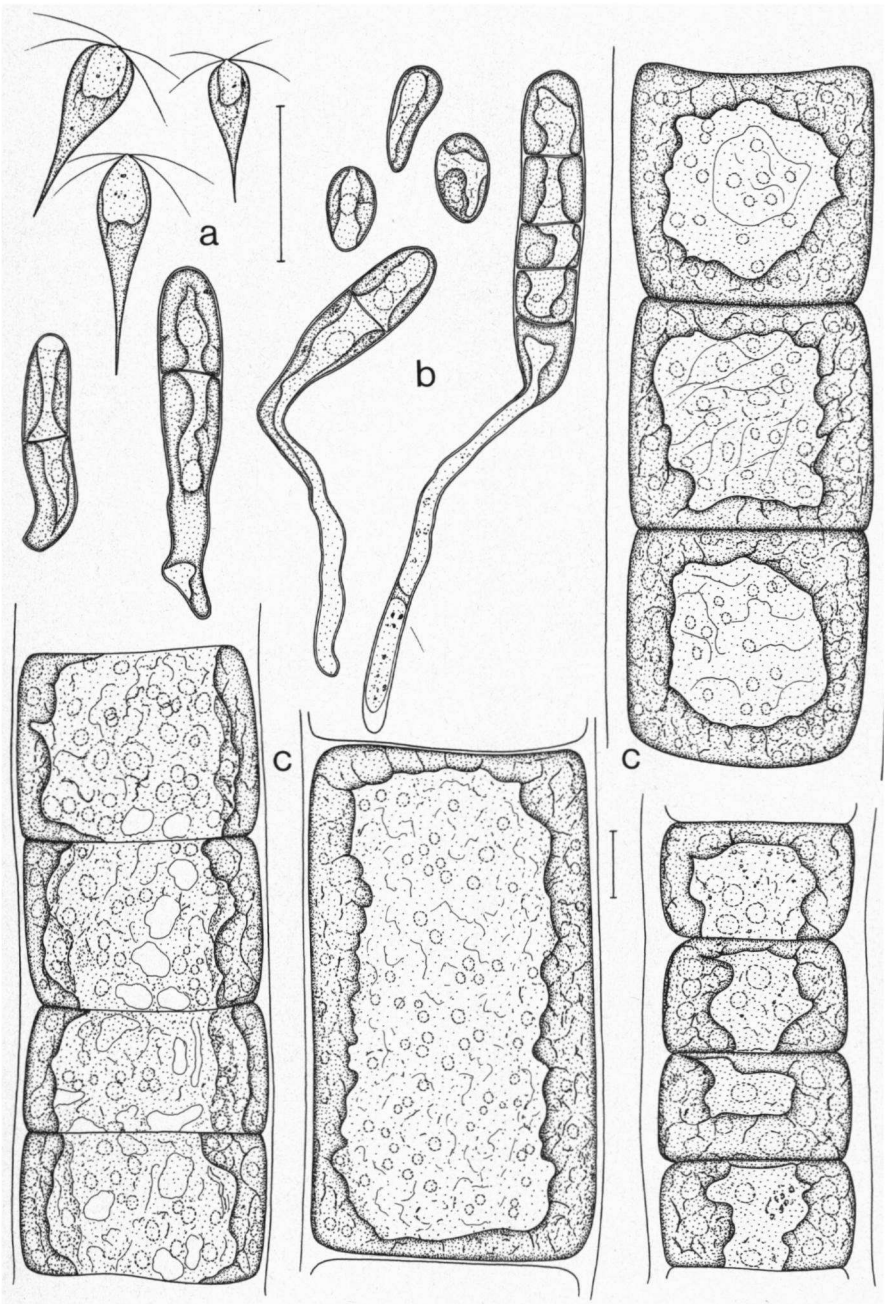

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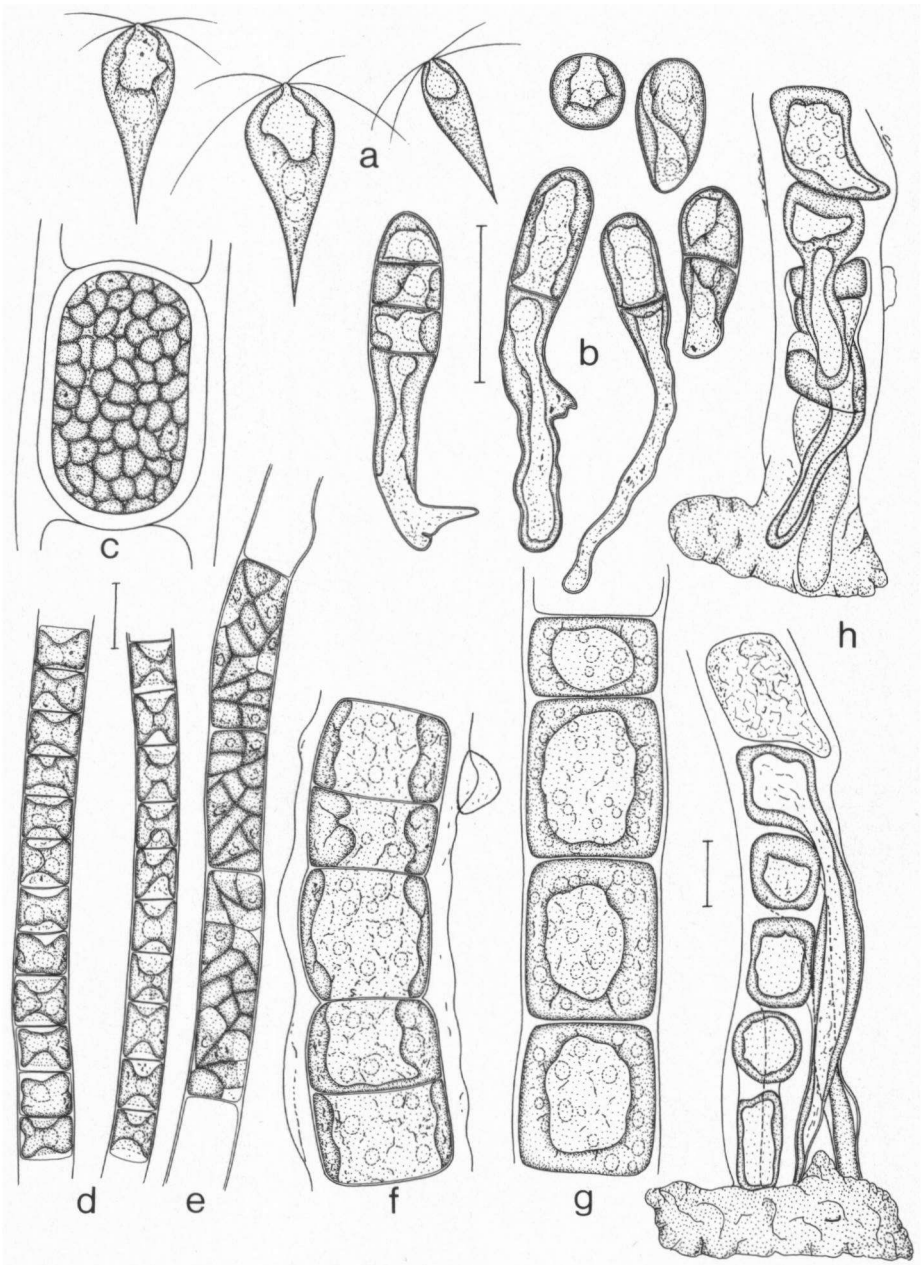

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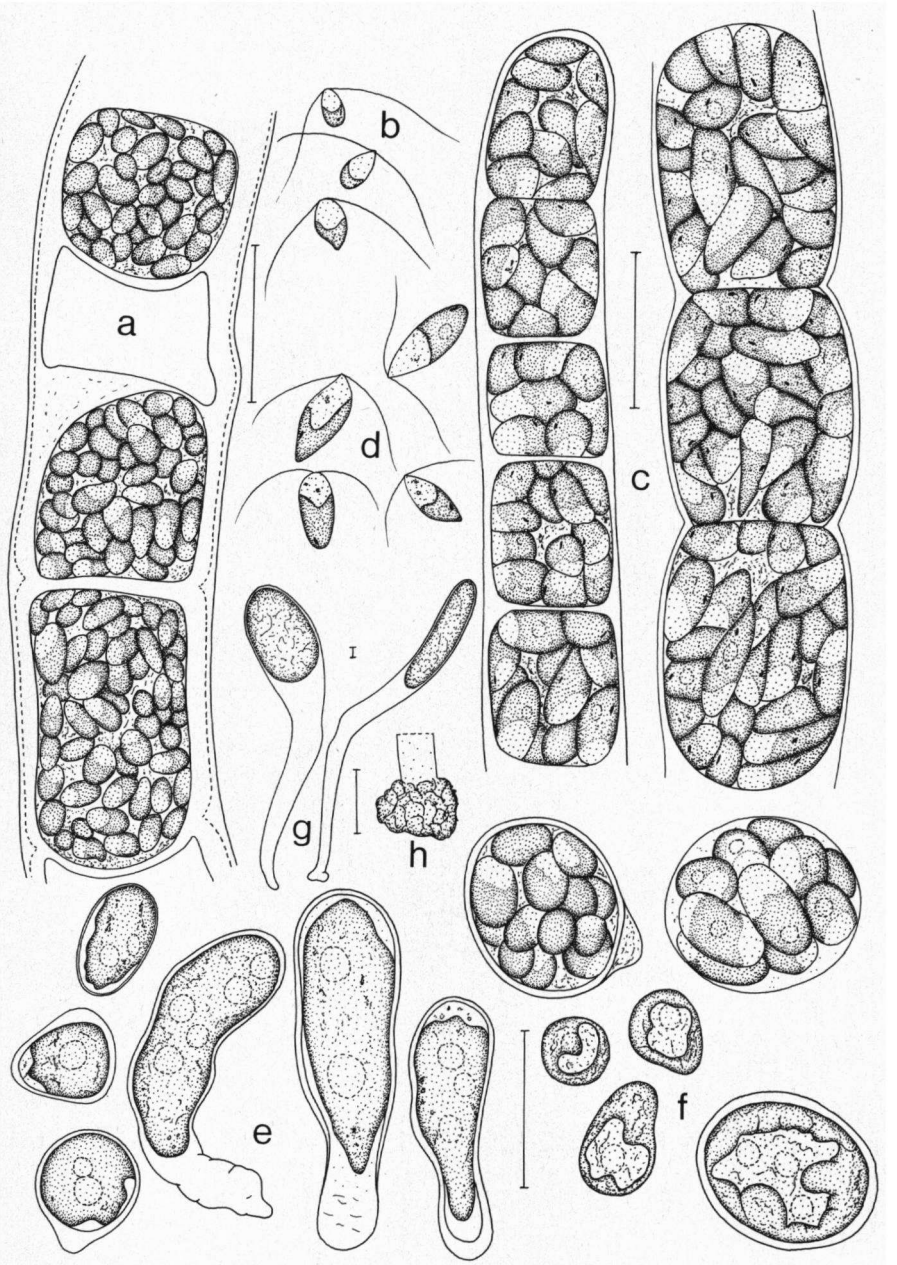
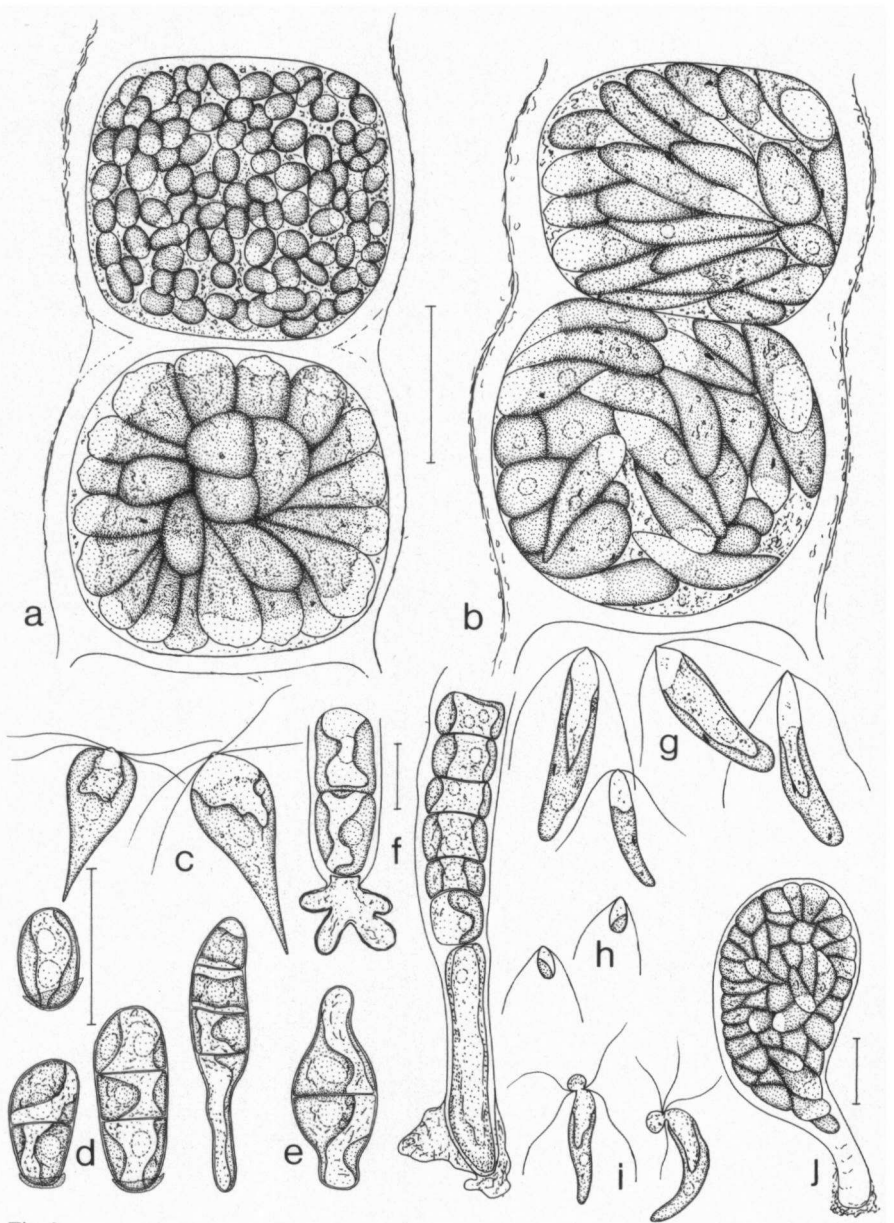


Fig. 7.



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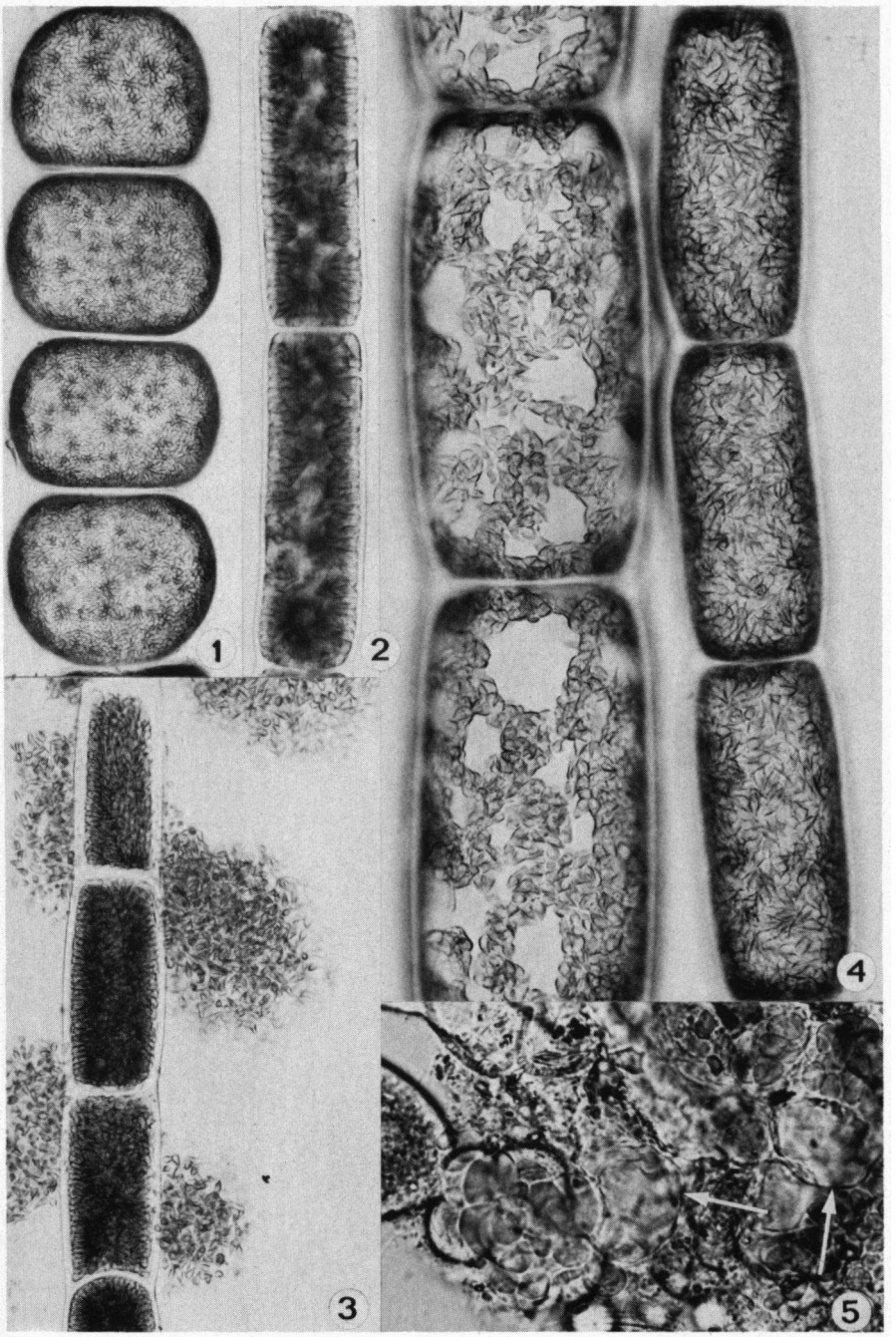
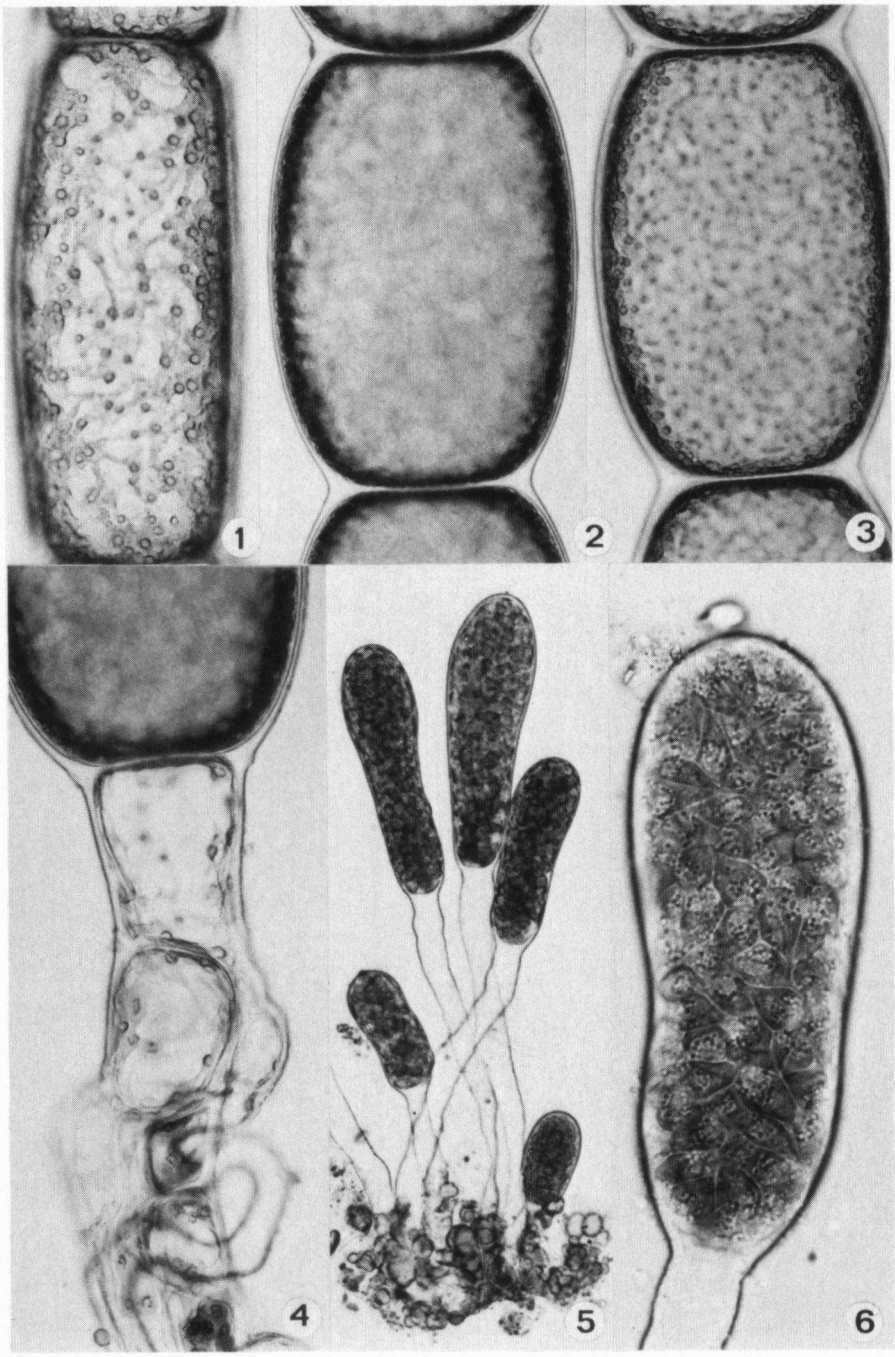


Plate 1.



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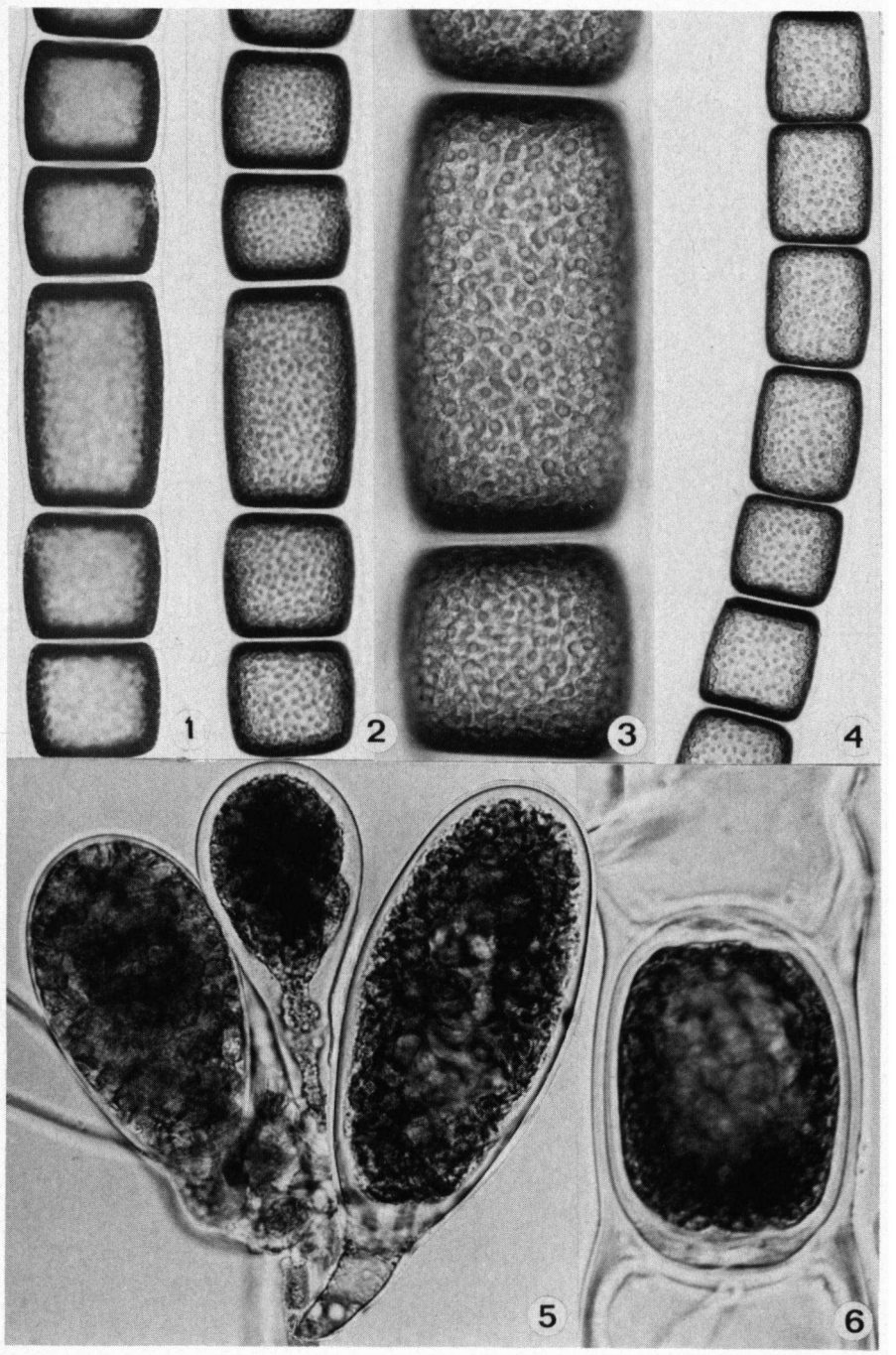

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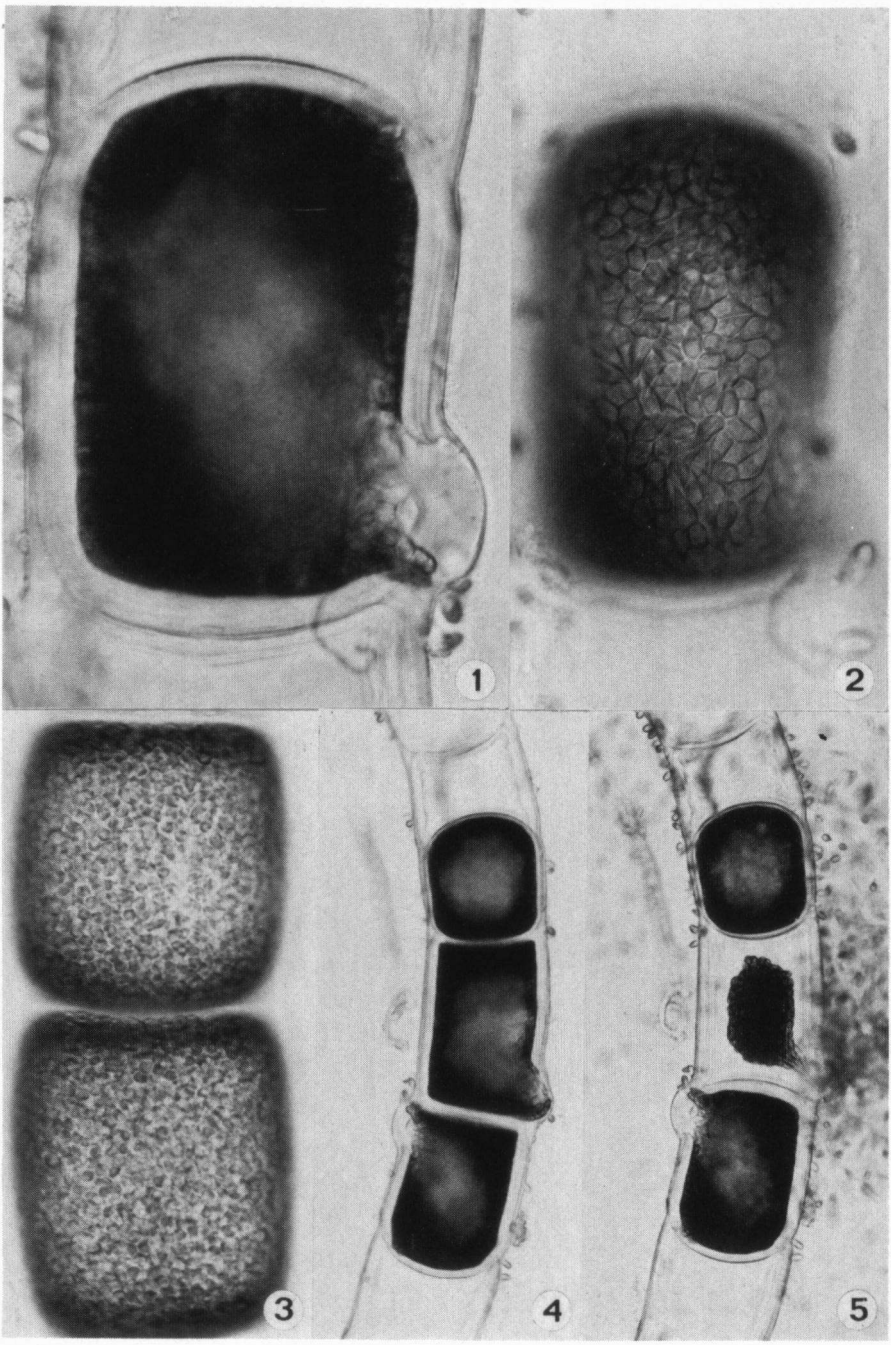

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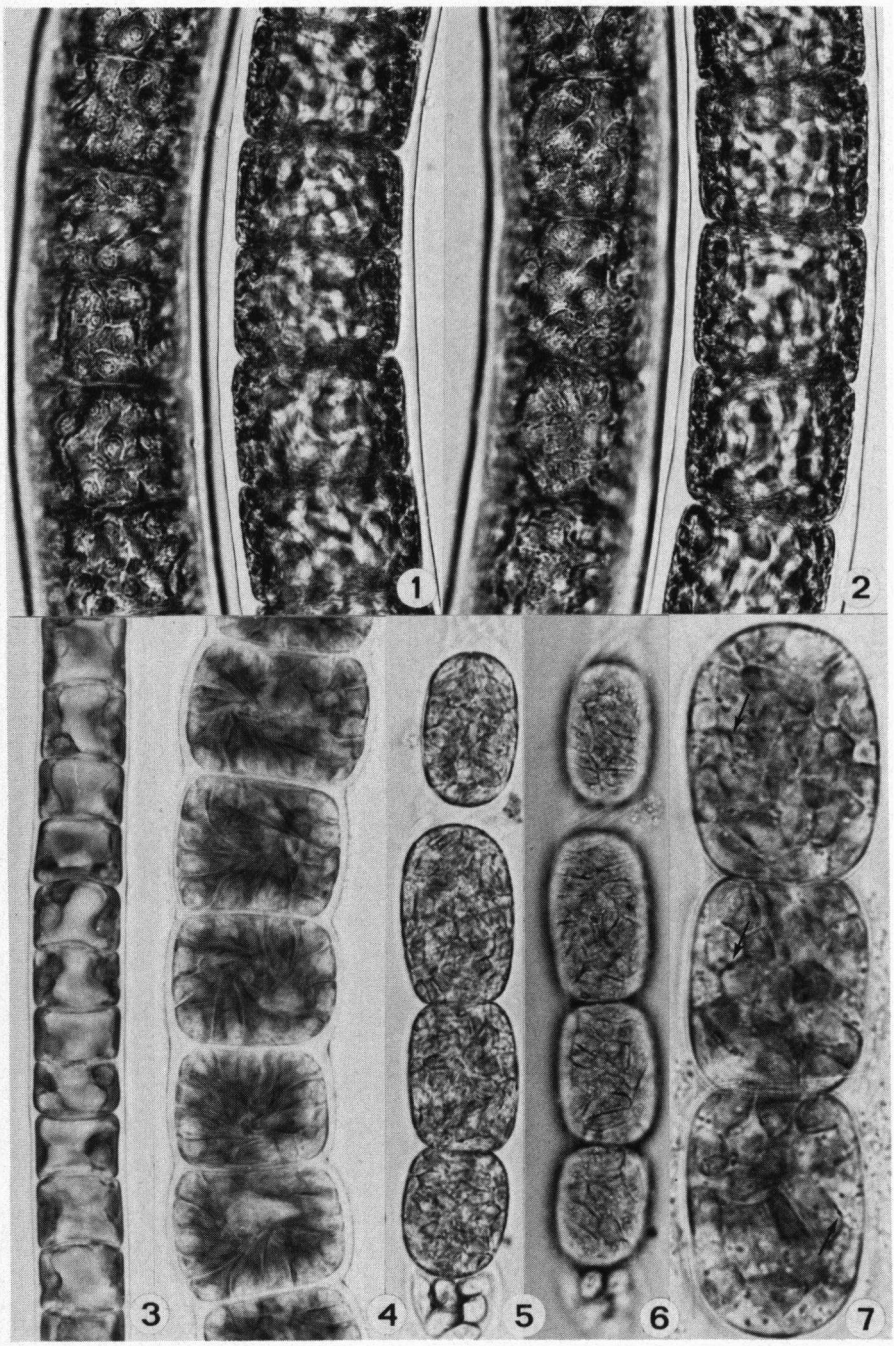
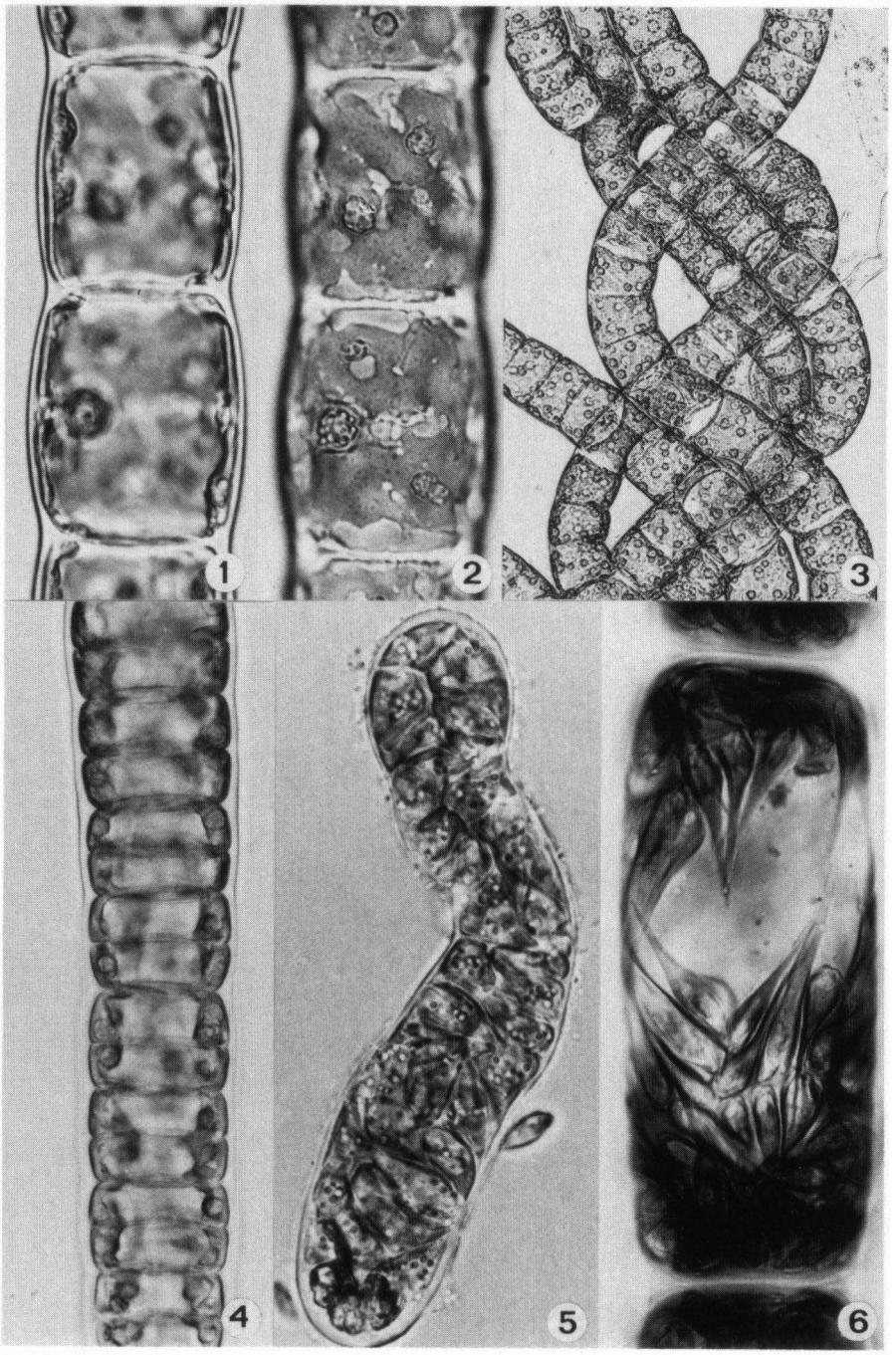


Plate 5.



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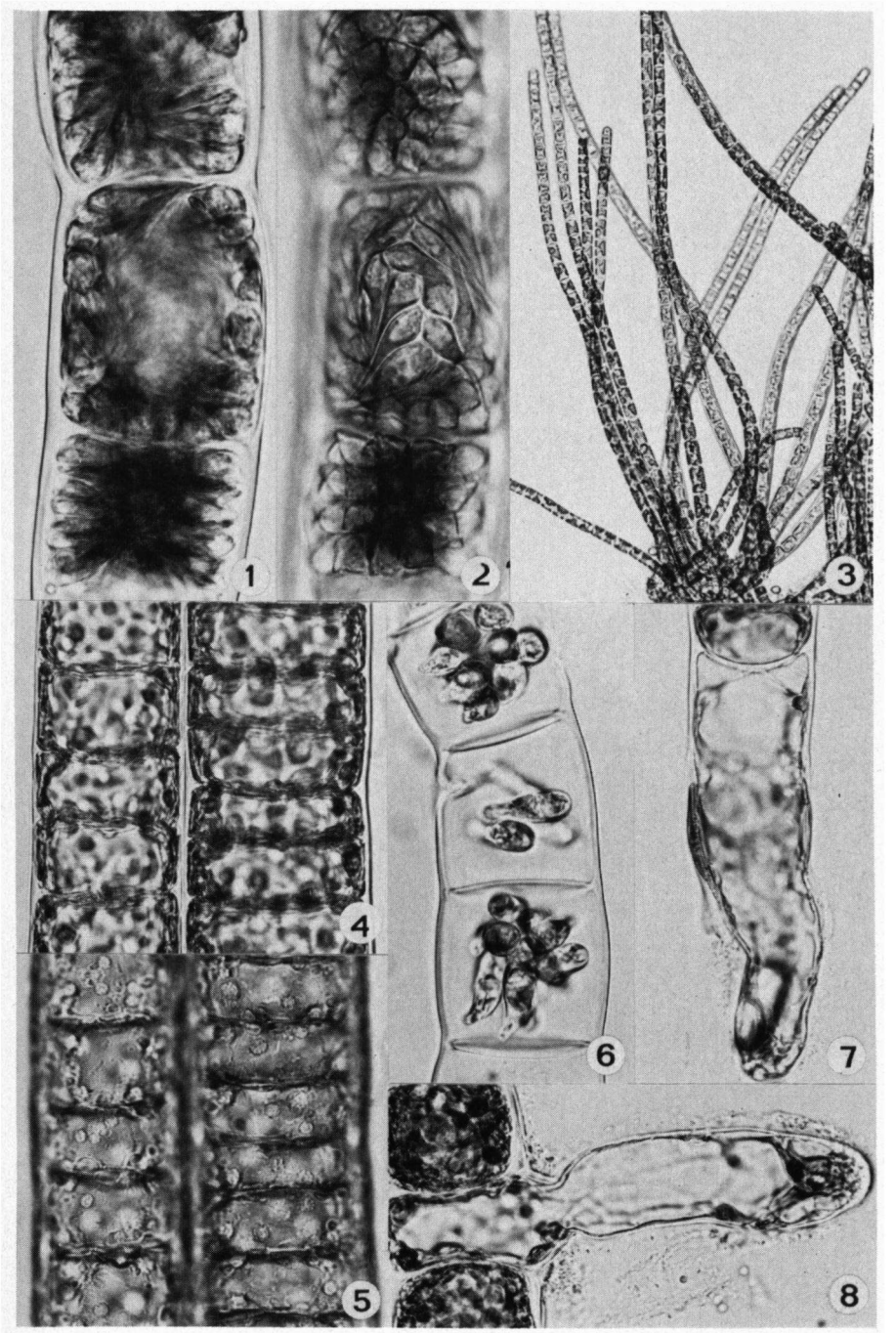

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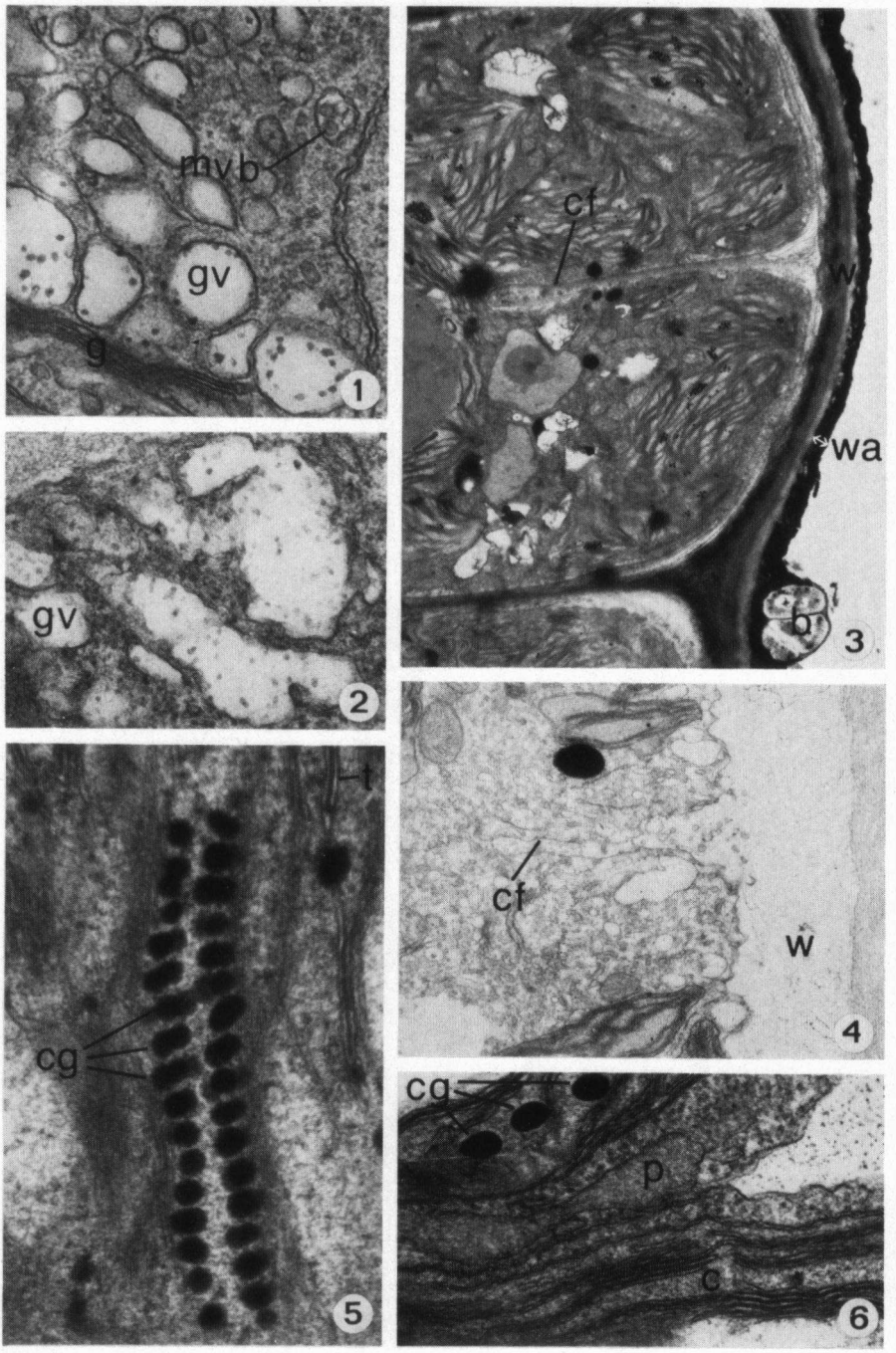

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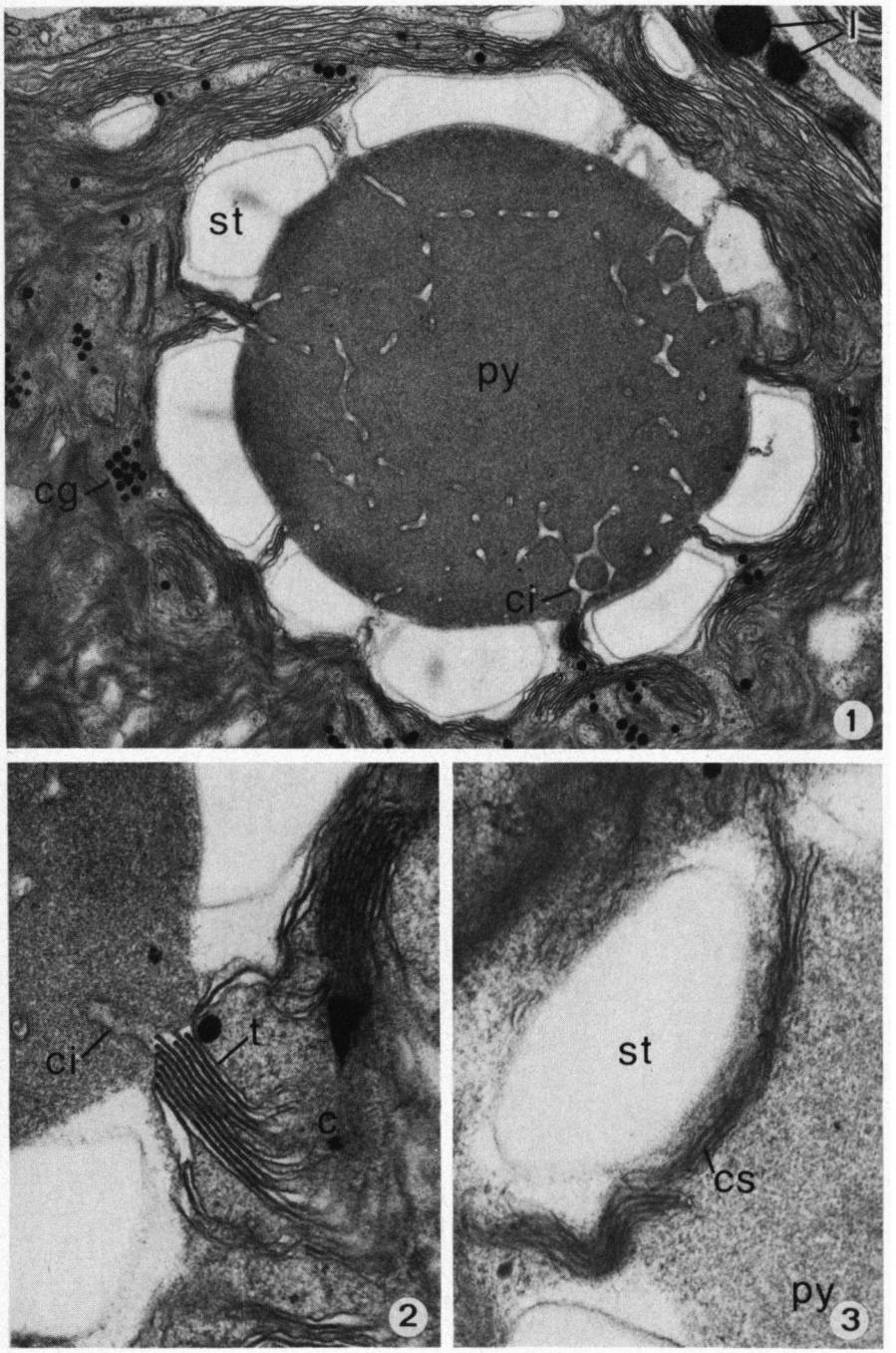

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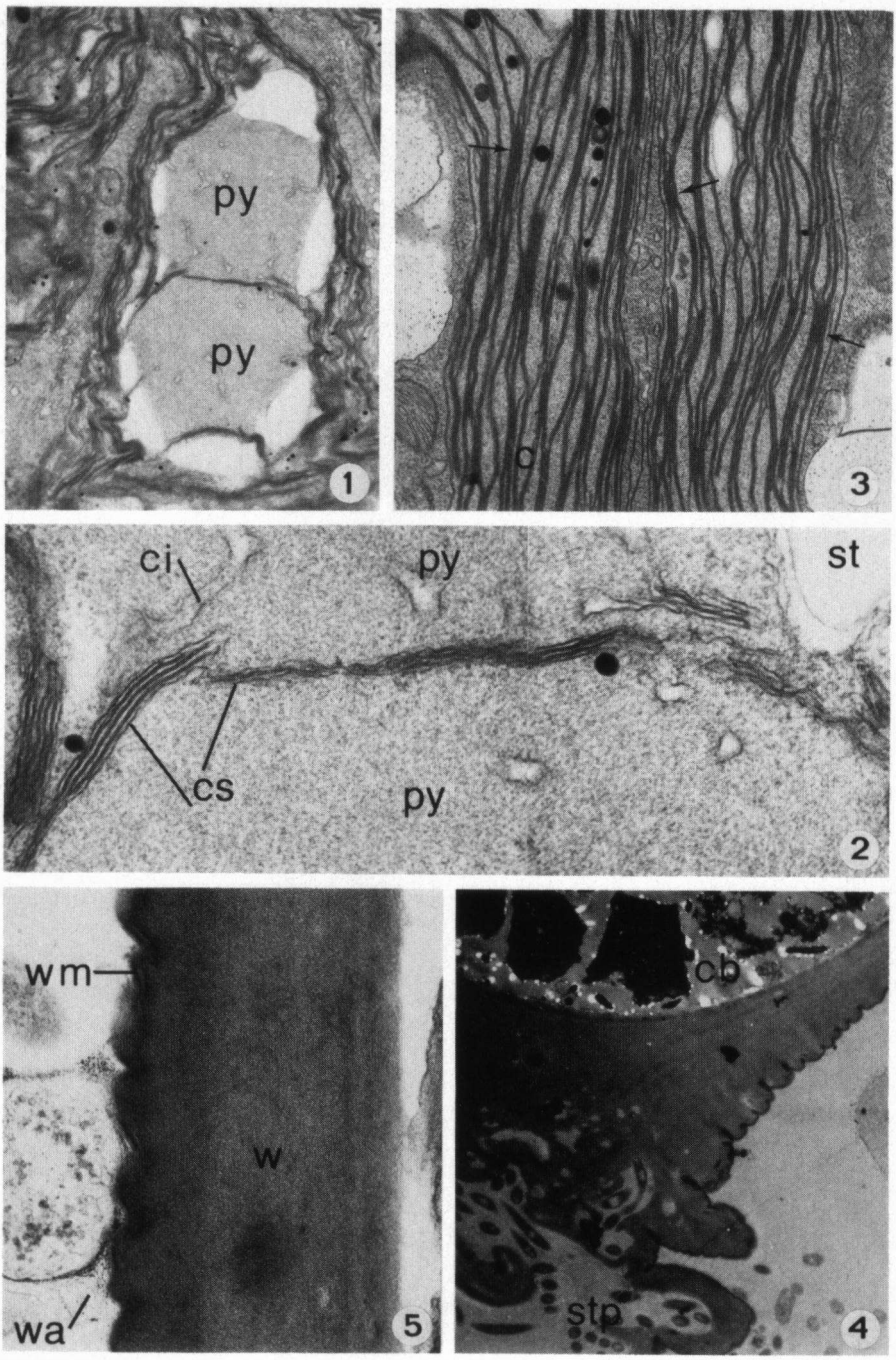

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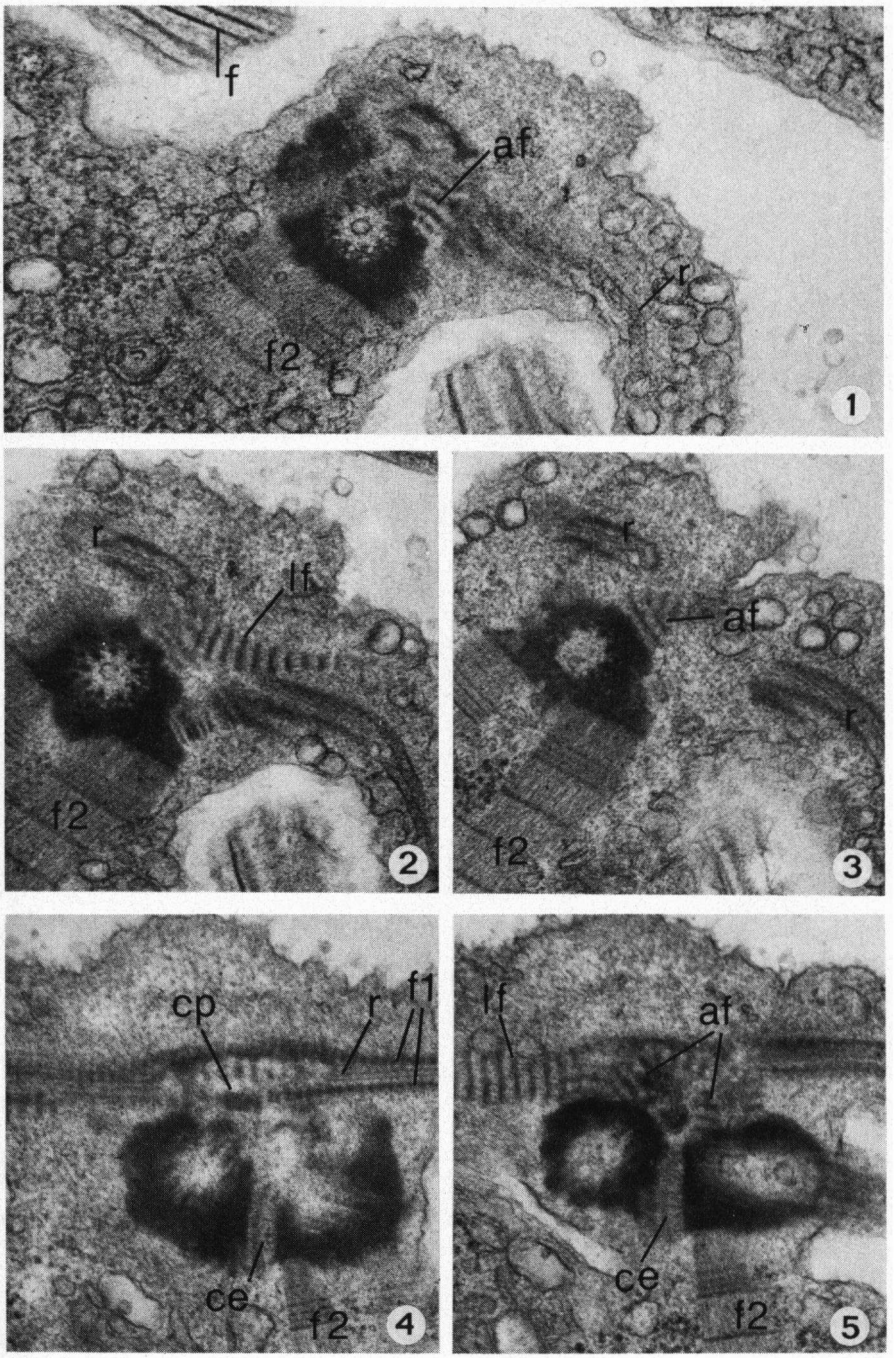

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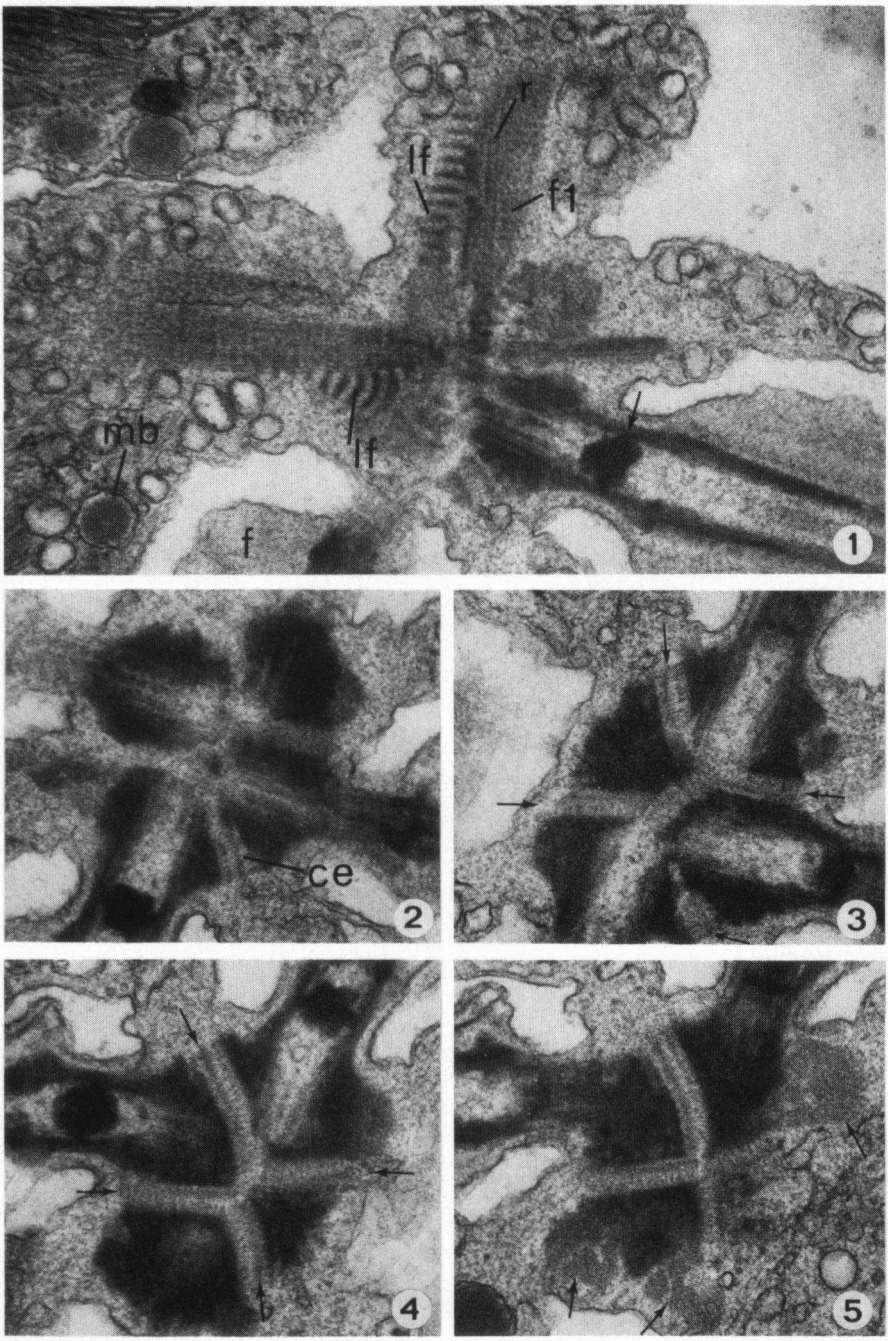

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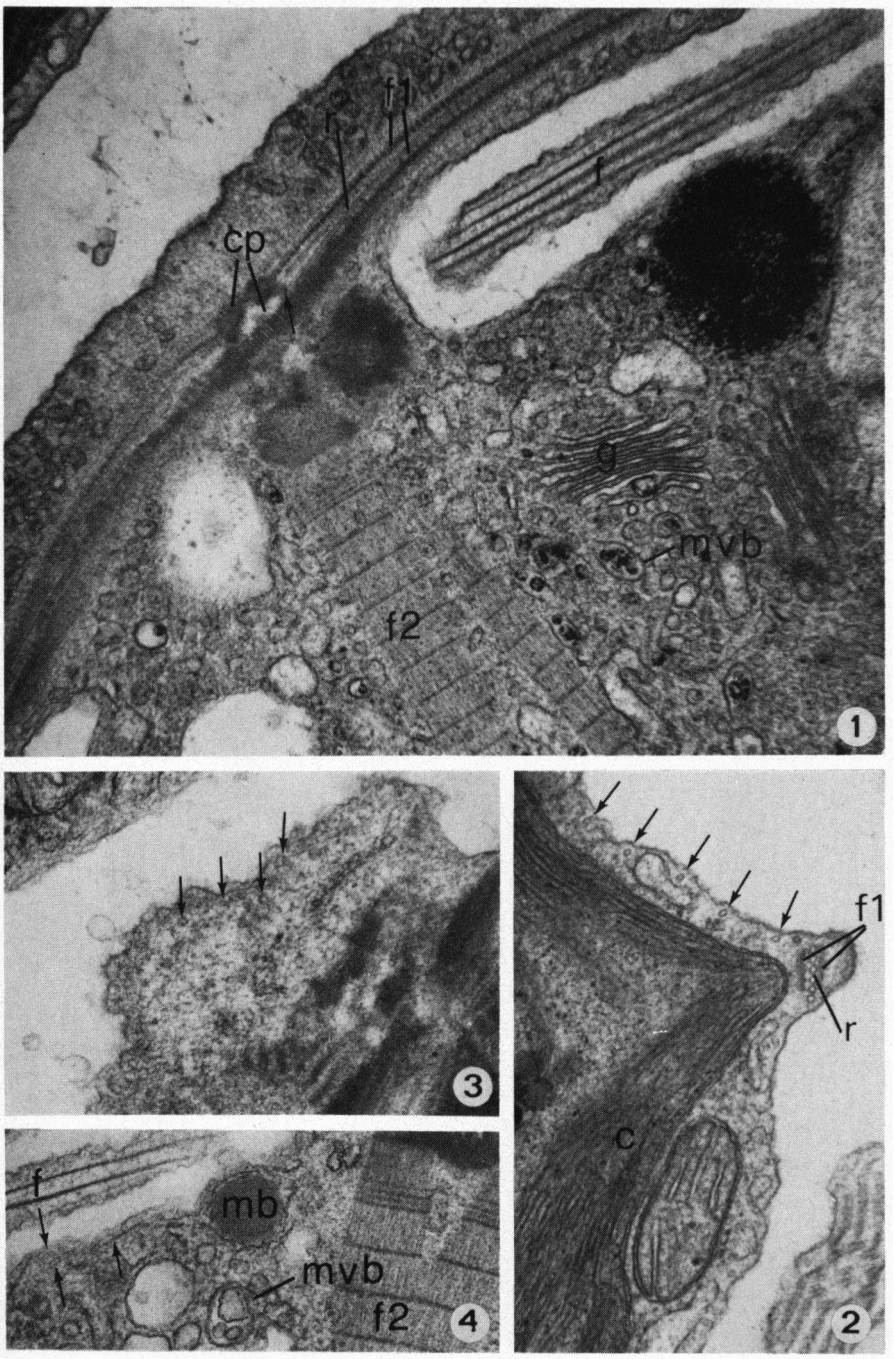

Plate 13.