The status of the Acrosiphoniales
(Chlorophyta)

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ABSTRACT
A taxonomic review of the green algal genera, Urospora, Chlorothrix, Spongomorpha and Acrosiphonia, reveals intergeneric relationships of these taxa justifying their retention in the order Acrosiphoniales.

Keywords: Taxonomy, Acrosiphoniales, Chlorophyta.

INTRODUCTION
The Acrosiphoniales, as conceived here, encompass green branched or simple filamentous seaweed, 2 to 15 cm high. They are largely confined to cold waters of both hemispheres, mostly growing in the intertidal zone on exposed or sheltered coasts.

The taxonomic position of these algae is still in a fluid state. For a long time, they were placed in the family Cladophoraceae because of similar habit. However, they differ from this family by a number of characters, especially pertaining to cell structure, reproduction, life cycles and growth (Jónsson 1962). Three genera were originally concerned: Urospora Areschoug, unbranched with multinucleate cells, Spongomorpha (Kützing) emend Wille and Acrosiphonia (J. Agardh) emend. Wille (Jónsson 1991), both branched, but the former with one nucleus per cell and the latter with multinucleate cells. These genera were removed to an independent family, the Acrosiphoniaceae (Jónsson 1959) and elevated later to the rank of order, the Acrosiphoniales (Jónsson 1962).

More recently a new genus, Chlorothrix Berger-Perrot, was tentatively assigned to the Acrosiphoniales (Berger-Perrot 1980, p.153; Berger-Perrot and Thomas 1982, footnote p. 355). This genus much resembles Urospora, but is provided with uninucleate cells as all members of the Ulotrichales, which are often considered as closely related to the Acrosiphoniales.

The aim of the present review is to give a better insight in genera composing the Acrosiphoniales.

CHARACTERISTICS OF GENERA


Dedicated to Professor Unnsteinn Stefánsson in honour of his contributions to oceanography and education.

Type specimen (holotype): slide no. 384, 24 02 1961, in Kornmann’s herbarium, Helgoland, as *Urospora speciosa* (Carm.) Leblond ex. Hamel.

The unbranched filaments, each up to 15 cm long and 8-40 µm broad, are attached to solid substrate by discoid expansion issued from the basal cell and/or unicellular laterally descending rhizoids. The growth is intercalary. The cell wall is mainly made up of three microfibrillar layers, the outermost rather dense and bordered on the outside by a thin, smooth envelope. The mature vegetative cells contain only one nucleus each. The chloroplast is girdle-shaped in younger plants, but becomes continuous, parietal, in fullgrown plants with one to several polypyramidal pyrenoids. The pyrenoid matrix is penetrated by tubular invaginations of the chloroplast stroma, a feature shared with all genera actually placed in Acrosiphoniales (Berger-Perrot and Thomas 1982).

The life cycle is heteromorphic haplodiplontic. The sexual reproduction is carried out by biflagellate ovoid isogametes, produced by filamentous gametophytes which are dioecious and haploid (chromosome number unknown). Zygotes develop into unicellular, coccoid or stalked sporophytes which yield quadriflagellate, acuminate and presumably meiotic zoospores giving rise to new filamentous gametophytes (only observed in *Chlorothrix kornmannii*). The asexual reproduction is brought about by quadriflagellate acuminate zoids similar to those of *Urospora* (Berger-Perrot 1980, 1981). However, no ultrastructural studies on flagellar apparatus of motile cells are available in *Chlorothrix*. Plasmodesmata have not been observed.

So far only three marine species have been described, all from Brittany, France and growing during winter on buoys and boats, at about the water line, and on hard substrates of various nature at the low water mark (Berger-Perrot 1980). One of these species has been reported from the Pacific coast of North America as *Urospora speciosa* (Carm.) Leblond ex Hamel (Hanic 1965).

The *Chlorothrix* genus seems to be an intermediate genus between Acrosiphoniales and Ulotrichales. Fine structural studies of mitosis, cytokinesis and flagellar apparatus are needed to establish its taxonomic position. The genus is placed in Acrosiphoniales pending further studies.


Synonym: *Hormiscia* E.M. Fries 1835 (*Conferva penicilliformis*).

Type species: *Urospora mirabilis* J.E. Areschoug 1866.


The plants of this genus consist of slender to coarse, unbranched filaments, rarely more than 10 cm long and up to 400 µm broad, attached by means of external descending rhizoids from cells in the basal part of the thallus. Mature vegetative cells are multinucleate. The cell wall is macrofibrillar, apparently 2-layered, the outermost electron-dense and covered by a thin gelatinous layer. Diffraction pattern by X-ray analysis of the cell wall resembles mercerized cellulose, indicating randomly arranged macrofibrils (Jónsson 1962). The neutral wall polysaccharides are composed of galactose, glucose, mannose, xylose and rhamnose, the latter two being the most abundant (Bachmann *et al.* 1976; Carlberg and Percival 1977). The chloroplast in young cells is an open girdle, covering when mature, the entire inner wall and is provided with many perforations. The pyrenoids are surrounded by numerous starch grains and penetrated by tubular chloroplast stroma invaginations as in all Acrosi-
phoniales (Lokhorst and Trask 1981; Berger-Perrot and Thomas 1982). No plasmodesmata have been detected in this genus.

All cells of the Urospora-filament, except basal cells, are able to undergo division. Cell division in an individual cell takes place in a four-day rhythm and is restricted to an active zone of cells, differing from day to day and generally proceeding in mature plants downwards to the base of the filament (Kornmann 1966; Lokhorst and Star 1983). Nuclear-cell division follows a highly unusual pattern initially described in Acrosiphonia (Jónsson 1960, 1962; Kornmann 1965; Hudson and Waaland 1974; cf. also Aruga et al. 1996). This process includes a considerable elongation of the cell, a formation of a hyaline cytoplasmic equatorial band and a migration of some of the nuclei of each cell. Nuclei in this band are in line and undergo synchronous division, forming two bands of daughter nuclei that move away from one another during ingrowth of a cleavage furrow in the region of the band. The non-migrated nuclei also divide. “Free” division of nuclei may also occur in not fully elongated cells without them undergoing cytokinesis (Kornmann 1966a). This process was also observed in germings of Acrosiphonia (Jónsson 1962).

During mitosis in lined-up nuclei, centrioles which are absent in interphase, become apparent. In some species the nuclear envelope is partially broken down, while in others it is maintained except for the occurrence of polar gaps. Numerous microtubules connect the chromosomes and the poles, but kinetochores are apparently absent. The centrioles take a lateral position near the spindle poles. In anaphase chromosomes migrate simultaneously towards opposite poles and in late anaphase a cylindrical interzonal spindle develops between the two sets of chromosomes. Later, these structures disappear and the resulting nuclei recover their original form. The ingrowing annular septum is preceded by a hoop of cytokinetic microtubules, not similar to phycoplasts observed in some other algae (Lokhorst and Star 1983).

Life cycles in Urospora are basically haplodiplontic and heteromorphic, with alteration of filamentous gametophyte and Codiolum-like sporophyte. Sexual reproduction of filaments is by biflagellate gametes and filaments are unisexual. Male gametes are ovoid to irregularly spindle-shaped, fast swimming with feebly developed chloroplast, inconspicuous stigma and no pyrenoid. X-rootlets are apparently lacking (Marshfield in Floyd and O’Kelly 1984, p. 114). The terminal cap is simple, the proximal sheath is a single large unit and there are no rhizoplasts. Proximal ends of basal bodies are overlapping, arranged with respect to each other in a 11/5 o’clock configuration. Neither body nor flagellar scales are present. Female gametes, rather slow in locomotion, are of an ovoid-elliptical shape, larger than male gametes and contain one chloroplast with one pyrenoid and a distinct eyespot. Ultrastructural features of the flagellar apparatus are characterized by the presence of cruciately arranged rootlets (X=3).

The reproduction is anisogamous. The zygotes develop into a stalked, in general free-living, epilithic Codiolum-stage producing quadriflagellate, acuminate and probably meiotic zoospores on ripening. The cell wall polysaccharides of the sporophyte differs from that of the gametophyte by its high contents of mannose (Carlberg and Percival 1977). Parthenogenetic development of both mating types into stalked or sessile Codiolum-stage is possible. Aplanospores in stalked sporophytes issued from female gametes have been reported in Urospora penicilliformis. Some species seem to have lost their sexual reproduction, whereas others represent geographically isolated sexual strains such as Urospora vancouveriana (Tilden) S.& G. (= Urospora wormskiioldii (Mert. in Hornem.) Rosenv.) from the Pacific coast of North America. The life cycle is temperature dependent, including besides the filamentous and the Codiolum-stage, special dwarf plants containing mainly glucose in their cell wall polysaccharides (Kornmann 1961; Bachmann et al. 1976).

Asexual reproduction of gametophytes is by acuminate, quadriflagellate zoospores and occasionally by aplanospores and akinetes arising as the gametes in ordinary cells. The exit aperture of sporangia is in general little differentiated. The zoids are enclosed within a vesicle which may or may not be released from the zoidangia. The vesicle, differentiated by the cell wall, is separated from this by an abscission zone (O’Kelly and Floyd 1984, p.128). The zoospores, morpho-
logically similar to those produced by the sporophyte, have one chloroplast containing one pyrenoid and a double layered indistinct stigma, and a flagellar apparatus, quite unique among algae (Kristiansen 1974; Lokhorst and Trask 1981; Slui
tman et al. 1982). The four flagella are inserted apically in cavities of cruciforme papillae. Each flagellum bears proximally undulating wings, projecting from peripheral microtubules of the flagellar axoneme. Basal bodies are associated with a striated fibrous complex, including two rhizoplasts, cruciately arranged but apparently not overlapping. The number of microtubules in microtubular roots is invariable, consistently nine in Urospora penicilliformis. Transverse lamellae rather than a single septum occur in the transition region of basal bodies and are without stellar or cartwheel patterns.

Experiments based on 14CO2-incorporation have revealed temperature correlated differences in metabolism between filamentous plants (5°C), Codium-plants (~10°C) and dwarf plants (~14°C) in U. wormskioldii, suggesting “temperature-sensitive differential gene expression and/or steps in metabolism” (Bachmann et al. 1976).

About 10 species are assigned to this genus (4 described in Western Europe; Lokhorst and Trask 1981), mostly growing on hard substrate in the middle-upper intertidal and in the splash zone. Urospora-species were the first multicellular organisms to colonize the virgin island of Surtsey, Iceland (Jónsson 1966).

SPONGOMORPHA Kützing1843, Phycologia generalis. p. 273: Wille, N. 1899, Bot. Not. 30 nov., fasc. 6, p. 281 (Spongomorpha (Küt
tzing) Wille).

crous, p. 82.


Type specimen (lectotype): specimen No. 7089 in Agardh’s herbarium (LD) as Converva un
cialis Lyngbye (cf. Tent. Hydrophytol. Danicae, Tab. 56); probable type locality: Okse

This is a monospecific genus. The plants form green pompoms (gametophytes) up to 2 cm high, composed of slender (20-30 µm), branched filaments which are basally attached by descending, often branched, multicellular rhizoids. Branches are spread in younger plants but intertwined in older plants, forming spongy tufts. The branching is intercalary and irregular, branches usually being single per node, arising subterminally from the upper cell pole with oblique crosswall at the axial cell. Branches have rounded tips, rarely hooked. The cell wall is thin in fast growing plants and histochemically of pecto-cellulosic nature. The chemical composition is not known. X-ray diagrams are somewhat different from those of Urospora and Acrosiphonia, although indicating randomly arranged substances (Jó
nsson 1962). The growth is limited to the apical cells. Under experimental conditions (14 h light/10 h dark cycle; 1150 lux; 15°C), elongation of filaments may reach 0.6 mm per day after three successive divisions of the apical cells. Such divisions are exclusively restricted to the dark phase. The apical cell division gives rise to two unequal cells, a short upper one, a new apical cell and a subapical cell, which is much longer (sometimes 2:5), depending on age and environmental conditions. The cells cut off from the apical cells undergo repeated division but no elongation. This results in a thallus composed of short inter
calary cells, sometimes isodiametric, in the lower part of the thallus and longer cells in the upper part (Kjellman 1893; Kornmann 1967).

The cells in Spongomorpha are strictly uni
nucleate. In the apical cell, the nucleus migrates towards the future zone of cell division. The nucleus of apical cells is much more conspicuous (10-12 µm in diameter with a large nucle
olus) than in intercalary cells. A cleavage furrow is visible at the light microscope level during mitosis. However, no ultrastructural details are available on mitosis and cytokine
sis. The chloroplast is single per cell, parietal, perforated and becomes dense towards the tip
in vigorously growing apical cells. The pyrenoids are polypyramidal, several in each cell. Their matrix is penetrated by tubules of the chloroplast stroma (unpublished observation). Plasmodesmata are present in crosswalls (unpublished observation).

The life cycle is fundamentally haplodiplontic and heteromorphic. The sexual reproduction occurs in haploid (n = 6-7 chromosomes) filamentous and apparently monoecious plants. Induction of gametogenesis is correlated with long-day conditions and cessation of growth, independent of temperature within a range of about 5-15°C. Gametes arise by sequential cleavage of the cell content. The gametangia are located in long rows in the middle region of the thallus. The liberation of gametes is through a circular non-crenulated pore in the upper part of the cell, provided with an operculum which is generally shed. The gametes are enclosed within a vesicle (modified cell wall material?) which is sometimes released without dissolution. The gametes are pear-shaped and biflagellate, with one chloroplast containing one pyrenoid and a distinct double-layered eyespot. The flagellar apparatus is provided with cruciately arranged microtubules and the root formula seems to be: X-2-X-2, where X=3. Electron microscope studies of the flagellar apparatus are still insufficient. Fusion of gametes is by isogamy or slight anisogamy. The zygotes develop into unicellular and uninucleate sporophytes, formerly described as Chlorochytrium inclusum Kjellman and Codiothecetum petrocelidis Kückuck, endophytes in various foliose and crustose algae. The sporophytes may be either stalked or stalkless, depending on the host-plant.

In culture, induction of sporogenesis is favored by the presence of the filamentous mother plants (Kornmann 1964). The sporophytes produce quadriflagellate, ovoid zoospores, probably following meiosis. These give rise to new filamentous gametophytes. Parthenogenetic gametes or zoospores in the filamentous phase have not been observed. On the other hand, “false” zygotes may be produced, when nuclear fusion is suppressed after the plasmogamy. Such binucleate pseudozygotes (n + n) do not develop into an unicellular sporophyte, but into filamentous micro-haploid plants (Jónsson 1986). A life cycle of this type, also observed in Acrosiphonia, simulates an haplodiplontic isomorphic life cycle.

The only species actually assigned to the genus Spongomorpha is Spongomorpha aeruginosa (L.) van den Hoek, 1963, p. 225). This species is distributed in temperate and cold temperate to cold marine waters of the North Atlantic and adjacent waters, growing in the eulittoral zone, often in rock pools, epiphytically on various larger algae. The epilithic form was described as Cladophora lanosa var. uncialis (Muell.) Thuret in Le Jolis, 1863. S. aeruginosa can penetrate into the Baltic where salinity is as low as 6.5. The species also occurs in the Black Sea (Zinova, 1967). The genus has not been reported from the Pacific. Some authors merge Spongomorpha and Acrosiphonia mainly on the basis of common vegetative characters. However, Wille’s (1899) distinction of uninucleate cells in Spongomorpha and multinucleate ones in Acrosiphonia justifies the separation of the two genera.


Plants belonging to this genus are branched upright filaments, variable in diameter from 50 (-60) to 250 µm and form 2 (-3) to 10 (-15) cm high cushions, soft and spreading when young, becoming stiff, compact and ropelike in older plants. The plants are attached to the substrates by multicellular, branched, downgrowing rhizoids issued from the lower pole of cells in the basal region, but occasionally by a pseudoparenchymatous discoid holdfast (= resting stage). Filaments generally increase in diameter towards the apices. Percurrent axes are inconspicuous or absent. The branching is irregular and always intercalary. The branches are usually alternate or opposite, but sometimes more or less unilaterally secund, appressed, with blunt or acute tip, straight or variously incurved and hooked, entangled. In general, plants are very variable in form depending on age and environmental factors as demonstrated by means of culture experiments (Jónsson 1962; Kornmann 1965; M.L. Hudson 1974). Mature cells are multinucleate. The cell wall is multilayered showing in an electron microscope a random microfibrillar structure and a thin surface membrane. X-ray analysis reveals randomly oriented fibrils (Jónsson 1962). Polysaccharides are composed of sulphated glucuronozylorhamnans as in *Urospora* (Percival 1979) (cf. chapter on *Urospora* “wall polysaccharides”).

The growth is mainly by division and elongation of the apical cells, the process being much similar to that occurring in *Spongomorpha* and to some extent in multinucleate *Urospora*. In *Acrosiphonia* the process includes the formation of a cytoplasmic band at a distance of about 1/4 to 1/5 of the length of the cell back from its tip and a migration of nuclei to this band. All nuclei situated above the band migrate and finally form a ring containing up to six nuclei in height and four nuclei in thickness, whereas other nuclei located in the lower part of the cell do not migrate. The next step is the synchronous mitosis of migrated nuclei in the band as well as of those situated at its proximity (Jónsson 1960, 1962; Kornmann 1965). During mitosis the nuclear envelope remains mostly intact, except for gaps at each pole permitting spindle microtubules to extend to the paired centrioles. No distinct kine-tochores have been observed (cf. also Aruga *et al.* 1996).

The centriole, absent in interphase nuclei, may be located approximately at right angles, suggesting migration of centrioles. An interzonal spindle is present. After mitosis, the original band containing daughter nuclei is displaced apically and, to some extent, also basally, whereas cytokinesis occurs approximately at the base of the original nuclear band. The cytokinesis is characterized by the ingrowth of a cleavage furrow preceded by a group of microtubules in a similar way as in *Urospora*. During this process the apical cell, which receives most of the daughter nuclei, continues to elongate, while elongation of the subapical cell is insignificant, if any. In intercalary cells nuclei also migrate to a band, occupying an equatorial position and containing only one layer of nuclei. After the synchronous mitosis, an equal number of nuclei is partitioned into each daughter cell. These cells do not elongate but continue to deposit cell wall material (P.R. Hudson and J.R. Waaland 1974). Plasmodesmata are present in crosswalls (unpublished observation).

Culture experiments indicate that apical cells in fast growing plants divide about one hour after entering the dark cycle in a 14 h-light/10 h-dark photoregime. Changes in temperature, light intensity and photoperiod affect this process as well as the general growth pattern in *Acrosiphonia* (Kornmann 1965; M.L. Hudson 1974).

The chloroplast is parietal, largely perforated in elongated cells, much more dense in older cells, and contains many polyhedral pyrenoids with the matrix penetrated by chloroplast stroma tubules as in *Chlorothrix, Urospora* and *Spongomorpha* (Berger-Perot and Thomas 1982; Lokhorst and Trask 1981; S. Jónsson unpublished material).

Life cycles are of two types; diplaphlontic heteromorphic and haplontic. Sexual reproduction occurs in haploid filamentous plants. These are either monoecious (*e.g.* *Acrosiphonia arcta* (Dillw.) J. Ag.) or dioecious (*e.g.* *Acrosiphonia duriuscula* (Ruprecht) Yendo). Gametogenesis is accomplished by synchronous division of nuclei, followed by a cleavage of cytoplasm but without participation of the voluminous central vacuole. Mature gametes are liberated through a semicir-

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cular aperture with crenated margin and an operculum which is generally not shed. The gametangia which arise from ordinary, intercalary cells occur either solitary or two, three or many together in rows. Induction of gametogenesis is correlated with the cessation of growth and long-day conditions, irrespective of temperature in the range of about 5-15°C. The gametes are released into a sac which sprouts out from the gametangium. On bursting the gametes become motile. They are pear-shaped or posteriorly acuminate and biflagellate, each containing a pyrenoid and a double layered stigma. The fine structural features of the flagellar apparatus include two overlapping basal bodies in 11/5 o’clock (counterclockwise) position, cruciately arranged microtubules (2-X-2-X, where X=3) and the presence of terminal caps. Other details include the presence of a non striated capping plate, covering two proximal sheaths, a tiny second proximal connecting fibre, striated bands linking three-membered rootlets to the proximal sheaths, an electron dense material partially covering the two-membered rootlets and a striated material underneath and, finally, an electron dense material inside the basal bodies. A mating structure is located in the upper part of the gamete. Scales and rhizoplasts are lacking (Miyaji and Hori 1984).

After the fusion of gametes, four roughly cruciately arranged basal bodies and eight sets of rootlets may be seen. Two basal bodies, each from opposite mating types, are almost in contact by their proximal ends, whilst two others are considerably displaced. This configuration suggests a rotation and sliding movements of basal bodies during gamete fusion. Four sets of rootlets (2-3-2-3) are associated in the plane of fusion. In the opposite plane, rootlets are always separated. Microtubules seem to play a morphogenetic role during gametic positioning (Jónsson and Chesnoy 1984). Zygotes, where normal karyogamy occurs, develop into Codium-like unicellular and uninucleate stalked cells. In the haplodiplontic life cycle, the Codium-like cells form quadriflagellate, ovoid zoospores which give rise to new filamentous gametophytes. Zoosporogenesis, which is not inhibited under a long-day regime, is accompanied by meiosis which takes place during the first division of the nucleus (Jónsson 1970). The chromosome number in Acrosiphonia arcta is n = 5. In the haplontic life cycle (e.g. Acrosiphonia sonderi from Iceland), meiosis also occurs during the first division of the nucleus but no zoospores are formed. The chromosome number of this species is n = 4. The hypnozygote germinates directly into a new haploid gametophytic filament (Jónsson 1969; see also Kornmann 1970, concerning the life cycle in the same species under the synonym of Acrosiphonia grandis Kjellm.). In both types of life cycles “false” binucleate zygotes are formed following suppression of karyogamy (Jónsson 1964 and 1964a). These produce directly new gametophytes in a similar way as in Spongomorpha. Apokaryogamic strains of this kind are particularly common in the Acrosiphonia arcta population of Helgoland (Jónsson 1971). Biflagellate zoids may also develop directly into new haploid plants and this is the rule in some geographical strains which have completely lost their sexuality, e.g. Acrosiphonia sonderi (Kütz.) Kornmann at Helgoland. Gametes giving parthenogenetically Codium-like plants have been reported. In laboratory cultures Acrosiphonia plants can easily be multiplied by fragmentation.

Members of this genus are widespread in cold temperate to cold marine waters (Kjellman 1893; Vinogradova 1979; Gabrielson et al. 1989). They occur as epiphytes on larger algae or epilithically in the intertidal and, occasionally, in the subtidal zone, sometimes penetrating into brackish waters (salinity 6). A profusion of species have been described, but the circumscription of species within the genus needs revision. In the Atlantic, the group is now reduced to three or four species (Caram and Jónsson 1972). Five species have been reported from the northern Pacific (Vinogradova 1979; Gabrielson et al. 1989), whereas 3 species are apparently present in the Indian Ocean (Silva et al. 1996).

DISCUSSION
Since the creation of the Acrosiphoniales by Jónsson in 1962, ultrastructural studies undertaken in different genera, have considerably strengthened the validity of this order. Of special interest are studies on mitosis and cytokinesis in Acrosiphonia (P. R. Hudson and Waaland 1974) and Urospora (Lokhorst and Star 1983). The
multinucleate cells in these morphologically quite different genera exhibit similar type of cell division, characterized by migration and synchronous divisions of the nucleus without participation of phycoplasts. This type of cytokinesis, already detected in 1960 (Jónsson 1960), has not been reported for other algae. Another criterion in support of the order Acrosiphoniales is the highly specialized flagellar apparatus in quadriflagellate, acinate zoids in *Urospora* (Kristiansen 1974; Sluiman *et al.* 1981). Flagella appear to be winged and no cartwheel or stellate pattern is observed. This is quite unique among algae. In *Chlorothrix*, acinate zoospores might also represent such a structure, but this has not yet been fully examined. Furthermore, it is noteworthy that pyrenoids, with their reticulate stroma invaginations, are found in all genera, including *Chlorothrix*. This character may indicate a close intergeneric relationship within the taxon. On the other hand, *Acrosiphonia* and *Spongomorpha* are allied genera, due to a common growth pattern restricted to the apical cells. This relatedness is accentuated by the presence of plasmodesmata in crosswalls. However their main difference consists in the number of nuclei per cell, one in *Spongomorpha* but many in *Acrosiphonia*.

The Acrosiphoniales may therefore be considered as a fairly coherent taxonomic unit. However, there is no unanimous agreement as to the taxonomic treatment of the group, except, perhaps, for its separation from the Cladophoraceae. Some taxonomists have accepted the Acrosiphoniales as initially defined (e.g. Vinogradova 1979), whereas other authors have rejected the ordinal status and proposed various amendments. Thus Kornmann (1966a, 1973) and Kornmann and Sahling (1977), on the basis of asexual acinate zoids in *Urospora* (as *Hormiscia*) have moved this genus to the Codiolaceae den Hartog (1st July 1959), which in fact is synonymous with Acrosiphoniaceae S. Jónsson (9th March 1959) and therefore illegitimate (Urosporaceae, fam. nov., is proposed here to replace the name Codiolaceae den Hartog 1st July 1959, p.111; T. *Urospora* Areschoug 1866). Kornmann (1973) claims a new order for *Urospora*, the Codiolales, and even a new class, Codiophyceae, to which are also assigned the Ulotrichales, Monostromatales and Acrosiphoniales, the latter including *Spongomorpha* and *Acrosiphonia*.

Another taxonomic treatment incorporates a division of the Acrosiphoniales into two units; Codiolaceae for *Urospora* and probably also *Chlorothrix*, and Acrosiphoniaceae to include *Spongomorpha* and *Acrosiphonia* (Silva 1982). This resolution has been followed by Christensen (1994) who, however, rejects the ordinal status of the taxon, but includes *Chlorothrix* in the illegitimate family Codiolaceae. These two families are placed by Christensen in Ulotrichales without special comments. Finally, *Urospora* may be found in Ulotrichaceae together with other genera, including *Ulothrix*, whereas the remaining members, reduced to *Spongomorpha* (*Acrosiphonia* is rejected), are retained in Acrosiphoniaceae within the order Ulotrichales (Burrows 1987).

Much more work remains to be carried out before the conflicting situation of the Acrosiphoniales can be settled.

**ACKNOWLEDGEMENTS**

I would like to thank Dr. Hjálmar Vilhjálmsson, Marine Research Institute, Reykjavík, for valuable editorial help and an anonymous reviewer for providing useful suggestions.

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