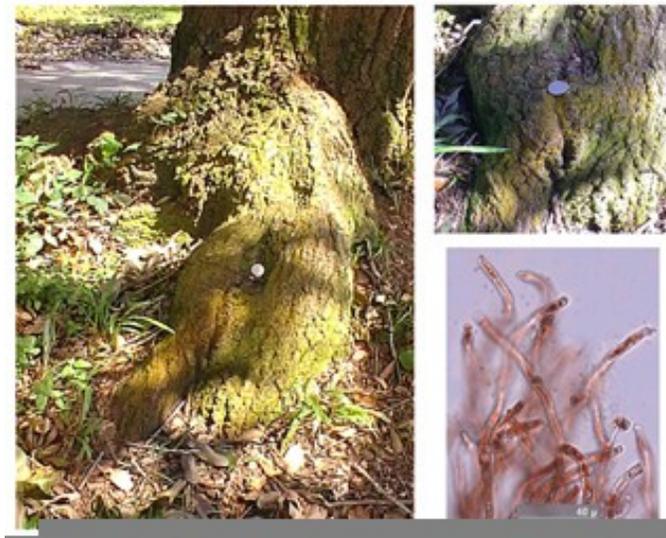


Constancea 83, 2002**University and Jepson Herbaria**

P.C. Silva Festschrift

The Trentepohliales Revisited

Juan M. López–Bautista¹, Debra A. Waters², and Russell L. Chapman^{2, 3,*}¹**Department of Biology, University of Louisiana at Lafayette,**²**Department of Biological Sciences, Louisiana State University,**³**Department of Oceanography and Coastal Sciences*****Corresponding Author: chapman@lsu.edu**

It is with pleasure and a touch of nostalgia that I convey the authors' dedication of this report to Paul Silva. For more than 30 years, my career, first as a University of California graduate student and then as a Louisiana State University faculty member, has benefitted not only from Paul Silva's knowledge and expertise on phycological matters taxonomic (including but not limited to questions related to the topic of this report, the Trentepohliales!), but also from his interest in and concern for phycology as a discipline. We, the authors, hope that this Festschrift will be but one of many expressions of appreciation and high regard for one of phycology's most important scholars. Paul Silva has been and is a very special colleague to generations of scientists around the U.S. and the world. Congratulations Paul!

Russell L. Chapman

June 2002

INTRODUCTION

The green algal order Trentepohliales (Chlorophyta) consists of a single family, the Trentepohliaceae, with six genera. These algae are not aquatic, but rather subaerial, growing on humid soil, rocks, buildings, tree bark (Fig. 1), leaves, stems, and fruit. Some species are endophytic or parasitic (Fig. 2), whereas others grow in close association with fungi, forming lichens (Chapman and Good 1983, Chapman and Waters 2002). The cells are uni- or multinucleate, with several parietal chloroplasts that can be discoid or band-shaped, sometimes appearing reticulate. Most trentepohlialean genera develop a

filamentous structure that forms either uniseriated, branched, erect tufts (Fig. 3) or laterally coherent, prostrate discs (Fig. 4). Others are highly reduced and produce only a short vegetative filament a few cells in length. Reproduction occurs by asexual quadriflagellate zoospores or sexual biflagellate gametes. (Bourrelly 1966, Chapman 1984, Silva 1982, Sluiman 1989, O'Kelly and Floyd 1990).

The main characteristics that distinguish the order Trentepohliales from other green chlorophycean algae are as follows:

- a. Differentiated reproductive cells;
- b. The presence of β -carotene and haematochrome (i.e., astaxanthin), which color the algal thallus yellow, orange, or red (Fig. 5);
- c. The absence of a pyrenoid in the chloroplasts;
- d. Unique flagellar apparatus;
- e. Transverse cell walls with plasmodesmata.

Reproduction and Life Histories

O'Kelly and Floyd's 1990 review acknowledged limited data on this subject. Early taxonomic treatments of the Trentepohliales, such as Printz's (1939), made no observations on life cycles, and later works have concentrated on various aspects of reproduction and life history in specific genera rather than the group as a whole. In the work that has been completed, two different life cycle strategies have been reported.

Thompson (1961) and Thompson and Wujek (1997) reported an alternation of heteromorphic generations for *Cephaleuros* and *Stomatochroom*. The haploid gametophyte produces stalked zoosporangia that release quadriflagellate zoospores, which repeat the gametophytic phase. On the same thallus, biflagellate isogametes are produced within sessile gametangia. Fertilization may take place within or outside the gametangia, and the mating system is homothallic. The zygote germinates to produce a dwarf sporophyte that develops small zoosporangia (microzoosporangia or meiozoosporangia) that, in turn, produce four or eight quadriflagellate zoospores (microzoospores or meiozoospores) (Thompson and Wujek 1997). The site of meiosis was tentatively placed in the dwarf zoosporangia (Thompson 1961), and later corroborated (equally tentatively) by Chapman and Henk who discovered synaptonemal complexes in the presumptive dwarf sporangia of *Cephaleuros virescens* (Chapman and Henk 1981).

The life cycles of both *Trentepohlia* and *Phycopeltis* have been described as an alternation of isomorphic generations (Chapman 1984, Thompson and Wujek 1997). The haploid gametophyte bears gametangia (in some species also zoosporangia) and produces biflagellate gametes. The zygote develops into a diploid sporophyte bearing only meiozoosporangia and quadriflagellate zoospores that germinate to form haploid gametophytes. The putative site of meiosis is the meiozoosporangium. Rindi and Guiry (2002a), however, reported that, "There is no evidence that an isomorphic alternance [sic] of diploid sporophytes and haploid gametophytes...normally takes place in Western Irish populations..." of *Trentepohlia*. Further, in their field and laboratory work, Rindi and Guiry (2002a) were unable to confirm sexual reproduction in Irish populations of *Trentepohlia*. Instead, they observed "Biflagellate swimmers behaving as asexual spores and reproducing the same morphological phase...."

Chapman (1984) observed that isomorphic alternation of generations is said to occur in *Trentepohlia* and *Phycopeltis* where the vegetative morphology is simpler, whereas a more complicated heteromorphic alternation is said to occur in the genera *Cephaleuros* and *Stomatochroom*, both of which have a complex vegetative morphology and possibly secondarily reduced morphology. [Thus, *Trentepohlia* and *Phycopeltis* could be interpreted as basal taxa.]

Representatives of the Trentepohliales display a characteristic abscission (described below) between the sporangium and the suffultory cell (or stalk cell). The sporangium and suffultory cell together form the sporangiate-lateral (Fig. 6), which together with the abscission process represent an important taxonomic character for the circumscription of the order Trentepohliales. Thompson and Wujek (1997) defined the suffultory cell as "the retrorsely bent cell that immediately

subtends a sporangium.” The area of contact between the suffultory cell and the sporangium has been the object of ultrastructural studies in *Cephaleuros* (Chapman 1976) and *Phycopeltis* (Good and Chapman 1978a). The head cell, which can be lateral or terminal on a sporangiophore (erect filament), bears the sporangiate–laterals. The process of abscission as described by Good and Chapman (1978a) involves a central area rich in plasmodesmata surrounded by a thickened area, or internal ring (Fig. 7). In the periphery of this abscission septum there is a second area of thickened wall material, the external ring; the region between the internal and external rings lacks plasmodesmata. During the development of the sporangium, the external ring splits or breaks apart all around the ring (circumscissile tearing), and the suffultory cell and the sporangium remain attached only at the central region. Under conditions of high humidity favorable for the swimming zoospores, the suffultory cell expands, holding the sporangium farther out from the head cell. Turgor probably causes the final separation of the sporangium.

Ultrastructure

The ultrastructural details of reproductive structures, quadriflagellate zoospores, and biflagellate gametes in the Trentepohliales have been reported by several phycologists. From studies on *Trentepohlia* (Graham and McBride 1975, Roberts 1984), *Cephaleuros* (Chapman 1976, 1980, 1981, Chapman and Henk 1982, 1983), *Phycopeltis* (Good 1978), and *Stomatochroon* (Good 1978), a pattern has emerged. The flagellate cells are compressed in a dorsiventral fashion with either two (gametes) or four (zoospores) flagella and four microtubular roots in a cruciate arrangement. The overlapping configuration of the basal bodies in the Trentepohliales is termed 11 o'clock–5 o'clock, or counter–clockwise (CCW), and has been cited as evidence for an affinity to the Ulvophyceae (Roberts 1984). It is important to point out that molecular phylogenetic studies using 18SSU nuclear rDNA as well as 18LSU mitochondrial RNA have confirmed the ulvophycean nature of the Trentepohliales (Zechman et al. 1990; López–Bautista et al. 1995, 1998, 2002; López–Bautista and Chapman 1999).

The flagellar apparatus in the Trentepohliales also shows distinct and unique features. One is the pair of columnar structures that resemble, and may be homologous to, the multilayered structures (MLS) typical of the unilateral flagellate cells such as those found in Charales. Van den Hoek et al. (1995) reported another unusual feature for the motile cells in the Trentepohliales: the four microtubular roots do not follow the usual arrangement of the x–2–x–2 pattern that is typical of the green algae with a cruciate flagellar root system. Instead, in *Trentepohlia* the arrangement is 6–4–6–4, and in other genera the arrangements also vary. Because the flagellate cells are strongly compressed dorsiventrally, the microtubular roots are appressed to the basal bodies, and each flagellum bears bilateral wing–like structures.

Chapman and Henk (1986) reported that vegetative cells of *Cephaleuros parasiticus* had a closed and centric mitosis; the interzonal spindle is present and at telophase is a distinct massive bundle of microtubules associated with membrane vesicles at the plane of cell division, forming a phragmoplast.

Waters et al. (1998) reported that immunofluorescence cytochemical studies revealed phragmoplast–mediated cytokinesis in *Trentepohlia odorata*. The phragmoplast was later confirmed with TEM work (Chapman et al. 2001. N.B. high–resolution images of the figures from this work are available online at <http://ijs.sgmjournals.org>. Enter volume 51:759–765.). Interestingly, the one example of metaphase observed in TEM showed an apparent open mitosis in *Trentepohlia*, in contrast to the closed mitosis observed in *C. parasiticus*, where the nuclear envelope was intact at metaphase (Chapman and Henk 1986). Chapman et al. (2001) concluded, however, that the overall processes are “nearly identical.” “Whether or not they are identical, it is clear that vegetative cell division in both involves a massive double–cone–shaped phragmoplast microtubular structure and the coalescence of phragmoplast vesicles to form a cell plate. In neither case is there any indication whatsoever of lateral infurrowing of lateral vegetative cell walls.” Both *Cephaleuros* and *Trentepohlia* exhibited a “clear temporal separation of karyokinesis and cytokinesis.”

Mattox and Stewart (1984) cited the importance of phragmoplast–mediated cytokinesis in assessing phylogenetic affinity in green algae. It is found only in a few charophycean algae (e.g., *Nitella missouriensis* [Turner 1968], *Chara fibrosa* [Pickett–Heaps 1967], *Coleochaete scutata* [Marchant and Pickett–Heaps 1973], *Spirogyra* sp. [Fowke and

Pickett–Heaps 1969, Sawitzky and Grolig 1995, Pickett–Heaps et al. 1999]), as well as in *Cephaleuros parasiticus* (Chapman and Henk 1986) and *Trentepohlia odorata* (Chapman et al. 2001, Waters et al. 1998). (Graham and McBride [1978] reported that “neither phycoplast nor phragmoplast microtubules were observed during cytokinesis” of a “sessile sporangium” of *Trentepohlia aurea*. The sessile sporangium was almost certainly a gametangium, and the mitoses and cytokineses observed gave rise to motile cells, thus the absence of either a phycoplast or phragmoplast was to be expected and not significant in terms of phylogeny. It would be interesting to see if phragmoplast–mediated cytokinesis does occur in vegetative cells of this species.) Although phragmoplast–mediated cell division in the Trentepohliales could link the group to the charophycean green algae and directly contradict the ulvophycean affiliation inferred from the CCW cruciate flagellar arrangement, the structures and processes of vegetative cytokinesis in *Trentepohlia* and *Cephaleuros* differ from those observed in streptophytes. Thus, one could argue for parallel evolution of the process (Chapman et al. 2001), especially as molecular systematics studies (discussed below), consistently favor an ulvophycean green algal alliance for the Trentepohliales.

Plasmodesmata are common in the charophycean lineage, and they are found in some of the orders in the chlorophycean lineage such as Ulotrichales, Ulvales, and Chaetophorales as well as in the Trentepohliales (Stewart et al. 1973). In the order Trentepohliales, plasmodesmata occur in the cross walls between the cells (Chapman and Good 1978, Chappell et al. 1978, Good 1978) in a central area that has been termed the “pit field” by Chappell et al. (1978). Plasmodesmata also occur in the central abscission zone of the zoosporangium (Fig. 7).

Karyology

An early account of karyology in Trentepohliales (Chowdary 1959) reported on the extremely small dot–like appearance of chromosomes in several unnamed species of *Trentepohlia* and in *Cephaleuros virescens*. Chowdary (1963) reported 22 chromosomes for *Physolinum monilia* (De Wildeman) Printz (for a taxonomical discussion of this species see Chowdary [1963] and Davis and Rands [1993]). Abbas and Godward (1964) reported a chromosome count of 18 for *Trentepohlia aurea* (Linnaeus) Martius. Other karyological studies on trentepohlialean algae (Jose and Chowdary 1977, 1978) reported chromosome numbers for 14 isolates of *Cephaleuros solutus* Karsten and *C. virescens* as well as several isolates from nine species of the genus *Trentepohlia*. The most current and comprehensive list of chromosome numbers in algae summarized the research of the previous 30 years (Sarma 1982). In that review, trentepohlialean algae (under the order Chaetophorales) were reported as having minute chromosomes in most of the taxa and chromosomal races in species of *Trentepohlia* and *Cephaleuros*.

Available data for chromosome numbers reported in 16 species of Trentepohliales are shown in Table 1. Chromosome numbers from trentepohlialean taxa range from [4]12 to 56 (Table 1). Jose and Chowdary (1978) noted that in the case of *Trentepohlia (sensu lato)*, several species have identical chromosome numbers. Conversely, a single species can exhibit “chromosomal” or “cytological” races with several chromosome numbers as in the case of *Trentepohlia aurea*, *Cephaleuros solutus*, and *C. virescens* Jose and Chowdary 1977, 1978). Recent microspectrophotometric studies using DNA–localizing fluorochrome DAPI report an estimate of 1.1 to 4.1 pg values for the algal nuclear genomes (López–Bautista et al 1998). The same report indicates a doubling sequence in nuclear DNA content for several taxa of Trentepohliales. An hypothesis for this phenomenon based on karyotype data was suggested: this doubling sequence in nuclear DNA content could be the result of the variation in chromosome numbers, thus indicating that evolution in this group has involved polyploidy accompanied by doubling of genome size.

Biochemistry

Some biochemicals have been found to be specific to the Trentepohliales. Kjosen (1972) reported on the alpha– and beta–carotenes of *Trentepohlia iolithus*, which together totaled 50% of the total carotenoids investigated. Feige and Kremer (1980) reported an unusual carbohydrate pattern in *Trentepohlia* species. Patterson and Van Valkenburg (1991) mentioned the presence of unusual carbohydrates that accumulate in cells of *Cephaleuros* and *Trentepohlia*, as well as polyhydroxy alcohols (polyols and alditols), considered rare among the green algae. Cholesterol made up 19% of the total sterol

extracted from *Cephaleuros*. Patterson and Van Valkenburg's (1991) report of the novel sterol 4, 24-dimethylcholest-7-enol, as a new algal sterol is also the first report of its being the principal sterol of any organism. Kremer and Kirst (1982) demonstrated that species of *Trentepohlia* showed the widest spectrum of accumulated alditols reported for any algal group. They suggested that the alditols were related to an aerophytic (subaerial) habit. Chapman and Good (1983) concurred with this suggestion but pointed out the need for more studies in this field.

Fossils

Eocene fossils identifiable as belonging to the Trentepohliales were reported by Tappan (1980). Dilcher (1965) reported a fossil fungus, *Pelicothallus villosus*, but after reexamination of the preserved thalli from leaf compressions from the Eocene 40 million years ago, it was redescribed (Reynolds and Dilcher 1984) and reinterpreted as a foliicolous alga with sporangiophores and hairs similar to those in *Cephaleuros*. Fossils of algae resembling the Dasycladales have been found from 500 mya and of Charales from 420 mya (van den Hoek et al. 1995). The presence of sporopollenin-like substances in the cell wall (Good and Chapman 1978b) of trentepohlialean algae should have helped preserve them and allowed them to fossilize easily. Since trentepohlialean fossils are found only as far back as the Eocene, one could suggest that the Trentepohliales must be of a more recent origin than the algae with an older fossil record (although this is certainly not the only explanation).

Ecology

The geographic distribution of the Trentepohliales is basically pantropical (Bourrelly 1966). Some taxa of *Trentepohlia* and *Phycopeltis*, however, have been reported from colder regions such as western Ireland (Rindi and Guiry 2002a) and northern Europe (Chapman 1984, O'Kelly and Floyd 1990). All Trentepohliales are subaerial, none having ever been found in aquatic habitats, freshwater or marine (although early authors included aquatic taxa that have since been removed from the group). The presence of sporopollenin-like substances in the cell walls (Good and Chapman 1978b), as well as a special pattern of carbohydrates and alcohols (Feige and Kremer 1980; Patterson and Van Valkenburg 1991), probably are adaptive features against desiccation in the subaerial habitat.

The ecological distribution of the Trentepohliales is also remarkable. *Trentepohlia* commonly occurs upon rocks, pilings, walls, tree bark, or wherever a solid substrate and favorable conditions of light and humidity are found (Bold and Wynne 1985). *Phycopeltis* is generally described as an epiphyllous alga, growing on the surface of leaves but potentially able to grow on any object (Thompson and Wujek 1997). *Cephaleuros* is more restricted in its habitat requirements. It is considered a strict epiphyte (Fig. 8), living beneath the cuticle above the epidermal cells or, deeper, in the tissue of leaves, twigs, and fruits of vascular plants (Chapman and Good 1983). *Cephaleuros virescens* seems to be the most common of the trentepohlialean community inhabiting tropical hosts. It has been reported from numerous host species, representing 218 genera and 62 families of vascular plants in the Gulf of Mexico coast of the southeastern United States, and in numerous hosts (119 genera) from Brazil (Holcomb 1986). *Stomatochroon* has an even more specialized habitat; it is found in the air chambers and stomata of leaves of tropical vascular plants (Bourrelly 1966).

Economic Importance

The economic importance of the Trentepohliales can be both positive and negative. Negative factors are damage to buildings and to economically important plants. Trentepohlialean algae are accounted among the factors responsible for the progressive mechanical degradation of buildings, or biodeterioration (Noguerol-Seoane and Rifon-Lastra 1997). Epilithic communities dominated by *Trentepohlia* sp. play an important role in creating the conditions for destruction of stone buildings in England, Scotland, and Spain (Wakefield et al. 1996; Noguerol-Seoane and Rifon-Lastra 1997). In tropical areas with conditions of high humidity, damage to concrete buildings caused by *Trentepohlia* is considered a serious problem and biocides for the control of *Trentepohlia odorata* have been evaluated (Tan et al. 1985).

Species of *Cephaleuros* are very common on the leaves of tropical trees and shrubs with economic importance such as tea (*Camellia sinensis*), pepper (*Piper nigrum*), coffee (*Coffea arabica*), oil palm (*Elaeis guineensis*), avocado (*Persea americana*), vanilla (*Vanilla planifolia*), guava (*Psidium guajava*), and cacao (*Theobroma cacao*), as well some citrus (*Citrus* spp.) cultivars. *Cephaleuros* infections can cause death (necrosis) of the cells just beneath the algal thallus (Thompson and Wujek 1997) and perhaps injure the host plants. *Cephaleuros* infections on tea and coffee plants have been called “red rust.” Thompson and Wujek (1997) suggested that it is a fungus (which sometimes forms an association with the alga to form a lichen) and not the algal growth that is responsible for the deleterious effects of the “red rust.” (In another case of a *Cephaleuros*/fungus mistaken identity, *Verulucia brasiliensis* was erroneously described as a new genus and species of fungus from the Amazon basin in Brazil [Reynolds and Dunn 1982], based on samples of a “fungus-like” alga, later recognized as *Cephaleuros parasiticus* Karsten [Reynolds and Dunn 1984].)

A different scenario is played out by *Cephaleuros parasiticus* and allied species, which develop intramatrically within the leaf tissue, causing necrosis in the lower epidermis. This species is a serious pest on *Magnolia grandiflora* (Fig. 2) in Florida. It has been noted, however, that the parasitic species of *Cephaleuros* are not as widespread in a variety of hosts as is *C. virescens* (Thompson and Wujek 1997).

Members of the Trentepohliales, and other subaerial algae, are exposed to more adverse environmental conditions than aquatic algae because water and mineral resources are suspended in the air as opposed to constituting a circumambient medium. Quality and quantity of these resources as well as pollutants in the air should have an effect on the algal biodiversity. Salleh and Kamsari (1994) reported an ecological study of *C. virescens* from the rubber tree (*Hevea brasiliensis*) in Malaysia. They found that rain and high temperatures were factors limiting the growth of *C. virescens* infections. Marche–Marchad (1981) reported that evapotranspiration, or ETP, was the limiting factor on a population of *Cephaleuros virescens* in Senegal and that decreasing ETP added to the community richness, density, and diversity. Marche–Marchad considered the trentepohlialean flora as an ETP indicator for the environment. More recently, Haapala et al. (1996) regarded *Trentepohlia umbrina* as an indicator of air pollution in forests around the eastern part of the Gulf of Finland. These studies advocate the use of the trentepohlialean flora as bioindicator of environmental conditions.

A potential for positive economical importance of the trentepohlialean flora lies not only in their usefulness as bioindicators, but in biotechnology. Carotenoids have been well documented (Kjosens 1972) and some are unique to this group (Czeczuga and Maximov 1996). Commercial production of carotenoids is currently based on *Dunaliella*, a green alga of saline habitats, but recent research (Tan et al. 1993) established *Trentepohlia* as a potential source for carotenoids since it appears to accumulate a larger quantity.

Lichens

Trentepohliales are well known to form lichenic associations with fungi (Alexopoulos et al. 1996; Chapman and Good 1983; Chapman and Waters 2002, Matthews et al. 1989). The phycobionts usually are representatives of the genera *Cephaleuros* (Fig. 8), *Phycopeltis*, and *Trentepohlia*. *Cephaleuros* has been described as the phycobiont in 14 species of obligately foliicolous lichens (Santesson 1952) in the genera *Strigula* and *Raciborskiella* (Chapman 1976). *Racodium* and *Coenogonium* are other genera of lichens with trentepohlialean phycobionts (Davis and Rands 1993). *Trentepohlia* has been found associated with eight families of loculoascomycetes and discomycetes just in one city in Louisiana (Tucker et al. 1991). Chapman (1976) has shown in *Strigula elegans* that fungal penetration of haustoria occurs in the phycobiont cells. Since some phycobiont cells are destroyed by the mycobiont, the author concluded that the phycobiont does not benefit from this association and the mycobiont is, in fact, parasitizing the trentepohlialean alga (the lichen and the nonlichenized phycobiont occur in the same habitat). In another study, Davis and Rands (1993) found that the common trentepohlialean phycobiont *Physolinum monile* is almost identical in its lichenized form to the free-living filaments of *P. monile*, which do have larger cells. An up-to-date review of lichenization in the Trentepohliales has been published recently (Chapman and Waters 2002).

Systematics of the Trentepohliales

The order Trentepohliales is represented by one family, Trentepohliaceae. Chapman (1984) discussed the appropriateness of the family name thus:

Although “Trentepohliaceae” is the better known and more widely used name, Papenfuss (1962) cited the precedence of “Chroolepidaceae” Rabenhorst (1868) over “Trentepohliaceae” Hansgirg (1886). Recently, P.C. Silva (personal communication) indicated that Rabenhorst had incorrectly constructed “Chroolepidaceae” and that the family name should have been “Chroolepaceae.” Thus, “Chroolepidaceae” has been eliminated, and it is reasonable to recommend the continued use of Trentepohliaceae because “Chroolepaceae” is virtually unknown and *Chroolepus*, although available as a valid name, is not currently applied to any genus. Despite the fact that *Byssus* Linnaeus may be an earlier taxonomic synonym of *Trentepohlia* Martius, there is no need to alter current nomenclatural usage (Ross and Irvine 1967) and, again, use of Trentepohliaceae is appropriate.

For a source of early names and authorities, the authors recommend the Index Nominum Algarum (<http://ucjeps.berkeley.edu/INA.html>) maintained by Paul C. Silva at the Herbarium of the University of California.

Early taxonomic treatments of the Trentepohliales were made by Karsten (1891), Hariot (1889, 1890, 1893), and De Wildeman (1888a, 1888b, 1888c, 1889, 1890, 1891). The major taxonomic accounts consist of the publications of Printz (1921, 1927, 1939). In his major revision Printz (1939) recognized only subaerial genera within the Trentepohliales: *Physolinum*, *Trentepohlia*, *Phycopeltis*, *Cephaleuros*, and *Stomatochroon*. He placed Trentepohliales into the order Chaetophorales (Printz 1964). A summary of his classification follows (Printz 1939):

Genus	Number of Species
<i>Trentepohlia</i>	36
<i>Phycopeltis</i>	12
<i>Cephaleuros</i>	13
<i>Stomatochroon</i>	1
<i>Physolinum</i>	1
Total	63

Trentepohlia Martius

(Synonyms: *Chroolepus* C. Agardh; *Amphiconium* Nees; *Dematium* Rebert.; *Mycinema* Hooker & Arnott; *Phytoconis* Bory; *Cystocoleus* Thwaites; *Coenogonium* Nylander; *Nylandera* Hariot)

Section I. *Chroolepus* (C. Agardh) Wille (*Eutrentepohlia* Hariot 1889)

- | | | |
|-------------------------|--------------------------|----------------------------|
| 1. <i>T. dialepta</i> | 8. <i>T. bossei</i> | 15. <i>T. villosa</i> |
| 2. <i>T. calamicola</i> | 9. <i>T. luteo-fusca</i> | 16. <i>T. jolithus</i> |
| 3. <i>T. abietina</i> | 10. <i>T. elongata</i> | 17. <i>T. lagenifera</i> |
| 4. <i>T. treubiana</i> | 11. <i>T. arborum</i> | 18. <i>T. santurcensis</i> |
| 5. <i>T. jucunda</i> | 12. <i>T. negerii</i> | 19. <i>T. umbrina</i> |
| 6. <i>T. cucullata</i> | 13. <i>T. uncinata</i> | 20. <i>T. odorata</i> |
| 7. <i>T. annulata</i> | 14. <i>T. aurea</i> | 21. <i>T. diffracta</i> |
| | | 22. <i>T. rigidula</i> |

Section II. *Heterothallus* Hariot 1890

- | | |
|-----------------------------|---------------------------------|
| | 27. <i>T.</i>
<i>cyanea</i> |
| 23. <i>T. leprieurii</i> | 28. <i>T.</i> |
| 24. <i>T. depressa</i> | <i>minima</i> |
| 25. <i>T. ellipsiocarpa</i> | 29. <i>T.</i> |
| 26. <i>T. dusenii</i> | <i>effusa</i> |
| | 30. <i>T.</i>
<i>diffusa</i> |

Section III. *Nylanderia* (Hariot 1889) Wille

- | | |
|---------------------------|-------------------------------------|
| 31. <i>T. peruana</i> | 34. <i>T.</i>
<i>tentaculata</i> |
| 32. <i>T. bogoriensis</i> | 35. <i>T. willei</i> |
| 33. <i>T. Lagerheimii</i> | 36. <i>T. prolifera</i> |

Phycopeltis Millardet

Phyllactidium Kützing; *Chromopeltis* Reinsch; *Hansgirgia* De Toni.

Section I. *Euphycopeltis* Wille

- | | |
|--------------------------|------------------------------------|
| 1. <i>P. epiphyton</i> | 3. <i>P.</i>
<i>arundinacea</i> |
| 2. <i>P. microcystis</i> | 4. <i>P. expansa</i> |

Section II. *Hansgirgia* (De Toni) Wille

- | | |
|---------------------------|-------------------------------------|
| 5. <i>P. treubii</i> | 9. <i>P. irregularis</i> |
| 6. <i>P. aurea</i> | 10. <i>P. prostrata</i> |
| 7. <i>P. maritima</i> | 11. <i>P.</i>
<i>amboinensis</i> |
| 8. <i>P. flabelligera</i> | 12. <i>P. nigra</i> |

Cephaleuros Kunze

- | | |
|--------------------------|---|
| 1. <i>C. solutus</i> | 9. <i>C. virescens</i> |
| 2. <i>C. laevis</i> | (<i>Mycoidea parasitica</i> , <i>C. mycoidea</i> , |
| 3. <i>C. purpureus</i> | <i>Phyllactidium tropicum</i>) |
| 4. <i>C. karstenii</i> | 10. <i>C. albidus</i> |
| 5. <i>C. pulvinatus</i> | 11. <i>C. minimus</i> |
| 6. <i>C. henningsii</i> | 12. <i>C. parasiticus</i> |
| 7. <i>C. candelabrum</i> | 13. <i>C. coffeae</i> |
| 8. <i>C. lagerheimii</i> | |

Stomatochroon Palm 1934

1. *S. lagerheimii*

Physolinum Printz 19211. *P. monile* (De Wildeman) Printz 1921

Another major publication concerning the Trentepohliales was the well-known textbook of Fritsch (1935). Fritsch envisioned the Trentepohliaceae as a wide ensemble of genera of green algae possessing a filamentous morphology and various differentiated reproductive structures (O'Kelly and Floyd 1990).

Genera included in the Trentepohliaceae by Fritsch (1935):

Section <i>Gongrosireae</i>	<i>Chloroclonium</i>	<i>Lochmium</i>
	<i>Chlorotylum</i>	<i>Pleurastrum</i>
	<i>Endophyton</i>	<i>Pseudendoconium</i>
	<i>Gongrosira</i>	<i>Pseudodictyon</i>
	<i>Leptosira</i>	<i>Sporocladus</i>
Section <i>Gomontieae</i>	<i>Gomontia</i>	<i>Tellamia</i>
Section <i>Trentepohlieae</i>	<i>Trentepohlia</i>	<i>Stomatochroon</i>
	<i>Cephaleuros</i>	<i>Rhizothallus</i>
	<i>Phycopeltis</i>	<i>Physolinum</i>

Smith (1950) placed the Trentepohliaceae into the order Ulotrichales, together with aquatic and subaerial forms. The genera included by Smith are as follows:

Cephaleuros
Ctenocladus
Fridaea
Gomontia
Gongrosira
Leptosira
Physolinum
Trentepohlia

Flint (1959) merged the monotypic genus *Physolinum* with *Trentepohlia*, a treatment widely accepted by many authors (Chapman 1984, Bourrelly 1966); but, based on new evidence, disputed by Davis and Rands (1993) and Davis (1994).

More recently, Thompson and Wujek (1992), based on "the nature of its superficial growth on leaves or twigs and a papilla pore basal on the sporangium," published a new genus, *Printzina* (Type: *Printzina lagenifera*). They described a new species and transferred several species of *Trentepohlia*, many of them from Hariot's (1890) section *Heterothallus*. The new species is *P. ampla*; the transferred species are:

P. lagenifera (= *Trentepohlia lagenifera*; *T. tenuis*; *T. procumbens*; *T. polymorpha*; *T. phyllophila*; *T. gracilis*)
P. lagenifera var. *africana* (= *T. lagenifera* var. *africana*)
P. lagenifera var. *rugulosa* (= *T. lagenifera* var. *rugulosa*)
P. bossei (= *T. bossei*; *T. bossei* f. *major*)
P. diffusa (= *T. diffusa*; *T. pinnata*)
P. dusenii (= *T. dusenii*)
P. effusa (= *T. effusa*; *T. setifera*; *T. effusa* var. *subtropica*)
P. lagerheimii (= *T. lagerheimii*)
P. luteo-fusca (= *T. luteo-fusca*)
P. santurcensis (= *T. santurcensis*)

Thompson and Wujek (1997) prepared a monograph of the Trentepohliales (except for the genera *Printzina*, which was covered in Thompson and Wujek [1992], and *Trentepohlia*) recognizing only subaerial genera within the Trentepohliales. Thompson and Wujek did not include *Physolinum*.

Cephaleuros Kunze

- | | | |
|----------------------------|--------------------------|---|
| 1. <i>C. solutus</i> | 5. <i>C. virescens</i> | 10. <i>C. pilosus</i> |
| 2. <i>C. drouetii</i> | 6. <i>C. expansus</i> | 11. <i>C. parasiticus</i> var. <i>nanus</i> |
| 3. <i>C. tumidae-setae</i> | 7. <i>C. lagerheimii</i> | 12. <i>C. minimus</i> |
| 4. <i>C. karstenii</i> | 8. <i>C. diffusus</i> | 13. <i>C. biolophus</i> |
| | 9. <i>C. henningsii</i> | |

Phycopeltis Millardet

- | | | |
|-----------------------------|-------------------------------|---------------------------|
| 1. <i>P. amboinensis</i> | 7. <i>P. flabellata</i> | 13. <i>P.</i> |
| 2. <i>P. arundinacea</i> | 8. <i>P. irregularis</i> | <i>terminopapillosa</i> |
| 3. <i>P. aurea</i> | 9. <i>P. minuta</i> | 14. <i>P. treubii</i> |
| 4. <i>P. costaricensis</i> | 10. <i>P. novae-zelandiae</i> | 15. <i>P. umbrina</i> |
| 5. <i>P. dorsopapillosa</i> | 11. <i>P. parva</i> | 16. <i>P. vaga</i> |
| 6. <i>P. epiphyton</i> | 12. <i>P. pilosa</i> | 17. <i>P.</i> |
| | | <i>pseudotreubii</i> |
| | | 18. <i>P. treubioides</i> |

Stomatochroon Palm 1934

1. *S. lagerheimii*
2. *S. coalitus*
3. *S. consociatus*
4. *S. reniformis*

The order Trentepohliales, as currently circumscribed (Thompson and Wujek 1997; but we include here also *Physolinum*, which was not recognized by Thompson and Wujek), includes one family, Trentepohliaceae, and six genera that can be separated by the following key:

Key to the Genera of Trentepohliales

1. Thallus reduced to few cells, endophytic *Stomatochroon*
1. Thallus well developed, with filaments free or coalesced to form discs ... 2
2. Aplanospores present, filaments free and moniliform *Physolinum*
2. Aplanospores absent, filaments with cylindrical or inflated cells ... 3
3. Filaments free; epiphytic or not; papilla-pore always basal, adjacent to the sporangium attachment ... 4
3. Filaments regularly coalesced to form discs; sometimes free; commonly associated with a host; papilla-pore basal or terminal ... 5
4. Sporangia globular-reniform; prostrate filaments well developed, scanty erect system *Printzina*
4. Sporangia ovoid; scanty prostrate system, profuse erect system *Trentepohlia*
5. Supracuticular or sometimes epilithic; papilla-pore terminal, opposite to the attachment of the sporangium *Phycopeltis*
5. Subcuticular; papilla-pore basal, adjacent to the attachment of the sporangium *Cephaleuros*

Trentepohlia Martius (nom. cons.)

(Named in honor of J.F. Trentepohl, German botanist).

Type species: *Trentepohlia aurea* Martius

Trentepohlia consists of branched heterotrichous filaments, with a scarce or absent prostrate system and a profuse erect system. Thallus grows on the bark of trees or on rock, are usually found in exposed habitats, often forming conspicuous masses, and are usually yellow to orange in color (Fig. 9). They can form lichenic associations in exposed habitats. Sporangia are ovoid; sporangiate–laterals, solitary or grouped, are borne terminally or on an enlarged terminal head–cell of a branched sporangiophore. Gametangia are terminal only. The life history consists of alternation of isomorphic generations (Thompson and Wujek 1997). *Trentepohlia* is the most species–rich genus of the order. Printz's (1939) work on the family is still the most complete treatment for this genus. After Thompson and Wujek (1997) transferred several species of *Trentepohlia* to *Printzina* and *Phycopeltis*, the following remain from Printz's (1939) list of species.

T. abietina (Flotow) Hansgirg; *T. annulata* Brand; *T. arborum* (C. Agardh) Hariot; *T. aurea* (Linnaeus) Martius; *T. bogoriensis* De Wildeman; *T. calamicola* (Zeller) De Toni & Levi; *T. cucullata* De Wildeman; *T. cyanea* Karsten; *T. depressa* (Muller) Hariot; *T. dialepta* (Nylander) Hariot; *T. diffracta* (Krempelhuber) Hariot; *T. ellipsiocarpa* Schmidle; *T. elongata* (Felles) De Toni; *T. jolithus* (Linnaeus) Wallroth; *T. jucunda* (Cesati) Hariot; *T. leprieurii* Hariot; *T. minima* Schmidle; *T. negerii* Brand; *T. odorata* (Wiggers) Wittrock; *T. peruana* (Kützing) Printz; *T. prolifera* De Wildeman; *T. rigidula* (Muller) Hariot; *T. tentaculata* (Hariot) De Wildeman; *T. treubiana* De Wildeman.; *T. uncinata* (Gobi) Hansgirg; *T. villosa* (Kützing) Hariot; *T. willei* (Tiffany) Printz.

***Printzina* Thompson & Wujek**

(Named in honor of Prof. H. Printz)

Type species: *Printzina lagenifera* (Hildebrand) Thompson & Wujek

Printzina is remarkably similar to *Trentepohlia* (see above), but generally more inconspicuous, with branched heterotrichous filaments, a scarce or absent erect system, a well developed prostrate system, and usually a green color (Fig. 10). Thalli grow on leaves, and are usually found in habitats protected from direct sunlight with high humidity. Sporangia are globular to reniform. Sporangiate–laterals are solitary and sessile on prostrate or erect filaments. The sporangial pore is positioned near the base of the sporangium. Gametangia are terminal or lateral. The life history consists of alternation of isomorphic generations (Thompson and Wujek 1997). The only taxonomic treatment of this genus is that of Thompson and Wujek (1992), which recognized nine species.

P. ampla Thompson & Wujek; *P. bossei* (De Wildeman) Thompson & Wujek; *P. diffusa* (De Wildeman) Thompson & Wujek; *P. dusenii* (Hariot, Wittrock, & Nordst.) Thompson & Wujek; *P. effusa* (Krempelhuber) Thompson & Wujek; *P. lagenifera* (Hildebrand) Thompson & Wujek; *P. lagerheimii* (De Wildeman) Thompson & Wujek; *P. luteo–fusca* (De Wildeman) Thompson & Wujek; *P. santurcensis* (Tiffany) Thompson & Wujek.

***Physolinum* Printz**

(Gr. physa=bladder + Gr. linon=thread)

Type species: *Physolinum monile* (De Wildeman) Printz

Physolinum is also similar to *Trentepohlia* (see above) with branched creeping filaments without a clear distinction between prostrate and erect systems. Thalli grow on the bark of trees or on rock, are usually green–orange to dark orange, and are composed of moniliform cells. Asexual reproduction is by aplanospores. Sexual reproduction is unknown. Printz (1921) erected the genus *Physolinum* based on his discovery of aplanospores. Flint (1959), citing similarities in zoospore production and branching system, merged *Physolinum* with *Trentepohlia*. More recently, Davis et al. (1989) reestablished this genus when studying samples, both free–living and lichenized, of an alga from central Missouri. They emphasized the presence of aplanospores and the absence of plasmodesmata in the cross walls as supporting recognition of the genus

Physolinum. Only one species is known, *Physolinum monile* (De Wildeman) Printz.

***Phycopeltis* Millardet**

(Gr. phykos=algae + L. pelta=shield)

Type species: *Phycopeltis epiphyton* Millardet

Phycopeltis grows in branched filaments that can be free or coalesce to form a pseudoparenchymatic thallus (monostromatic) (Fig. 11) with or without dorsal papillae (“glandular cells” of Thompson and Wujek 1997) and erect filaments (hairs). Thalli are irregular, lobate or orbicular in shape, always grow superficially upon a plant host or inert surface (they are never parasitic), and are yellow–green to dark orange. Sporangiate–laterals are solitary; they can be sessile (no stalk or pedicel), or appear medially or terminally on erect filaments (Fig. 12). The sporangial pore is distal. Gametangia are intercalary or terminal. The life history consists of alternation of isomorphic generations (Thompson and Wujek 1997). A helpful feature distinguishing *Phycopeltis* from other foliicolous genera (*Trentepohlia*, *Physolinum*, *Printzina*, and *Cephaleuros*) is the terminal papilla–pore on the sporangium, which is opposite to the end of attachment (Thompson and Wujek 1997), whereas in the other genera it is basal and adjacent to the area of attachment. The modern taxonomic treatment of the genus includes 18 species (Thompson and Wujek 1997).

P. amboinensis (Karsten) Printz; *P. arundinacea* (Mont.) De Toni; *P. aurea* Karsten; *P. costaricensis* Thompson & Wujek; *P. dorsopapillosa* Thompson & Wujek; *P. epiphyton* Millardet; *P. flabellata* Thompson & Wujek; *P. irregularis* (Schmidle) Wille; *P. minuta* Thompson & Wujek; *P. novae–zelandiae* Thompson & Wujek (however this species may be a synonym of *P. expansa*, according to Rindi and Guiry [2002b]); *P. parva* Thompson; *P. pilosa* Thompson & Wujek; *P. pseudotreubii* Thompson & Wujek; *P. terminopapillosa* Thompson & Wujek; *P. treubii* Karsten; *P. treubioides* Thompson & Wujek; *P. umbrina* (Kützing) Thompson & Wujek (transferred from *T. umbrina* [Kützing] Bornet by Thompson and Wujek [1997]); *P. vaga* Thompson & Wujek.

***Cephaleuros* Kunze**

(Gr. kephale=head + Gr. eurys=breadth)

Type species: *C. virescens* Kunze

Cephaleuros consists of branched filaments, free or coalescing to form a pseudoparenchymatous thallus (usually polystromatic) in the form of irregular discs. The thallus grows below the cuticle or sometimes below the epidermis of the host plant (Fig. 13). *Cephaleuros*, is usually reported as an obligate epiphyte and may be parasitic. The thallus (orange to red–brown) consists of a prostrate portion that is branched irregularly with irregular cells and an erect portion of unbranched hairs, with cylindrical cells, either sterile or fertile, protruding through the cuticle (Fig. 14). Haustorial cells are sometimes present inside the plant host's tissue. Sporangiphores bear one or more head cells subtending sporangiate–laterals (Fig. 15, 16). Gametangia are terminal or intercalary on the prostrate cell filaments. The life history consists of alternation of heteromorphic generations (Thompson and Wujek 1997), with the sporophyte reduced to a dwarf plant (the stalk cell, head cell, one or more suffultory cells, and the meiosporangia). *Cephaleuros* is one of the most studied genera among the Trentepohliales, in part for its worldwide distribution, in part for the obvious presence on and sometimes damage to economically important host plants. The modern treatment of this genus by Thompson and Wujek (1997) included 13 species.

C. biolophus Thompson & Wujek; *C. diffusus* Thompson & Wujek; *C. drouetii* Thompson; *C. expansus* Thompson & Wujek; *C. henningsii* Schmidle; *C. karstenii* Schmidle; *C. lagerheimii* Schmidle; *C. minimus* Karsten; *C. parasiticus* Karsten; *C. pilosus* Thompson & Wujek; *C. solutus* Karsten; *C. tumidae–setae* Thompson & Wujek; *C. virescens* Kunze.

Our preliminary data on *Cephaleuros virescens* collected worldwide and analyzed using the gene 18SSU rDNA suggest that “*Cephaleuros virescens*” encompasses several species with similar morphology, and, therefore, new species and descriptions are needed to recognize these unknown entities. There is an urgent need for modern revisionary studies, using

molecular tools such as gene sequencing and phylogenetic analysis, to evaluate the systematics of this poorly understood group (and the Trentepohliales as a whole).

***Stomatochroon* Palm emend. Thompson & Wujek**

(Gr. stomatos=pl. mouth + Gr. chros=color of skin)

Type species: *Stomatochroon lagerheimii* Palm

Stomatochroon grows as an endophyte in the substomatal chamber and through the intercellular spaces of the host, either as a branching system of filaments or reduced to a single massive and lobed anchoring cell. The thallus is green to orange. Terminal cells become enlarged through the stomata and produce unicellular hairs and clavate sporangiophores distally and gametangia laterally. Sporangioophores are unicellular with either solitary or whorled sporangiate laterals (Fig. 17, 18, 19). The life history consists of alternation of heteromorphic generations (Thompson and Wujek 1997). For a description of the invasion of angiosperm mesophyll by *Stomatochroon* see Timpano and Pearlmutter (1983). *Stomatochroon* was originally described by Palm (1934) from a single species, *S. lagerheimii*. Thompson and Wujek (1997) amended the original description upon adding three new species.

S. coalitus Thompson & Wujek; *S. consociatus* Thompson & Wujek; *S. lagerheimii* Palm; *S. reniformis* Thompson

Hypotheses on Molecular Systematics and Phylogeny

Mattox and Stewart (1984) proposed one of the most widely accepted systems of classification of the green algae. These authors analyzed the ultrastructural data for flagellate cells and cell division accumulated in the previous 20 years. They proposed a system with five classes: Micromonadophyceae, Pleurastrphyceae, Ulvophyceae, Chlorophyceae, and Charophyceae. Mattox and Stewart (1984) described this classification as "more natural than any previous system," but acknowledged that the Micromonadophyceae (which included, among others, *Micromonas*, *Pedinomonas*, *Pyramimonas* and *Scourfieldia*) was an unnatural group because it was defined by primitive features.

Charophycean taxa were represented by the orders Chlorokybales, Klebsormidiales, Coleochaetales, Zygnematales, and Charales. The class Ulvophyceae included the following:

1. all of the coenocytic or siphonous forms (except coenocytic members of the Chlorococcales and genera of the Sphaeropleaceae);
2. marine species of *Ulothrix* and those freshwater species of *Ulothrix* that have codium stages or other ulvophycean features;
3. any other genera that produce a codium stage;
4. all marine branched filaments that were formerly classified in the Chaetophorales;
5. genera usually included in the Ulvales (except *Schizomeris*);
6. *Pseudendoclonium*, *Trichosarcina*, *Pseudendocloniopsis*, *Ctenocladus*, and *Smithsoniella*; and the Trentepohliaceae.

The Pleurastrphyceae of Mattox and Stewart (1984) consisted of Tetraselmiales and Pleurastrales, and the Chlorophyceae included Chlamydomonadales, Volvocales, Chlorococcales, Sphaeropleales, Chlorosarcinales, Chaetophorales, and Oedogoniales.

The system proposed by Mattox and Stewart (1984) is often the starting point for modern discussions of green algal systematics and evolution (McCourt 1995), and its importance lies in the fact that it is based on correlated characters on which phylogenetic predictions can be made.

Conflicting views have been advanced about the systematic position of the Trentepohliales among the several classes of

green algae. The presence of MLSs in the flagellar apparatus and the demonstration of a phragmoplast-type cytokinesis in *Cephaleuros parasiticus* (Chapman and Henk 1986) and *Trentepohlia odorata* (Chapman et al. 2001) suggest an affinity with the class Charophyceae. However, taxonomic features of the Trentepohliales such as the CCW flagellar apparatus components can be cited as evidence for an affinity with the Ulvophyceae (Roberts 1984), where Mattox and Stewart (1984) placed them, but without discussion. Based on biochemical, biophysical, and physiological features, Raven (1987) classified the Trentepohliales among a third class, the Pleurastrophyceae. Moreover, it was noted that the Trentepohliales even share a rare ultrastructural feature (presumptive mating structures, or PMSs, in the gametes) with members of a fourth class, the Chlorophyceae (Chapman and Henk 1983, 1985). Therefore, the Trentepohliales exhibit some features associated with four of the five major classes of green algae in the system proposed, appropriately, by Mattox and Stewart (1984), but the bulk of the evidence has focused the major discussions on ulvophycean versus charophycean affinities of this enigmatic order. The order remains incompletely characterized for phylogenetic purposes (O'Kelly and Floyd 1990).

Recently, molecular studies have challenged the concept of the green algae as a natural group (for a review see Chapman et al. 1999; Waters and Chapman 1996). Molecular evidence consistently supports (a) the monophyly of all the green algae plus land plants, forming the group Viridiplantae (Cavalier-Smith 1981) or Chlorobionta (Bremer 1985), and (b) within the Viridiplantae, the presence of two major lineages of green algae. One of the lineages comprises the charophycean algae and their descendents, the land plants, forming together a monophyletic group named Streptophyta. The charophycean algae include at least five orders: the Chlorokybales, Klebsormidiales, Zygnematales, Coleochaetales, and Charales. The second line, or chlorophycean lineage, consists exclusively of the remaining green algae, forming the monophyletic group Chlorophyta (Friedl 1997; Melkonian et al. 1995). The term "chlorophyte" has often been used to denote all green algae; however, it should now be used only as an informal designation for green algae in the Chlorophyta.

Phylogenetic analysis of different groups of algae using genes has been very successful. The nuclear-encoded small subunit ribosomal DNA (18SSU rDNA) and chloroplast-encoded large subunit ribulose-1,5-bisphosphate carboxylase/oxygenase (*rbcL*) are the most common genes for this purpose. We used the 18SSU rDNA gene to analyze phylogenetic relationships of representatives of the Trentepohliales (Fig. 20) among the green algae. This gene is considered an excellent tool for phylogenetic inference (Chapman and Buchheim 1991, Hamby and Zimmer 1992). A considerable database has been assembled of representatives of the major groups of green plants (<http://ucjeps.berkeley.edu/bryolab/greenplantpage.html>).

For our analysis, DNA was amplified by PCR (Fig. 21) using universal primers (Hamby et al. 1988). Purified DNA amplification products were sequenced with internal primers in an automated sequencer. The sequences were assembled using Sequencher and visually inspected and manually adjusted with MacClade. Regions in the data matrix that could not be unambiguously aligned were excluded from the analyses. Representatives of green plants and two outgroup taxa (glaucocystophytes) were used to construct a general data matrix that was used as input for distance and maximum parsimony. All analyses were performed with the PAUP* 4.0 package (Swofford 1999) on a G4 Macintosh computer. Hierarchical likelihood ratio tests were employed using Modeltest V.3.0 (Posada and Crandall 1998). A neighbor-joining analysis using the maximum likelihood model parameters selected by Modeltest was performed.

The maximum likelihood analysis (Figure 22) positioned the trentepohlialean taxa unequivocally within the chlorophycean lineage, the Chlorophyta. The Chlorophyta lineage forms a monophyletic group. Present results based on nuclear-encoded SSU rDNA confirm the previous reports from both SSU data and chloroplast-encoded LSU rubisco data on the existence of two lineages of Viridiplantae. Since some branches of this phylogram are short, the specific topology shown herein should not be considered to be more than a preliminary hypothesis of relationships, that certainly warrants further study. The land plants within the streptophyte clade diverged from the Charophyceae as expected from previous reports. As predicted by Mattox and Stewart (1984), the micromonadophycean taxa are not a natural or monophyletic group but rather a series of basal divergences forming a grade. This paraphyletic group is also known as Prasinophyceae, and the use of this term has been recommended by Sym and Pienaar (1993). Similar results supporting the paraphyletic nature of this group have been reported (Nakayama et al. 1998, Fawley et al. 1999). In general, the prasinophytes are considered as the modern representatives of the earliest green algae (Graham and Wilcox 2000). Despite the fact they are not a monophyletic group, their basal position is well supported.

The representatives of the order Trentepohliales are included with the ulvophycean taxa, and this clade is the sister group of the remaining green algae, the Chlorophyceae and Pleurastrrophyceae (*sensu* Mattox and Stewart). Pleurastrrophyceae is polyphyletic (as shown by Friedl and Zeltner 1994). A new class, Trebouxiophyceae, was erected by Friedl (1995) to include many coccoid green algae that completely lack a motile stage (autosporic coccoids) and members of the Microthamniales (*sensu* Melkonian 1982, 1990 or Pleurastrales *sensu* Mattox and Stewart 1984) based on rDNA sequence comparisons (Friedl 1995, 1997). The Chlorophyceae analyzed in the present study formed a clade and comprised two distinct lineages defined by ultrastructural details of the flagellar apparatus: one group with a clockwise basal body configuration (CW group) and the other group with directly opposed basal bodies (DO group) (Lewis et al. 1992, Nakayama et al. 1996).

The maximum likelihood analysis consistently positioned the taxa of Trentepohliales within the ulvophycean clade. The monophyly of the Trentepohliales is not surprising since some features such as the sporangium-associated apparatus (Fig. 16) and the flagellar apparatus are unique for this order. Both ulvophycean and Trentepohliales taxa share a CCW basal body configuration as well as an alternation of generations. Based on preliminary partial nuclear-encoded SSU rDNA sequence data, Zechman et al. (1990) also related the Trentepohliales to the Ulvophycean clade. The phylogram (Fig. 22) also indicates that the “advanced” taxa (marine orders Siphonocladales/Cladophorales complex and Dasycladales) are the most closely related to the trentepohlialean algae. One could speculate that the trentepohlialean group presumably diverged from an ulvophycean-like macroscopic filamentous marine ancestor. (It is interesting that trentepohlialean taxa cultured in the laboratory can grow either in freshwater or marine media.)

The phylogram indicates that *Phycopeltis* and *Trentepohlia sensu lato* are basal. In contrast, *Cephaleuros* is a derived monophyletic clade. Furthermore, analysis of isolates of *Cephaleuros virescens* from the United States, Taiwan, and South Africa indicate that this taxon may consist of different species sharing a convergent morphology (as suggested by karyological data above). A recent report (López-Bautista et al. 2002) also indicates that a solitary versus grouped sporangiate lateral is a phylogenetic marker in this order.

CONCLUSION

The presence of phragmoplast-mediated cytokinesis in *Cephaleuros* (Chapman and Henk 1986) and *Trentepohlia odorata* (Chapman et al. 2001) remains an enigma. This mode of cytokinesis, which probably involves several genes, is well documented in some charophycean algae and is the typical cytokinesis in land plants. The unexpected presence of the phragmoplast in the chlorophycean lineage raises questions about the homology of this cytokinetic process. Of special attention is the fact that in both lineages, chlorophycean and charophycean, the phragmoplast-mediated cytokinesis is associated with terrestrial (subaerial) habits. Perhaps the solution to this puzzle and the evolutionary history of the development of the phragmoplast may remain in a thorough study of the ultrastructural cytokinetic apparatus and the analysis of the phragmoplast-associated protein, phragmoplastin (López-Bautista et al. 2002), in the basal groups of the charophycean lineage and representatives of the Trentepohliales. Also, the possibility of lateral gene transfer (LGT) should not be dismissed, though it is improbable for various reasons. First, the phragmoplast-mediated cytokinesis undoubtedly involved several genes, and a suite of genes (one or more operons?) would have to be laterally transferred. Second, the rather intimate association of *Cephaleuros* spp. with phragmoplast-containing land plant hosts hints at the possibility of some mechanism for LGT, but *Trentepohlia* does not exhibit such a close relationship with land plant hosts when growing epiphytically. Third, the “morphology” of the phragmoplast-mediated cytokinesis in *Cephaleuros* and *Trentepohlia* is not identical to that in the land plants.

Future research just might provide evidence for some bizarre LGT or, conversely, provide significant evidence for non-homology and parallel evolution. Either way, the uniqueness of the Trentepohliales continues to underscore that they are a challenging and interesting group of green algae that should continue to be studied—perhaps especially in the tropics where they are abundant and diverse, but are disappearing as fast as their habitats are disappearing.

Download all figures. N.B.: very big file**REFERENCES**

Abbas, A. and Godward, M. 1964.

Cytology in relation to taxonomy in Chaetophorales. *Journal of the Linnean Society. Botany* 58: 499–507.

Alexopoulos, C.J., Mims, C.W., and Blackwell, M. 1996.

Introductory Mycology. John Wiley and Sons. Fourth edition. 869 pp.

Bold, H.C. and Wynne, M. 1985.

Introduction to the algae. Prentice–Hall, Inc. Second Edition. 720 pp.

Bourrelly, P. 1966.

Les algues d'eau douce. Initiation à la systématique. I. Les algues verts. Boubee, Paris. 511 pp.

Bremer, K. 1985.

Summary of green plant phylogeny and classification. *Cladistics* 1: 369–385.

Cavalier–Smith, T. 1981.

Eukaryote kingdoms: seven or nine? *Biosystems* 14: 461–481.

Chapman, R.L. 1976.

Ultrastructure of *Cephaleuros virescens* (Chroolepidaceae; Chlorophyta). I. Scanning electron microscopy of zoosporangia. *American Journal of Botany* 63: 1060–1070.

Chapman, R.L. 1980.

Ultrastructure of *Cephaleuros virescens* (Chroolepidaceae; Chlorophyta). II. Gametes. *American Journal of Botany* 67: 10–17.

Chapman, R.L. 1981.

Ultrastructure of *Cephaleuros virescens* (Chroolepidaceae; Chlorophyta). III. Zoospores. *American Journal of Botany* 68: 544–556.

Chapman, R.L. 1984.

An assessment of the current state of our knowledge of the Trentepohliaceae. In Irvine, D. & John, D. (eds.) *Systematics of the Green Algae*. Academic Press, London, pp. 233–250.

Chapman, R.L., Borkhsenius, O., Brown, R.C., Henk, M.C., and Waters, D.A. 2001.

Phragmoplast-mediated cytokinesis in *Trentepohlia*: results of TEM and immunofluorescence cytochemistry. *International Journal of Systematic and Evolutionary Microbiology* 51: 759–765.

Chapman, R.L. and Buchheim, M. A.

1991. Ribosomal RNA gene sequences: Analysis and significance in the phylogeny and taxonomy of green algae. *Critical Reviews in Plant Science* 10: 343–368.

Chapman, R.L., Buchheim, M.A., Delwiche, C.F., Friedl, T., Huss, V.A., Karol, K.G., Lewis, L.A., Manhart, J., McCourt, R.M., Olsen, J.L., and Waters, D.A. 1999.

Molecular systematics of the green algae. In Soltis, D.E., Soltis, P.S., and Doyle, J.J. (eds.) *Molecular Systematics of Plants II*. Kluwer Publishers Boston. Pp. 508–540.

Chapman, R.L. and Good, B.H. 1976.

Observations on the morphology and taxonomy of *Phycopeltis hawaiiensis* King (Chroolepidaceae). *Pacific Science* 30: 187–195.

Chapman, R.L. and Good, B.H. 1978.

Ultrastructure of plasmodesmata and cross walls in *Cephaleuros*, *Phycopeltis* and *Trentepohlia* (Chroolepidaceae; Chlorophyta). *British Phycological Journal* 13: 241–246.

Chapman, R.L. and Good, B.H. 1983.

Subaerial symbiotic green algae: Interactions with vascular plant hosts. In Goff, L.J. (ed.) *Algal Symbiosis: A Continuum of Interaction Strategies*. Cambridge Univ. Press, London and New York. Pp. 173–204.

Chapman, R.L. and Henk, C. 1981.

Observations on the putative dwarf sporophyte of *Cephaleuros* Kunze (Chlorophyta; Chroolepidaceae). *Proceedings of the Thirteenth International Botanical Congress*, 1981 p. 162.

- Chapman, R.L. and Henk, C. 1982.
Cruciate flagellar apparatus and multilayered structures in *Cephaleuros virescens* gametes. *Proceedings of the First International Phycological Congress*, 1982, a8.
- Chapman, R.L. and Henk, C. 1983.
Ultrastructure of *Cephaleuros virescens* (Chroolepidaceae; Chlorophyta). IV. Absolute configuration analysis of the cruciate flagellar apparatus and multilayered structures in the pre- and post-release gametes. *American Journal of Botany* 70: 1340–1355.
- Chapman, R.L. and Henk, C. 1985.
Observations on habitat, morphology and ultrastructure of *Cephaleuros parasiticus* (Chlorophyta) and a comparison with *C. virescens*. *Journal of Phycology* 21: 513–522.
- Chapman, R.L. and Henk, C. 1986.
Phragmoplasts in cytokinesis of *Cephaleuros parasiticus* (Chlorophyta) and a comparison with *C. virescens* vegetative cells. *Journal of Phycology* 22: 83–88.
- Chapman, R.L. and Waters, D.A. 2002.
Lichenization of the Trentepohliales. In Seckbach, J. (ed.) *Symbiosis*. Kluwer Academic Publishers. The Netherlands. Pp. 359–371.
- Chappell, D.F., Stewart, K.D., and Mattox, K.R. 1978.
On pits and plasmodesmata of Trentepohliacean algae (Chlorophyta). *Transactions of the American Microscopical Society* 97: 88–94.
- Chowdary, Y. 1959.
Cytology of *Trentepohlia* and *Cephaleuros*. In: *Proc. Symp. Algology*. UNESCO–ICAR. New Delhi. 65–69 pp.
- Chowdary, Y. 1963.
On the cytology and systematic position of *Physolinum monilia* Printz. *Nucleus* 6: 44–48.
- Czeczuga, B. and Maximov, O. 1996.
Carotenoids in the cells of the alga *Trentepohlia gobii* Meyer. *Acta Societatis Botanicorum Poloniae* 65(3–4): 273–276.
- Davis, J.S. 1994.
Coenogonium missouriense, a new lichen species from Missouri. *The Bryologist* 97: 186–1989.
- Davis, J.S. and Rands, D.G. 1993.
Observations on lichenized and free-living *Physolinum* (Chlorophyta, Trentepohliaceae). *Journal of Phycology* 29: 819–825.
- Davis, J.S., Rands, D.G., and Lachapelle, M. 1989.
Heavily lichenized *Physolinum* (Chlorophyta) from a dimly lit cave in Missouri. *Journal of Phycology* 25: 419–428.
- De Wildeman, E. 1888a.
Les espèces du genre *Trentepohlia* Mart. (*Chroolepus* Ag.). *Bulletin de la Société Royale de Botanique de Belgique* 27: 22–25.
- De Wildeman, E. 1888b.
Observations sur quelques formes du genre *Trentepohlia* Mart. *Bulletin de la Société Royale de Botanique de Belgique* 27: 136–144.
- De Wildeman, E. 1888c.
Observations sur quelques formes d'algues terrestres épiphytes. *Bulletin de la Société Royale de Botanique de Belgique* 27: 119–126.
- Dilcher, D.L. 1965.
Epiphyllous fungi from Eocene deposits in western Tennessee, USA. *Paleontographica* 116: 1–54.
- Fawley, M.W., Qin, M., and Yun, Y. 1999.
The relationship between *Pseudoscourfieldia marina* and *Pycnococcus provasolii* (Prasinophyceae, Chlorophyta): evidence from 18S rDNA sequence data. *Journal of Phycology* 35: 838–843.
- Feige, G.B., and Kremer, B.P. 1980.
Unusual carbohydrate pattern in *Trentepohlia* species. *Phytochemistry* 19: 1844–1845.
- Flint, E.A. 1959.

- The occurrence of zoospores in *Physolinum* Printz. *New Phytologist* 58: 267–270.
- Fowke, L.C. and Pickett–Heaps, J. 1969.
Cell division in *Spirogyra*. I. Mitosis. *Journal of Phycology* 5: 240–259.
- Friedl, T. 1995.
Inferring taxonomic positions and testing genus level assignments in coccoid green lichen algae: a phylogenetic analysis of 18S ribosomal RNA sequences from *Dictyochloropsis reticulata* and from members of the genus *Myrmecia* (Chlorophyta, Trebouxiophyceae *cl. nov.*). *Journal of Phycology* 31: 632–639.
- Friedl, T. 1997.
The evolution of the green algae. *Plant Systematics and Evolution* 11(Suppl): 87–101.
- Friedl, T. and Zeltner, C. 1994.
Assessing the relationships of some coccoid green lichen algae and the Microthamniales (Chlorophyta) with 18S ribosomal RNA gene sequence comparisons. *Journal of Phycology* 30: 500–506.
- Fritsch, F.E. 1935.
The Structure and Reproduction of the Algae. Vol. 1. Cambridge Univ. Press. London and New York.
- Good, B.H. 1978.
Ultrastructural and biochemical studies on the epiphytic subaerial green alga *Phycopeltis epiphyton* Millardet. Ph. D. dissertation, Louisiana State University, Baton Rouge.
- Good, B.H. and Chapman, R.L. 1978a.
Scanning electron microscope observations on zoosporangial abscission in *Phycopeltis epiphyton* (Chlorophyta). *Journal of Phycology* 14: 374–376.
- Good, B.H. and Chapman, R.L. 1978b.
The ultrastructure of *Phycopeltis* (Chroolepidaceae; Chlorophyta). I. Sporopollenin in the cell walls. *American Journal of Botany* 65: 27–33.
- Graham, L.E. and McBride, G.M. 1975.
The ultrastructure of multilayered structures associated with flagellar bases in motile cells of *Trentepohlia aurea*. *Journal of Phycology* 11: 86–96.
- Graham, L.E. and McBride, G.M. 1978.
Mitosis and cytokinesis in sessile sporangia of *Trentepohlia aurea* (Chlorophyceae). *Journal of Phycology* 14: 132–137.
- Graham, L.E. and Wilcox, L.W. 2000.
Algae. Prentice–Hall, USA, pp. 640.
- Haapala, H., Goltsova, N., Seppala, R., Huttunen, S., Kouki, J., Lamppu, J., and Popovichev, B. 1996.
Ecological condition of forests around the eastern part of the Gulf of Finland. *Environmental Pollution* 91: 253–265.
- Hamby, R.K., Sims, L., Issel, L., and Zimmer, E. 1988.
Direct ribosomal RNA sequencing: optimization of extraction and sequencing methods for work with higher plants. *Plant Molecular Biology Reporter* 6: 175–192.
- Hamby, R.K. and E.A. Zimmer. 1992.
Ribosomal RNA as a phylogenetic tool in plant systematics. In P.S. Soltis, D.E. Soltis, and J.J. Doyle (eds.) *Molecular Systematics of Plants*. Chapman and Hall, New York. pp. 50–91.
- Hansgirg, A. 1886.
Prodromus der Algenflora von Böhmen. Erster Theil... *Archiv für die Naturwissenschaftliche Landesforschung von Böhmen* 5(6) 1–96.
- Hariot, P. 1889.
Note sur le genre *Cephaleuros*. *Journal de Botanique [Morot]* 3: 274–276, 284–288.
- Hariot, P. 1890.
Notes sur le genre *Trentepohlia* Mart. *Journal de Botanique [Morot]* 4: 50–53, 85–92, 192–196.
- Hariot, P. 1893.
Les trois *Trentepohlia*. *Journal de Botanique [Morot]* 7: 216.
- Hoek, C. van den, Mann, D., and Jahns, H. 1995.
Algae: an introduction to phycology. Cambridge Univ. Press. Cambridge. 623 pp.

Holcomb, G.E. 1986.

Hosts of the parasitic alga *Cephaleuros virescens* in Louisiana and new host records for the continental United States. *Plant Disease* 70: 1080–1083.

Jose, G. and Chowdary, Y. 1977.

Karyological studies on *Cephaleuros* Kunze. *Acta Botanica Indica* 5: 114–122.

Jose, G. and Chowdary, Y. 1978.

On the cytology of some *Trentepohlias* from India. *Acta Botanica Indica* 6: 159–166.

Karsten, G. 1891.

Untersüchungen über die Familie der Chroolepideen. *Annales du Jardin Botanique de Buitenzorg* 10: 1–66.

Kjosen, H. 1972.

Synthetic and Spectroscopic Studies of Carotenoids. University of Trondheim. Dissertation. Norway. 239 pp.

Kremer, B.P. and Kirst, G.O. 1982.

Biosynthesis of photosynthates and taxonomy of algae. *Zeitschrift für Naturforschung* 37: 761–771.

Lewis, L.A., Wilcox, L.W., Fuerst, P.A., and Floyd, G.L. 1992.

Concordance of molecular and ultrastructural data in the study of zoosporic chlorococcalean green algae. *Journal of Phycology* 28: 375–380.

López–Bautista, J.M. and Chapman, R.L. 1999.

Molecular and microspectrophotometric analyses and phylogeny of the subaerial Trentepohliales (Chlorophyta). *Journal of Phycology* 35(Suppl.): 21.

López–Bautista, J., Chapman, R.L., Rindi, F., and Guiry, M. 2002.

Molecular systematics of the subaerial green algal family Trentepohliaceae (Chlorophyta, Trentepohliales) inferred from 18 SSU rDNA sequences. *Botany 2002, Publ. Abst.* 348: 89.

López–Bautista, J.M., Kapraun, D.F., and Chapman, R.L. 1998.

Karyology and nuclear genome quantification in the order Trentepohliales (Chlorophyta). *Journal of Phycology* 34(Suppl): 35.

López–Bautista, J.M., Nedelcu, A.M., and Chapman, R.L. 1998.

Continuous mitochondrial large subunit ribosomal RNAs in *Cephaleuros parasiticus* Karsten (Trentepohliales, Chlorophyta): phylogenetic implications. *Journal of Phycology* 34(Suppl): 35.

López–Bautista, J.M., Waters, D.A., and Chapman, R.L. 1995.

Phylogenetic affinities of the Trentepohliales (Chlorophyta) inferred from small subunit rRNA gene sequences. *Journal of Phycology* 31(Suppl): 7.

López–Bautista, J., Waters, D.A., and Chapman, R.L. 2002.

Phragmoplast in green algae and the evolution of cytokinesis. *International Journal of Systematic and Evolutionary Microbiology* (In press).

Marchant, H.J. and Pickett Heaps, J. 1973.

Mitosis and cytokinesis in *Coleochaete scutata*. *Journal of Phycology* 9: 461–471.

Marche–Marchad, J. 1981.

Quelques données écologiques sur *Cephaleuros virescens* Kunze et les lichens dont il est la gonidie. *Cryptogamie: Algologie* 2: 289–301.

Matthews, S.W., Tucker, S., and Chapman, R.L. 1989.

Ultrastructural features of mycobionts and trentepohliaceous phycobionts in selected subtropical crustose lichens. *Botanical Gazette* 150: 417–438.

Mattox, K.R. and Stewart, K.D. 1984.

Classification of the green algae: A concept based on comparative cytology. In Irvine, D.E.G. and John, D.M. (eds.) *Systematics of the Green Algae*. Academic Press, London and Orlando. Pp. 29–72.

McCourt, R.M. 1995.

Green algal phylogeny. *Trends in Ecology and Evolution* 10: 159–163.

Melkonian, M. 1982.

Two different types of motile cells within the Chlorococcales and the Chlorosarcinales: taxonomic implications. *British Phycological Journal* 17: 236.

Melkonian, M. 1990.

- Chlorophyte orders of uncertain affinities: order Microthamniales. In Margulis, L., Corliss, J.O., Melkonian, M., and Chapman, D. (eds.) *Handbook of Protoctista*. Jones and Bartlett Publishers, Boston, pp. 652–664.
- Melkonian, M., Marin, B., and Surek, B. 1995.
Phylogeny and evolution of the algae. In Arai, R., Kato, M. and Doi, Y. (eds.) *Biodiversity and Evolution*. The National Science Museum Foundation, Tokyo, pp. 153–176.
- Nakayama, T., Marin, B., Kranz, H., Surek, B., Huss, V., Inouye, I., and Melkonian, M. 1998.
The basal position of scaly green flagellates among the green algae (Chlorophyta) is revealed by analyses of nuclear-encoded SSU rRNA sequences. *Protist* 149: 367–380.
- Nakayama, T., Watanabe, S., Mitsui, K., Uchida, H., and Inouye, I. 1996.
The phylogenetic relationships between the Chlamydomonadales and Chlorococcales inferred from 18S rDNA sequence data. *Phycological Research* 44: 47–56.
- Noguerol-Seoane, A. and Rifon-Lastra, A. 1997.
Epilithic phycoflora on monuments. A survey of San Esteban de Ribas de Sil Monastery (Ourense, NW Spain). *Cryptogamie: Algologie* 18: 351–361.
- O'Kelly, C.J. and Floyd, G.L. 1990.
Chlorophyte orders of uncertain affinities: Order Trentepohliales. In Margulis, L., Corliss, J.O., Melkonian, M., and Chapman, D.J. (eds.) *Handbook of Protoctista*. Jones and Bartlett Publ., Boston, pp. 658–660.
- Palm, B.T. 1934.
On parasitic and epiphyllous algae: II. *Stomatochroon*, a genus of stomaticolous Chroolepideae. *Arkiv för Botanik* 25: 1–16.
- Papenfuss, G.F. 1962.
On the circumscription of the green algal genera *Ulvella* and *Pilinia*. *Phykos* 1: 6–12.
- Patterson, G.W. and S. Van Valkenburg. 1991.
Sterols of *Cephaleuros* (Trentepohliaceae), a parasitic green alga. *Journal of Phycology* 27: 549–551.
- Pickett-Heaps, J. 1967.
Ultrastructure and differentiation in *Chara* sp. II. Mitosis. *Australian Journal of Botany* 20: 883–894.
- Posada, D. and Crandall, K.A. 1998.
Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- Printz, H. 1921.
Subaërial algae from South Africa. *Kongelige Norske Videnskabers Selskabs Skrifter* 1920(1). 41 pp. XIV pls.
- Printz, H. 1927.
Trentepohliaceae. In Engler, A. and Prantl, K. (eds.) *Die natürlichen Pflanzenfamilien*. Verlag von Wilhelm Engelmann. Pp. 217–225.
- Printz, H. 1939.
Vorarbeiten zu einer Monographie der Trentepohliaceae. *Nytt Magazin for Naturvidenskaberne* 80: 137–210.
- Printz, H. 1964.
Die Chaetophorales der Binnengewässer. Eine systematische Übersicht. *Hydrobiologia* 24: 1–76.
- Rabenhorst, L. 1868.
Flora europea algarum aquae dulcis et submarinae. Sectio III. Algas chlorophyllophyceas, melanophyceas et rhodophyceas complectens. Kummer, Leipzig.
- Raven, J.A. 1987.
Biochemistry, biophysics and physiology of chlorophyll b-containing algae: implications for taxonomy and phylogeny. *Progress in Phycological Research* 5: 1–122.
- Reynolds, D.R. and Dilcher, D.L. 1984.
A foliicolous alga of Eocene age. *Review of Palaeobotany and Palynology* 43: 397–403.
- Reynolds, D.R. and Dunn, P.H. 1982.
Foliicolous fungi from Brazil: the new genus *Veralucia*. *Mycologia* 74: 854–857.
- Reynolds, D.R. and Dunn, P.H. 1984.
A fungus-like alga. *Mycologia* 76: 719–721.
- Rindi, F. and Guiry, M.D. 2002.

- Diversity, life history, and ecology of *Trentepohlia* and *Printzina* (Trentepohliales, Chlorophyta) in urban habitats in western Ireland. *Journal of Phycology* 38: 39–54.
- Roberts, K.R. 1984.
The flagellar apparatus in *Batophora* and *Trentepohlia* and its phylogenetic significance. In Irvine, D.E.G. and John, D.M. (eds.) *Systematics of the Green Algae*. Academic Press, London and Orlando, pp. 331–341.
- Ross, R. and Irvine, L.M. 1967.
The typification of the genus *Byssus* L. (1753). *Taxon* 16: 184–186.
- Saitou, N. and Nei, M. 1987.
The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution* 4: 406–425.
- Salleh, A. and Kamsari, S. 1994.
Studies on *Cephaleuros virescens* Kunze, a parasitic alga from Malaysia. In Phang, E. (ed.) *Algal Biotechnology in the Asia-Pacific Region*. University of Malaysia, pp. 274–278.
- Santesson, R. 1952.
Foliicolous lichens. I. A revision of the obligately foliicolous, lichenized fungi. *Symbolae Botanicae Upsalienses* 12: 1–590.
- Sarma, Y. 1982.
Chromosome number in algae. *Nucleus* 25: 66–108.
- Silva, P.C. 1950.
Generic names of algae proposed for conservation. *Hydrobiologia* 2: 252–280.
- Silva, P.C. 1982.
Chlorophycota. In Parker, S.P. (ed.) *Synopsis and Classification of Living Organisms. Vol. I*. McGraw-Hill, New York. Pp. 133–161.
- Sluiman, H. 1989.
The green algal class Ulvophyceae: an ultrastructural survey and classification. *Cryptogamic Botany* 1: 83–94.
- Smith, G.M. 1950.
The Freshwater Algae of the United States. Mc Graw-Hill. 2nd edition. New York.
- Stewart, K.D., Mattox, K.R., and Floyd, G.L. 1973.
Mitosis, cytokinesis, the distribution of plasmodesmata, and other cytological characteristics in the Ulotrichales, Ulvales, and Chaetophorales: phylogenetic and taxonomic considerations. *Journal of Phycology* 9: 128–141.
- Suematu, S. 1960.
The somatic nuclear division in *Trentepohlia aurea*, the aerial alga. *Bulletin of Liberal Arts College, Wakayama University, Natural Science* 10: 111.
- Swofford, D.L. 1999.
PAUP: Phylogenetic Analysis Using Parsimony (*and other methods)*. Version 4. Sinauer Associates. Sunderland, Massachusetts.
- Sym, S.D. and Pienaar, R.N. 1993.
The class Prasinophyceae. *Progress in Phycological Research* 9: 281–376.
- Tan, C., Lee, Y., and Ho, K. 1993.
Effect of light intensity and ammonium-N on carotenogenesis of *Trentepohlia odorata* and *Dunaliella bardawil*. *Journal of Applied Phycology* 5: 547–549.
- Tan, K., Wee, Y., and Ho, K. 1985.
Laboratory evaluation of biocides for the control of *Trentepohlia odorata*. *International Biodeterioration* 21(1): 5–10.
- Tappan, H. 1980.
The paleobiology of plant protists. W.H. Freeman. San Francisco.
- Thompson, R.H. 1961.
The life cycles of *Cephaleuros* and *Stomatochroon*. *Proceedings of the Ninth International Botanical Congress* 2 (abstr.): 397.
- Thompson, R.H. and Wujek, D. 1992.

Printzina gen. nov. (Trentepohliaceae), including a description of a new species. *Journal of Phycology* 28: 232–237.

Thompson, R.H. and Wujek, D. 1997.

Trentepohliales: Cephaleuros, Phycopeltis, and Stomatochroon. Morphology, Taxonomy, and Ecology. Science Publishers. India. 149 pp.

Tucker, S.C., Matthews, S.W., and Chapman, R.L. 1991.

Ultrastructure of subtropical crustose lichens. In Galloway, D.J. (ed.) *Tropical Lichens: Their Systematics, Conservation, and Ecology.* Clarendon, Oxford, pp. 171–191.

Turner, F.R. 1968.

An ultrastructural study of plant spermatogenesis: Spermatogenesis in *Nitella*. *Journal of Cell Biology* 37: 370–393.

Wakefield, R., Jones, M., Wilson, M., Young, M., Nicholson, K., and Urguhart, C. 1996.

Investigations of decayed sandstone colonized by a species of *Trentepohlia*. *Aerobiologia* 12: 19–25

Waters, D., Brown, R., López–Bautista, J., and Chapman, R.L. 1998.

Phragmoplast–mediated cytokinesis in *Trentepohlia odorata* (Chlorophyta): An immunofluorescent cytological study. *Journal of Phycology* 34(Suppl): 62–63.

Waters, D.A. and Chapman, R.L. 1996.

Molecular phylogenetics and the evolution of green algae and land plants. In Chaudhary, B.R. and Agrawal, S.B. (eds.) *Cytology, Genetics and Molecular Biology.* SPB Academic Publishing, Amsterdam, pp. 337–349.

Zechman F.W., Theriot, E.C., Zimmer, E., and Chapman, R.L. 1990.

Phylogeny of the Ulvophyceae (Chlorophyta): cladistic analysis of nuclear–encoded rRNA sequence data. *Journal of Phycology* 26: 700–710.

ACKNOWLEDGEMENTS

This paper is partially based on the dissertation of Juan M. López–Bautista of Louisiana State University at Baton Rouge (2000). We thank D. F. Kapraun, S. Fredericq, F. Rindi, M. Guiry, and G. E. Holcomb. The research was funded in part by NSF grant DEB–9408057, Sigma Xi, and DOE/NSF/USDA Joint Program on Collaborative Research in Plant Biology (USDA grant 94–37105–0173).

The Trentepohliales Revisited

Juan M. López–Bautista, Debra A. Waters, and Russell L. Chapman

Table 1. Chromosome numbers reported in some members of the Trentepohliales. ^a As cited by Sarma (1982).

Species	Chromosome Number	Reference
<i>Cephaleuros solutus</i> Karsten	12, 14	Jose and Chowdary 1977
<i>C. virescens</i> Kunze in Fries	18, 36 (24,27,32)	Jose and Chowdary 1977, Chowdary 1959
<i>Physolinum monile</i> (de Wildeman) Printz	22	Chowdary 1963

<i>Printzina bossei</i> (de Wildeman) Thompson & Wujek	48	Chowdary 1962 ^a , Jose and Chowdary 1978
<i>P. dusenii</i> (Hariot) Thompson & Wujek	18	Chowdary 1962 ^a
<i>P. effusa</i> (Krempelhuber) Thompson & Wujek	18	Jose and Chowdary 1978
<i>P. lagenifera</i> (Hildebrand) Thompson & Wujek	4	Chowdary 1962 ^a
<i>P. santurcensis</i> (Tiffany) Thompson & Wujek	16	Jose and Chowdary 1978
<i>Trentepohlia abietina</i> (Flotow) Hansgirg	16	Jose and Chowdary 1978
<i>T. aurea</i> (Linnaeus) Martius	16	Suematu 1960
<i>T. aurea</i> (Linnaeus) Martius	18	Abbas and Godward 1964
<i>T. aurea</i> (Linnaeus) Martius	56	Jose and Chowdary 1978
<i>T. cucullata</i> de Wildeman	48	Jose and Chowdary 1978
<i>T. elongata</i> (Felles) de Toni	24	Chowdary 1962 ^a
<i>T. jucunda</i> (Cesati) Hariot	42	Jose and Chowdary 1978
<i>T. treubiana</i> de Wildeman	56	Jose and Chowdary 1978
<i>T. umbrina</i> (Kützing) Bornet	12	Chowdary 1962 ^a
<i>T. uncinata</i> (Gobi) Hansgirg	56	Jose and Chowdary 1978