

New records of Trentepohliales (Ulvophyceae, Chlorophyta) from Africa

by

Fabio Rindi*¹, Michael D. Guiry² and Juan M. López-Bautista¹

¹Department of Biological Sciences, The University of Alabama, P.O. Box 870345,
425 Scientific Collections Building, Tuscaloosa, AL 35487-0345, U.S.A.

²AlgaeBase Centre, Martin Ryan Institute, National University of Ireland, Galway, Ireland

With 31 figures

Rindi, F., M.D. Guiry & J.M. López-Bautista (2006): New records of Trentepohliales (Ulvophyceae, Chlorophyta) from Africa. - Nova Hedwigia 83: 431-449.

Abstract: The diversity and distribution of the Trentepohliales have been investigated in detail in several regions of Europe and Asia. However, the information available for other continents is relatively limited and very little is known for these algae in Africa. New records of Trentepohliales for Africa were obtained in the course of surveys conducted in 2005 in South Africa, Namibia and Tanzania. For *Phycopeltis epiphyton*, *Trentepohlia abietina* and *Trentepohlia flava*, these are the first documented records for the continent. A species of *Printzina*, probably an undescribed taxon, was collected from trees in Tanzania. The new collections allowed the rediscovery and characterization of some poorly known species, of dubious taxonomic validity, such as *Trentepohlia afra* and *T. chinensis*. Additional records of widespread species, such as *Phycopeltis arundinacea* and *Trentepohlia umbrina*, were also obtained. The morphology and distribution of the species collected are described and the taxonomic and biogeographical implications of the new records are discussed.

Introduction

The order Trentepohliales includes subaerial green algae widespread in tropical and temperate regions with humid climates, where they occupy a wide range of habitats and occur on a great range of substrata (Chapman 1984; Ettl & Gärtner 1995; Thompson & Wujek 1997). This order is distinguished from all other green algae by the unique combination of the following features: presence of β -carotene and haematochrome (which colour the thallus yellow, orange or red), absence of pyrenoids in the chloroplast, a unique flagellar apparatus, transverse cell walls with

*Author to whom correspondence should be addressed; e-mail: frindi@bama.ua.edu

plasmodesmata, and presence of a unique reproductive structure, the sporangiate lateral. The sporangiate lateral is a highly modified branch; it consists of an apical cell (the suffultory cell) that is swollen basally and tapers apically into a short neck, on which a spherical or oval zoosporangium is borne (Fig. 1). At maturity, the zoosporangium is shed and carried by the wind, contributing to the dispersal of these algae. Due to such unusual combination of features, the position of the Trentepohliales at the class level has been long uncertain (Chapman et al. 2001; López-Bautista et al. 2002). Only recently, molecular data have provided conclusive evidence that the Trentepohliales are members of the class Ulvophyceae (López-Bautista & Chapman 2003). However, despite more than 200 years of intensive study, the taxonomy at genus and species level is still affected by many unsolved problems. As presently circumscribed, the order includes five genera: *Cephaleuros* Kunze ex Fries 1832, *Phycopeltis* Millardet 1870, *Printzina* Thompson & Wujek 1992, *Stomatochroom* Palm 1934 and *Trentepohlia* Martius 1817 (the taxonomic validity of *Physolinum* Printz 1920 is controversial and, in the recent literature, this genus has generally not been separated from *Trentepohlia*). Although the morphological separation of the genera is straightforward, recent evidence based on SSU rRNA sequences suggests that the characters traditionally used for the separation at the genus level have no phylogenetic significance, and a radical revision of the generic arrangement of the group will be probably necessary (López-Bautista et al. 2006). Delimitation at the species level is also often difficult. To date, species-level identification in the Trentepohliales is almost entirely based on gross morphology, which in some species is known to encompass considerable variation. Several species of *Trentepohlia* and *Printzina*, the genera most intensively studied, are reported to be very polymorphic (Hariot 1889a; Printz 1920, 1939; Rindi & Guiry 2002a). Although for the typical forms of most species the identification is relatively straightforward, not infrequently field-collected specimens show an intermediate morphology and are difficult or impossible to identify unambiguously. The distinction of species of *Cephaleuros* and *Phycopeltis* is often based on subtle characters, for which the range of variation is poorly understood (e.g., Rindi & Guiry 2002b; Neustupa 2005). Furthermore, descriptions and illustrations available for several species in the main taxonomic treatments of this group are poor and inadequate, since failing to depict or describe some important characters. For these reasons, basic investigations on the diversity and ecology of these algae should be considered still very valuable, especially when they provide new information for geographical areas for which little or nothing is known (Rindi et al. 2005).

For historical reasons, Europe and some parts of Asia are the regions for which the diversity of the Trentepohliales has been studied best. Relatively recently, several studies have provided important contributions for North and Central America (Dillard 1989; Thompson & Wujek 1997; John 2003), South America (Akiyama 1971; Tracanna 1989), Australia (Cribb 1958, 1963, 1964, 1968, 1970), New Zealand (Sarma 1986) and the Pacific islands (Brooks 2004; Rindi et al. 2005). There is no doubt that, to date, Africa is the continent for which by far the least is known about the Trentepohliales. Some taxa were described for material collected on this continent in the 19th century (Montagne 1846, Reinsch 1877, Hariot 1893). In a study of subaerial algae from Natal, South Africa, Printz

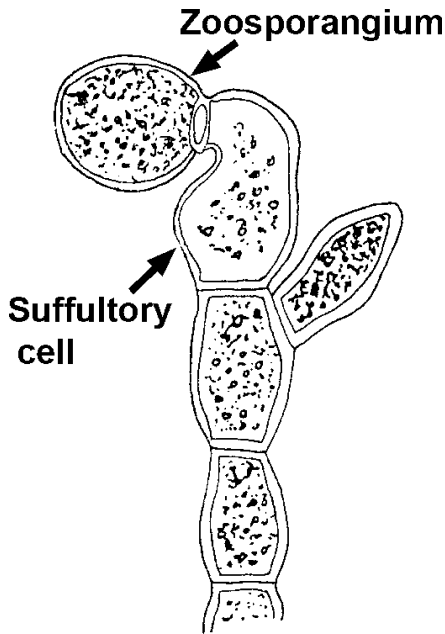


Fig. 1. Structure of the sporangiate lateral.

(1920) reported records of several species of *Phycopeltis* and *Trentepohlia*, with a detailed description of their morphology. Flint (1959) described the growth and reproduction in culture of a strain of *Physolinum monile* (De Wildeman) Printz from Nigeria. Apart for these studies, the information available for African Trentepohliales is extremely limited and fragmentary. Other records of *Trentepohlia* are available for Algeria, Congo, Morocco and South Africa (Harriot 1891, 1913, Feldmann 1947, Gauthier-Lièvre 1954, Woodhead & Tweed 1958, Joska & Bolton 1996). Records of *Cephaleuros* have been reported by Thompson & Wujek (1997) for Cameroon, Kenya, South Africa and Tanzania. However, these records usually include very few or no details on morphology and ecology; Thompson & Wujek's (1997) records are part of more general treatments and no details specific to the African material are included. In this paper, we report on some Trentepohliales collected in the course of trips to several African localities in 2005. These collections led to the discovery of several interesting taxa. Since some of these have been poorly characterized in the previous literature, we believe that accurate descriptions and illustrations will be very helpful for comparative purposes. Some of the species recorded have not been previously reported for Africa; for an entity attributable to *Printzina*, the morphology does not match any of the species currently attributed to the genus and there is the possibility that this might represent an undescribed species. For each entity, morphology and ecology are described in detail and the taxonomic and biogeographical implications of the records are discussed.

Materials and methods

Collections were made at several locations in separate trips. Samples from Zanzibar, Tanzania, were collected by one of us (MDG) in April 2005, mainly from bark of trees and leaves. A large set of samples from several localities in the provinces of Western Cape and Eastern Cape, South Africa, was obtained by the same collector in September-October 2005; in this case, samples were also collected from natural rocks and artificial surfaces (painted concrete). Collections from tree bark were made by JMLB in the province of Kwa-Zulu Natal in August 2005. Finally, a collection obtained from bark and leaves of coastal trees at Swakopmund, Namibia, in July 2005, was kindly supplied by Dr Willem Prud'homme van Reine (Rijksherbarium Leiden, the Netherlands). Collection details are reported for each entity recorded. Due to the exotic nature of the host plants to the authors, the brief duration of the trips and the lack of local colleagues able to provide identification, for collections obtained from leaves and tree bark the host plants could not be determined. Voucher specimens are deposited in the Phycological Herbarium, National University of Ireland, Galway (GALW). The material was examined by light microscopy. Microphotographs were taken by a Nikon DXM1200 digital camera and mounted in plates using Adobe Photoshop CS (version 8.0). A larger set of photographs of the species collected is available in AlgaeBase (www.algaebase.org).

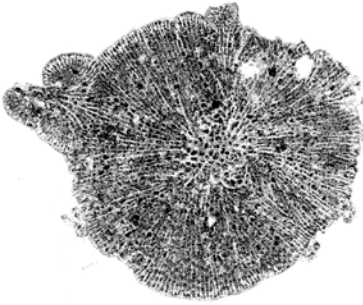
Results and discussion

Phycopeltis arundinacea (Montagne) De Toni

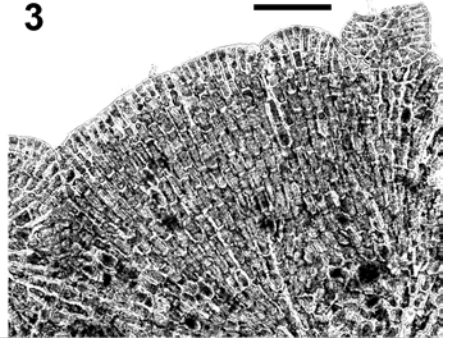
This species occurred on leaves of several tree species in Nature's Valley, Tsitsikamma National Park and Robberg Nature Reserve, South Africa, in September 2005. At Robberg, specimens were also found on a plastic tree label. Specimens growing freely consisted of rounded disks (Fig. 2), with a regular smooth margin (Fig. 3), and were up to 1.5 mm in diameter. When the margins of two individual specimens met, they stopped growing in the area of contact and their growth continued in other directions; this produced thalli with an irregular outline. Vegetative cells were 8-17 μm long (mainly 10-13) and 5-12 μm wide (mainly 7.5-9.0), the length:width ratio ranging between 1 and 2.5 (mainly \sim 1.5). Sporangiate laterals occurred on most specimens examined. They were produced randomly in the central parts of the thallus, in intercalary position, and were absent in the marginal parts. The sporangiate laterals were formed by an oval zoosporangium occurring at the top of a suffultory cell with a retorted neck. The suffultory cells were produced directly from vegetative cells and there was no evidence of production of a stalk cell or a sporangiophore (Fig. 4). The zoosporangium was 12-20 μm wide and 15-25 μm long; the ostiole was opposite to the attachment of the sporangium (Fig. 5). Mature gametangia were not seen with any certainty. In several large thalli, however, many discoloured cells occurred in the central parts. These might have been empty gametangia that had discharged gametes; this, however, could not be confirmed since these parts were frequently invaded by fungal hyphae, which made observation difficult, and no ostioles could be observed with certainty.

Figs 2-9. *Phycopeltis arundinacea* and *Phycopeltis epiphyton*. Figs 2-5. *Phycopeltis arundinacea*. Fig. 2. Habit (scale = 100 μm). Fig. 3. Detail of margin (scale = 50 μm). Fig. 4. Surface view of thallus, with some zoosporangia in development (scale = 20 μm). Fig. 5. Detail of a mature zoosporangium (scale = 20 μm). Figs 6-9. *Phycopeltis epiphyton*. Fig. 6. Habit of a young specimen (scale = 30 μm). Fig. 7. A mature, reproductive specimen (scale = 40 μm). Fig. 8. Detail of thallus with gametangia (scale = 20 μm). Fig. 9. Detail of gametangia after release of gametes; note ostioles (arrowheads) (scale = 10 μm).

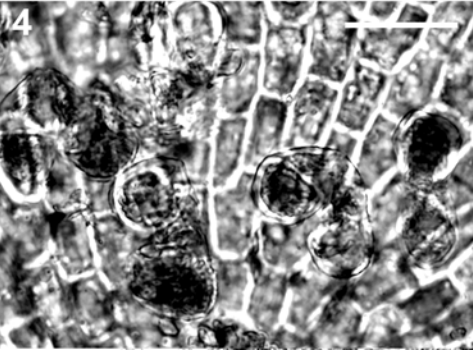
2



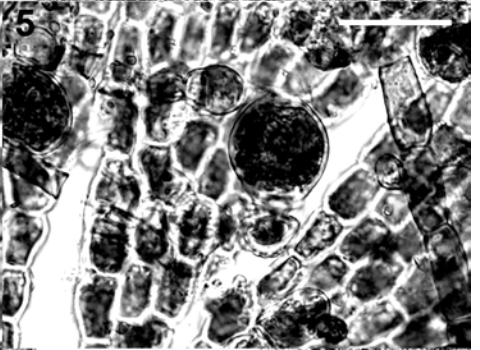
3



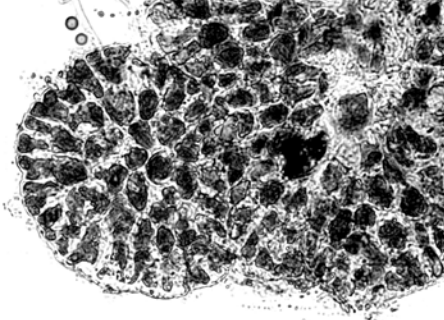
4



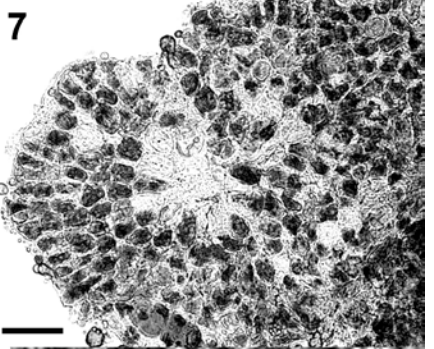
5



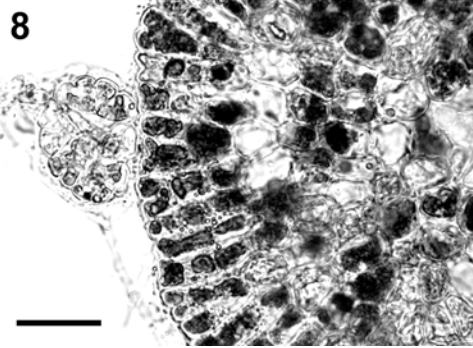
6



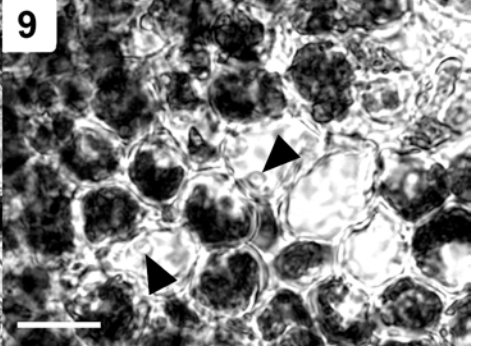
7



8



9



Phycopeltis arundinacea has been reported for several regions of Europe and Asia, both temperate and tropical (see Rindi et al. 2004 and Neustupa 2005, for a summary of the geographical distribution). Thompson & Wujek (1997) mentioned that *Phycopeltis arundinacea* is also present in the New World tropics; however, the taxonomic identity of the material that they referred to this species is not clear, as the description that they provided for it is not in complete agreement with the morphology of the type material (see discussion in Rindi & Guiry 2002b, Rindi et al. 2004 and Neustupa 2005). Apart from the original description from Algeria (Montagne 1846, as *Phyllactidium arundinaceum*), at present the only documented record for Africa is that of Printz (1920) from Saldanha Bay, on the west coast of South Africa, and from the environs of Durban, Kwa-Zulu Natal, South Africa. In the present collections, we could not observe with certainty gametangia, which are reported to occur on thalli that also produce sporangiate laterals in collections from other regions (Rindi & Guiry 2002b; Neustupa 2003; Rindi et al. 2003; Neustupa 2005). However, the morphology of the material is in good agreement with collections of *Phycopeltis arundinacea* from several locations in Europe (Rindi & Guiry 2002b, Rindi et al. 2003, 2004) and is characterized by a combination of characters that allow it to be discriminated from similar species, such as *Phycopeltis expansa* Jennings (Jennings 1895), *P. novae-zelandiae* Thompson & Wujek (Thompson & Wujek 1997), *P. theaensis* Neustupa (Neustupa 2003) and *P. javanica* Neustupa (Neustupa 2005). It seems therefore reasonable to refer the present collections to this species.

Phycopeltis epiphyton Millardet

Specimens attributable to this species formed a fine, dense cover on leaves of some shrubs and trees in Tsitsikamma National Park and Robberg Nature Reserve, South Africa, in September 2005. The normal shape of individual thalli was rounded or polygonal, with entire margins (Fig. 6); specimens were up to 150-160 μm in diameter. The material examined formed very crowded populations on the leaves on which this species occurred. Relatively large portions of leaves were covered by an extensive layer formed by many joined specimens. Growth stopped when the margin of a thallus came into contact with neighbouring thalli and continued in directions where space was available; in this way, many specimens assumed an irregular outline. In most thalli, the central parts were formed by empty gametangia and living vegetative cells occurred only in the marginal parts (Fig. 7). Vegetative cells were 4-8 μm wide (mainly 5-7) and 8-15 μm long (mainly 9-11). Gametangial specimens started to become reproductive when the thallus reached a diameter of 60-70 μm ; the cells situated in the centre of the thallus became gametangia and released gametes (Fig. 8). This pattern extended gradually to more peripheral parts of the thallus. Mature gametangia were globular or polygonal, 12-18 μm in diameter; the ostiole was produced in a corner of the gametangium (Fig. 9). No sporangiate laterals were observed.

Phycopeltis epiphyton is the type species of the genus and is reported as pantropical (Thompson & Wujek 1997); however, this is the first documented record for Africa. The morphology of the material from South Africa is in good agreement with the original description of this species from the Black Forest, Germany (Millardet 1870) and reports from other regions of Europe (Rindi et al. 2004) and Asia (Krishnamurthy 2000; Neustupa 2003).

Printzina cf. lagenifera (Hildebrand) Thompson & Wujek

This alga was collected from a concrete pillar supporting a small suspension bridge at the resort of Storms River, Tsitsikamma National Park, South Africa, in September 2005. The material consisted of irregular masses with a pseudoparenchymatous habit, producing a thin layer on the substratum, with no clear distinction between erect and prostrate parts. The cells were globular, elliptical or barrel-shaped, 6-12 μm wide (mainly 7-9) and 1-2 times as long as wide (Fig. 10). No reproductive structures were observed.

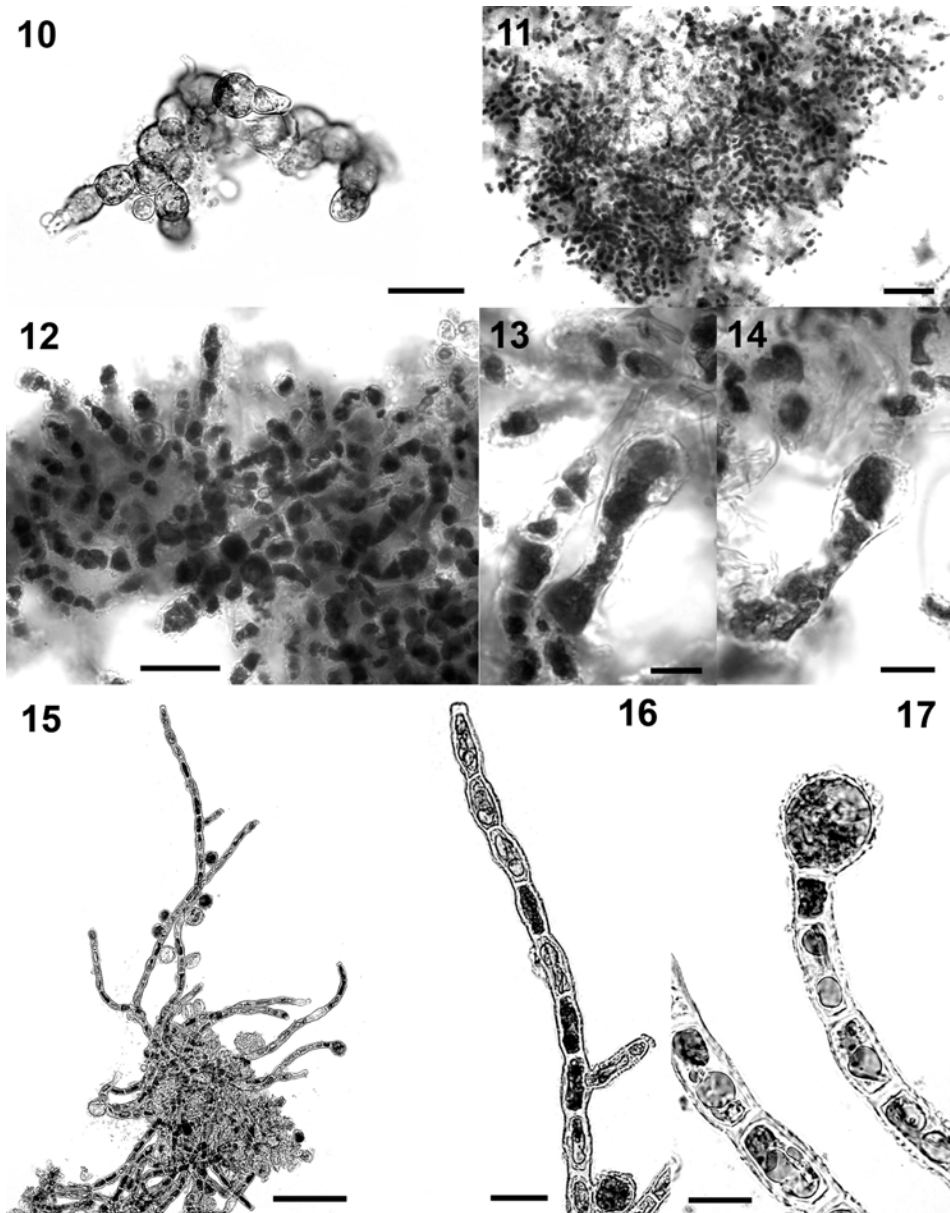
The identification of the material described here must be regarded as somewhat tentative. The vegetative morphology of the specimens is in agreement with that of *Printzina lagenifera*, as generally described in the literature. It is widely accepted, however, that this alga is very polymorphic, showing a considerable range of variation in colour, habit and branching pattern (Hariot 1889a; Nakano & Handa 1984; Rindi & Guiry 2002a; Rindi et al. 2005). We believe that forms attributed to it are likely to represent a complex of cryptic species with similar morphology; molecular data will be necessary to clarify their relationships. Since no gametangia with elongated neck (which is considered the diagnostic character of *Printzina lagenifera*) were observed in the material collected, the specimens examined here cannot be separated with certainty from similar species (for example *Printzina ampla* Thompson & Wujek; Thompson & Wujek 1992) and are referred to this species only provisionally.

Printzina sp.

This alga formed an orange, thin mat on bark of trees on Zanzibar in April 2005.

The thallus appeared to consist primarily of a network of prostrate filaments from which curved, irregularly branched erect axes were produced. These were, however, densely compacted and produced a pseudoparenchymatous thallus, in which the distinction between erect and prostrate parts was usually not clear (Figs 11, 12). The cells varied greatly in shape; they were mainly globular, elliptical or barrel-shaped, but in the erect axes they were often regularly cylindrical (Fig. 12). The cells were 7-17 μm wide (mainly 8-10), 1-2 times as long as wide; apical cells were longer (up to 4 times as long as wide) and devoid of apical caps. Sporangiate laterals were relatively common. The suffultory cell was produced in lateral or apical position, either directly on the main axes or on short branchlets. The neck arose excentrically and was comparatively long (Fig. 13); the zoosporangium was spherical, 10-16 μm in diameter (Fig. 14). Although no empty sporangia could be observed, the ostiole seemed to be opposite to the point of insertion.

In respect of the extensive development of the prostrate parts and the spherical shape of the zoosporangium, this alga is clearly referable to *Printzina*. However, none of the species included in this genus by Thompson & Wujek (1992) are in complete agreement with the combination of habit, cell size, cell shape and sporangial morphology observed for the Zanzibarian material. *Printzina santurcensis* (Tiffany) Thompson & Wujek corresponds well to it for size and shape of the cells and zoosporangia. However, the original description (Tiffany 1936, as *Trentepohlia santurcensis*) and other reports on this species (Jose & Chowdary 1980; Thompson



Figs 10-17. *Printzina* cf. *lagenifera*, *Printzina* sp. and *Trentepohlia abietina*. Fig. 10. *Printzina* cf. *lagenifera*. Detail of a fragment (scale = 20 μ m). Figs 11-14. *Printzina* sp. Fig. 11. Habit (scale = 50 μ m). Fig. 12. Detail of thallus (scale = 30 μ m). Fig. 13. A sporangiate lateral with immature zoosporangium (scale = 10 μ m). Fig. 14. Detail of a sporangiate lateral with zoosporangium (scale = 10 μ m). Figs 15-17. *Trentepohlia abietina*. Fig. 15. Habit of some erect axes (scale = 80 μ m). Fig. 16. Detail of an erect axis (scale = 20 μ m). Fig. 17. Detail of a presumptive gametangium (scale = 10 μ m).

& Wujek 1992) did not provide many details on its habit and seem to suggest that the erect parts are well developed and subdichotomously branched, which does not agree with the morphology of the material from Zanzibar. As no currently recognized species of *Trentepohlia* or *Phycopeltis* agree with this alga either, we believe that it may represent an undescribed entity. We feel, however, that further collections (possibly repeated in time) are desirable for a better characterization.

Trentepohlia abietina (Flotow) Hansgirg

Thin orange cushions referable to this alga were collected from bark of a palm tree in the Durban Botanical Gardens in August 2005 and bark of an unidentified tree at Stormy River, Eastern Cape, South Africa, in September 2005. The thallus consisted of erect axes up to 400 µm tall, irregularly branched, arising from a limited system of prostrate axes (Fig. 15). Cells of erect axes were cylindrical or slightly swollen (Fig. 16), 7-10 µm wide (mainly 7.5-8.0) and 1.5-5 times as long as wide (mainly 2-3). Cells of the prostrate parts were globular or elliptical, 8-12 µm in diameter. In the Stormy River collection, the septa between adjacent cells showed great variation in thickness; whereas some septa were much thicker than the adjacent lateral walls, in other cases no noticeable difference was observed. No similar variation was observed in the material from Durban, in which the septa were consistently thin. In both collections the cell walls were ornamented by thin spiral strands, which could be observed in detail only at high magnifications. Apical cells bore frequently a pectic cap. Presumptive gametangia were the only reproductive structures observed. They were borne on the erect axes in lateral or apical position; in the collection from Durban, they often occurred in lateral series on 2-3 consecutive cells. At maturity they were globular, 10-20 µm in diameter. In the collection from the Stormy River, the wall was covered by thin scales (Fig. 17). No release of swimmers was observed.

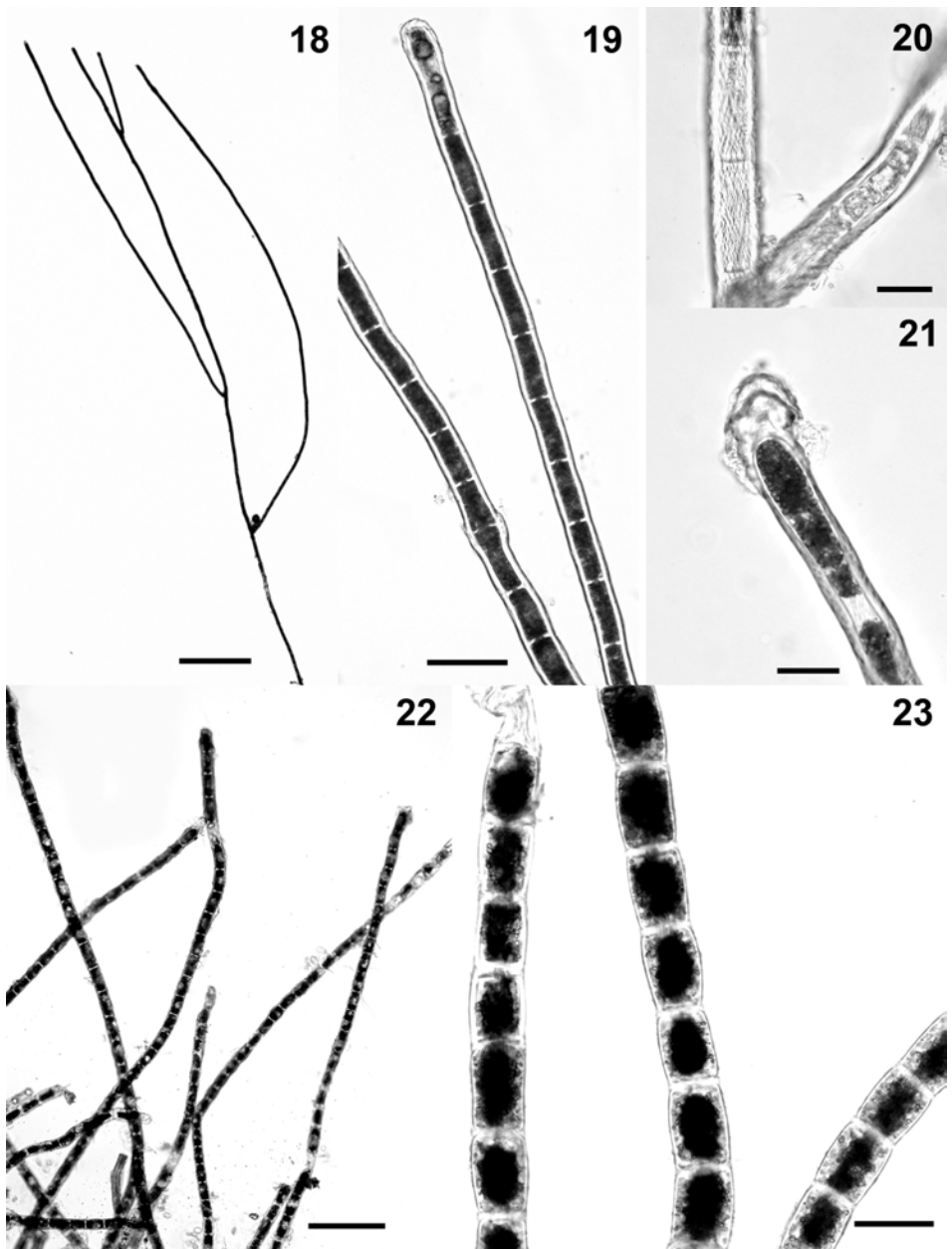
Trentepohlia abietina is one of the most widespread species of the genus, having been largely reported for many temperate and tropical regions throughout the world (De Wildeman 1900; Jose & Chowdary 1980; Tracanna 1989; Ettl & Gärtner 1995; John 2002; Rindi et al. 2005). This is the first documented record for Africa, although the material reported by Printz (1920) as *Trentepohlia aurea* (Linnaeus) Martius is probably referable to it. Despite reports suggesting the possible conspecificity of *Trentepohlia abietina* and *T. aurea* (Hariot 1989b, 1890; Printz 1920; John 2002), in our experience the morphology of *T. abietina* is generally stable and there is little possibility of confusion with European specimens of *T. aurea*; recently, the taxonomic separation of these species has been confirmed by molecular data (López-Bautista et al. 2006). Several forms and varieties have been described for *Trentepohlia abietina*. The morphology of the material from the Stormy River is in general agreement with *Trentepohlia abietina* var. *tenue*, as characterized by Cribb (1970). This variety is mainly distributed in tropical and subtropical regions and it differs from specimens of *Trentepohlia abietina* from Europe and other temperate regions for the ornamentation of the cell wall and the thickness of the septa (Cribb 1970). Our specimens have a slightly larger cell width (7-10 µm, mainly 7.5-8.0) than the material described by Cribb (1970) from Queensland (2-10 µm, mainly 5-8); the range of variation, however, is comparable. The material from Durban is also close to the

variety *tenue*, but it does not show the thickening of the septa reported as typical of this taxon. It is not clear, however, how taxonomically relevant this character is, since considerable variation was observed in the Stormy River material. In the past, great importance has been attached to this feature and specimens from South-eastern Asia with thick septa have been described as a separate species, *Trentepohlia crassisepta* Karsten (Karsten 1891). However, examination of the present collections and specimens from other tropical localities (Rindi et al. 2005) has shown a wide range of variation in the ornamentation of the cell wall and thickness of the septa; we therefore agree with previous studies (Hariot 1889b; Cribb 1970) that these differences are probably not relevant at the species level. Their possible taxonomic significance for delimitation of intraspecific taxa needs to be assessed in combination with molecular data.

Trentepohlia afra (Massalongo) Cribb

Numerous specimens belonging to this species were discovered on 23 September 2005 on the Table Mountain (Cape Town, Western Cape, South Africa), growing as bright orange tufts on shaded rocky surfaces. The tufts consisted of long erect axes, poorly branched or unbranched (up to 1 cm tall), arising from a limited prostrate system (Fig. 18). The cells were regularly cylindrical, 20-30 µm wide (mainly 24-28), 2-4 times as long as wide (Fig. 19); shape and size of the cells were similar in the erect and prostrate parts. In healthy cells, the carotenoid pigments were abundant and dispersed into many small, tiny droplets, which gave the alga a uniformly dark red colour when observed microscopically. The cell walls were consistently thick, up to 5-6 µm, and finely ornamented by numerous tiny strands, which gave the cell surface a corrugated appearance (Fig. 20). Plasmodesmata between adjacent cells were very apparent, being large and clearly protruding from each cell into the adjacent upper cell. The apical cells were invariably provided with a thick pectic cap (Fig. 21); some were considerably enlarged. Lateral branches arose as lateral protrusions from the top corners of cells. Some intercalary cells were swollen, suggesting that restart of growth took place from a larger apical cell. No reproductive structures were observed.

The vegetative morphology of *Trentepohlia afra* is very characteristic and it is impossible to confuse with any other species, even in absence of reproductive structures. *Trentepohlia afra* has long been considered conspecific with either *Trentepohlia flava* (W.J.Hooker & Arnott) Cribb (= *Trentepohlia polycarpa* Nees & Montagne) or *Trentepohlia aurea* (Hariot 1889c; Printz 1939). Cribb (1970), however, considered that the larger size of the cells, the ornamentation, the thickness of the wall and the habit of the apical caps distinguished this species from both *T. aurea* and *T. flava*; we agree with his opinion. *Chroolepus montis-tabulae* Reinsch, based by Reinsch (1877) on material from the Table Mountain in South Africa and transferred by De Toni (1889) to *Trentepohlia*, is a later synonym for this species. Cribb (1970) showed that *Chroolepus afrum* Massalongo (Massalongo 1861) is an earlier name for this entity and based on it the new combination *Trentepohlia afra*. To date, the known distribution of this species is restricted to Southern Africa. However, the fact that it has usually been considered a synonym of other species makes it impossible to assess with certainty its distributional range; it is possible that future collections will reveal a much wider distribution.



Figs 18-23. *Trentepohlia afra* and *Trentepohlia chinensis*. Figs 18-21. *Trentepohlia afra*. Fig. 18. Habit of an erect axis (scale = 500 μm). Fig. 19. Apical parts of erect axes (scale = 60 μm). Fig. 20. Detail of cell walls (note superficial corrugation) (scale = 40 μm). Fig. 21. Detail of apical cell with thick pectic cap (scale = 30 μm). Figs 22-23. *Trentepohlia chinensis*. Fig. 22. Habit of erect axes (scale = 150 μm). Fig. 23. Detail of cells of erect axes (scale = 30 μm).

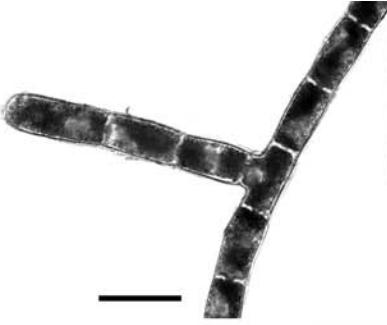
Trentepohlia chinensis (Harvey) Hariot

This alga was found in three separate collections, all obtained from tree bark: Zanzibar, Tanzania, April 2005; Durban Botanical Gardens, South Africa, August 2005; Tsitsikamma National Park, Eastern Cape, South Africa, 25 September 2005. This species formed a dense brownish fur over the substratum. The thallus consisted of long erect axes, up to 4 mm tall, arising from a scanty system of prostrate axes. The erect axes were mostly unbranched in the sample from Tsitsikamma (Fig. 22); some irregular and sparse branching occurred in the material from Zanzibar and Durban. Cells were cylindrical, slightly inflated or barrel-shaped, 12-25 μm wide (Fig. 23); with regard to this character, the material from Durban showed a larger range of variation (12-25 μm) than the populations from Zanzibar and Tsitsikamma (20-25 μm). In the specimens from Tsitsikamma the width:length ratio was higher (cells 1.5-3 times as long as wide, mainly 2-2.5) than in the collections from Durban and Zanzibar (cells 1-3 times as long as wide, mainly 1.2-1.8). When present, lateral branches arose in the middle of the cells and were borne at a 90° angle (Fig. 24). Apical cells were blunt, dome-shaped, and no apical caps were observed. Cells of the prostrate parts were similar in size and shape to those of the erect axes. Plasmodesmata between adjacent cells were often very obvious. Large amounts of carotenoid pigments occurred in the material from Tsitsikamma, in which they showed a characteristic distribution, forming numerous small droplets arranged in a parietal layer. The production of these pigments seemed to be associated with the chloroplasts (which, when observable, looked like small parietal plates forming a more or less extensive network). Characteristically, in many cells the layer of carotenoid pigments was not uniform, giving the impression of one or more holes (Fig. 25). Fungal hyphae were commonly mixed with the alga, especially in the collection from Durban. No reproductive structures were observed in any collection.

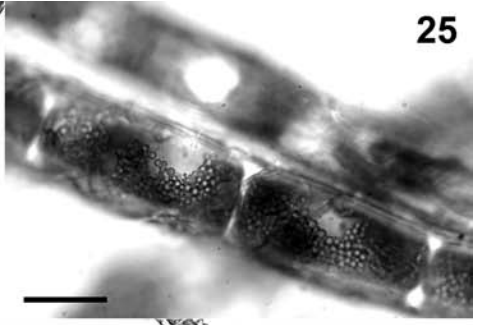
Trentepohlia chinensis was based by Hariot (1889b) on *Chroolepus chinensis* Harvey, described by Harvey (1860) for material collected from rocks in Hong Kong. The morphological characterization of this species is problematic. Harvey's (1860) original description is brief and does not mention several features that are important in the infrageneric taxonomy of *Trentepohlia*. Hariot (1889b) examined authentic material of this species and provided additional information, including cell size, new records and illustrations of a specimen from Madagascar. Cribb (1970), however, examined the type specimen and remarked on some discrepancies between its morphology and the description of Hariot (1889b). In particular, he noted that the width: length ratio of the cells was longer than reported by Hariot and that the filaments tapered distinctly

Figs 24-31. *Trentepohlia chinensis*, *Trentepohlia flava* and *Trentepohlia umbrina*. Figs 24-25. *Trentepohlia chinensis*. Fig. 24. Detail of branching (scale = 50 μm). Fig. 25. Detail of cell pigmentation (scale = 20 μm). Figs 26-29. *Trentepohlia flava*. Fig. 26. Habit of erect axes (scale = 40 μm). Fig. 27. Detail of erect axes showing corrugation of the cell walls (scale = 40 μm). Fig. 28. Detail of prostrate parts (scale = 40 μm). Fig. 29. Detail of a presumptive gametangium, containing unreleased presumptive gametes (scale = 20 μm). Figs 30-31. *Trentepohlia umbrina*. Fig. 30. Habit (scale = 20 μm). Fig. 31. Upper view of a presumptive gametangium (note ostiole in the centre) after release of presumptive gametes (scale = 20 μm).

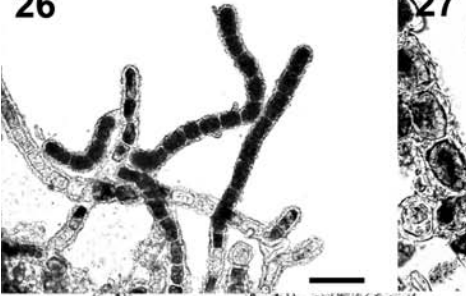
24



25



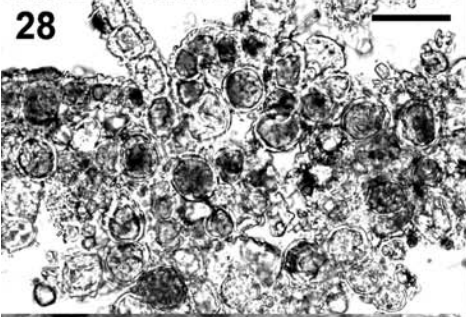
26



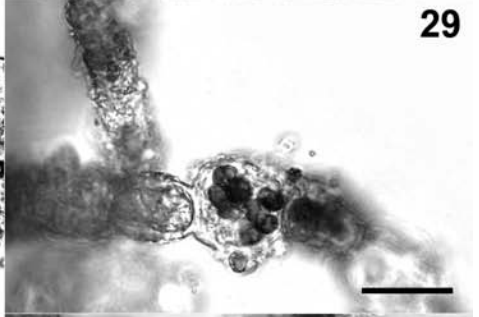
27



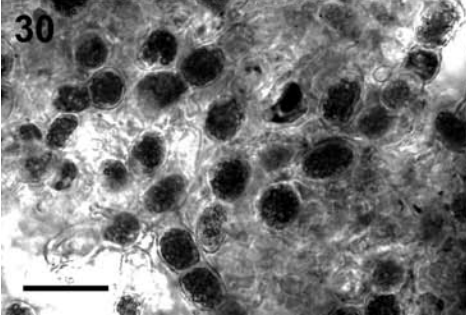
28



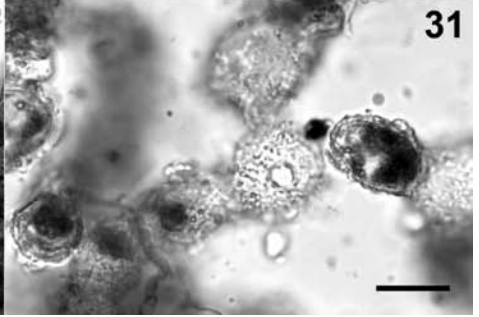
29



30



31



towards the apex, which is clearly not the case in the figure of Hariot (1889b: 379). Cribb (1970) concluded that, if the figure is typical of Hariot's concept of *Trentepohlia chinensis*, it is unlikely to represent the same species as the type specimen; he therefore regarded this species as a doubtful entity. In our opinion, the three collections from Africa examined in this study are clearly representative of the same taxon, and Hariot's *Trentepohlia chinensis* is the species to which they are morphologically closest. The examination of our samples suggests that this alga is polymorphic and several features (development of branching, cell width, length:width ratio of cells) are subjected to a relatively wide range of variation. It looks therefore possible that Harvey's type material and Hariot's alga represent different morphological variants of the same entity. Further collections, combined with culture studies, are necessary to understand better the morphological variability of this species; in particular, examination of reproductive material is much needed. We agree with Cribb (1970) that, until further collections from the type locality become available, the relationship between the Chinese and the African populations needs reassessment. We also agree that this species is very similar to *Trentepohlia arborum* (C.Agardh) Hariot. Habit, branching pattern and cell size are virtually identical in the two species, although *Trentepohlia arborum* usually has a lighter colour, apical cells attenuated and a generally higher length:width cell ratio (Printz 1939; Islam 1960; Cribb 1970; Rindi et al. 2005).

Trentepohlia flava (W.J.Hooker & Arnott) Cribb

This species formed a velvety coating on stems and leaves of shrubs and trees in the coastal region of Swakopmund, Namibia, in July 2005. It was also collected from the painted concrete wall of a cottage-like building in the De Hoop Nature Reserve, Western Cape, South Africa, on 3 October 2005. The alga consisted of erect axes, up to 700-800 μm tall, arising from a well-developed system of prostrate filaments. The erect filaments were straight or curved, poorly branched or unbranched (Fig. 26). When present, branches mainly occurred in the lower parts, without a regular arrangement; branches with *Scytonema*-like appearance were observed occasionally. New branches were issued as protrusions from the top corner of the cells. In the material from Swakopmund the prostrate filaments were loose, whereas in the sample from De Hoop the basal part consisted of strictly entangled filaments forming a compact, almost pseudoparenchymatous layer. In the erect parts, the cells were cylindrical or slightly inflated, 10-20 μm wide (mainly 15-18 for Swakopmund, 14-16 for De Hoop), 1-3 times as long as wide (Fig. 27). Most cells of the erect axes had a thick cell wall (up to 5 μm), heavily corrugated by spiral strands and scales. Apical cells were either blunt or sharpened, with a variably developed cap. Whereas in the sample from Swakopmund the cells of the prostrate parts were similar in shape and size to those of the erect parts, in the material from De Hoop they were mostly globular or elliptical, 13-20 μm in diameter (Fig. 28); for both samples, the corrugation observed in the erect parts was either absent or weakly developed. Presumptive gametangia were observed in the sample from De Hoop. They were globular or urn-shaped, 20-25 μm in diameter, and occurred either terminally at the top of the erect axes or in intercalary position (Fig. 29). Some sporangiate laterals, produced either on apical cells or at the top of short lateral branches, were observed in the sample from Swakopmund. The zoosporangia were globular or subglobular,

20-30 μm in diameter, with the ostiole opposite to the attachment. The neck of the suffultory cell was initially straight, but in fully developed sporangiate laterals it was more or less markedly bent.

Considerable uncertainty has long surrounded the exact circumscription of this species, which is mostly reported in the literature as *Trentepohlia polycarpa* Nees & Montagne or *Trentepohlia aurea* var. *polycarpa* (Nees & Montagne) Hariot. By examination of a large number of relevant herbarium specimens, Cribb (1970) reassessed its taxonomic position and geographical distribution, and renamed it *Trentepohlia flava*. Our specimens are generally in good agreement with the morphological characterization provided by this author and we largely agree with his conclusions. Our records, however, show that this species is not strictly confined to America, as believed by Cribb. It is noteworthy that several documented records confirmed by Cribb (1970: 18) exist for some of the southernmost regions of America (Patagonia, Tierra del Fuego, Strait of Magellan and Falkland Islands). The presence of *Trentepohlia flava* in southern Africa, which in past geological eras has been connected to such parts of South America, is therefore not particularly surprising. The samples from Namibia and South Africa represent the first documented records of this species for Africa. Hariot (1889c: 373) mentioned a record (as *Trentepohlia polycarpa*) from Cape of Good Hope; however, in consideration of Hariot's incorrect circumscription of this species (see discussion in Cribb 1970), this record cannot be confirmed.

***Trentepohlia umbrina* (Kützing) Bornet**

Material attributable to this species was found in three collections. In one from Zanzibar and one from Tsitsikamma National Park, South Africa, the alga formed a brownish-orange mat on tree bark; in one from Plettenberg Bay, South Africa, it formed small dark red masses, with more or less hemispherical to irregular shape, on natural rocks. Thalli of this species consisted of many entangled filaments, forming compact masses without a distinction between erect and prostrate parts. When removed, the thalli were easily fragmented into short filaments. The cells varied in shape from globular to almost cylindrical, but were mostly subglobular or elliptical (Fig. 30). They were 9-25 μm wide; the material from Zanzibar was more robust (mainly 18-22 μm), than the material from South Africa (mainly 10-14 μm). In the population from Zanzibar, the cell walls were finely ornamented by many small dot-like protrusions. Presumptive gametangia were present in the population from Zanzibar (Fig. 31); they were globular, 20-26 μm in diameter and, during microscopical observation, they released large numbers of biflagellate, presumptive gametes, which were not observed to fuse. No reproductive structures were observed in the material from South Africa.

Trentepohlia umbrina is one of the most widespread species of the genus; records exist for almost all regions of the world where Trentepohliales have been collected. The morphology of this species is generally stable and its identification is usually straightforward, although its exact separation from *Trentepohlia odorata* has been source of controversy in the past (Hariot 1989a). The original collections of this species (as *Chroolepus umbrinum* Kützing; Kützing 1843) were made from tree bark in southern Germany and the occurrence on this type of substratum is considered an

important character for its identification (Printz 1939, 1964). Recent investigations, however, have shown that material referable to this species also occurs on stone and artificial surfaces (Rindi & Guiry 2002a; Rindi et al. 2003; present study). With regard to morphology, there is no basis for a different taxonomic attribution of populations occurring on tree bark from populations occurring on stone; nevertheless, a confirmation of the genetic identity of different populations based on molecular methods is desirable.

The new records documented in this study include trentepohlialean taxa with pantropical (*Phycopeltis arundinacea*, *P. epiphyton*, *Trentepohlia abietina*, *T. umbrina*) and endemic distributions (*Trentepohlia afra*), and other taxa for which the uncertain delimitation at the species level precludes a precise assessment of the distribution (*Printzina* sp., *Trentepohlia chinensis*, *T. flava*). The phylogeography of the Trentepohliales represents an interesting evolutionary puzzle; its clarification is presently prevented by poor understanding of the taxonomic and evolutionary relationships among members of this group. A detail taxonomic assessment at species and genus level, based on a combination of morphological, molecular and physiological data and a careful examination of many herbarium specimens, is essential to clarify phylogeographic patterns in this order. We are currently analysing the evolutionary history of this group by phylogenetic analyses based on sequences of several molecular markers; such data are essential for testing hypotheses concerning biogeographic patterns, clarifying the taxonomy of problematic taxa (e.g., the *Printzina lagenifera* complex) and assessing in detail the taxonomic identity and distribution of some species that are currently regarded as widespread. Such information will provide a framework that will be of great importance to understand the evolution and biogeography of other groups of subaerial algae; it will also be particularly valuable because the Trentepohliales have their centre of diversity in tropical and subtropical regions. Humid tropical and subtropical forests host a large number of habitats that are favourable for the development of a rich and diverse subaerial algal flora. The information available on subaerial algae of tropical regions is generally limited and, in particular, very little is known about algae of tropical rainforests. This is particularly worrying both because these are among the most endangered ecosystems on the planet and because recent investigations have shown that many new taxa, including some major evolutionary surprises, can be expected to be discovered in these environments (Neustupa 2003, Neustupa & Sejnohová 2003, Neustupa 2005, Rindi et al. 2006). Algal and microbial communities of tropical and subtropical forests represent an untapped biological resource for studies on systematics and evolution, and a better knowledge of their diversity is urgently needed.

Acknowledgements

We are very grateful to Dr Willem Prud'homme van Reine (Rijksherbarium, Leiden, the Netherlands) for providing the collection of *Trentepohlia flava* from Namibia. JMLB and FR acknowledge financial support by the National Science Foundation (Systematics Program DEB-0542924). MDG's collections in South Africa and Tanzania were made in the course of surveys for which travel expenses were partially funded by the European Commission, under an International Scientific Cooperation Project (SEAWEEAFRICA, contract ICA4-CT-2001-10030).

References

- AKIYAMA, M. (1971): On some Brazilian species of Trentepohliaceae. - Mem. Fac. Educ. Shimane Univ., Nat. Sci. **5**: 81-95.
- BROOKS, F.E. (2004): [Plant-parasitic algae \(Chlorophyta: Trentepohliales\) in American Samoa. - Pacific Sci. **58**: 419-428.](#)
- CHAPMAN, R.L. (1984): An assessment of the current state of our knowledge of the Trentepohliaceae. - In: IRVINE, D.E.G. & D.M. JOHN (eds): Systematics of the green algae: 233-250. Academic Press, London.
- CHAPMAN, R.L., R.C. BORKHSENIUS, R.C. BROWN, M.C. HENK & D.A. WATERS (2001): Phragmoplast-mediated cytokinesis in *Trentepohlia*: results of TEM and immunofluorescence cytochemistry. - [Int. J. Syst. Evol. Microbiol. **51**: 759-765.](#)
- CRIBB, A.B. (1958): The genus *Trentepohlia* in South-Eastern Queensland. - Pap. Dept. Bot. Univ. Queensland **3**: 193-201.
- CRIBB, A.B. (1963): Further records of *Trentepohlia* from South-eastern Queensland. - Pap. Dept. Bot. Univ. Queensland **4**: 75-81.
- CRIBB, A.B. (1964): Notes on *Trentepohlia* from Queensland including one growing on a spider. - Pap. Dept. Bot. Univ. Queensland **4**: 99-108.
- CRIBB, A.B. (1968): Some *Trentepohlias* new to Australia. - *Phykos* **7**: 3-8.
- CRIBB, A.B. (1970): A revision of some species of *Trentepohlia* especially from Queensland. - Proc. Roy. Soc. Queensland **82**: 17-34.
- DE TONI, G.B. (1889): Sylloge Algarum Omnium Hucusque Cognitarum. Vol. 1. Chlorophyceae. - Privately published, Patavii (Padova).
- DE WILDEMAN, E. (1900): Les algues de la flore de Buitenzorg. - E.G. Brill, Leiden.
- DILLARD, G.E. (1989): Freshwater algae of the Southeastern United States. Part 2. Chlorophyceae: Ulotrichales, Microsporales, Cyndrocapsales, Sphaeropleales, Chaetophorales, Cladophorales, Schizogoniales, Siphonales and Oedogoniales. - Biblioth. Phycol. **83**: 1-163. J. Cramer, Stuttgart.
- ETTL, H. & G. GÄRTNER (1995): Syllabus der Boden-, Luft- und Flechtenalgen. - Gustav Fischer Verlag, Stuttgart, Jena and New York.
- FELDMANN, J. (1947): Le *Trentepohlia effusa* (Kempelhub.) Hariot aux environs d' Alger. - Bull. Soc. Hist. Nat. Afrique N. **38**: 92-93.
- FLINT, E.A. (1959): The occurrence of zoospores in *Physolinum* Printz. - [New Phytol. **58**: 267-70.](#)
- GAUTHIER-LIÈVRE, L. (1954) : Algues africaines nouvelles, rares ou imparfaitement connues. - Bull. Soc. Hist. Nat. Afrique N. **45**: 98-125.
- HARIOT, P. (1889a): Notes sur le genre *Trentepohlia* Martius (Suite). - [J. Bot. \(Morot\) **3**: 393-405.](#)
- HARIOT, P. (1889b): Notes sur le genre *Trentepohlia* Martius (Suite). - [J. Bot. \(Morot\) **3**: 377-388.](#)
- HARIOT, P. (1889c): Notes sur le genre *Trentepohlia* Martius (Suite). - *J. Bot. (Morot)* **3**: 366-375.
- HARIOT, P. (1890): Notes sur le genre *Trentepohlia* Martius (Suite). - *J. Bot. (Morot)* **4**: 85-92.
- HARIOT, P. (1891): Quelques algues du Brésil et du Congo. - *Notarisia* **6**: 1217-1220.
- HARIOT, P. (1893): Les trois genres *Trentepohlia*. - *J. Bot. (Morot)* **7**: 216.
- HARIOT, P. (1913): Algues d' eau douce du Maroc. - Bull. Soc. Bot. France **60**: 40-43.
- HARVEY, W.H. (1860): Characters of new algae, chiefly from Japan and adjacent regions, collected by Charles Wright in the North Pacific exploring expedition under Captain James Rodgers. - Proc. Amer. Acad. Arts Sci. **4**: 327-335.

- ISLAM, N. (1960): Some subaerial green algae from East Pakistan. - Trans. Amer. Microscop. Soc. **79**: 471-479.
- JENNINGS, A.V. (1895): On two new species of *Phycopeltis* from New Zealand. - Proc. Roy. Irish Acad. **3**: 753-766.
- JOHN, D.M. (2002): Order Trentepohliales. - In: JOHN, D.M., B.A. WHITTON & A.J. BROOK (eds): The freshwater algal flora of the British Isles: 475-479. Cambridge University Press, Cambridge.
- JOHN, D.M. (2003): Filamentous and plant-like green algae. - In: WEHR, J.D. & R.G. SHEATH (eds): Freshwater algae of North America. Ecology and classification: 311-349. Academic Press, San Diego.
- JOSE, G. & Y.B.K. CHOWDARY (1980): New records of *Trentepohlias* from India. - Nova Hedwigia **32**: 725-731.
- JOSKA, M.A. & J.J. BOLTON (1996): Filamentous freshwater macroalgae in South Africa - a literature review and perspective on the development and control of weed problems. - Hydrobiologia **340**: 295-300.
- KARSTEN, G. (1891): Untersuchungen ueber die Familie der Chroolepideen. - Ann. Jard. Bot. Buitenzorg **10**: 1-66.
- KHRISHNAMURTHY, V. (2000): Algae of India and neighbouring countries. I. Chlorophycota. - Science Publishers, Enfield, New Hampshire.
- KÜTZING, F.T. (1843): Phycologia generalis. - F.A. Brockhaus, Leipzig.
- LÓPEZ-BAUTISTA, J.M., D.A. WATERS & R.L. CHAPMAN (2002): The Trentepohliales revisited. - Constancea **83** [http://ucjeps.berkeley.edu/constancea/83/lopez_etal/trentepohliales.html]
- LÓPEZ-BAUTISTA, J.M. & R.L. CHAPMAN (2003): Phylogenetic affinities of the Trentepohliales inferred from small-subunit rDNA. - Int. J. Syst. Evol. Microbiol. **53**: 2099-2106.
- LÓPEZ-BAUTISTA, J.M., F. RINDI & M.D. GUIRY (2006): Molecular systematics of the subaerial green algal order Trentepohliales: an assessment based on morphological and molecular data. - Int. J. Syst. Evol. Microbiol. **56** (in press).
- MASSALONGO, A.B. (1861): Lichenes Capenses quos collegit in itinere 1857-1858 Dr. Wawra medicus Navis (Corvetta) Caes. R. Carolinae. - Mem. Reale Ist. Veneto Sci. **10**: 33-90.
- MILLARDET A., 1870 - De la germination des zygospores des genres *Closterium* et *Staurastrum* et sur un genre nouveau d'algues chlorospores. - Mém. Soc. Sci. Nat. Strasbourg **6**: 37-50.
- MONTAGNE, C. (1846): Phyceae. - In: DURIEU DE MAISONNEUVE, M.C. (ed.): Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. Sciences physiques. Botanique. Cryptogamie: 1-197. Imprimerie Nationale, Paris.
- NAKANO, T. & HANDA, S. (1984): Observations on *Trentepohlia lagenifera* (Hild.) Wille (Chlorophyceae, Trentepohliales). - Jap. J. Phycol. **32**: 354-363.
- NEUSTUPA, J. (2003): The genus *Phycopeltis* (Trentepohliales, Chlorophyta) from tropical Southeast Asia. - Nova Hedwigia **76**: 487-505.
- NEUSTUPA, J. (2005): Investigations on the genus *Phycopeltis* (Trentepohliaceae, Chlorophyta) from South-East Asia, including the description of two new species. - Cryptog. Algal. **26**: 229-242.
- NEUSTUPA, J. & SEJNOHOVÁ (2003): *Marvania aerophytica* sp. nov., a new subaerial tropical green alga. - Biologia (Bratislava) **58**: 503-507.
- PRINTZ, H. (1920): Subaerial algae from South Africa. - Kongel. Norsk. Vidensk. Selsk. Skr. (Trondheim) **1920** (1): 3-41.
- PRINTZ, H. (1939): Vorarbeiten zu einer Monographie der Trentepohliaceen. - Nytt Mag. Naturvidensk. **80**: 137-210.

- PRINTZ, H. (1964): Die Chaetophorales der Binnengewässer. Eine systematische Übersicht. - Hydrobiologia **24**: 1-376.
- REINSCH, P.F. (1877): Contributiones ad floram algarum aquae dulcis promontorii Bonae Spei. - J. Linn. Soc., Bot. **16**: 232-248.
- RINDI, F. & M.D. GUIRY (2002a): Diversity, life history and ecology of *Trentepohlia* and *Printzina* (Trentepohliales, Chlorophyta) in urban habitats in Western Ireland. - J. Phycol. **38**: 39-54.
- RINDI, F. & M.D. GUIRY (2002b): The genus *Phycopeltis* (Trentepohliaceae, Chlorophyta) in Ireland: a taxonomic and distributional reassessment. - Phycologia **41**: 421-431.
- RINDI, F., M.D. GUIRY, A.T. CRITCHLEY & E. AR GALL (2003): The distribution of some species of Trentepohliaceae in France. - Cryptog. Algol. **24**: 133-144.
- RINDI, F., J.M. LÓPEZ-BAUTISTA, A.R. SHERWOOD & M.D. GUIRY (2006): Morphology and phylogenetic position of *Spongiochrysis hawaiiensis* gen et sp. nov., the first known terrestrial member of the Cladophorales (Ulvothyceae, Chlorophyta). - Int. J. Syst. Evol. Microbiol. **56**: 913-922.
- RINDI, F., J.L. MENÉNDEZ, M.D. GUIRY & J.M. RICO (2004): The taxonomy and distribution of *Phycopeltis* (Trentepohliaceae, Chlorophyta) in Europe. - Cryptog. Algol. **25**: 3-17.
- RINDI, F., A.R. SHERWOOD & M.D. GUIRY (2005): Taxonomy and distribution of *Trentepohlia* and *Printzina* (Trentepohliales, Chlorophyta) in the Hawaiian Islands. - Phycologia **44**: 270-284.
- SARMA, P. (1986): The freshwater Chaetophorales of New Zealand. - Nova Hedwigia Beih. **58**: 1-169.
- THOMPSON, R.H. & WUJEK, D.E. (1992): *Printzina* gen. nov. (Trentepohliaceae), including a description of a new species. - J. Phycol. **28**: 232-237.
- THOMPSON, R.H. & D.E. WUJEK (1997): Trentepohliales: *Cephaleuros*, *Phycopeltis* and *Stomatochroon*. Morphology, Taxonomy and Ecology. - Science Publishers, Enfield, New Hampshire.
- TIFFANY, L.H. (1936): Wille's collection of Puerto Rican freshwater algae. - Brittonia **2**: 165-175.
- TRACANNA, B.C. (1989): Trentepohliales (Chlorophyta): el género *Trentepohlia* Martius para las provincias de Salta y Tucumán (Argentina). I. - Lilloa **37**: 47-59.
- WOODHEAD, N. & TWEED R.D. (1958): A check list of tropical West African algae (fresh and brackish water). - Hydrobiologia **11**: 299-395.

Received 31 January 2006, accepted in revised form 13 March 2006.