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Trentepohliales (Ulvophyceae, Chlorophyta) from Panama

by

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With 39 figures

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Abstract: The green algal order Trentepohliales represents one of the most diverse and widespread groups of terrestrial algae in tropical regions; however, little published information on this group is available for Central and tropical South America. The diversity and distribution of these algae in central Panama were investigated in the course of a fieldtrip in May 2007. At the time of the survey species of Trentepohliales were a quantitatively dominant component of the terrestrial microalgal vegetation, being widespread on a large variety of natural and artificial substrata. Collections made from three sites (Barro Colorado Island, Gamboa and Summit Garden) revealed the presence of at least 24 taxa (1 *Cephaleuros*, 6 *Phycopeltis*, 4 *Printzina* and 13 *Trentepohlia* species). Two species (*Trentepohlia minima* and *T. treubiana*) were new records for the Americas. Other interesting records included *Printzina bosseae*, *Trentepohlia chapmanii*, *T. depressa* and *T. dusenii*, species rarely recorded in the Americas. Several taxa could not be identified unambiguously and we believe that some of these probably represent undescribed species, for which an assessment based on molecular data will be needed.

Introduction

In tropical regions, species of subaerial algae are a rich and widespread component of the terrestrial microflora. In the past, these organisms have mainly attracted attention as practical nuisances for their biodeterioration of artificial substrata (Wee & Lee 1980, Gaylarde et al. 2006) and for infecting plants of economic importance (Chapman & Waters 2001; Brooks 2004). Relatively little information is available on the diversity and systematics of subaerial tropical algae (López-Bautista et al. 2007). Green algae of the order Trentepohliales are generally reported as the most common subaerial microchlorophytes in tropical regions (Fritsch 1907; López-Bautista et al. 2002). Their

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red, orange or yellow patches (due to the presence of β-carotene and haematochrome) are in striking contrast to the dominant blackish-grey colour produced by cyanobacteria in tropical subaerial habitats (Fritsch 1907). In general, investigations of the Trentepohliales have provided considerable floristic and taxonomic detail. However, most investigations were carried out in Europe and other temperate zones (mainly for historical and logistic reasons). In the tropics, our knowledge of the diversity and taxonomy of the Trentepohliales is very uneven in terms of geographical coverage. Detailed studies have been carried out in several tropical regions, such as Queensland (Cribb 1958a, 1963, 1964, 1968, 1970, 1993, 1996), India and Bangladesh (Brühl & Biswas 1923; Islam 1960; Saxena 1961; Islam 1972; Jose & Chowdary 1980; Panikkar & Sindhu 1993; Krishnamurthy 2000), the area of Bogor in Indonesia (De Wildeman 1891, 1900), Samoa (Brooks 2004), the Hawaiian Islands (Rindi et al. 2005) and French Guiana (Rindi & López-Bautista 2007, 2008). No information, however, is available for most tropical zones, including vast areas (such as central Amazonia and central Africa) where species diversity may be expected to be very high. Recent molecular data have shed light into the systematics and phylogenetic relationships of the Trentepohliales, suggesting that the classification of this order will need major rearrangements and that the species diversity may be much higher than currently appreciated (López-Bautista & Chapman 2003; López-Bautista et al. 2006; Rindi et al., in preparation). Several morphological characters which have been considered of great importance in traditional taxonomic schemes (Printz 1939; Sarma 1986; Thompson & Wujek 1997) appear to have no phylogenetic relevance. The circumscription of species in this order will need to be reassessed and based on a combination of molecular data and phylogenetically significant morphological data. For these reasons, a detailed morphological and ecological characterization of the members of the order is of fundamental importance. Traditional studies concerning diversity, taxonomy and ecology are therefore still very valuable, especially for geographical areas for which there is currently no published information (Rindi et al. 2006).

Acting as a land bridge between North and South America, Panama is a region of great biogeographical significance, characterized by a geographically and biologically diverse environment. The presence of many protected areas (16% of the total surface of the country) and numerous field stations of the Smithsonian Tropical Research Institute have made it one of the most studied and best-known tropical regions in the world. The number of studies concerning biological diversity and ecology carried out in the area is very large and detailed information is available for almost every taxonomic group. Thus far, however, terrestrial algae have been entirely neglected and no information is available about the Trentepohliales of Panama. Thompson & Wujek (1997), in their monograph of the genera *Cephaleuros*, *Phycopeltis* and *Stomatochroon*, reported numerous records from nearby countries, such as Colombia, Costa Rica and El Salvador; for some species, they also mentioned a general widespread presence in Central America. However, they did not make any mention of specific records from Panama. In May 2007 we had the opportunity to visit central Panama in the course of a one-week fieldtrip, aimed at surveying the subaerial algal flora of this area. Species of Trentepohliales appeared to be a quantitatively dominant component of the subaerial microalgal vegetation and were widespread on a large variety of natural and artificial substrata. The numerous collections made

revealed the high species diversity of these algae in the area and led to several records of great floristic interest. Here we describe in detail the morphology, ecology and distribution of the specimens collected; these results provide a core of information of fundamental importance for future investigations on the Trentepohliales in Central America. Some specimens were isolated in culture and used for molecular work (sequencing of the *rbc*L and 18S rRNA genes). Such information will be presented in a separate report (Rindi et al., in preparation).

Materials and methods

Collections of Trentepohliales were made in the period 19-26 May 2007. The island of Barro Colorado (approximately 9°10.152'N, 79°50.01'W), situated in the Gatun Lake (which is part of the Panama Canal system), is the location where most of the sampling took place. Barro Colorado is an artificial island with a surface area of 15 km^2, which was separated from the mainland by the creation of the Gatun Lake in 1913. Since 1923 it has been part of a large protected area, the Barro Colorado Nature Monument (BCNM). Apart from a limited portion occupied by a permanent research station of the Smithsonian Tropical Research Institute (STRI), Barro Colorado Island is covered by a dense rainforest, which has remained unaffected by major human impacts since the establishment of the BCMN protected area. Additional sampling was carried out on the mainland in the area of Gamboa (9°70.38'N; 79°41.934'W) and from the Summit Zoological and Botanical Garden (9°04.038'N; 79° 38.724'W), in the area of Balboa. Samples were collected from sites where the presence of orange, yellow or red patches indicated the presence of Trentepohliales. Collections were made from a large variety of natural and artificial substrata, including tree bark, leaves, rotting wood, concrete walls, metal sheeting and bars, plastic nets and tubes, and textile fabric curtains. For material collected from tree bark and leaves, an attempt was made to identify the host plants; however, due to the largely exotic nature of the host plants to the authors, this was usually not possible. The specimens were placed in sealable plastic bags and mailed to the laboratory at the University of Alabama, where the material was examined microscopically and identified at the best possible level of taxonomic resolution. Photomicrographs were taken with an Olympus BX51 Microscope equipped with DIC and a QColor 3 digital camera, and mounted in plates using Adobe Photoshop CS2.

Results

Cephaleuros sp.

Alga producing lesions with round or oval outline and cushion-like habit on leaves of tree (Fig. 1). A ring of thick-walled cells, of black colour, was often produced by the host plant around the lesion. Thalli pseudoparenchymatous, with a ramulated prostrate part. Sterile erect filaments usually absent, occasionally present in some specimens. Sporangiophores abundant, 400-700 µm tall; their cells were 50-100 µm long, 18-20 µm wide in the basal parts and 12-16 µm wide in the apical parts. Many sporangiate laterals occurred at the top of the sporangiophores (Fig. 2). Zoosporangia were 23-26 × 32-35 µm in size.

This alga occurred on leaves of some trees in the area of the STRI pier in Gamboa and in the area of the STRI research station on Barro Colorado Island. The type of lesion suggested that the alga parasitically penetrated the leaves of the host plant. However, the details of the morphology of the ramuli could not be observed, and we therefore prefer not to propose an identification at the species level.

Phycopeltis cf. ***amboinensis*** (G.Karsten) Printz

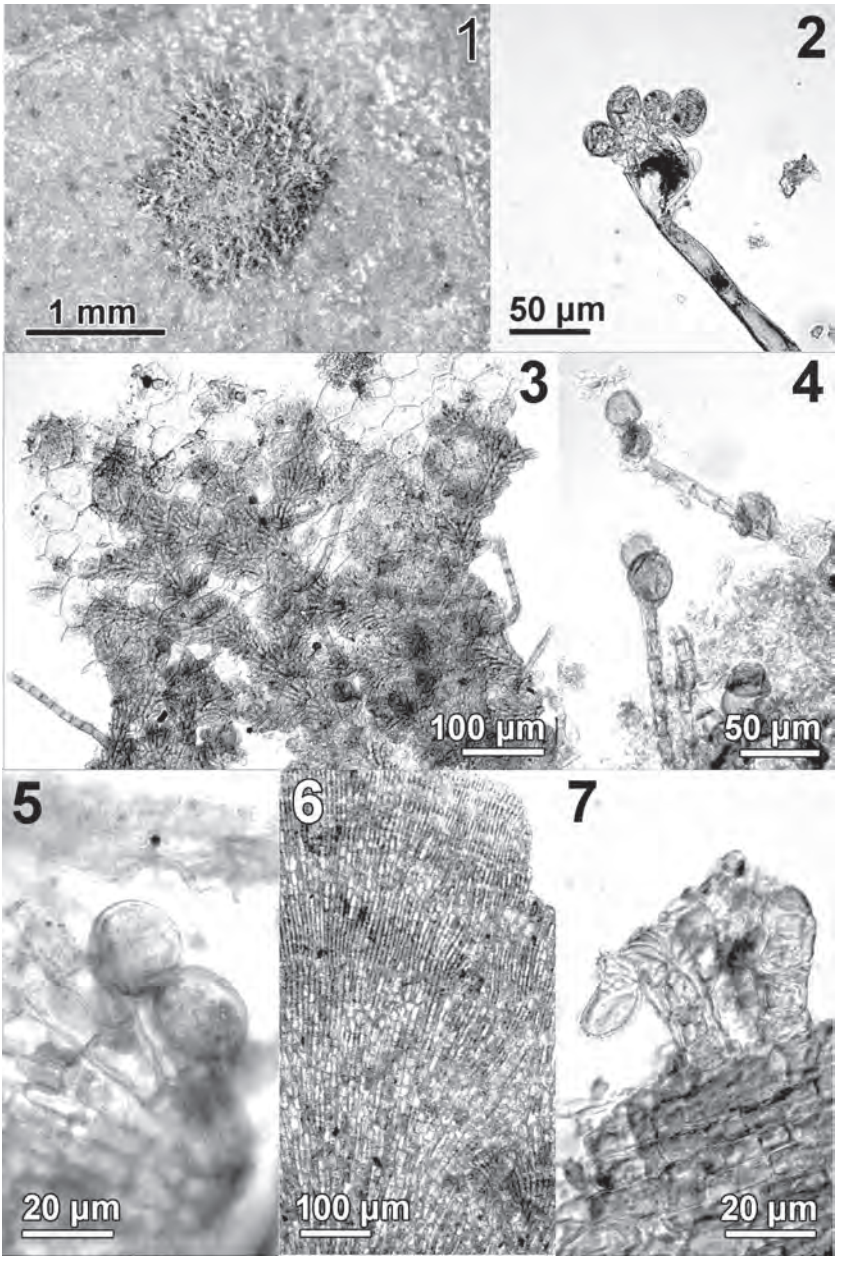
Alga forming a spreading thallus with ramulated habit, brown in colour (Fig. 3); the ramuli may become closely adherent to produce a more or less closed disk. Individual ramuli narrow, formed by 1-2 central cells. Cells 5-10 × 12-27 µm in size (mainly 6-9 × 14-17 µm). Erect filaments common, formed by up to 15 cells, 10-13 µm wide and 2-3 times as long as wide. The erect filaments often supported at their top 1 or 2 enlarged cells (approximately 20 µm wide), which were presumed to be gametangia (Fig. 4). Gametangia occurred also at the apices and along the margins of the ramuli (Fig. 5); they were globular, 18-20 µm in diameter. Sporangiate laterals were not observed.

This alga was found on leaves of several trees in the forest of Barro Colorado Island. Among the species of *Phycopeltis* currently known, it is morphologically most similar to *P. amboinensis* (G. Karsten) Printz, originally described from Ambon, Indonesia (Karsten 1891) and widely recorded in the tropics (Printz 1939; Thompson & Wujek 1997; Neustupa 2003). However, in *P. amboinensis* the cells are longer than in our specimens (22-32 µm; Thompson & Wujek 1997); Neustupa (2003) also reported that *P. amboinensis* rarely produced closed disks, which were common in the material from Barro Colorado. For these reasons, the identification of our specimens is best regarded as provisional.

Phycopeltis cf. ***arundinacea*** (Montagne) De Toni

Alga forming closed disks with smooth or slightly lobed margin, up to 3-4 mm in diameter. Cells 5-11 × 11-28 µm in size (mainly 7.5-9.0 × 15-20). Gametangia and zoosporangia normally occurred on different thalli, but some specimens bearing both were also observed. Gametangia were globular or ovoid at maturity, 12-15 × 15-20 µm in size; they were produced in intercalary position, forming irregular concentric rings in some thalli (Fig. 6). Sporangiate laterals occurred also with intercalary arrangement; they were randomly scattered across the surface of the thallus, but they were usually absent in the most peripheral parts. After discharge of the zoosporangium, the sporangiate laterals developed into sporangiophores, which consisted of 1, 2 or 3 cells, 10-12 µm wide and 0.5-1.5 times as long as wide (Fig. 7).

This alga was common on leaves of several trees in the forest of Barro Colorado and in the area around the STRI pier in Gamboa. It shares similarities with several species of *Phycopeltis* in producing closed disks, but its morphology is not in complete agreement with any of them. It differs from *Phycopeltis novae-zelandiae* R.H.Thompson & Wujek (1997) in having gametangia and zoosporangia on the same thalli; from *P. theaensis* Neustupa (2003) in the larger size and the absence of dorsal papillae; from *P. expansa* A. Jennings (1895) in the number of cells of the sporangiophores (more than 1). European specimens of *Phycopeltis arundinacea* (Montagne) De Toni, that we consider representative of the type material (see discussion in Rindi & Guiry 2002a and Rindi et al. 2004), are also close to the material from Panama; however, they do not produce sporangiophores. Thompson & Wujek (1997) identified as *P. arundinacea* a tropical alga with much larger cells and sporangiophores; we recently collected this entity in French Guiana (Rindi & López-Bautista 2008), reporting it as *P.* cf. *arundinacea*. Our specimens from Panama



Figs 1-7. *Cephaleuros* sp., *Phycopeltis* cf. *amboinensis* and *Phycopeltis* cf. *arundinacea*. Figs 1-2. *Cephaleuros* sp. Fig. 1. Habit on surface of leaf. Fig. 2. Detail of sporangiophore with apical sporangiate laterals. Figs 3-5. *Phycopeltis* cf. *amboinensis*. Fig. 3. Habit. Fig. 4. Detail of erect filaments with enlarged cells (presumed to be gametangia) at their top. Fig. 5. Detail of two gametangia produced on the margin of a ramulus. Figs 6-7. *Phycopeltis* cf. *arundinacea*. Fig. 6. Detail of thallus with numerous gametangia. Fig. 7. Detail of two sporangiophores.

have generally shorter cells, but otherwise correspond well with this alga. Therefore, pending a reassessment of the taxonomy of this group based on molecular data, we use this provisional identification for the Panamanian material.

Phycopeltis cf. ***aurea*** G.Karsten

Alga forming closed disks with smooth or undulated margins, up to 4 mm in diameter (Fig. 8). Gametangia and zoosporangia distributed on different thalli. Cells of gametophytes 4-7 × 8-12 µm (mainly 5-6 × 9-10 µm); cells of sporophytes 6.0-7.5 × 10-15 µm (mainly 6-7 × 11-13 µm). Gametangia were produced either by terminal or intercalary cells of the radiating filaments (Fig. 9); at maturity they were scattered across the thallus, 5-15 × 20-35 µm in size (Fig. 10), occasionally arranged in more or less concentric rings, absent from the most peripheral parts in some thalli. Sporangiate laterals and sporangiophores randomly scattered across the thallus, except the most marginal parts. Zoosporangia 12.5-15.0 × 15-17 µm in size. Sporangiophores formed by 4-8 cells as long as wide, 15-25 µm wide (Fig. 11); residuals of old sporangiate laterals accumulating on a side of the sporangiophore (Fig. 11). Old sporangiophores were eventually broken and only the thickened walls of the basal parts remained in situ; these were observable in surface view as thick brown rings.

This alga was common on the leaves of trees in the forest of Barro Colorado. We believe that this is a robust form of *Phycopeltis aurea* G.Karsten, a species originally described from Java (Karsten 1891) and widespread in the tropics (Printz 1939; Thompson & Wujek 1997; Neustupa 2003). However, since thalli of *P. aurea* are usually not larger than 1 mm (Printz 1939; Neustupa 2003) and have slightly smaller cells than our specimens (Thompson & Wujek 1997; Neustupa 2003), our material cannot be attributed to this species with complete certainty.

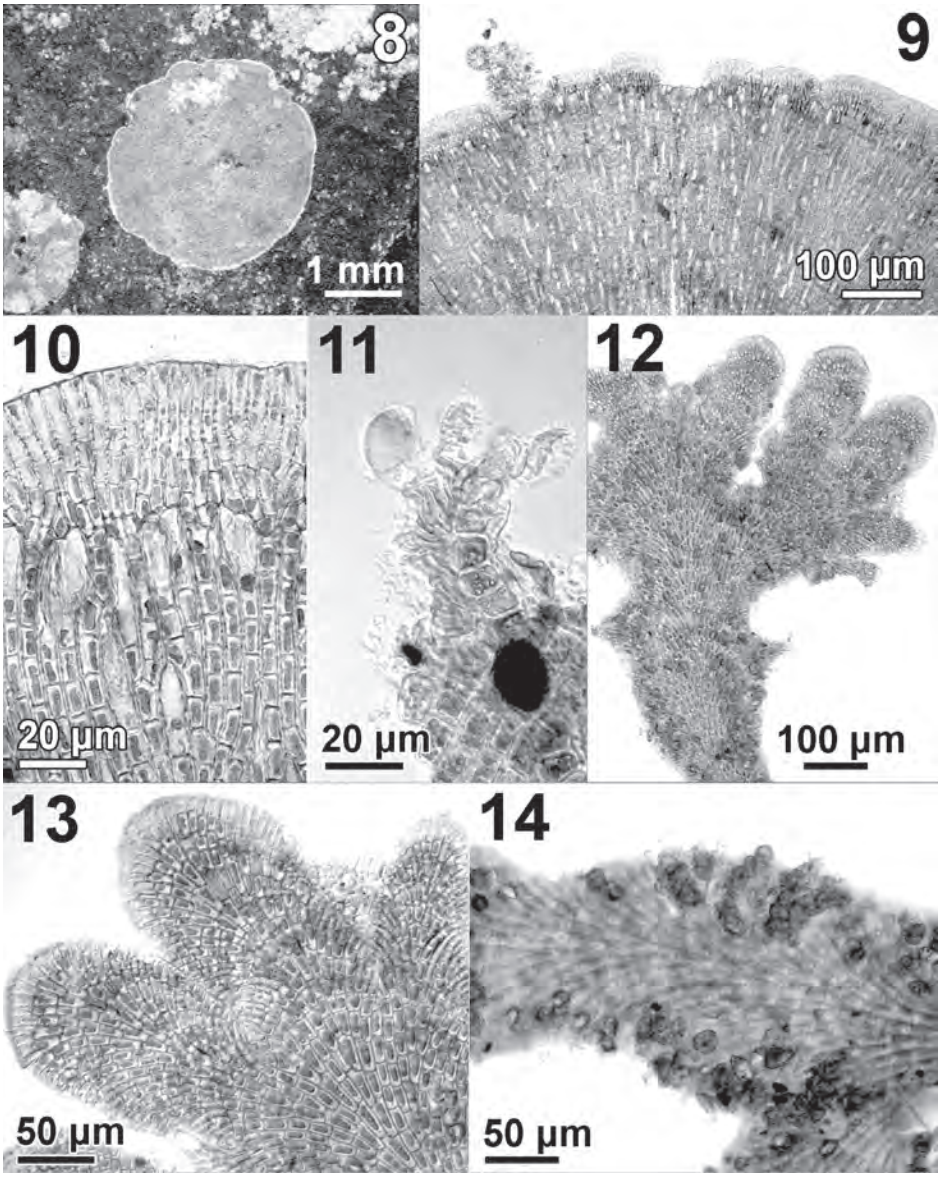
Phycopeltis epiphyton Millardet

Alga of small size (up to 100 µm in diameter), consisting of closed rounded disks with regular margin. Vegetative cells 2-4 µm wide and 3-8 µm long. Gametangia common, produced mostly in the central parts of the thallus but also present in the peripheral parts; they were globular at maturity, about 10 µm in diameter. Sporangiate laterals not observed.

This species was found on leaves of trees, mixed with other *Phycopeltis* spp., in the forest of Barro Colorado. Overall its morphology is in good agreement with the original description (Millardet 1870) and subsequent records from the tropics and temperate regions (Printz 1939; Thompson & Wujek 1997; Neustupa 2003; Rindi et al. 2004).

Phycopeltis cf. ***flabellata*** R.H.Thompson & Wujek

Alga with ramulated thallus, with ramuli openly spreading or appressed to form more or less closed disks up to 4 mm in diameter (Fig. 12). Ramuli large in the basal parts, becoming thinner in the apical parts, where they consist of 1-2 central filaments (Fig. 13). Cells 5-9 × 12-26 µm in size (mainly 6.0-8.5 × 15-20 µm). Sporangia and gametangia apparently produced on separate thalli; most specimens examined were sporangial. Sporangiate laterals and sporangiophores frequent, produced primarily



Figs 8-14. *Phycopeltis* cf. *aurea* and *Phycopeltis* cf. *flabellata*. Figs 8-11. *Phycopeltis* cf. *aurea.* Fig. 8. Habit of thallus on surface of leaf. Fig. 9. Peripheral part of a thallus with gametangia. Fig. 10. Detail of some gametangia produced near the margin of thallus. Fig. 11. Detail of a sporangiophore. Figs 12-14. *Phycopeltis* cf. *flabellata*. Fig. 12. Habit of a ramulus in a thallus with open branching. Fig. 13. Detail of apical parts. Fig. 14. Arrangement of sporangiate laterals and sporangiophores in the subapical parts of a ramulus.

in subapical position along the margins of the ramuli (Fig. 14); in older thalli, however, they were scattered more or less randomly across the thallus. Zoosporangia ovoid, 10-15 × 12-18 µm in size. Sporangiophores formed by 1-3 cells as long as wide or shorter, 12.5-16.0 µm wide. Gametangia not observed.

This alga occurred on leaves of trees at several sites in the forest of Barro Colorado. *Phycopeltis flabellata*, described by Thompson & Wujek (1997) from Puerto Rico, is the species to which it is morphologically closest. However, *P. flabellata* normally does not form closed thalli with more or less regular margin as observed in our material; furthermore, gametangial thalli, which are a common occurrence in *P. flabellata*, were not observed with certainty in the material from Barro Colorado. *Phycopeltis vaga*, described by the same authors from Maricao, Puerto Rico (Thompson & Wujek 1997: 90), shows also considerable morphological similarity to our material. This species, however, is reported to produce sporangia and gametangia on the same thalli (Thompson & Wujek 1997), a situation which was not observed in the collections from Barro Colorado. For these reasons, further collections are desirable in order to clarify the identity of our specimens.

***Phycopeltis* sp.**

This alga formed a dense compact layer on plastic tubes, produced by the adhesion and overgrowth of numerous individual thalli. For this reason, the morphology of individual adult specimens was very difficult to observe. The juvenile specimens showed a regular continuous margin and a rounded or polygonal shape; they were reminiscent of *Phycopeltis epiphyton*. In the mass formed by the aggregation of adult thalli, the discoid shape was usually impossible to observe (Fig. 15) and many specimens produced filamentous growths more similar to *Trentepohlia* than to *Phycopeltis*, with cells cylindrical or barrel-shaped (Fig. 16). Cells 4-9 µm wide (mainly 5-7 µm), 1-2 times as long as wide. Presumptive gametangia were the most common reproductive structures. They were produced in intercalary position (Fig. 15); at maturity they were globular to ovoid, 10-20 µm wide. Sporangiate laterals rarely observed, produced also in intercalary position; no production of sporangiophores was observed.

This alga was found on PVC (Polyvinyl Chloride) pipes in the forest of Barro Colorado Island, not far from the STRI station. The unusual habit, most probably due to the particular substratum on which the alga was growing, makes it impossible to refer it with certainty to any species of *Phycopeltis* currently known.

Printzina bosseae (De Wildeman) R.H.Thompson & Wujek

Alga forming irregular yellowish-green tufts on tree bark. Thallus consisting of erect axes variously branched, arising from a limited prostrate system. Cells cylindrical, 1.2-2 times (mostly 1.5) as long as wide, 12-15 µm wide. Branching irregular; new branches often arising from the suffultory cells (either from the body or the neck), either before or after the discharge of the zoosporangia. Several enlarged intercalary cells were observed in the erect axes, indicating restart of growth from suffultory cells after the discharge of the zoosporangium. The septa between adjacent cells were often thickened, and the plasmodesmata easily observable. Apical cells blunt, dome-shaped

devoid of pectic caps. Zoosporangia common. Suffultory cells markedly inflated, with a septum separating the body of the cell from the neck at maturity. Zoosporangium globular, 25-30 μm in diameter, with ostiole opposite to the attachment.

This species was collected from bark of trees in the area of the STRI station on Barro Colorado Island and in a public park in Gamboa (where it was mixed with other trentepohlialean species). This is the second record for the Americas of this species, which was recently recorded for French Guiana by Rindi & López-Bautista (2008); reported also for Guadaloupe by Bourrelly & Manguin (1952). The morphology of the material from Panama shows great similarity to the variety *P. bosseae* var. *brevicellulis*, described by Cribb (1970) from Queensland. However, it differs from it by the thick septa and the evident plasmodesmata, which did not occur in the Queensland population used by Cribb (1970) to erect this variety.

Printzina lagenifera (Hildebrand) R.H.Thompson & Wujek

Alga forming brownish-orange mats on bark of tree. Thallus consisting of irregular masses produced by the mixture of numerous filaments densely intertwined, without distinction between erect and prostrate parts. Cells elliptical or subglobular, constricted at the junctions with adjacent cells, occasionally more or less cylindrical, 5-10 μm wide (mainly 7.0-7.5 μm). Presumptive gametangia produced in apical, lateral or intercalary position; they were flask-shaped, 8-15 μm in diameter, with the ostiole occurring at the top of a more or less long neck.

This species was collected from the bark of a tree in a public park in Gamboa. Its morphology corresponds well with *P. lagenifera* as generally circumscribed (Hariot 1889; De Wildeman 1900; Printz 1920, 1939; Thompson & Wujek 1992), in particular for the presence of flask-shaped gametangia with a long neck.

Printzina cf. ***lagenifera*** (Hildebrand) R.H.Thompson & Wujek

Specimens of *Printzina* for which the identity could not be confirmed were collected at several sites and from several substrata (bark of rotting tree near Gatun Lake in the STRI station area on Barro Colorado Island; metal posts in rainforest on Barro Colorado Island; on concrete walls in Gamboa and in the Summit Garden). For all these collections, the vegetative morphology was in agreement with *Printzina lagenifera*. However, the lack of reproductive structures or, in some cases, the absence of the well-developed neck typical of the gametangia in this species, did not allow an unambiguous identification.

Printzina **sp.**

Alga forming a thin red coating on the surfaces colonized. The thallus consisted of two well-differentiated portions. The basal part was formed by prostrate filaments densely intertwined, consisting of globular, elliptical or barrel-shaped cells (Fig. 17). The erect part consisted of short erect filaments, up to 250 μm tall, with two different morphologies. Some axes were thin, became tapered in the upper portions and had sharply pointed tips (Fig. 18); some of them were pigmented for the whole length, whereas in others the apical parts consisted of dead cells with thick walls. Other axes

were thicker and not tapered in the upper parts, and usually supported one or two sporangiate laterals. In the prostrate parts the cells were 7.5-14.0 µm wide (mainly 9-12 µm). In the pointed erect axes, the diameter was about 4 µm in the basal parts and decreased to 2.0-2.5 µm near the tip; in the erect axes with sporangiate laterals it was 4-9 µm. Presumptive gametangia occurred on both prostrate and erect axes. In the erect axes, they were borne laterally in the basal parts of the pointed filaments; in this case they were elliptical or ovoid, about 10 µm wide. If produced on the cells of the prostrate system, they were globular or flask-shaped, 10-16 µm in diameter, usually provided with a short beak (Fig. 19). The sporangiate laterals occurred singly or in couples at the top of the erect axes (Figs 20, 21); when two sporangiate laterals were produced, the cell bearing them was not enlarged. The zoosporangia were globular, 10-14 µm wide; the ostiole occurred in basal position, near the attachment.

This alga was collected on 20 May 2007 in the area of the STRI station on Barro Colorado Island, where it produced red patches on the painted concrete surface of a fire hydrant cabinet. For the extensive development of the prostrate parts and the striking separation between erect and prostrate portions, its morphology corresponds with the genus *Printzina*. However, none of the species of *Printzina* currently known shows a combination of morphological characters as observed in the material from Barro Colorado. We believe that this entity may represent an undescribed species, but further collections are desirable to assess in detail its identity.

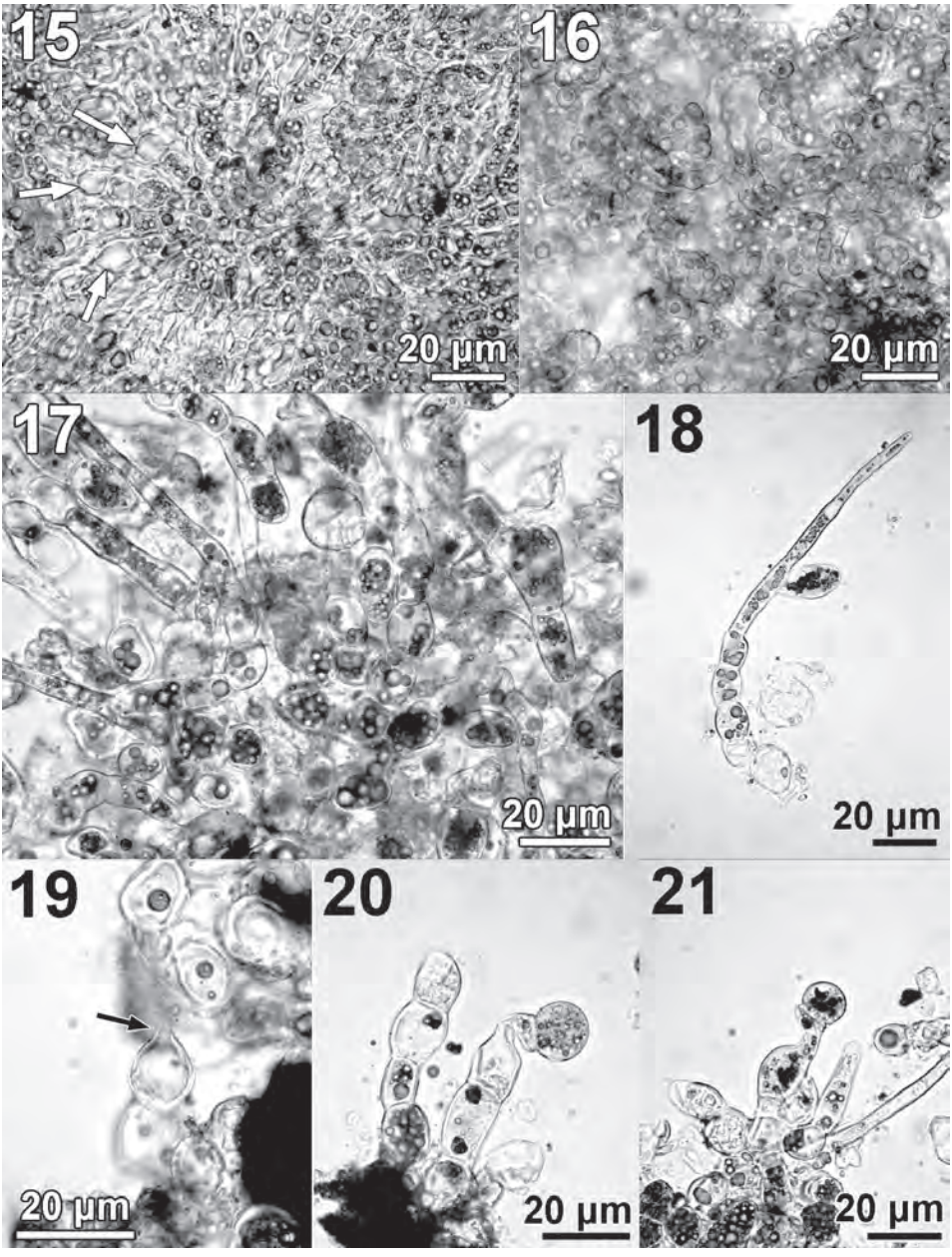
Trentepohlia abietina (Flotow) Hansgirg

Alga producing yellow-orange patches on tree bark. Thallus consisting of erect axes up to 400 µm tall, arising from a limited prostrate system. Cells of the prostrate parts barrel-shaped, 8-12 µm wide; cells of the erect axes cylindrical or slightly inflated, 3-6 times as long as wide, 4-10 µm wide. Most apical cells provided with a small apical cap; in some specimens, cell wall corrugated by thin spiral ornamentations. Presumptive gametangia present but not abundant; they were globular, produced in lateral position on the erect axes, 10-12 µm in diameter.

Specimens of *T. abietina* were collected from bark of tree in a public park in Gamboa, mixed with other species (*Printzina bosseae*, *Trentepohlia rigidula*, *Trentepohlia* sp.). The record from Panama extends the known distribution of this species, which has been frequently reported in the tropics (De Wildeman 1900; Islam 1972; Cribb 1987; Rindi et al. 2005)

Trentepohlia arborum (C.Agardh) Hariot

Alga forming dense fluffy tufts, up to 5 mm tall, orange to light green, on a large variety of substrata. Cells cylindrical, 14-25 µm wide (mainly 18-20 µm), 1.5-5.0 times as long as wide (mainly 2.5-4.0). Apical cells variable in shape, blunt to more or less pointed, devoid of pectic caps. Erect axes poorly or not branched, arising from a limited prostrate system; new branches arising at 90° angle from the center of cells. Presumptive gametangia globular or subglobular, lateral on the erect axes or on short lateral branches, 25-37 µm in diameter. Sporangiate laterals borne at the top of the erect axes, in clusters of 2-8 on an enlarged apical cell. Each sporangiate



Figs 15-21. *Phycopeltis* sp. and *Printzina* sp. Figs 15-16. *Phycopeltis* sp. Fig. 15. Surface view of specimen with empty gametangia (indicated by arrows). Fig. 16. Detail of growth with irregular filamentous habit, *Trentepohlia*-like. Figs 17-21. *Printzina* sp. Fig. 17. Detail of prostrate portion of the thallus. Fig. 18. An individual erect axis with pointed, tapered apex. Fig. 19. A presumptive gametangium produced on the prostrate system; note the short beak (arrow). Fig. 20. Two enlarged erect axes, one of which supporting a sporangiate lateral. Fig. 21. Detail of a sporangiate lateral.

lateral consisted of a suffultory cell with heavily retorted neck on which an elliptical or kidney-shaped zoosporangium, 18-22 × 25-30 µm, was produced The ostiole of the zoosporangium was adjacent to the attachment.

Trentepohlia arborum was one of the most common trentepohlialean species in the area investigated at the time of the study. On Barro Colorado Island it was found on tree bark, leaves (where it typically produced green tufts on the margins), plastic tubes and plastic nets; in Gamboa it was collected from leaves; in the Summit Park it was found on concrete surfaces at the base of animal cages. The morphology of the material from Panama corresponds well with the traditional circumscription of this widespread species, which has been reported from all tropical regions in which the Trentepohliales have been studied.

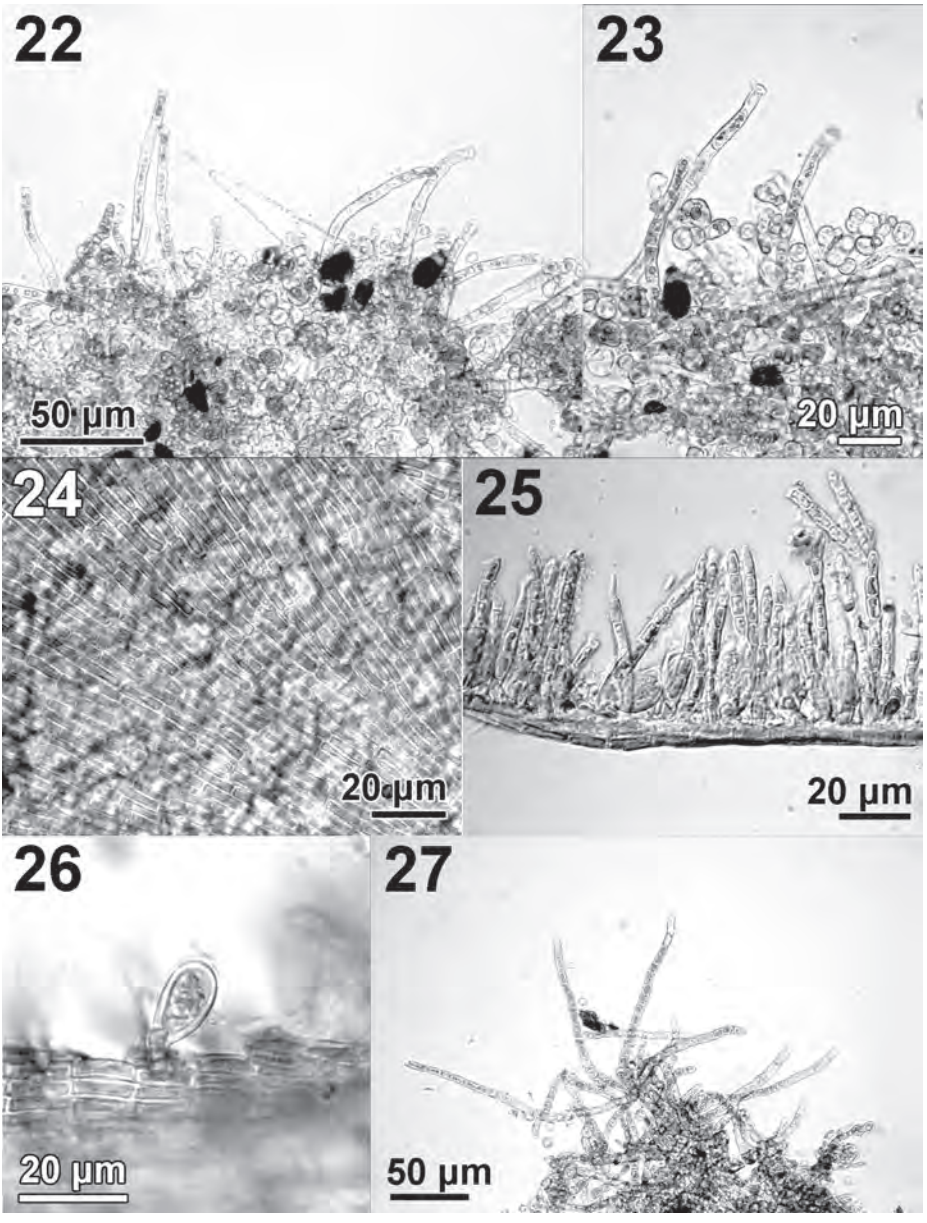
Trentepohlia chapmanii Rindi & López-Bautista

Alga producing a greenish-yellow coating on a painted metal fence. Thallus consisting of a dense mat with marked separation between erect and prostrate parts. The prostrate axes were densely intertwined and produced a pseudoparenchymatous layer of variable thickness; its cells were globular or elliptical, 7-10 µm (mainly 7.5-8.0 µm). The erect axes arose from the upper surface of the prostrate layer and were up to 200 µm tall (Fig. 22); they were formed by 4-5 cells, 4-6 µm wide, 3-8 times as long as wide (Fig. 23). The apical cells were often slightly pointed, usually with a small pectic cap at the tip. A tiny spiral corrugation could be observed at strong magnification in the cell wall of many erect axes. No reproductive structures were observed.

This species was collected in Gamboa, where it produced a thin coating on a painted metal fence. *Trentepohlia chapmanii* was recently described by Rindi & López-Bautista (2007) for specimens collected from coastal bamboo reeds at Fort Diamant, French Guiana. The material from Gamboa did not show a basal layer with a *Phycopeltis*-like habit as observed in the French Guianean specimens; apart for this, every other detail of the vegetative morphology was in very good agreement with the type material. The present record suggests that *T. chapmanii* is probably widespread in Central and tropical South America, and that it deserves to be looked for in detail in other tropical regions.

Trentepohlia depressa (Müller Arg.) Hariot

Alga forming bright green patches on leaves of trees, easily peeled off the substratum. Thallus consisting of two well distinct portions. The prostrate portion consisted of a regular disk with *Phycopeltis*-like habit, formed by radiating filaments with dichotomous branching (Fig. 24); its cells were rectangular, cylindrical, 4-5 µm wide, 2-4 times as long as wide. The erect part consisted of short axes (about 50 µm tall), unbranched or poorly branched, arising at 90° angle from the prostrate filaments (Fig. 25); their cells were cylindrical, 1-2 times as long as wide, 4-6 µm wide. The apical cells of the erect axes were pointed, devoid of pectic caps. Overall, the amount of carotenoids produced was very limited and the colour of the alga was bright green. Presumptive gametangia were abundant, borne laterally on the first or second basal cells of the erect axes. They were elliptical or ovoid in shape, 12.0-12.5 × 17.5-20.0 µm (Fig. 26). In well-developed gametangia the cell wall was usually thick, formed by 2 or 3 concentric layers.



Figs 22-27. *Trentepohlia chapmanii*, *Trentepohlia depressa* and *Trentepohlia dusenii*. Figs 22-23. *Trentepohlia chapmanii*. Fig. 22. Habit of erect axes arising from the prostrate system. Fig. 23. Detail of some erect axes. Figs 24-26. *Trentepohlia depressa*. Fig. 24. Detail of the prostrate system, with *Phycopeltis*-like habit, as observed in underneath view in a thallus peeled off the substratum. Fig. 25. Habit of thallus observed in cross-section. Fig. 26. Detail of presumptive gametangium. Fig. 27. *Trentepohlia dusenii*. Habit of some erect axes arising from prostrate portion of the thallus.

This species is one of the most interesting records of the present investigation. It was so far known only from Brazil, as reported in the original description (Müller Arg. 1882). The morphology of our material is in good agreement with descriptions available in previous studies (Hariot 1890; Printz 1939).

Trentepohlia dusenii Hariot

Alga forming compact green mats on metal surfaces. Thallus consisting of a compact prostrate layer formed by many filaments densely intertwined, from which numerous erect axes, mostly unbranched and up to 300 µm tall, arose (Fig. 27). Cells of the prostrate portion elliptical or globular, 5-9 µm wide. Cells of the erect axes cylindrical or slightly inflated, 1-2 times as long as wide, variable in width. Many axes (presumed to represent the gametophyte generation) were 3.5-7.5 µm wide (mainly 5.5-6.0 µm); other axes, which bore sporangiate laterals and represented the sporophyte generation, were 8-11 µm wide (Fig. 28). Apical cells of the erect axes slightly pointed, bullet-shaped, devoid of pectic caps. Sporangiate laterals were the most common reproductive structures. They occurred singly at the top of the erect axes. The suffultory cell was tall, only slightly enlarged, and supported a globular zoosporangium 12-15 µm in diameter (Fig. 29). The ostiole was located in basal position, near the attachment with the suffultory cell. Some erect axes showed some inflated intercalary cells, which appeared to be suffultory cells from which the growth had restarted after discharge of the zoosporangium. Very few presumptive gametangia were observed. They were subglobular or ovoid, 10-15 µm in diameter, apical or lateral on the erect axes, or produced at the top of short lateral branches (Fig. 30).

This species was collected from a metal vice placed in a shaded site beside the boat dock at the STRI station on Barro Colorado Island. This collection represents the second report of *T. dusenii* for the Americas, after our recent record for French Guiana (Rindi & López-Bautista 2007, 2008). In general, this species has been rarely found; the only other records available refer to Cameroon (original description by Hariot in Wittrock & Nordstedt 1893), Queensland (Cribb 1963) and India (Jose & Chowdary 1980). The record for Panama confirms that this species is probably much more widely distributed in the tropics than currently appreciated. The apparent preference for shaded, sheltered habitats and the bright green colour, which make it prone to be easily confused with mosses or other terrestrial green algae, are probable reasons why it has been largely undetected.

Cf. ***Trentepohlia ellipsicarpa*** var. ***africana*** Schmidle

Alga forming bright green mats on the surface of leaves, easily peeled off the substratum. Prostrate part formed by creeping axes variably branched, irradiating from a central part but not producing a compact closed disk; however, they issued lateral branches that grew filling the gaps between the axes (Fig. 31). Numerous erect axes arose from the prostrate portion; they were mostly unbranched, up to 150 µm tall, and their apical cells were more or less pointed, sometimes quite sharply (Fig. 32). The cells were cylindrical; in the prostrate parts they were 5.0-7.5 µm wide and 2.5-5.0 times as long as wide; in the erect parts they were 4-8 µm wide and 2-4 times as long as wide. Carotenoid pigments occurred in very limited amounts and the alga had a bright green

colour. The presumptive gametangia were produced on the prostrate axes or laterally on the basal parts of the erect axes; less frequently they occurred on higher parts of the erect axes. They were elliptical or ovoid, 12.5-15.0 µm in diameter (Fig. 33). Sporangiate laterals occurred singly at the top of the erect axes or, less frequently, in a lateral position. The suffultory cells were distinctly enlarged, 12.5-15.0 µm wide (Fig. 34). Mature zoosporangia were rarely found and were mostly observed discharged; they were subglobular or ovoid, 10-15 µm in diameter. Restart of growth from suffultory cells after discharge of the zoosporangium was commonly observed, as indicated by the presence of some enlarged intercalary cells in the erect axes.

This alga was collected from the leaves of several trees in the rainforest of Barro Colorado Island. *Trentepohlia ellipsicarpa* var. *africana* Schmidle, originally described from Cameroon, is the entity that is morphologically closest to it. We have not been able to see the original description of this taxon (Schmidle 1902); however, following the circumscriptions of Printz (1939) and Cribb (1993), its vegetative and reproductive morphology are very similar to our material from Barro Colorado, and the habitat occupied appears also to be the same. Our specimens differ somewhat from *T. ellipsicarpa* var. *africana* in having comparatively longer cells in the erect axes, larger cells in the prostrate parts, and clearly pointed apical cells; Printz (1939) reported also the presence of intercalary gametangia, which were not observed in our collections. In consideration of these differences, the identification of our material should be considered preliminary; the availability of further collections will be necessary for a precise determination.

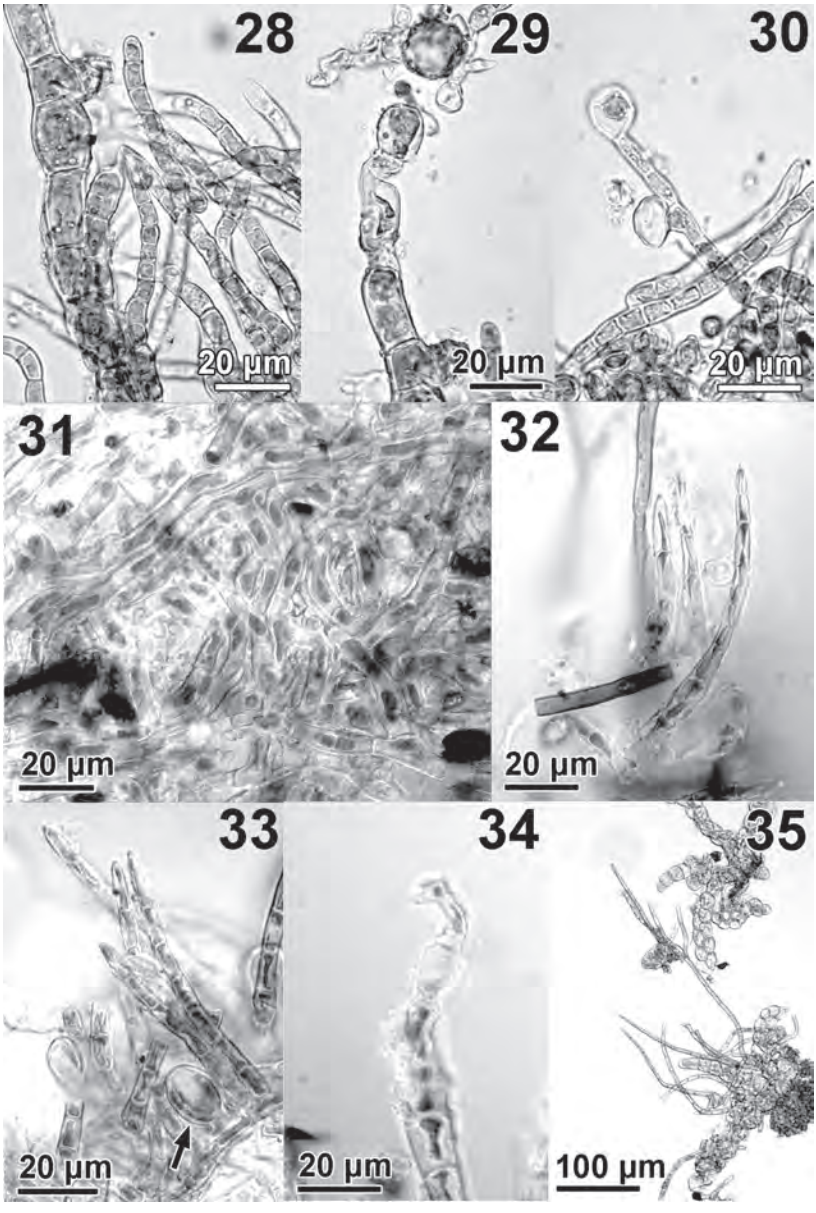
Trentepohlia minima Schmidle

Alga found mixed with mosses on tree bark (Fig. 35). Thallus with clear separation between erect and prostrate parts. Prostrate axes sparsely branched; erect axes unbranched, thin, gradually tapering, with sharply pointed tips. Cells 4-5 µm wide in the prostrate axes and in the basal parts of the erect axes, 2.5-3.0 µm wide in the upper parts of the erect axes. Cells 3-8 times as long as wide. Presumptive gametangia globular or subglobular, 10-13 µm in diameter, with a short neck, borne on the cells of the prostrate axes or laterally in the lower parts of the erect axes (Fig. 36).

This species was mixed with mosses and lichens forming a green powdery layer on the bark of a palm tree in the rainforest of Barro Colorado Island. *Trentepohlia minima* was based by Schmidle (1897: 318) on specimens growing in the grooves of the filaments of *Phycopeltis treubii* var. *expansa* Schmidle in New Guinea. Although the substratum of growth is different and some morphological details do not correspond completely (for example, in our specimens the apical cells are clearly more than 2 times as long as wide), we consider that the morphology of the material from Barro Colorado is in sufficiently good agreement with the original description and subsequent reports (Printz 1939) to refer it confidently to this species. This is the first record for the Americas of *T. minima*, which was so far known only from the type locality in New Guinea.

Trentepohlia peruana **(Kützing) Printz**

Alga forming yellow spongy mats on bark of tree. Thallus consisting of a dense basal layer with pseudoparenchymatous structure, formed by many entangled prostrate



Figs 28-35. *Trentepohlia dusenii*, cf. *Trentepohlia ellipsicarpa* var. *africana* and *Trentepohlia minima*. Figs 28-30. *Trentepohlia dusenii*. Fig. 28. Detail of some erect axes; note a thick erect axis of sporophyte and many thin axes of gametophyte. Fig. 29. Detail of a sporangiate lateral. Fig. 30. An erect axis with two gametangia. Figs 31-34. Cf. *Trentepohlia ellipsicarpa* var. *africana*. Fig. 31. Detail of postrate system as observed in underneath view in a thallus peeled off the substratum. Fig. 32. Detail of an erect axis showing pointed apical cell. Fig. 33. A gametangial thallus with a presumptive gametangium (arrow). Fig. 34. A sporangiate lateral in which the zoosporangium was released. Fig. 35 *Trentepohlia minima*. Habit of thallus mixed with fragments of mosses.

axes. Numerous short filaments emerge from the upper surface of such layer; their cells are globular, elliptical or barrel-shaped, 7.0-12.5 µm wide, and their dorsal surface often produces one or two hair-like protrusions, 40-50 µm tall and 2.5-3.0 µm wide. In some cells the cell wall is corrugated by numerous thin, irregular scales. Presumptive gametangia common, globular or subglobular, 10-15 µm in diameter, produced in apical or lateral position on the cells of the emerging filaments. Sporangiate laterals rarely observed, produced singly at the apex of emerging filaments; they consisted of small suffultory cells with a strongly retorted neck which supported a globular zoosporangium, 15-16 µm in diameter at maturity. The ostiole of the zoosporangium was opposite to the attachment.

This species was collected from bark of trees at Colorado Point on Barro Colorado Island, and in a public park in Gamboa. The morphology of our specimens is in good agreement with the circumscription of this species presented by Cribb (1970), who examined the type specimen of *Bulbotrichia peruana* Kützing (the basionym of *T. peruana*) and several morphologically similar taxa.

Trentepohlia rigidula (Müller Arg.) Hariot

Alga forming compact crusts on tree bark, very variable in colour (usually dark red, but also pink, orange or yellow). The thallus was a filamentous mat in which sometimes a prostrate and an erect system can be recognized, but more frequently it consisted of an irregular mass formed by entangled filaments without evident differentiation of erect and prostrate parts. Cells barrel-shaped, elliptical or subglobular, 12-21 µm wide (mainly 14-18 µm), usually with a strong constriction at the junctions with adjacent cells. Cell walls occasionally smooth, but more often densely corrugated by numerous thin scales. Presumptive gametangia abundant, globular, ovoid or dome-shaped, 20-26 µm in diameter; they were produced in apical, lateral or intercalary position and were also covered by numerous tiny scales. When occurring in intercalary position, the presumptive gametangia had often one side markedly more flattened than the other.

At the time of the survey, this was the most common trentepohlialean species in the area investigated. It was found on the bark of numerous trees both on Barro Colorado Island and at the sites visited on the mainland. The best-developed populations were found at weather-exposed sites, where the cell walls were densely covered by scales. Specimens of *T. rigidula* with smooth walls were found mixed with *Printzina* cf. *lagenifera* on metal poles in the rainforest of Barro Colorado; in this case the morphology corresponded to *Trentepohlia monilia* De Wildeman [= *Physolinum monile* (De Wildeman) Printz], an entity that, following Cribb (1970), we consider conspecific with *T. rigidula*. The record from Panama extends the known geographical distribution of *T. rigidula*, which has been widely reported in the tropics (Hariot 1889; Printz 1939; Sarma 1986).

Trentepohlia treubiana De Wildeman

Alga forming brownish-orange tufts on tree bark. Thallus consisting of erect axes poorly branched, up to 350 µm tall, arising from a limited prostrate system (Fig. 37). Cells cylindrical, sometimes slightly inflated, 1-2 times as long as wide, 7-10 µm wide

(mainly 7.5-9.0 µm). In the older parts of the thallus the septa between adjacent cells were relatively thick and the cell walls had a brownish-red colour. Apical cells blunt, devoid of pectic caps; new branches arising from either the corners or the central parts of the cells. Presumptive gametangia abundant, globular or subglobular, 18-25 µm in diameter, produced on the erect axes in apical, lateral or, more frequently, intercalary position; when intercalary, they often occurred in series of 2, 3 or 4 adjacent gametangia (Figs 38, 39).

Trentepohlia treubiana was collected from the bark of a tree in the dormitory area of the STRI station on Barro Colorado Island. This is the first record for the Americas of this species, which was described by De Wildeman (1896: 89) for material from Bogor (formerly Buitenzorg) and Tjikeumeuh, Java, Indonesia; it has also been reported from Papua New Guinea (Cribb 1958b) and India (Jose & Chowdary 1980). Although our specimens have slightly larger cells (7-10 µm instead of 5-7 µm), in every other respect they agree with De Wildeman's material and in particular share with it the morphological character considered diagnostic of this species, the intercalary gametangia in multiple series.

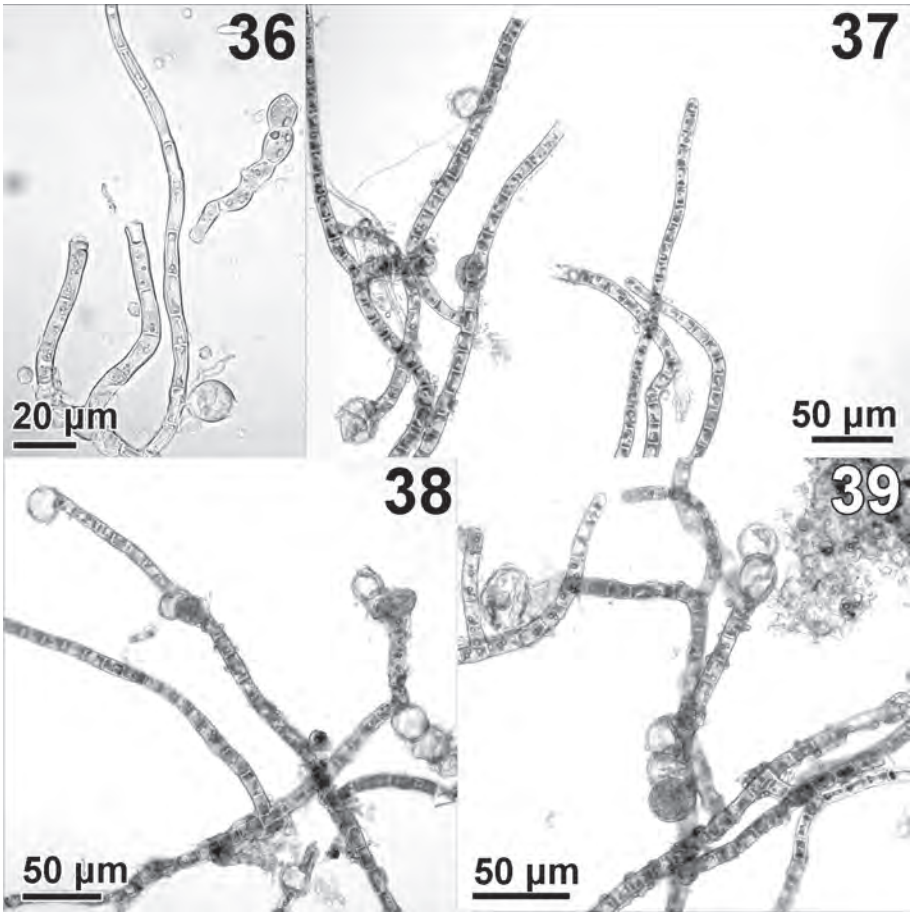
Cf. ***Trentepohlia umbrina*** (Kützing) Bornet

Alga forming a thin orange mat on bark of a palm tree. Thallus forming a pseudoparenchymatous mass produced by numerous entangled filaments; no distinction was noticeable between erect and prostrate parts. Cells globular or barrel-shaped, mostly as wide as long, 5-10 µm wide (mainly 7-8 µm). Under pressure, the thallus was easily broken into many few-celled fragments; cells were not constricted at the junction with adjacent cells. Presumptive gametangia common, produced apically, laterally or in intercalary position. They were subglobular or flask-shaped, 10-15 µm in diameter, with the ostiole at the top of a short neck.

This alga was found on the exfoliation of a palm tree bark in the area of the STRI station on Barro Colorado Island, on the side facing Basilisk Bay. Its morphology is not in complete agreement with any species of *Trentepohlia* or *Printzina* currently known. For the globular or barrel-shaped cells and for the tendency to fragment into short filaments, this alga is similar to *Trentepohlia umbrina* (Kützing) Bornet, which has been widely reported for temperate and tropical regions. The size of the cells, however, is smaller in our alga and no flask-shaped gametangia with a neck occur in *T. umbrina* (Printz 1939; Ettl & Gärtner 1995; Rindi & Guiry 2002b). In the latter character, our alga is similar to *Printzina lagenifera* and *P. ampla* R.H.Thompson & Wujek; however, in these species the cells are mostly elliptical and more or less constricted at the junctions with the other cells, and in *P. ampla* there is an evident distinction between erect and prostrate parts (De Wildeman 1891; Hariot 1889; Printz 1939; Thompson & Wujek 1992). Pending availability of further collections, the identity of our alga is best regarded as uncertain.

***Trentepohlia* sp. 1** (F256)

Alga consisting of little-branched erect axes arising from a limited prostrate system. Cells cylindrical, 2 times as long as wide, 7-13 µm wide. In the older parts of the



Figs 36-39. *Trentepohlia minima* and *Trentepohlia treubiana*. Fig. 36. *Trentepohlia minima*. Detail of a specimen bearing a presumptive gametangium. Figs. 37-39. *Trentepohlia treubiana*. Fig. 37. Habit of erect axes. Figs 38-39. Erect axes bearing intercalary gametangia in series.

thallus the cell wall has a brownish orange colour and it is more or less thickened; the septa are also thick, with evident plasmodesmata. The apical cells are blunt, devoid of pectic caps. Presumptive gametangia globular, produced in apical position, 12-15 µm in diameter.

This alga was collected from tree bark near Colorado Point, on Barro Colorado Island. For cell size and the orange-brownish colour of the cell wall, it is in agreement with *Printzina luteofusca* (De Wildeman) R.H.Thompson & Wujek (described as *Trentepohlia luteofusca* by De Wildeman 1891 from Fort de Kock, Sumatra, Indonesia). The alga from Barro Colorado, however, does not bear the whorls of detachable cells reported for *P. luteofusca* and the apical cells do not show the inflated shape

reported as typical of this species (Printz 1939; Cribb 1970). The availability of further collections is necessary to clarify its taxonomic identity.

***Trentepohlia* sp. 2** (F270)

Alga forming a brownish-green cover on tree bark. Thallus consisting of short erect axes mostly unbranched, arising from a well-developed prostrate system with markedly different morphology. Cells of the erect axes cylindrical, 7-9 µm wide, 2-4 times as long as wide; cells of the prostrate axes globular or elliptical, 10-20 µm wide. Apical cells of the erect axes obtuse or slightly pointed, devoid of apical caps. Sporangiate laterals infrequent, occurring singly at the top of the erect axes. Zoosporangium globular, about 10 µm in diameter.

This alga was found on bark of tree in a public park in Gamboa, mixed with *Trentepohlia rigidula*. Its morphology does not correspond with any species of *Trentepohlia* currently known. *Trentepohlia abietina* has similar size and habit, but our specimens have larger and more swollen cells in the prostrate parts; furthermore, thalli of *T. abietina* collected in the same area bore pectic caps, which were not observed in this alga. We believe that this may possibly be an undescribed species, but further collections will be necessary to clarify its identity.

Unidentified forms

Our collections included a number of specimens for which not even identification at the genus level could be proposed. This was in particular the case for some samples collected from unusual substrata, such as metal bars, mosquito nets and textile fabric curtains in the dormitories of the STRI research station on Barro Colorado Island. These algae formed irregular masses without distinction of prostrate and erect parts, reminiscent of *Trentepohlia* or *Printzina*; several cells, however, had an irregular shape (polygonal or dichotomously or polytomously lobed) similar to those of *Phycopeltis*.

Discussion

The present study has revealed the presence of not less than 24 taxa of Trentepohliales in central Panama, as identified by morphology. Four of the five genera currently belonging to the order were recorded; despite of careful observation, we were not able to locate any specimens of *Stomatochroon*. This genus is known exclusively from tropical regions and its presence in Panama is expectable, considering that records from Costa Rica, Colombia and Venezuela are available (Thompson & Wujek 1997). However, the small size and elusive habit (thalli growing endophytically in the leaves of vascular plants, with sporangiate laterals issuing from the stomata) make specimens of this genus particularly difficult to observe. Although it is generally accepted that the Trentepohliales are most abundant and diverse in tropical zones, the information available about the diversity of these algae in Central and tropical South America is still limited. Thompson & Wujek (1997) reported detailed information and records of *Cephaleuros*, *Phycopeltis* and *Stomatochroon* for several countries of Central America; however, they did not include *Trentepohlia* and *Printzina*

in their treatment. Some investigations focused on these genera have been carried out in other parts of South America (Akiyama 1971; Tracanna 1989). However, French Guiana is the only region in this geographical area for which a comprehensive survey of the trentepohlialean flora has been carried out (Rindi & López-Bautista 2008). This investigation, which was based on the same methods and in which the main collector (FR) was the same as in this study, led to the collection of 28 different taxa. Based on these investigations and data available for other regions (De Wildeman 1900; Phillips 2002), we believe that the presence of at least 30 trentepohlialean taxa is the normal situation for tropical regions with humid climates. In the case of Panama, it is likely that the actual number of taxa present may be considerably higher than recorded here. Some collections made in this study, for which we were not able to provide identification at the genus level, may well represent additional taxa. Furthermore, for logistical reasons our collections were mostly made on Barro Colorado Island, since it was not possible to travel extensively on the mainland. It is likely that collections made in coastal areas and types of habitats different from those occurring in the area sampled would have resulted in a higher number of taxa. A differentiation between the trentepohlialean flora of humid rainforest habitats and that of exposed coastal areas was highlighted by Rindi & López-Bautista (2008) for French Guiana. Whereas species of *Phycopeltis* and some *Trentepohlia* and *Printzina* show a clear preference for rainforest habitats, many *Trentepohlia* and *Cephaleuros* species are associated with more exposed habitats, characterized by direct sunlight exposure and higher temperature (Rindi & López-Bautista 2008). We believe that similar differences will also be revealed for Panama, once the necessary information becomes available.

The present investigation led to two new records for the Americas (*Trentepohlia minima* and *T. treubiana*), as well as the discovery of several species rarely reported (*Printzina bosseae*, *Trentepohlia chapmanii*, *T. depressa*, *T. dusenii*). Both in this investigation and in our previous study for French Guiana (Rindi & López-Bautista 2008) we experienced great difficulty in identifying specimens of *Phycopeltis* and *Cephaleuros*, and only a few unambiguous species-level identifications were possible for these genera. Most of our specimens did not show complete correspondence with the descriptions available in the main treatments of these genera (Printz 1939; Thompson & Wujek 1997) and other studies referring to tropical regions (Neustupa 2003, 2005). This may be in part due to the fact that in several species the range of morphological variation is possibly wider than currently appreciated. However, the diversity of these genera (*Phycopeltis* in particular) in tropical regions is generally considered to be very high (Thompson & Wujek 1997; Neustupa 2003) and we suspect that several taxa recorded in our investigations represent undescribed species. Molecular data will be of fundamental importance to clarify the taxonomy of these organisms and of the whole order in general. Unfortunately, in the case of *Phycopeltis* high-quality molecular data are more difficult to produce than for other trentepohlialean algae; algae of this genus are virtually impossible to isolate in culture, making it very difficult to obtain clean material free of contaminants to be used for DNA extraction. For *Printzina* and *Trentepohlia*, inference based on sequences of the *rbc*L and SSU rRNA genes suggests that morphology grossly underestimates genetic diversity and that the actual number of species is probably much higher than

currently appreciated (Rindi et al., in preparation). Some species widely distributed in the tropics, such as *Printzina lagenifera* and *Trentepohlia arborum*, appear to represent a complex of cryptic species rather than individual entities. Overall, the body of molecular, morphological and ecological information that is emerging from our studies and other recent investigations on the Trentepohliales points strongly to the importance of the conservation of natural habitats in the tropics. The association between diversity of Trentepohliales and tropical rainforests implies that the destruction of these environments is a major threat to trentepohlialean algae, and presumably to many other taxa of terrestrial algae. Areas such as the Barro Colorado Nature Monument represent repositories of great importance for these organisms, and a great increase in the number of similarly protected areas in other regions of the tropics would be highly desirable for the conservation of these algae.

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