Cryptogamie, Algol., 2004, 25 (1): 3-17

The taxonomy and distribution of *Phycopeltis* (Trentepohliaceae, Chlorophyta) in Europe

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(Received 2 October 2003, accepted 23 November 2003)

Abstract — Two species of *Phycopeltis* (Trentepohliaceae, Chlorophyta) were found to occur epiphytically on leaves of ivy in Asturias, north-western Spain. The larger species, consisting of disk-shaped thalli up to 1400 µm wide, with vegetative cells 9-18 µm long and 5-11 µm wide, is referred to *Phycopeltis arundinacea* (Montagne) De Toni. Its morphology is in good agreement with similar material recently collected from Ireland and northern France. The smaller species (up to 180 µm in diameter) corresponds with the original description of *Phycopeltis epiphyton* Millardet, the generitype, originally based on material from the Black Forest, southern Germany. This provided the opportunity to reassess the morphology of the species by examining a living population comparable to the original material for the first time since its original description. *Phycopeltis epiphyton* from Asturias had gametangial and zoosporangial reproduction on different plants. Gametangia were produced in the central parts of the thallus and were up to 16 µm wide and 20 µm long; zoosporangia were produced apically, on the margin of the thallus, and were 12-24 µm wide. A comparison of European *P. epiphyton* with descriptions and illustrations reported for the same species for tropical localities suggests that caution should be used in the assessment of the morphology and distribution of this species. Records of *P. epiphyton* from Britain also should be critically reassessed. A provisional lectotype is designated for *P. epiphyton*.

Distribution / Europe / *Phycopeltis* / Spain / Taxonomy / Trentepohliaceae /

Résumé — La taxinomie et la distribution de *Phycopeltis* (Trentepohliaceae, Chlorophyta) en Europe. Deux espèces de *Phycopeltis* (Trentepohliaceae, Chlorophyta) ont été trouvées, épiphytes sur des feuilles de lierre, dans les Asturies, nord-ouest de l'Espagne. La plus grande espèce, consistant en thalles en forme de disque pouvant atteindre jusqu'à 1400 µm de largeur, avec des cellules végétatives de 9-18 µm de longueur et 5-11 µm de largeur, est attibuée à *Phycopeltis arundinacea* (Montagne) De Toni. Sa morphologie est en bonne conformité avec du matériel semblable récolté récemment en Irlande et dans le nord de la France. La plus petite espèce (pouvant mesurer jusqu'à 180 µm de diamètre) correspond à la description originale de *Phycopeltis epiphyton* Millardet, l'espèce type du genre, basée à l'origine sur du matériel de la Forêt Noire en Allemagne du sud. Cela procure l'opportunité de reconsidérer la morphologie de l'espèce en examinant une population vivante comparable au matériel d'origine, pour la première fois depuis sa description originale. Le *P. epiphyton* des Asturies présente une reproduction par des gamétocystes et des zoospo-

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rocystes sur plusieurs échantillons. Les gamétocystes sont produits dans les parties centrales du thalle et mesurent jusqu'à 16 µm de largeur et 20 µm de longueur; les zoosporocystes sont formés apicalement sur les marges du thalle et ont de 12 à 24 µm de largeur. Une comparaison de *P. epiphyton* d'Europe avec des descriptions et illustrations de la même espèce rapportées de localités tropicales suggère qu'il faille faire preuve de prudence pour réévaluer la morphologie et la distribution de cette espèce. Des mentions de *P. epiphyton* en Grande Bretagne doivent aussi être sérieusement reconsidérées. Un lectotype provisoire est désigné pour *P. epiphyton.* Traduit par la Rédaction.

Distribution / Espagne / Europe / *Phycopeltis* / Taxinomie

INTRODUCTION

Phycopeltis is a genus of subaerial green algae widespread in tropical regions (Printz, 1939; Chapman, 1984; Thompson & Wujek, 1997) and occasionally recorded for temperate regions (Printz, 1964; Sarma, 1986; López-Bautista *et al*., 2002b). *Phycopeltis epiphyton* Millardet is the generitype of *Phycopeltis*; this species was erected by Millardet (1870, p. 48) for material occurring on needles of fir (*Abies* P. Miller) and leaves of ivy and blackberry in the area of Freiburg im Breisgau (Black Forest, southern Germany).

Currently, two species of *Phycopeltis* are reported for Europe, *P. epiphyton* and *P. arundinacea* (Montagne) De Toni. For *P. epiphyton*, however, the only record for continental Europe is the original description. *P. epiphyton* has been also recorded from a few, widely separated localities in the British Isles (John, 2002). The occurrence in Ireland of another species of *Phycopeltis* was reported by Scannell (1965). Initially she referred her material to *Phycopeltis expansa* Jennings; after further investigations, however, she considered that her material was *P. arundinacea* (Montagne) De Toni and regarded *P. arundinacea* and *P. expansa* as conspecific (Scannell 1978, 1982). In a recent reinvestigation, the attribution of Irish material to *P. arundinacea* was confirmed (Rindi & Guiry, 2002), highlighting the widespread distribution of this alga in Ireland. There are also recent records for Britain (John, 2002; Orange, 2003). More recently, we collected material attributable to the same species in a deciduous woodland in Brittany (Rindi *et al*., 2003), which was the first record of *P. arundinacea* for continental Europe.

Identification and clarification of taxonomic problems in *Phycopeltis* present numerous difficulties and require careful observations (for detailed discussion, see Tompson & Wujek, 1997; Rindi & Guiry, 2002; Neustupa, 2003). A number of morphological characters are known to be taxonomically significant. However, as remarked by Thompson & Wujek (1997), several of these characters may be influenced by environmental factors and a detailed assessment should be made on healthy, well-growing specimens; our observations on Irish *P. arundinacea* led us to agree with these authors (Rindi & Guiry, 2002). Difficulties in the assessment of these characters may have been the source of uncertainties and resulted in literature reports that are not completely correct. *P. epiphyton* is one species for which this might be the case, and we agree with Neustupa (2003) that the identity of populations from different climatic zones should be critically reassessed.

Recently, the presence of algae attributable to the genus *Phycopeltis* in deciduous woodlands of Asturias (north-western Spain) was noted. Microscopical

examination of the material revealed the presence of large populations of *P. arundinacea* and *P. epiphyton*. For *P. epiphyton*, in particular, this was a discovery of great interest. The morphology of the material was in perfect agreement with the alga described by Millardet (1870). This provided, for the first time since the original description, the possibility of examination of a living population referable with some certainty to the original material. Since *P. epiphyton* is the type species of the genus, an unambiguous assessment of its morphology is particularly desirable. We describe here the morphology of the material collected. On the basis of this record, examination of herbarium specimens and literature reports, we propose a critical reassessment of the geographical distribution of the two European species. We also present some recommendations and guidelines for future work aimed to clarify taxonomic and distributional problems in *Phycopeltis*.

MATERIALS AND METHODS

Specimens of *Phycopeltis* were collected at several sites in Asturias, north-western Spain, from July 2002 to April 2003; collection details are given in Tab. 1.

Phycopeltis occurred epiphytically on the leaves of ivy (*Hedera helix* L.). For each collection several leaves, each with visible orange patches of *Phycopeltis*, were collected and mailed within a few days to Ireland in sealed plastic bags. This procedure did not noticeably affect the morphology of the algae, which were still in good condition on arrival. Specimens of *Phycopeltis* were removed and exam-

Table 1. Collections of *Phycopeltis* examined.

Date	*Locality*	*Coordinates*	*Type of habitat*	*Species*
1 Jul. 2002	Cudillero	6º 10' 30.9 '' W	In *Eucalyptus-Pinus* woodland	*P. arundinacea, P. epiphyton*
18 Oct. 2002		43º 33' 32.4 '' N		*P. arundinacea*
2 Dec. 2002				*P. arundinacea*
10 Feb. 2003				*P. arundinacea*
4 Apr. 2003	Cadavedo	6º 21' 4.7 '' W 43º 32' 58'' N	In deciduous woodland, near stream	*P. arundinacea*
5 Apr. 2003	La Caridad	6º 49' 25.6'' W 43º 33' 17.9'' N	In deciduous woodland, near stream	*P. arundinacea*
8 Apr. 2003	El Escañorio	5º 55' 27.9'' W 43º 31' 4.8'' N	In deciduous woodland, near stream	*P. arundinacea*
23 Apr. 2003	Playa de Oleiros	6º 12' 34.9'' W 43º 34' 43.5'' N	*Pinus* woodland	*P. arundinacea*
23 Apr. 2003	Cudillero	6º 10' 30.9 '' W	In *Eucalyptus* woodland	*P. arundinacea*
24 Apr. 2003		43º 33' 32.4 '' N	In *Eucalyptus* woodland, near stream	*P. arundinacea*

ined by light microscopy (at least 20 specimens for each collection). The size of the thallus was measured for each specimen (as diameter of the plant in micrometers) and the reproductive condition was noted (absence of reproductive structures; presence of zoosporangia; presence of gametangia); for at least 5 specimens randomly selected, length and width of 6 vegetative cells (also randomly selected) were measured.

Voucher specimens have been deposited in the Phycological Herbarium, National University of Ireland, Galway (GALW) and in the Herbarium of the Departamento de Biología de Organismos y Sistemas, Universidad de Oviedo (FCO). Specimens of European *Phycopeltis* conserved in other herbaria, in particular the Herbarium of the Natural History Museum, London (BM) were also examined. Microphotographs of *Phycopeltis* were taken by a Nikon DXM1200 digital camera and mounted in plates using Adobe Photoshop 4.0®.

OBSERVATIONS

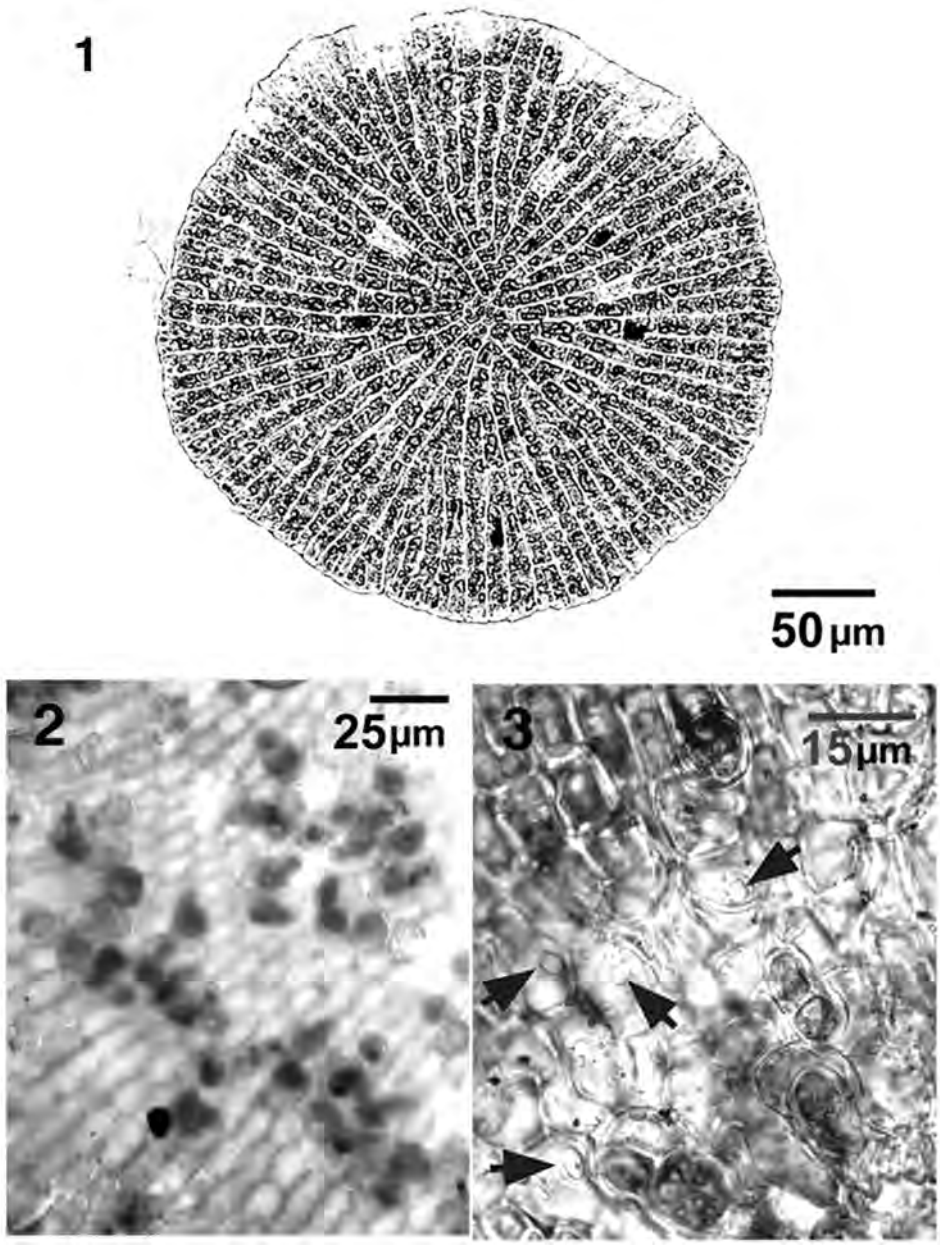
All sites where *Phycopeltis* was found consisted of woodlands, either mixed or primarily *Eucalyptus* sp.; the area in which most collections were made is located on the outskirts of the town of Cudillero. *Phycopeltis* was locally abundant, but with a very irregular and patchy distribution; in some areas it seemed much more abundant than in similar areas located a few tens of meters apart. Leaves of ivy at the basis of trees located beside small streams seemed to be a particularly favoured habitat.

Phycopeltis arundinacea was the most common species in the samples; it was recorded in all collections made. *Phycopeltis epiphyton* was found only in a single collection, made at Cudillero in July 2002. The leaves of ivy collected on that occasion were covered by many small orange patches and microscopical examination revealed the simultaneous presence of *P. arundinacea* and *P. epiphyton*. In surface view, the two species were very distinct and easily recognisable. *P. epiphyton* was small, up to 180 µm in diameter, with rounded or irregularly polygonal outline; *P. arundinacea* was much larger, up to ~1400 µm wide, with a regularly circular outline in well-growing specimens. Despite repeated collections in the same area, it was not subsequently possible to rediscover *P. epiphyton*.

Phycopeltis arundinacea

We refer to this species algae consisting of orange disks, produced by the adhesion of dichotomous filaments radiating from the centre of the thallus (Fig. 1), up to 1400 µm in diameter. The edge was smooth and regular in well-growing specimens, but thalli with a more-or-less lobed margin were frequently observed. When the margins of two individual plants met, they stopped growing in the area of contact and their growth continued in other directions; this produced growths with irregular outline. Vegetative cells were 9-19 µm long (mostly 13-16 µm) and 5-11 µm wide (mostly 6.5-8 µm), the length:width ratio ranging between 1.5 and 2.5 (mostly ~2). Cell size data for individual collections are reported in Tab. 2.

Sporangiate laterals were the most common reproductive structures, occurring on most specimens examined; these were produced in intercalary positions. Mature sporangiate laterals were usually concentrated in the central parts of the thallus, without any particular order (Fig. 2). In some specimens, however,



Figs 1-3. *Phycopeltis arundinacea* from Asturias. Fig. 1. Habit of an individual thallus. Fig. 2. Surface view of a zoosporangial specimen, showing detail of zoosporangia. Fig. 3. Surface view of a thallus, showing details of sporangiate laterals and some presumptive empty gametangia (arrows).

Table 2. Cell size of *Phycopeltis arundinacea* (mean ± standard deviation; n = 30).

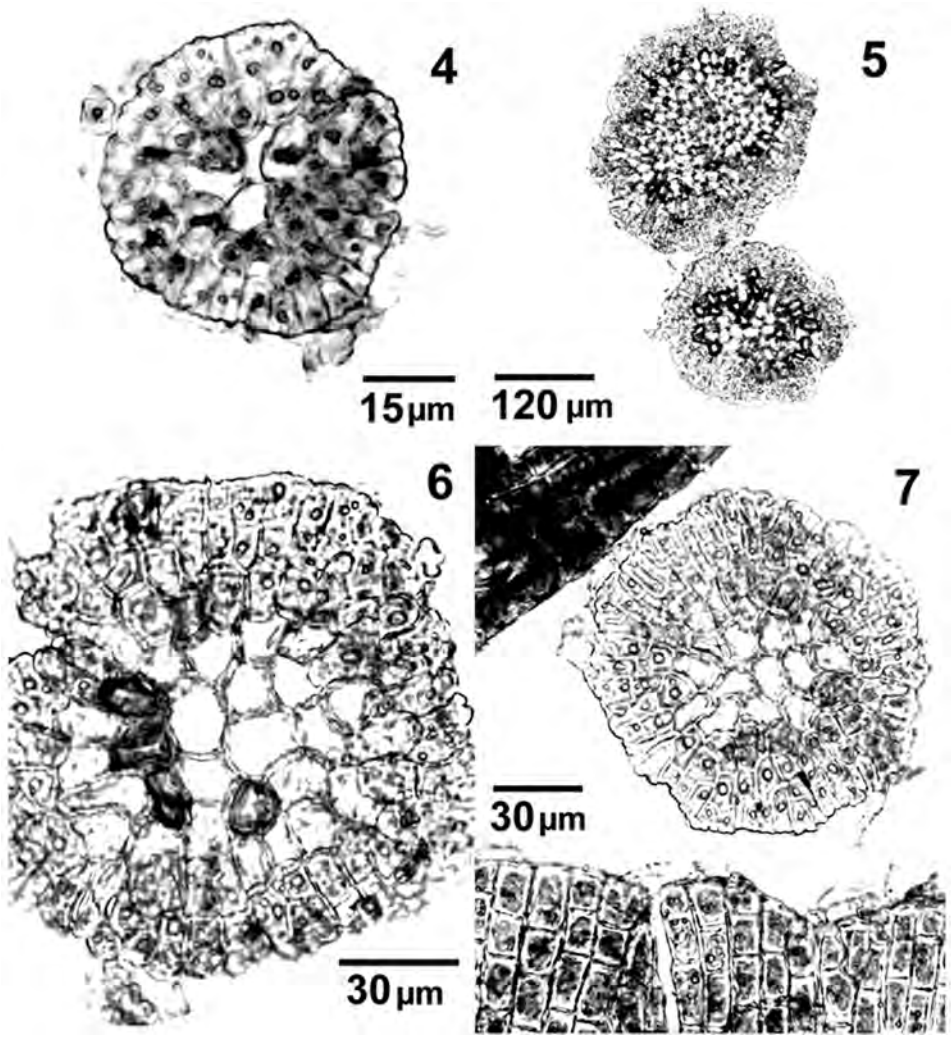
Date	*Locality*	*Length (µm)*	*Width (µm)*	*Length:Width Ratio*
1 Jul. 2002	Cudillero	15. 32 ± 1.44	7.66 ± 0.89	2.02 ± 0.29
18 Oct. 2002	Cudillero	14.91 ± 1.47	7.59 ± 1.02	2.06 ± 0.3
2 Dec. 2002	Cudillero	16.12 ± 1.53	7.76 ± 1.15	2.14 ± 0.33
10 Feb. 2003	Cudillero	15.2 ± 1.69	7.63 ± 0.8	2.01 ± 0.32
4 Apr. 2003	Cadavedo	15.12 ± 1.54	7.75 ± 1.10	1.96 ± 0.35
5 Apr. 2003	La Caridad	13.42 ± 1.18	7.32 ± 0.52	1.84 ± 0.2
8 Apr. 2003	El Escañorio	14.4 ± 1.49	7.68 ± 1.08	1.91 ± 0.37
23 Apr. 2003	Playa de Oleiros	12.9 ± 1.16	7.27 ± 0.75	1.79 ± 0.24
23 Apr. 2003	Cudillero	15.52 ± 1.58	7.65 ± 0.73	2.04 ± 0.25
24 Apr. 2003	Cudillero	14.97 ± 1.78	7.53 ± 0.63	1.99 ± 0.27

they occurred in irregularly concentric rings or were scattered all over the surface of the thallus, except the marginal parts. Production of sporangiate laterals on the margin was rare, usually occurring in parts of a thallus in direct contact with another individual. The sporangiate laterals were formed by an oval zoosporangium, 12-20 µm long and 8-16 µm wide, produced on the top of a retorted suffultory cell. The suffultory cells appeared to be produced directly by the vegetative cells and there was no evidence of production of a stalk cell or a sporangiophore. No release of zoospores from the zoosporangia was observed. The position of the opening of the sporangium could not be detected; in attached zoosporangia it was not observable, becoming evident probably only at the moment of the detachment of the zoosporangium.

Gametangia were not frequently observed. Specimens bearing gametangia were much more common in some collections than in others; in particular, they were abundant in the collection from Playa de Oleiros and relatively common in the collection from El Escañorio. In these collections, gametangia were usually the only reproductive structures in the plants on which they occurred, but thalli in which both gametangia and zoosporangia were simultaneously present were also observed. In other collections mature gametangia were rarely observed; however, the presence of discoloured cells, showing in surface view a hole with the appearance of a presumptive gametangial ostiole, was noted in several thalli with zoosporangia (Fig. 3). Mature gametangia were oval or globular, 10-20 µm wide and 15-30 µm long, most common in the centre and in the intermediate parts of the thallus, rarely arranged in roughly concentric rings. No release of gametangia was observed.

Phycopeltis epiphyton

Specimens referred to this species were greenish-orange discs with entire, rounded or polygonal margins. Size of individual specimens mostly varied between 40 and 120 µm; no individual specimens wider than 180 µm were



Figs 4-7. Gametangial specimens of *Phycopeltis epiphyton* from Asturias. Fig. 4. A young thallus with three empty gametangia in the centre. Fig. 5. Two large gametangial specimens with the central parts formed by empty gametangia. Fig. 6. A reproductive gametangial specimen; darker cells are air-filled, empty gametangia. Fig. 7. A reproductive specimen; note difference of cells size with *Phycopeltis arundinacea* (bottom).

observed. Occasionally, separate thalli in marginal contact produced growths with an irregular shape.

Gametangial specimens started to become reproductive when individual thalli were 50-60 µm in diameter (Fig. 4). At this stage, the cells situated in the centre of the thallus, which had a larger size, became gametangia and release of gametes took place. Production of gametangia and release of gametes followed a strictly centrifugal pattern; gradually, with the growth of the thallus, all cells form-

ing the central parts became enlarged and turned into gametangia. Typically, adult gametangial specimens of *P. epiphyton* were formed by a large, central portion consisting of empty gametangia and a relatively limited peripheral portion formed by pigmented cells, usually the 3-4 marginal cells (Figs. 5, 6, 7). The only exception to this situation was represented by specimens coming in marginal contact with other specimens, in which case growth ceased and the marginal cells became also gametangia. The vegetative cells occurring in the marginal parts were rectangular, or with an irregularly dichotomous shape, 3-6 μm wide and 8-14 μm long. Mature gametangia were variable in shape, globular to polygonal, up to 16 μm wide and 20 μm long.

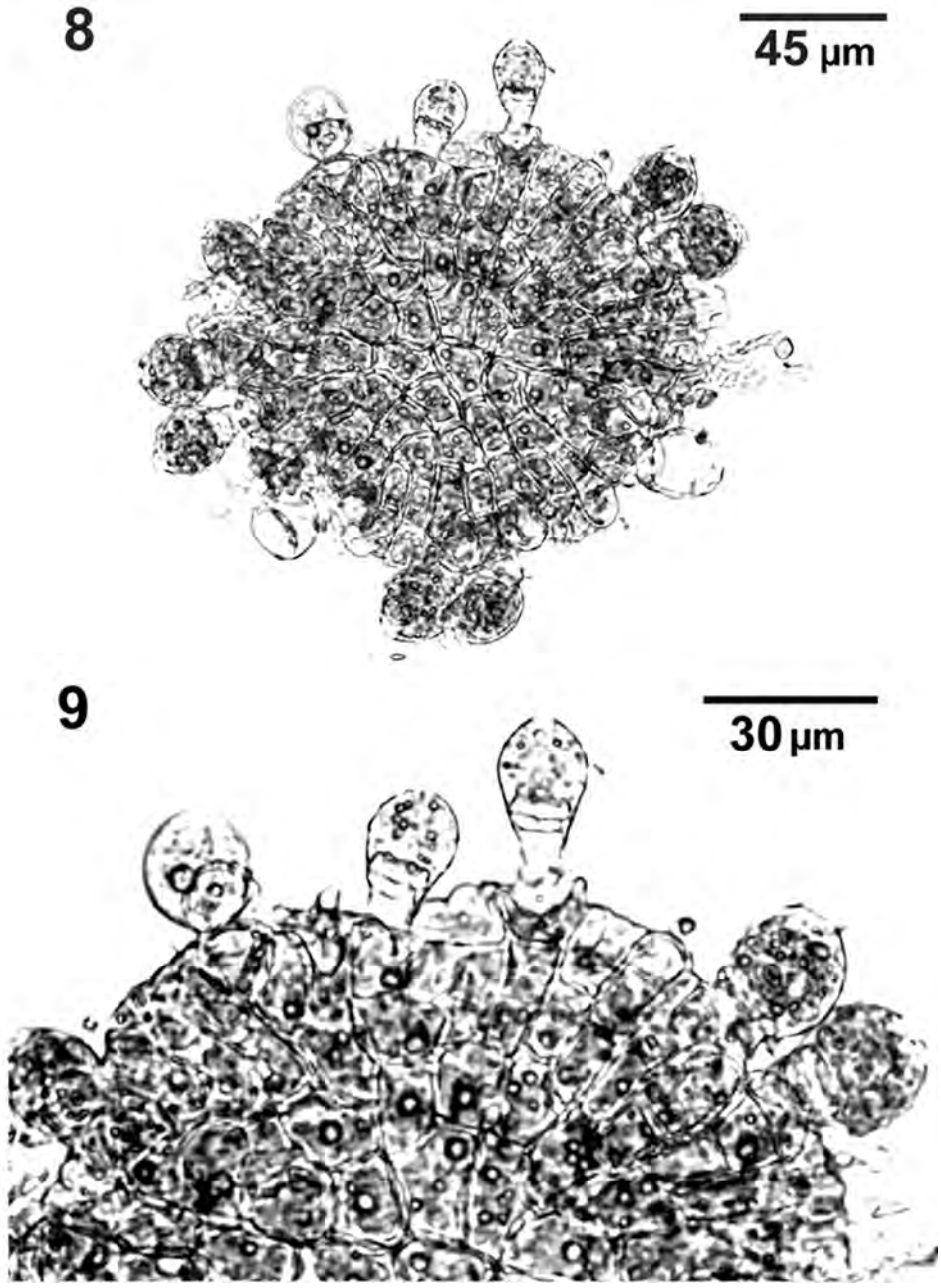
Sporangial specimens also showed a tendency to become reproductive at early stages; production of sporangiate laterals started in thalli 50-60 μm in diameter (Fig. 8). The sporangiate laterals were produced terminally, on apical cells or sister cells produced by dichotomy of apical cells; no production of sporangiate laterals in other parts of the thallus was observed. The sporangiate laterals consisted of suffultory cells supporting oval or globular zoosporangia; the zoosporangia were 12-24 μm in diameter (Fig. 9). The opening occurred in the apical part of the zoosporangium. Production of gametangia and zoosporangia was clearly segregated to different specimens; the simultaneous presence of zoosporangia and gametangia on the same thallus was never observed.

Among the samples of *Phycopeltis* from other herbaria that we examined, only a specimen located in BM was referable with certainty to *P. epiphyton*. The sample consisted of needles of fir (*Abies pectinata* De Candolle = *Abies alba* P. Miller) colonised by *Phycopeltis*; the material was collected by Wilhelm Schmidle near St. Peter in the Black Forest, southern Germany (about 25 km from Freiburg im Breisgau, the type locality). The sample includes a permanent slide in which several specimens, of variable size, are conserved; the morphology of these is identical to both Millardet's (1870) original description and figures and our material from Asturias. Most thalli are very small, 30-40 μm in diameter (Figs 10, 11) and devoid of reproductive structures. One specimen, however, is larger (~ 115 μm in diameter) and has the central part bleached, consisting of empty gametangia (Fig. 12), in good agreement with Millardet's material.

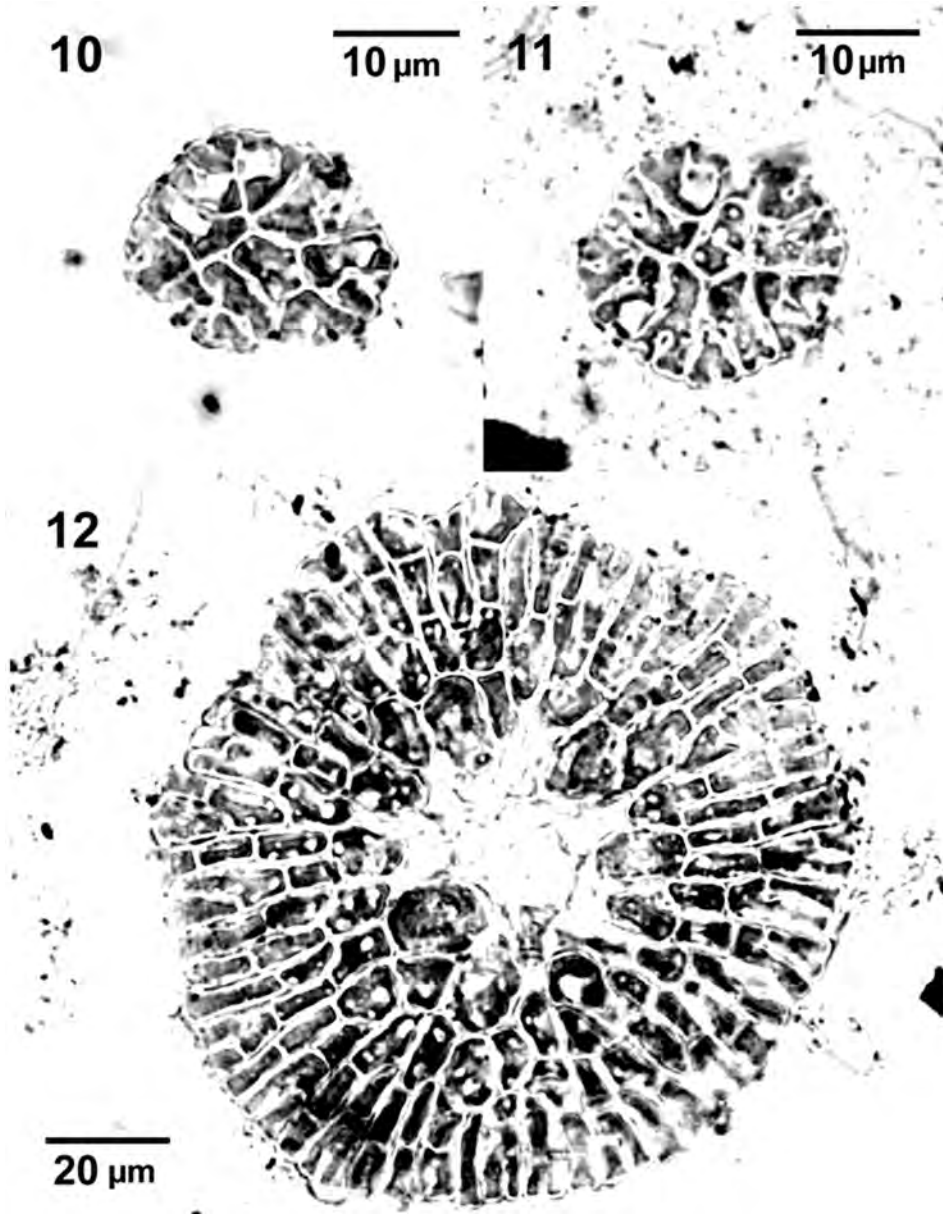
DISCUSSION

The presence of two species of *Phycopeltis* in a region of Atlantic Europe is a record of considerable interest; Asturias is the first region of Europe for which the simultaneous presence of two species has been documented.

We consider *Phycopeltis arundinacea* to be the most suitable entity for the specific attribution of the larger species of *Phycopeltis* occurring in Asturias. The Spanish material is in complete agreement with specimens from Ireland that we referred to *P. arundinacea* after examination of the type material of *Phyllactidium arundinaceum*, described by Montagne (1846) for algae growing on reeds in Algeria (Rindi & Guiry, 2002). More recently, we have also collected specimens with the same morphology in Brittany, northern France (Rindi *et al*., 2003). However, it is evident that the morphology of this alga is subject to a degree of variation due to environmental factors, and several species morphologically close to *P. arundinacea* have been described. The similarity with two species from New



Figs 8-9. Zoosporangial specimens of *Phycopeltis epiphyton* from Asturias. Fig. 8. Habit of a zoosporangial specimen. Fig. 9. Details of the margin of the same plant, showing sporangiate laterals.



Figs 10-12. Gametangial specimens of *Phycopeltis epiphyton* from St. Peter, Black Forest, Germany; material collected by Schmidle and deposited in BM. Figs. 10, 11. Two young specimens. Fig. 12. A larger, reproductive specimen with the central parts consisting of empty gametangia.

Zealand, *Phycopeltis expansa* Jennings and *Phycopeltis novae-zelandiae* Thompson & Wujek, was noted in a previous study (Rindi & Guiry, 2002). *Phycopeltis expansa* is separated from *P. arundinacea* by the structure of the sporangiate-lateral: whereas the suffultory cell is borne directly on a vegetative cell in *P. arundinacea*, a stalk cell occurs in *P. expansa* (Jennings, 1895; Printz, 1939; Sarma, 1986). *Phycopeltis novae-zelandiae* differs from *P. arundinacea* for the arrangement of the gametangia (distributed in regular rings) and the type of life history (obligate alternation of generations in *P. novae-zelandiae*, whereas gametangial and zoosporangial reproduction may occur on the same thalli in *P. arundinacea*). Recently, Neustupa (2003) described *Phycopeltis theaensis* on the basis of material occurring on leaves of tea (*Thea sinensis* Linnaeus) at Pahang, Cameron Highlands, Malaysia. Neustupa (2003) described accurately the characters separating *P. theaensis* from similar species; the presence of sporangiophores and dorsal glandular papillae and a higher width:length ratio of the vegetative cells are the characters separating this species from European populations of *P. arundinacea*. On the basis of the evidence currently available, we consider it reasonable to regard *P. arundinacea*, *P. expansa*, *P. novae-zelandiae* and *P. theaensis* as distinct species, but we also remark that the separation between these entities is based on subtle characters, for several of which the complete range of variation is poorly known. Observations on European material suggest that the arrangement of gametangia may be very variable and that the assessment of the relative distribution of gametangia and zoosporangia requires careful examination of a large number of specimens. The structure of the sporangiate lateral should also be assessed on a large number of specimens and it is not clear how variable this feature may be. In Irish specimens, the absence of a stalk cell seems to be a fairly constant character (Rindi & Guiry, 2002), but for species in which a stalk cell or a sporangiophore occur, no details are available about the consistency of this character. For example, in *P. expansa*, in which a stalk cell occurs, Sarma (1986) includes some illustrations of sporangiate laterals in which the suffultory cell apparently occurs directly on the mother vegetative cell. Glandular papillae and empty gametangia are also structures that may look very similar in surface view. In specimens from Ireland, France and Spain we have frequently observed discoloured cells bearing an ostiole on the upper surface (e.g., Rindi & Guiry, 2002, Fig. 10; Rindi *et al*., 2003, Fig. 5; this paper, Fig. 3). On the basis of illustrations available in the literature (e.g., Fig. 31 in Millardet, 1870; Fig. 5 of pl. 3 in Karsten, 1891) we regarded these cells as presumptive empty gametangia. However, the glandular papillae illustrated by Neustupa (2003, Fig. 21) for *P. theaensis* have a similar appearance. Careful observation is clearly important and caution should be exercised in the interpretation of these structures.

It is evident that further studies on all the aspects of the biology of these species are desirable, especially molecular analyses. In any case, pending such investigations, we consider that at present there is no need to reject any of the records currently available for *P. arundinacea*. This species should be therefore regarded as an entity with widespread distribution. In temperate areas, it occurs in Algeria, the type locality (Montagne, 1846), South Africa (Printz, 1920), Ireland (Rindi & Guiry, 2002), Britain (John, 2002), northern France (Rindi *et al*., 2003) and northern Spain (this study); however, we suspect that in Atlantic Europe this species has been largely overlooked and has a much wider distribution. Records for tropical areas include India and Bangladesh (Khrishnamurthy, 2000), Vietnam (De Wildeman, 1890), Malaysia (Neustupa, 2003) and Indonesia (Neustupa, 2003). The species is generally reported as widespread in tropical areas (Printz, 1939), both in the Eurasia and America (Thompson & Wujek, 1997).

The determination of specimens of *Phycopeltis epiphyton* collected in this study is unambiguous. It is disappointing that no further collections of this species were possible; however, the population sampled at Cudillero in July 2002 was large and included specimens of variable size and habit, belonging to both phases of the life history. We therefore believe that this population offers a good representation of the range of morphological variability of authentic *P. epiphyton*, even considering that it is in complete agreement with Schmidle's material conserved in BM (which was collected in the same geographical area of Millardet's material, the Black Forest). We attempted to locate the original specimens of Millardet, both for comparative purposes and to designate a lectotype. According to Stafleu & Cowan (1981: 489) Millardet's herbarium is conserved in BORD, with further material in PC and STU; however, we could not locate original specimens of *P. epiphyton* in any of these herbaria. We therefore propose the Figure 29 of Millardet (1870) be designated as provisional lectotype of *P. epiphyton*, until authentic specimens can be located.

In any case, the original description and illustrations of Millardet (1870) are extremely clear and there is no doubt that the material collected in Asturias corresponds perfectly with Millardet's alga. In particular, it agrees very well with two features that Millardet (1870) stressed: the small size and the tendency to become reproductive at an early stage. We consider this an important point because, although these characters are generally considered of limited taxonomic importance (Thompson & Wujek, 1997), our observations indicate that these are consistent and reliable features of the morphology of *P. epiphyton*. It is also noteworthy that the information available in the recent literature about these characters is quite contradictory. Ettl & Gärtner (1995) and Krishnamurthy (2000) also reported that individual specimens of *P. epiphyton* are not larger than 120-130 µm. John (2002), however, reported that British specimens of *P. epiphyton* are up to 1 mm wide; although the details reported by this author for most morphological characters are in agreement with *P. epiphyton*, we have never observed specimens larger than 180 µm. Thompson & Wujek (1997) provided a detailed description of *P. epiphyton*, including many pictures of excellent quality. Although details of cell size and primary reproductive structures are in good agreement with our observations, other characters do not match the morphology of European specimens. For European material, there is no evidence documenting the existence of plants bearing simultaneously gametangia and zoosporangia. No sporangiate laterals in intercalary position have been observed and no evidence of the presence of sporangiophores is available. Furthermore, several illustrations in Thompson & Wujek (1997) depict material that appears more robust and shows little resemblance both to the original illustrations of Millardet (1870) and our specimens. This suggests that the specific attribution of specimens from extra-European localities should be treated with caution. Unfortunately, after the death of Professor Rufus Thompson in 1980, most of his personal collections at the University of Kansas were lost (D.E. Wujek, personal communication), which makes it impossible to compare Thompson's material with European collections. It is certainly possible that the morphological features of the European specimens do not reflect the complete, potential range of morphological variation of *P. epiphyton*; we remarked that this is also possible in the case of *P. arundinacea* (Rindi & Guiry, 2002). It is possible that, although originally described for Germany, *P. epiphyton* is primarily a tropical or subtropical alga, which in the warm humid climates of the tropics achieves the best vegetative and reproductive development. In this case, it would be reasonable to believe that tropical specimens have a generally larger size and produce secondary reproductive structures not observable in European specimens.

In this regard, it is interesting that the only collection of *P. epiphyton* in Asturias was made in summer. This seems to suggest that in Asturias the environmental conditions are generally not favourable for the growth and reproduction of the alga and that good development takes place only in summer, when the climatic conditions are more similar to those of tropical regions. At present, however, this is mere speculation and more collections from other sites in Europe will be necessary. Whatever is the case, however, it is evident that generalisations on the morphology and distribution of this species need very careful assessment. We propose that, for the present, the distribution of *P. epiphyton* should be considered restricted to Europe, southern Germany and Asturias being the only regions for which the presence of the alga can be confirmed. We are very sceptical about records of *P. epiphyton* for Britain. The examination of a population of *P. epiphyton* reinforced our opinion that this species does not occur in Ireland or, at best, it is extremely rare (Rindi & Guiry, 2002), and we did not find any British specimens referable to *P. epiphyton* in BM (collections deposited under this name are from other locations or are misidentifications). We strongly suspect that *P. epiphyton* does not occur in Britain and that reports of this species are misidentifications of *P. arundinacea*; further studies will be necessary to reassess the identity of the British specimens of *Phycopeltis*. Records of *P. epiphyton* for tropical and subtropical countries include India (Khrishnamurthy, 2000), Malaysia (Neustupa, 2003), Indonesia (Neustupa, 2003), Samoa (Schmidle, 1897, considering *Phycopeltis microcystis* Schmidle a synonym of *P. epiphyton*), USA (Good & Chapman, 1978; Thompson & Wujek, 1997), El Salvador, Costa Rica and Colombia (Thompson & Wujek, 1997). We suggest that, for all of these, determination should be regarded as presumptive.

Further work, combining different approaches, will be necessary for a better understanding of the relationships of species of *Phycopeltis*. Molecular data, in particular, which are at present limited for the Trentepohliaceae (López-Bautista *et al*., 2002a; López-Bautista *et al*., 2003), will be of critical importance to assess the specific boundaries in the genus. Due to the small size and the incospicuous habit of *Phycopeltis*, the availability of techniques of extraction suitable to obtain DNA from very small amounts of material will be very important.

Since the genus has a primarily tropical and subtropical distribution, sampling effort should concentrate primarily on collections from tropical localities. However, for an unambiguous clarification of many taxonomic problems, the availability of molecular data from material from the type localities and referable with absolute certainty to the original descriptions is an essential requirement. In the case of *P. epiphyton*, a molecular assessment should be based on sequences from European material.

Acknowledgements. FR and MDG are grateful for financial support to the Higher Education Authority, Ireland, PRTLI Programme Cycle 2, Environmental Change Institute, National University of Ireland, Galway. Professor Paul C. Silva and Dr Daniel E. Wujek provided very useful information. Jenny Bryant (Natural History Museum, London) kindly provided assistance with collections deposited in BM.

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