

Sexual structures in *Ptilothamnion sphaericum* and *Pterosiphonia complanata* (Ceramiales, Rhodophyta) from the Atlantic Iberian Peninsula

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Abstract

Sexual structures of *Ptilothamnion sphaericum* and *Pterosiphonia complanata* are described for the first time. Spermatangial heads of *P. sphaericum* are densely clustered in short lateral branchlets, each cell of which bears up to three spermatangial heads. They consist of a stalk cell and 3–4 axial cells bearing a cluster of spermatangial mother cells that cut-off 1–2 spermatangia. The last two cells in female axes of *P. sphaericum* are relatively short, with the hypogenous cell longer and more similar to vegetative cells. The subapical cell bears three periaxial cells: two sterile and the supporting cell, which bears a four-celled carpogonial branch and one sterile cell. The hypogenous cell bears 1–2 involucral filaments prior to fertilization. These features support the placement of *P. sphaericum* in the genus *Ptilothamnion*. Spermatangial branches of *Pterosiphonia complanata* are borne on unbranched modified trichoblasts. They consist of an elongate suprabasal cell that bears a fertile central axis from which four periaxial cells arise, bearing quadrangular spermatangial mother cells that bear the spermatangia. Spermatangial branches have 1 (–3) apical sterile cells. Procarps of *P. complanata* consist of a four-celled carpogonial branch and two sterile cells borne on the supporting cell. These features are similar to all *Pterosiphonia* species for which they have been described.

Keywords: *Pterosiphonia complanata*; *Ptilothamnion sphaericum*; reproductive morphology; Rhodomelaceae; Wrangeliaceae.

Introduction

Ptilothamnion sphaericum (P.L. Crouan et H.M. Crouan ex J. Agardh) Maggs et Hommersand and *Pterosiphonia complanata* (Clemente) Falkenberg are common species along the Atlantic Iberian Peninsula. Nevertheless, their sexual structures remain unknown. The order Ceramiales

includes nine families (Choi et al. 2008) subdivided into infrafamilial taxa. *P. sphaericum* belongs to the tribe Spermotamninae, which is in the reinstated family Wrangeliaceae (Choi et al. 2008). *P. complanata* belongs to the tribe Pterosiphoniae in the family Rhodomelaceae (Hommersand 1963, Maggs and Hommersand 1993, Womersley 2003).

Callithamnion sphaericum P.L. Crouan et H.M. Crouan was described by J. Agardh based on sporophytic plants from Brest, Atlantic France (Agardh 1851). Subsequently, Maggs and Hommersand (1993) provided a detailed description of vegetative and sporangial plants based on new collections from the southwestern British Isles. In the absence of sexual reproductive structures, Maggs and Hommersand (1993) transferred the species to *Ptilothamnion* rather than *Spermotamnion* on the basis of the vegetative morphology (rhizoids and erect axes borne in a median position on prostrate axial cells) and the sessile polysporangia. Nevertheless, the differentiation of genera in Spermotamninae is mainly supported by the female reproductive structure and the assignment of any species in their absence is tenuous (Ballantine and Wynne 1998, Womersley 1998). *P. sphaericum* was the only species of the genus in which sexual structures remained unknown (Maggs and Hommersand 1993, Bárbara et al. 2001, Stegenga et al. 2002), whereas they are widely known in congeners (Stegenga et al. 2002, Schneider et al. 2010). *P. sphaericum* was recently recorded for the first time off the Iberian Peninsula (Bárbara et al. 2001), and later discovered in numerous sites (Díaz and Bárbara 2005). Presently, it is considered a common species on sand-covered rocks along the Atlantic Iberian Peninsula. It remained overlooked due to its small size and poor knowledge of its habitat.

Interestingly, the relationship between *Ptilothamnion sphaericum* and *P. polysporum* Gordon-Mills et E.M. Wollaston has not been previously investigated, although the species are similar in vegetative and sporangial morphology, as shown in a comparative table for *Ptilothamnion* species presented by Stegenga et al. (2002). *Ptilothamnion polysporum* was originally described from southern Africa and western Australia (Wollaston 1984), while *P. sphaericum* remained poorly known. Apart from the type locality, further descriptions of *P. polysporum* were provided from other sites in southern Africa (Stegenga et al. 1997, 2002, Rull Lluch and Gómez Garreta 2002).

Fucus complanatus Clemente was described based on vegetative material from Tarifa, Atlantic Spain (Cremades 1993); Falkenberg transferred it to *Pterosiphonia* (Schmitz and Fal-

kenberg 1897). Since then, this species has been widely reported in Europe and northern Africa, including Atlantic and Mediterranean coasts (Guiry and Guiry 2010). In spite of the great number of reports, male structures and procarps remain unknown (Norton and Parkes 1972, Cullinane et al. 1980, Maggs and Hommersand 1993), and cystocarps are the only structures that have been described (Gayral 1958, 1966, Rull Lluich 2002). The genus *Pterosiphonia* contains 20 species (Guiry and Guiry 2010), each distinguished on vegetative features (Maggs and Hommersand 1993). Male structures have been described in nine species of *Pterosiphonia* (Hommersand 1963, Abbott and Hollenberg 1976) and female plants have been reported for 11 species, but a complete description of procarps is available for just four of them (Suneson 1940, Hommersand 1963). The uniformity of reproductive structures is considered an important feature of Rhodomelaceae (Scagel 1953). Nevertheless, characters such as the origin of spermatangial branches, the presence of vegetative apical cells on spermatangial branches and the shape of cystocarps are useful features in the separation of species in *Polysiphonia sensu lato* (Stuercke and Freshwater 2008), a well-studied genus (with numerous species) in the Rhodomelaceae. Therefore, it would appear important to improve knowledge of reproductive structures in *Pterosiphonia*, as they may provide new characteristics for species discrimination.

In the present paper, we describe the sexual structures of *Ptilothamnion sphaericum* and *Pterosiphonia complanata* for the first time. A discussion of the generic status of *P. sphaericum* and the differences between this species and *P. polysporum* is provided, as well as a discussion of the features of sexual structures of *P. complanata* among related species.

Materials and methods

An extensive collection of seaweeds from sand-covered rocks was made in the intertidal and upper subtidal of more than 70 sites from the Atlantic Iberian Peninsula between 2000 and 2009. Material of *Ptilothamnion sphaericum* was collected on 77 sampling dates from 45 sites and material of *Pterosiphonia complanata* was collected on 44 sampling dates from 44 sites. Samples were preserved in 4% formalin in seawater at 4°C and stored in the dark for later study. Specimens were stained in aniline blue and mounted in 20% Karo® Syrup (ACH Foods, Memphis, TN, USA) and 80% distilled water. Preserved specimens were deposited in the herbarium of the Universidade de Santiago de Compostela (SANT). Herbarium abbreviations follow the online *Index Herbariorum* <<http://sweetgum.nybg.org/ih/>>.

Sexual specimens of *Ptilothamnion sphaericum*

Spain (1) Santander: Oyambre (43°23'58"N, 4°24'17"W), 11-ix-2006, epiphytic on *Pterosiphonia ardreana* Maggs et Hommersand on sand covered rocks in the lower intertidal, P. Díaz, female plants, SANT-Algae 21775; (2) Asturias: La Isla (43°28'74"N, 5°13'13"W), 10-x-2006, lower intertidal, epiphytic on *Halopithys incurva* (Hudson) Batters on rocks

covered by sand, P. Díaz, A. Secilla and S. Calvo, male and female plants, SANT-Algae 21773; (3) A Coruña: Playa de Barrañán (43°18'47"N, 8°33'29"W), 5-xi-2002, epiphytic on *Ahnfeltia plicata* (Hudson) E.M. Fries on sand covered rocks in the lower intertidal, I. Bárbara, P. Díaz and T. Novo, female and polysporangial plants, SANT-Algae 21777; (4) A Coruña: Playa de Lourido (43°05'37"N, 9°13'15"W), 1-ii-2006, epiphytic on *A. plicata* on sand covered rocks in the lower intertidal, P. Díaz and I. Bárbara, male and female plants, SANT-Algae 21776, 22517.

Portugal (5) Douro Litoral: Leça de Palmeira (41°12'07"N, 8°42'59"W), 16-xi-2004, epiphytic on *A. plicata* on sand covered rocks in the lower intertidal, P. Díaz, monoecious plants with male and female axis, SANT-Algae 21774.

Sexual specimens of *Pterosiphonia complanata*

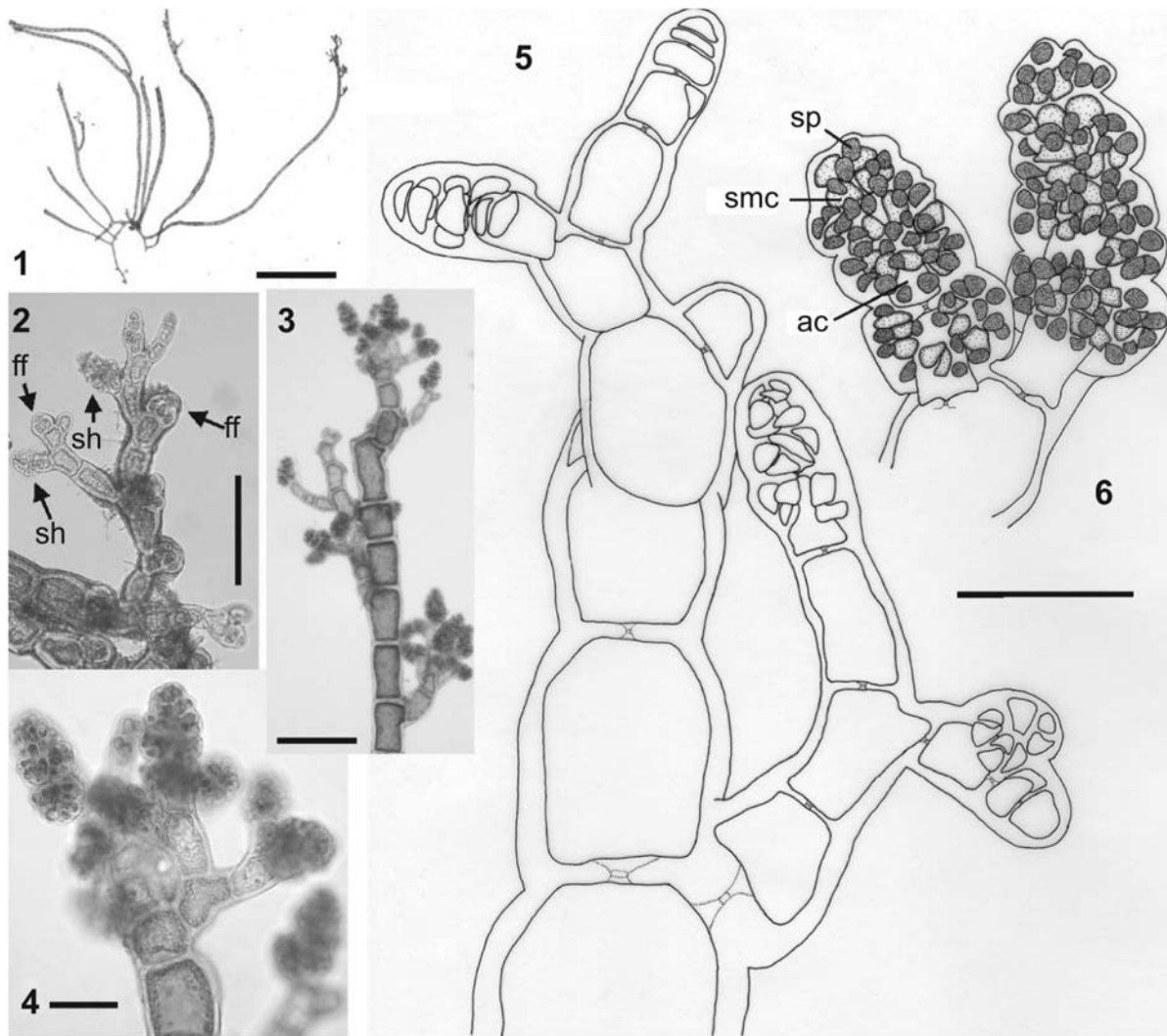
Portugal (1) Beira Litoral: Buarcos (40°10'55"N, 8°54'21"W), 13-xi-2004, on sand covered rocks in the lower intertidal, P. Díaz, male, female and tetrasporangial plants, SANT-Algae 16603.

Results

Ptilothamnion sphaericum (Figure 1)

Gametophytes dioecious or monoecious (Figure 2). Spermatangial heads densely aggregated on upper parts of erect filaments, borne on 3–5-celled lateral branchlets (Figures 3–5). Lateral branchlets are simple or once-branched and irregularly alternate. Up to three spermatangial heads borne terminally or laterally on each cell of the branchlets (Figures 4–6). Spermatangial heads are ovoid to short cylindrical, (40) 45–60 (70) × (30) 35–45 (50) µm. They consist of a stalk cell and 3–4 axial cells bearing a dense cluster of spermatangial mother cells that cut-off 1–2 spherical spermatangia 4–5 µm in diameter and enclosed in a mucilage sheath.

Female fertile axes are borne terminally on branches and branchlets that are located in upper parts of erect filaments (Figures 7–10). Female plants are often densely branched at the apex as a result of the successive growth of overtopping involucrel filaments of the first-formed fertile axis, which then develop further female branches (Figure 9). At times, the apical cell of unfertilized procarps resumes vegetative growth and the resulting axes also form further female branches. The fertile axis consists of comparatively short apical and subapical cells, and the hypogenous cell is longer and similar to vegetative cells below the procarp (Figures 11–13). The hypogenous cell bears 1–2 opposite involucrel filaments. Three periaxial cells arise from the subapical cell, becoming two sterile cells and the supporting cell. The supporting cell bears a four-celled carpogonial branch with a long trichogyne and also produces another single sterile cell (Figure 13). Post-fertilisation development was not observed in our collections.



Figures 1–6 *Ptilothamnion sphaericum*: male structures.

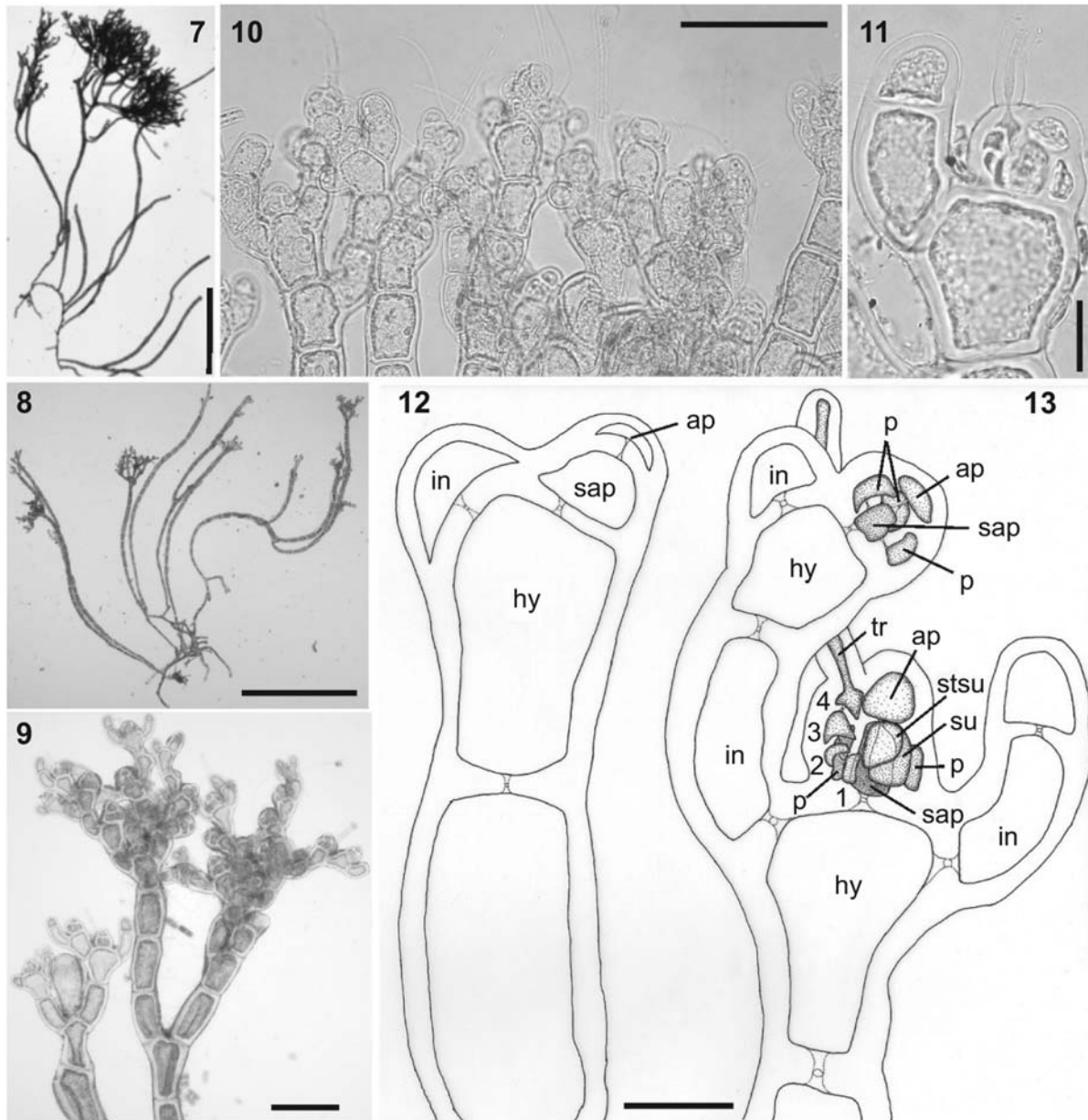
(1) Habit of a male plant. (2) Apical part of a monoecious plant showing spermatangial heads (sh) and female fertile axes (ff). (3, 4) Spermatangial heads borne densely aggregated on lateral branchlets. (5) Early development of spermatangial heads. (6) Two mature spermatangial heads borne on the terminal cell of a branchlet, showing axial cells (ac), spermatangial mother cells (smc) and spermatangia (sp). Scale bars: Figure 1: 1.5 mm; Figures 2, 3: 150 μm ; Figures 4–6: 40 μm .

Ptilothamnion sphaericum was collected on sand-covered rocks on 45 beaches along the Atlantic Iberian Peninsula, but sexual structures were observed only in collections from five of these sites (Figure 14). Sexual structures were observed only in winter and autumn: male gametophytes (February, October and November); female gametophytes (September, October and November). Monoecious gametophytes were collected in November 2004. *P. sphaericum* was found forming dense turfs on sand-covered rocks or as epiphyte on *Ahnfeltia plicata* (Hudson) E.M. Fries, *Halopithys incurva* (Hudson) Batters and other species that usually have their basal parts buried by a layer of sand. However, sexual structures were found only on epiphytic plants, which consisted of tufted specimens generally smaller and less branched (to 1.5 cm) than specimens from turfs (to 3 cm long). Polysporangia were more frequently observed than

sexual structures and were collected at 21 sites. Furthermore, *P. sphaericum* was found in maërl beds from the Atlantic Iberian Peninsula, where it was collected at 18 sites on 33 sampling dates. This material consisted of small plants (to 1 cm long) generally vegetative, bearing polysporangia in only one sample (V. Peña pers. comm.).

Pterosiphonia complanata

Gametophytes dioecious. Spermatangial axes located at the apices of main erect axes and branches, densely clustered, and forming one per segment in spiral arrangement (Figures 15–19). Spermatangial axes (Figure 19) borne on the supra-basal cell of an unbranched modified trichoblast; cylindrical and incurved, (150–) 200–240 (–275) \times (40–) 50–75 (–95) μm , with 1 (–3) sterile apical cells when mature. Sperma-



Figures 7–13 *Ptilothamnion sphaericum*: female structures.

(7, 8) Habit of female plants. (9, 10) Upper part of erect axes with procarp. (11) Detail of a procarp. (12) Initial stage of procarp development: apical cell (ap), subapical cell (sap), hypogenous cell (hy), basal cell of the involucre (in). (13) Stages in the development of the procarp: apical cell (ap), subapical cell (sap), hypogenous cell (hy), basal cells of the involucre (in), pericentral cells (p), supporting cell (su), sterile cell on supporting cell (stsu), four-celled carpogonial branch (1–4), trichogyne (tr). Scale bars: Figures 7, 8: 2 mm; Figures 9, 10: 150 μm ; Figures 11–13: 25 μm .

tangial axes consist of an elongate suprabasal cell that bears the fertile central axis from which four periaxial cells arise, bearing quadrangular spermatangial mother cells, (7-) 12–15 (-18) μm , that bear ovoid spermatangia, 5 μm in diameter.

Procarp are formed on modified trichoblasts in the upper parts of erect axes (Figures 20, 22). They consist of a four-celled carpogonial branch and two sterile cells borne on the supporting cell (Figure 21). Cystocarps (Figures 22–24) are globular to ovoid when mature, (450-) 500–600 (-650) μm ,

with an ostiole (90-) 130–190 (-225) μm . Carposporangia are clavate at maturity (Figures 25, 26), (120-) 125–150 (-175) \times (20-) 25–30 (-35) μm . Pericarps consisting of axial filaments bearing on the outside a layer of polygonal cells (27-) 30–40 (-45) \times (30-) 35–45 (-60) μm arranged in straight longitudinal rows and decreasing in size towards the ostiole, and an outer layer of irregularly shaped cortical cells (5-) 10–20 (-25) \times (10-) 15–25 (-40) μm .

Pterosiphonia complanata was collected at 44 sites along the Atlantic Iberian Peninsula from sand-covered rocks. Male

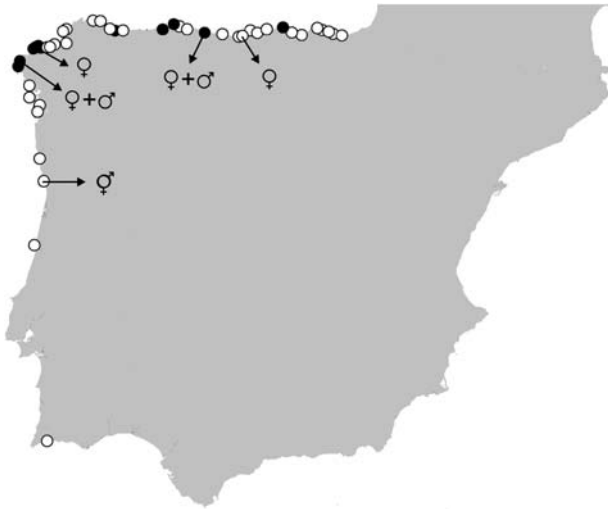
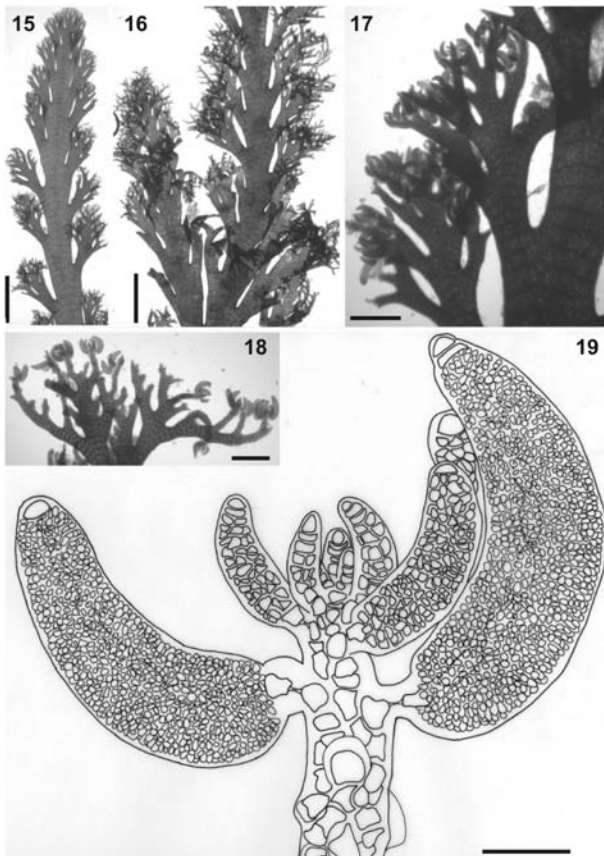
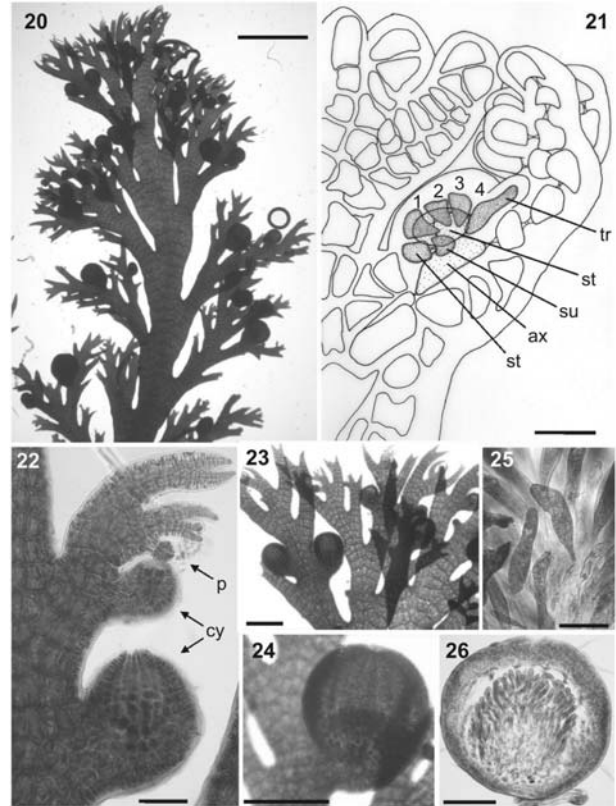


Figure 14 *Ptilothamnion sphaericum*: distribution map showing occurrence on sand-covered rocks of the Atlantic Iberian Peninsula. Black and white symbols indicate collections of sporangial plants and plants without polysporangia, respectively; collections of gametophytes are indicated with ♂, ♀ and ♀.



Figures 15–19 *Pterosiphonia complanata*: male structures. (15, 16) Apical parts of male plants. (17, 18) Spermatangial branches borne on the apices of branches. (19). Stages in the development of spermatangial branches on a branch apex. Scale bars: Figures 15, 16: 1.5 mm; Figures 17, 18: 400 μm ; Figure 19: 50 μm .



Figures 20–26 *Pterosiphonia complanata*: female structures. (20) Apical part of a female plant. (21) Procarp consisting of an axial cell (ax), the supporting cell (su), the four-celled carpogonial branch (1–4), which ends with a trichogyne (tr), and two sterile cells (st). (22) Axis with a procarp (p) and cystocarps (cy). (23, 24) Clavate carposporangia. (25) Globular cystocarps. (26) Transverse section of a cystocarp. Scale bars: Figure 20: 1.5 mm; Figure 21: 15 μm ; Figures 22, 25: 80 μm ; Figures 23, 24: 400 μm ; Figure 26: 250 μm .

and female gametophytes and tetrasporangial plants were collected in Buarcos in November 2004 growing on sand-covered rocks from the lower intertidal. In addition, two plants collected at Ria of A Corvia (in 1984 and 1989) with male and female structures were found in herbarium (SANT-Algae 1619, 4330).

Discussion

Ptilothamnion sphaericum

The occurrence of sexual structures is rare in *Ptilothamnion sphaericum* throughout its distribution range. Gametangia were found in only five of 75 collections, and only on epiphytic thalli, as reported for *P. polysporum* (Stegenga et al. 2002). Sporangia were more frequently observed than sexual structures. Populations of *P. sphaericum* from the Atlantic Iberian Peninsula appear to reproduce effectively by extensive growth of prostrate axes followed by fragmentation of thalli (Díaz and Bárbara 2005), as in the British Isles (Maggs

and Hommersand 1993). Off the Atlantic Iberian Peninsula, extensive populations of *P. sphaericum* were found only on sand-covered rocks, where the species sometimes constituted near monospecific turfs, but it was most commonly mixed with other turf-forming species (Díaz and Bárbara 2005). Turf-forming species are usually characterized by a high capacity for vegetative propagation (Airoldi 1998), and sexual reproduction is often very rare (Díaz et al. 2009), or even unknown (Rindi et al. 1999).

The genus *Ptilothamnion* belongs to the tribe Spermotamninae, which includes 12 genera (Womersley 1998, Alongi et al. 2007) separated mainly by features of the female structures shown in Table 1. Furthermore, the production of erect filaments and rhizoids from about the mid sections of prostrate axis cells is a feature that, in combination with other characters, distinguishes the genus *Ptilothamnion* from other members of the tribe Spermotamninae (Maggs and Hommersand 1993, Ballantine and Wynne 1998, Stegenga et al. 2002). The tribe Spermotamninae is placed in the recently reinstated family Wrangeliaceae (Choi et al. 2008). This family, together with the Callithamniaceae, Inkyuleaceae and Spyridiaceae, has been separated from the Ceramiaceae *sensu lato* based on anatomical and molecular data (Choi et al. 2008).

Male structures of *Ptilothamnion sphaericum* consist of compact spermatangial heads. They are in agreement with the genus and, in general, with the tribe Spermotamninae (Gordon 1972, Stegenga et al. 2002) and the family Wrangeliaceae (Choi et al. 2008). Spermatangial heads are the most common morphology of male structures in these taxa (Womersley 1998), but some exceptions occur. For example, male structures of *Hommersandiella* and *Stegengaea* consist of spermatangia in loose penicillate tufts and in umbellate clusters, respectively (Alongi et al. 2007). For this reason, in combination with some features of the female filament, the placement of both genera in the tribe Spermotamninae is doubtful (Alongi et al. 2007). Although male structures have been considered relatively unimportant as taxonomic features, they are probably useful in separation of genera or tribes (Gordon 1972, Itono 1977).

Female structures of *Ptilothamnion sphaericum* are in agreement with the genus *Ptilothamnion* (Table 1). Although post-fertilization stages of *P. sphaericum* were not observed in our collections, other reproductive and vegetative features corroborate its placement in *Ptilothamnion*, and they differ from other genera of Spermotamninae (Table 1). Therefore, the placement of *Callithamnion sphaericum* P.L. Crouan *et* H.M. Crouan *ex* J. Agardh in the genus *Ptilothamnion* (Maggs and Hommersand 1993) is here validated on the basis of sexual structures. Recent research on the Ceramiales based on molecular and anatomical data supports previous emphasis on procarp structure as a key indicator of phylogenetic relationships and systematics for families of the Ceramiales and related orders (Choi et al. 2008). The family Wrangeliaceae is characterized by procarps located on a subapical cell of a short fertile axis with 2–3 periaxial cells, one bearing an abaxial four-celled carpogonial branch and a sterile cell, the latter being absent in some *Wrangelia* spp. (Choi

et al. 2008) and in other genera, such as *Hommersandiella* (Alongi et al. 2007). The genus *Ptilothamnion* and taxa of Wrangeliaceae agree in general with this procarp structure, although there are several exceptions. For example, procarps in the Spongocloniae are characterised by a three-celled female axis with carpogonial branches cut-off directly from the subterminal cell and two periaxial cells from the third cell (Womersley 1998). Another example is the presence of a unique periaxial cell on the subapical cell (=supporting cell) of the procarp of *Hommersandiella* and *Stegengaea*, both doubtfully placed in the Spermotamninae (Alongi et al. 2007). On the other hand, some features of female structures vary among tribes of Wrangeliaceae, which in combination with vegetative and other reproductive characters, support their separation. For example, the position of procarps is one of the most important features used in separation of the tribes of Ceramiaceae *sensu lato* (Gordon 1972). The high variability in the features of procarps in Ceramiales is not only relevant to the taxonomy of families and tribes, but is also important in the separation of genera. In this regard, the tribe Spermotamninae is probably the most extreme example in the family Wrangeliaceae since the separation of genera is based entirely on female structures (Gordon 1972, Womersley 1998).

Although the gametophytes of *Ptilothamnion sphaericum* were mainly dioecious, the material from Leça de Palmeira, Portugal was monoecious. *Ptilothamnion* was described as dioecious by Maggs and Hommersand (1993), but Womersley (1998) found some monoecious gametophytes of *P. schmitzii* Heydrich from Australia among mostly dioecious plants, similar to observations on *P. sphaericum* in the present study.

Ptilothamnion sphaericum is similar to *P. polysporum* in vegetative morphology (Stegenga et al. 2002). Additionally, both species produce sessile polysporangia, differing from the majority of species in the genus that usually produce tetrasporangia (Stegenga et al. 2002). The two species differ in spermatangial head arrangement. In *P. polysporum*, they are borne alternately on erect axes, with each axis cell bearing only one spermatangial head (Wollaston 1984, Stegenga et al. 1997, 2002). Conversely, in *P. sphaericum*, spermatangial heads are borne densely aggregated on short lateral branchlets, with each branchlet cell bearing up to three spermatangial heads. The arrangement of spermatangial heads in clusters on small-celled lateral branchlets was previously described only for *P. rupicola* (“*rupiculum*”) Gordon-Mills (Gordon-Mills 1977), although in this species, the spermatangial heads are borne only one per cell. A third different type of spermatangial head arrangement is the terminal one on erect axes. Spermatangial head arrangement has been previously used in the separation of *Ptilothamnion* species (Gordon-Mills 1977, Searles and Schneider 1989, Womersley 1998) and it provides a useful character in the differentiation of *P. polysporum* and *P. sphaericum*.

Pterosiphonia complanata

The occurrence of sexual structures on *Pterosiphonia complanata* is rare; they were observed in only one sample

Table 1 Comparison of *Ptilothamnion sphaericum* with genera in the tribe Spermothamnieae (Wrangeliaceae).

	Length of hyogenous cell vs. subapical cell	Outer involucrel filaments/pericarp	Pericentral cells in subapical cell	Auxiliary cells bearing carposporophyte	Sporangia	No. species	References
<i>Ptilothamnion sphaericum</i>	Much longer	1–2 Prefertilization/ not observed	3	Not observed	P	–	Present paper
<i>Ptilothamnion Thuret ex Le Jolis</i>	Much longer	1–4 Pre-post-fertilization/ absent	2–3	1	T/P	12	Gordon (1972), Maggs and Hommersand (1993), Ballantine and Wynne (1998), Womersley (1998), Stegenga et al. (2002)
<i>Gordoniella Itono</i>	Much longer	Absent/absent	3	2	T	1	Itono (1977)
<i>Hommersandiella Alongi, Cormaci et G. Furnari</i>	Much longer	Absent/absent	1	1	T	1	Huisman (1985), Alongi et al. (2007)
<i>Interthamnion Gordon</i>	Similar	4 Post-fertilization/absent	3	2	T	1	Gordon (1972), Womersley (1998)
<i>Lejolisia Bornet</i>	Similar, except <i>L. aegagropila</i>	Absent/present	3	1	T	6	Bornet (1859), Gordon (1972), Womersley (1998)
<i>Lomathamnion Gordon</i>	Similar	Absent/absent	2	1	T	1	Gordon (1972), Womersley (1998), Alongi et al. (2007)
<i>Ptilothamnionopsis Dixon</i>	Much longer	Absent/absent	3	1	T	1	Dixon (1971), Gordon (1972), Bird et al. (1981)
<i>Rhpidothamnion Huisman</i>	Much longer	Absent/absent	3	1	T	1	Stegenga (1989), Womersley (1998)
<i>Spermothamnion Areschoug</i>	Similar	1–4 Pre-post-fertilization/ absent	3	2	T/P	23	Gordon (1972), Maggs and Hommersand (1993), Womersley (1998)
<i>Stegengaea Alongi, Cormaci et G. Furnari</i>	Similar	Absent/absent	1	1	P	1	Stegenga (1984), Alongi et al. (2007)
<i>Tiffaniella Doty et Meñez</i>	Similar	Absent/absent	3	2	T/P	8	Doty and Meñez (1960), Gordon (1972), Womersley (1998)
<i>Woelkerlingia Alongi, Cormaci et G. Furnari</i>	Much longer	Absent/absent	2	1	T/P	2	Alongi et al. (2007), Schneider and Wynne (2008)

P, polysporangium; T, tetrasporangium.

Table 2 Comparison of species of the genus *Pterosiphonia*.

	Type locality/ distribution	Pericentral cells	Cortication	Spermatangial branches		Female structures		References	
				On modified trichoblast	Arrangement	Sterile apical cells	No. cells in carpogonial branches		Shape of cystocarps
<i>P. ardreana</i> Maggs <i>et</i> Hommersand	Nerope rocks, Padstow, England/ British Isles to Portugal, Mediterranean	9–12	Absent	Unknown	Unknown	Unknown	Unknown	Maggs and Hommersand (1993)	
<i>P. baileyi</i> (Harvey)	Monterey Bay, California/California	12–14	Present	No data	No data	No data	Globular	Harvey (1853), Dawson (1963a), Smith (1969), Abbott and Hollenberg (1976)	
<i>P. bipinnata</i> Falkenberg	Kamchatka, Russia/ Japan, Kamchatka, Alaska, California	11–13 (18)	Absent	No data	No data	3–4	Globular	Smith (1969), Abbott and Hollenberg (1976)	
(Postels <i>et</i> Ruprecht) Falkenberg									
<i>P. cloiophylla</i> (C. Agardh) Falkenberg	Cape of Good Hope, S. Africa/S. Africa	5–6	Present	Unbranched	Distichous to spiral	No data	4	Globular	Hommersand (1963), Stegenga <i>et al.</i> (1997)
<i>P. complanata</i> (Clemente) Falkenberg	Cádiz, Spain/British Isles to Namibia, Mediterranean	5	Present	Unbranched	Spiral	1 (-3)	4	Globular/ ovoid	Gayral (1958), Palminha (1958), Gayral (1966), Maggs and Hommersand (1993), Rull Lluich (2002), Present work Baardseth (1941)
<i>P. concinna</i> Baardseth	Tristan da Cunha/ Tristan da Cunha	5	Present, slight	Unknown	Unknown	Unknown	Unknown	Unknown	Dawson (1963a,b), Smith (1969), Abbott and Hollenberg (1976)
<i>P. dendroidea</i> (Montagne) Falkenberg	Callao, Peru and Chile/Alaska to Chile	8–12	Absent	No data	Distichous	1 or more	Unknown	Unknown	Levring (1941)
<i>P. disticha</i> Levring	Juan Fernandez/Juan Fernandez	4	Present	Unknown	Unknown	Unknown	Unknown	Unknown	Hollenberg (1970), Abbott and Hollenberg (1976)
<i>P. farlowii</i> G.J. Hollenberg	California/California	10–12	Absent	Unknown	Unknown	Unknown	Unknown	Unknown	Kylin (1925), Hollenberg and Abbott (1966)
<i>P. gracilis</i> Kylin	Washington/British Columbia to California	10–14	Absent	Unknown	Unknown	Unknown	No data	No data	Hollenberg (1969), Wynne (1985)
<i>P. hamata</i> E.S. Zinova	Commander Islands, Kamchatka/Commander Islands to British Columbia	6	Absent	Unknown	Unknown	Unknown	No data	Ovoid- spheroidal	Martens (1868), De Toni (1903)
<i>P. javanica</i> (G. Martens) De Toni	Palabuan, Java/Java	8–12	Absent	Unknown	Unknown	Unknown	Unknown	Unknown	

(Table 2 continued)

	Type locality/ distribution	Pericentral cells	Cortication	Spermatangial branches		Female structures		References
				On modified trichoblast	Arrangement	Sterile apical cells	No. cells in carpogonial branches	
<i>P. parasitica</i> (Hudson) Falkenberg	Yorkshire, England/Iceland to Morocco and Azores, Mediterranean	7-8	Absent	Unbranched	Spiral	1-3	4	Ovoid to globular Suneson (1940), Maggs and Hommersand (1993)
<i>P. paucicorticata</i> E. Y. Dawson	Galapagos/Galapagos	8-9	Present, incomplete	Unknown	Unknown	Unknown	Unknown	Dawson (1963b)
<i>P. pennata</i> (C. Agardh) Sauvageau	Mediterranean (not specified)/Widely distributed, Atlantic and Pacific	9-11	Absent	Unbranched	Distichous	1-2	No data	Ovoid/ Urceolate Dawson (1963a), Schneider and Searles (1991), Lee et al. (1992), Maggs and Hommersand (1993), Abbott (1999), Womersley (2003)
<i>P. pinnulata</i> (Kützting) Maggs et Hommersand	Genoa, Italy/British Isles to Spain, Mediterranean, California and Japan	6-8	Absent	Unbranched	Distichous/ spiral	1	No data	Ovoid Masuda (1973), Abbott and Hollenberg (1976), Maggs and Hommersand (1993)
<i>P. pusilla</i> Levring	Juan Fernandez/ Chile Islands	4	Slight	Unknown	Unknown	Unknown	4	Ovoid to globular Levring (1941), Silva and Chacana (2005)
<i>P. spinifera</i> (Kützting) Ardre	Peru/Peru, Brazil, S. Africa	8-11	Absent	Unknown	Unknown	Unknown	Unknown	Unknown Hollenberg and Abbott (1966), André (1967), Yoneshigue and Villaca (1986), Stegenga et al. (1997) Stegenga et al. (1997)
<i>P. stangeri</i> (J. Agardh) Falkenberg	Port Natal, S. Africa/S. Africa	5-6	Present, slight	Unbranched	No data	No data	Unknown	Unknown
<i>P. tanakae</i> S. Uwai et M. Masuda	Hiroshima, Japan/Japan	7-10	Usually ecorticate	Unbranched	Spiral	1-3	4	Ovoid to globular Uwai and Masuda (1999c)

among 44 collections at different sites along the Atlantic Iberian Peninsula. Tetrasporangia were more frequent, but they are also unusual. These facts suggest that persistence of populations may occur predominantly by means of vegetative propagation.

The sexual structures described in this work agree in their main features with previous observations in other species of the genus. Spermatangial branches of *Pterosiphonia complanata*, which are borne on unbranched modified trichoblasts, are cylindrical and have 1 (-3) sterile apical cells when mature. These features have been observed in six species of *Pterosiphonia* and they seem to be uniform in the genus (Table 2); however, male structures of several species are not known in detail, or are unknown. The arrangement of spermatangial branches is the only character that varies (Table 2). Nevertheless, the variations seem to be related to development stage, since a shift from alternate-distichous to a spiral pattern was described in *P. cloiophylla* (C. Agardh) Falkenberg (Hommersand 1963) and *P. pinnulata* (Kützting) Maggs et Hommersand [Masuda 1973, as *P. pennata* (C. Agardh) Sauvageau]. In the majority of the Rhodomelaceae, the spermatangia are borne on special fertile trichoblasts with short monosiphonous stalks (Hommersand 1963) and the features of spermatangial structures vary between infrafamilial taxa. Most genera of the tribe Pterosiphonieae have spermatangial structures on unbranched modified trichoblasts (Womersley 2003), but *Kintarosiphonia*, *Heterostroma* and *Pollexfenia* have spermatangial structures on branched trichoblasts (Kraft and Wynne 1992, Uwai and Masuda 1999a, Womersley 2003). Spermatangial structures are usually cylindrical in the Pterosiphonieae, but *Pterochondria* has discoid antheridial branches (Hollenberg 1942). Finally, most genera and species of the tribe have spermatangial branches with sterile apical cells, but these are absent in *Symphyocladia punila* (Yendo) Uwai et Masuda (Uwai and Masuda 1999b). The two first features of spermatangial branches (cylindrical vs. discoid, and branched vs. unbranched) seem to be uniform within each genus, and they are useful in the separation of genera in the tribe Pterosiphonieae. Conversely, although the number of sterile apical cells in spermatangial branches apparently remains uniform in the genus *Pterosiphonia*, it varies between species of *Symphyocladia* and seems to be useful only in the delineation of species.

Procarps of *Pterosiphonia complanata* agree with the general structure for Rhodomelaceae, consisting of a supporting cell and a (three-) four-celled carpogonial branch, together with a lateral sterile group (Maggs and Hommersand 1993, Womersley 2003). Procarps of *P. complanata* have four-celled carpogonial branches, as in the four congeners for which they are described (Table 2). This feature has been considered virtually uniform in the Rhodomelaceae (Scagel 1953), but Iyengar and Balakrishnan (1949) reported three-celled carpogonial branches for the first time in *Polysiphonia platycarpa* Børgesen. Since then, studies of species of Rhodomelaceae show that there is a considerable number of taxa within *Polysiphonia sensu lato* with three-celled carpogonial branches (i.e., Kim and Lee 1999). Presently, the number of cells in the carpogonial branch is one of the most important

features in the segregation of the genus *Neosiphonia* from *Polysiphonia sensu lato* (Kim and Lee 1999, Choi et al. 2001). Furthermore, three-celled carpogonial branches are characteristic of *Kintarosiphonia* (Uwai and Masuda 1999a), a genus in the Pterosiphonieae based on *Pterosiphonia fibrillosa* Okamura. Therefore, it is important to detail the structure of procarps of more species of Rhodomelaceae in order to improve knowledge on the taxonomic value of this recently assessed feature.

Cystocarps of *Pterosiphonia complanata* are globular to ovoid, similar to those of most species in the genus (Table 2). The shape of cystocarps (urceolate vs. globose/subglobose) has been also considered an important character in separating species in *Polysiphonia sensu lato* (Kim and Lee 1999). A unique description of urceolate cystocarps in *Pterosiphonia* was provided for *P. pennata* from Hawaii (Abbott 1999). Conversely, the cystocarps of *P. pennata* from Australia are globose (Womersley 2003). This may indicate that species from Hawaii and Australia are different entities or that this feature is not constant for *Pterosiphonia*; its taxonomic value must be carefully considered.

The features of sexual structures in *Pterosiphonia* are generally highly uniform. Nevertheless, these structures are unknown in the majority of species, while in several taxa some of them have not been detailed. Further investigations on the morphology of sexual structures in *Pterosiphonia* are required to determine their taxonomic value. The finding of additional new taxonomic characters for species delineation would be desirable in a genus that is based on few vegetative characters and in which several synonymies between species have been suggested (Rull Lluch 2002, Díaz and Bárbara 2004, Gabrielson et al. 2004).

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