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Gonimophyllum buffhamii Batters (Delesseriaceae, Rhodophyceae) from the Iberian Peninsula: description of morphological and reproductive structures

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Abstract – *Gonimophyllum buffhamii*, a red algal hemiparasite on *Acrosorium ciliolatum* and *Cryptopleura ramosa* (Delesseriaceae), is rare along the coasts of the Iberian Peninsula. We describe male gametophytes with spermatangial sori and tetrasporophytic plants for the first time in this area. The species is reported for the first time on *A. ciliolatum* along the Iberian Peninsula. A comparison is made with the three other species of the genus in order to facilitate their separation.

***Gonimophyllum* / *Acrosorium* / *Cryptopleura* / *Delesseriaceae* / reproduction / phenology / seaweeds / Iberian Peninsula**

Résumé – ***Gonimophyllum buffhamii* Batters (Delesseriaceae, Rhodophyceae) dans la Péninsule Ibérique : description des structures morphologiques et reproductives.** *Gonimophyllum buffhamii*, hémiparasite sur *Acrosorium ciliolatum* et *Cryptopleura ramosa* (Delesseriaceae), est rare dans la Péninsule Ibérique. Nous décrivons les gamétophytes mâles, avec des sores spermatangiaux, et les tétrasporophytes pour la première fois dans ce secteur ; l'espèce est reportée sur le *A. ciliolatum* pour la première fois dans la Péninsule Ibérique. Une comparaison est faite avec les autres trois espèces du genre *Gonimophyllum* afin de les différencier.

***Gonimophyllum* / *Acrosorium* / *Cryptopleura* / *Delesseriaceae* / reproduction / phénologie / algues marines / Péninsule Ibérique**

INTRODUCTION

The genus *Gonimophyllum* was described by Batters (1892) based on *G. buffhamii* Batters (type species). The genus includes hemiparasitic marine red algae consisting of globose clusters of small compressed and lobed blades, with reproductive structures similar to those of its host. *Gonimophyllum*, like its hosts, *Acrosorium ciliolatum* (Harvey) Kylin and *Cryptopleura ramosa* (Hudson)

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L. Newton, belongs to the tribe Cryptopleureae of the family Delesseriaceae (Wynne, 2001). It is an adelphoparasite (Feldmann & Feldmann, 1958; Goff, 1982) by being taxonomically very closely related to its host, and having similar reproductive structures and secondary pit connections. The parasitism does not seem to have severe injurious effects on the host, whose cells are not destroyed. Hyperparasitism, a condition in which a parasite also becomes parasitized, occurs in the family Delesseriaceae (Zuccarello *et al.,* 2004), with *G. buffhamii* becoming parasitzed by *Harveyella mirabilis* (Reinsch) F. Schmitz *et* Reinke.

Four species are currently assigned to the genus: *Gonimophyllum africanum* M.T. Martin *et* M.A. Pocock, *G. buffhamii*, *G. insulare* Wagner and *G. skottsbergii* Setchell. A fifth species, *G. australe* Skottsberg, was transferred by Kylin (1924) to a segregate genus *Gonimocolax* (Guiry & Guiry, 2010). *Gonimophyllum africanum,* which was described from the South African coast (Martin & Pocock, 1953; Stegenga *et al.,* 1997), has also been reported from Uruguay (Coll & Oliveira, 1999) and from Brazil (Villaça *et al.*, 2008). *Gonimophyllum buffhamii,* described from the coast of Kent in England, is relatively abundant in the South of England and Ireland (Maggs & Hommersand, 1993; Hardy & Guiry, 2003); it has also been reported from the French coast of the English Channel (Dizerbo & Herpe, 2007) and on the northwestern Iberian Peninsula (Escudero *et al.,* 2009). *Gonimophyllum insulare* was described from plants collected on Half Moon Bay, New Zealand (Wagner, 1954) and has also been reported from Argentina (Mendoza, 1970). *Gonimophyllum skottsbergii* with a type locality of San Francisco, California (Setchell, 1923), is restricted to the northern coasts of Pacific North America, from British Columbia (Scagel *et al.,* 1989) to central California (Abbott & Hollenberg, 1976).

The first report of *Gonimophyllum buffhamii* in the Iberian Peninsula was made for Ría of Pontevedra (Miranda, 1934); the plants were cystocarpic and were growing on *Cryptopleura ramosa*. The species has been reported for the western coasts of Galicia (Granja *et al.,* 1992; Bárbara & Cremades, 1996; Veiga *et al.,* 1998a, b; Bárbara *et al.,* 2005), always growing on *C. ramosa*, at sites of Coruña or Pontevedra provinces. Recently, it was reported for Asturias province (Escudero *et al.,* 2009).

Along the Iberian Peninsula, *G. buffhamii* was until now only found as sterile or cystocarpic plants. In this study we provide accurate descriptions of vegetative and reproductive features (including male and tetrasporophytic plants).

MATERIAL AND METHODS

The studied individuals of *Gonimophyllum buffhamii* have been located on samples of *Cryptopleura ramosa* and *Acrosorium ciliolatum* collected in lower littoral and infralittoral habitats by the authors as well as on material preserved in Iberian herbaria: BCN-Phyc, BIO-Algae, HGI-Algues, IEL-Algae, MA-Algae, MACB, MGC-Phyc and Po-Algae, SANT-Algae (Holmgren & Holmgren, 1998). The collected samples were preserved in 5% formalin/sea water. Herbarium material was rehydrated in soapy water. Photographs were made with a Nikon Coolpix 8400 camera connected either to a Nikon Labophot-2 light microscope or to a Nikon SM2-2T stereomicroscope. A total of 420 samples of *C. ramosa* and *A. ciliolatum* from the coasts of the Iberian Peninsula and the Balearic Islands were studied. Representative specimens of *Gonimophyllum buffhamii* have been observed in the material listed below:

Asturias: 29TPJ52: Ría del Eo, 3-August-1979, *M. J. Fernández Pérez*, MACB 5501; [epiphyte on *Cryptopleura ramosa,* with cystocarps].

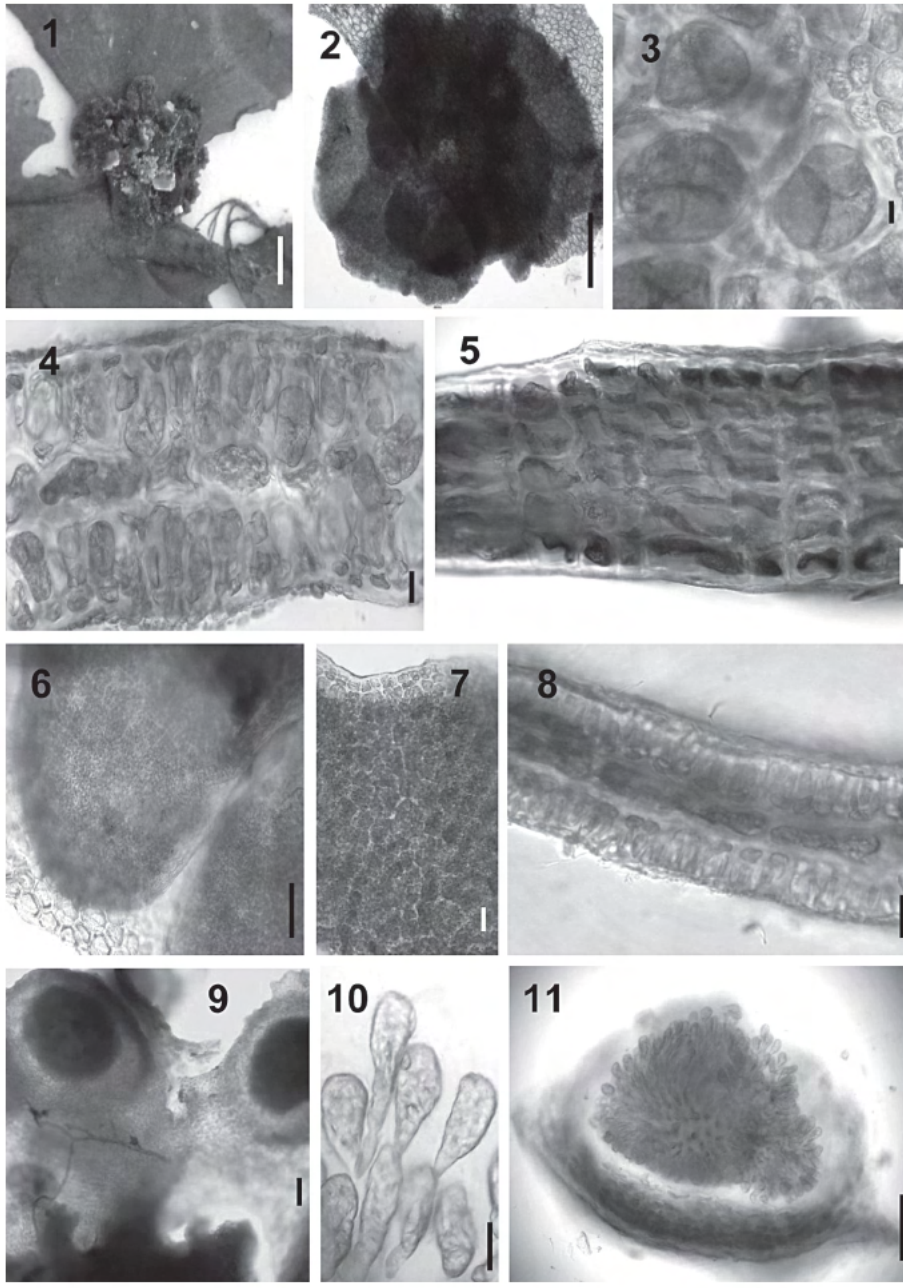
La Coruña: 29TMH85: Cabo Cee, Corcubión, Ría de Corcubión, infralittoral (-6 m), epiphyte on *Cryptopleura ramosa*, 25-June-1999, *C. López Varela*, SANT-Algae 11700 [with cistocarps]. **29TMH87:** Cabo Vilano, Camariñas, infralittoral (-3 m), epiphyte on *Cryptopleura ramosa*, 17-June-1999, *C. López Varela*, SANT-Algae 11268 [with cistocarps]. **29TMH98:** Punta Morelo, Laxe, infralittoral (-7 m), epiphyte on *Cryptopleura ramosa*, 17-June-1999, *C. López Varela*, SANT-Algae 11108 [with tetrasporangia]. **29TNH09:** Os Cortellos, Cabo Roncudo, Ponteceso, infralittoral (-5 m), epiphyte on *Cryptopleura ramosa*, 17-June-1999, *A. J. Veiga Villar*, SANT-Algae 11696; [with spermatangia]. **29TNH19:** A Redonda, Malpica, infralittoral (-6 m), epiphyte on *Acrosorium venulossum*, 31-August-1998, *C. López Varela*, SANT-Algae 10873 [with spermatangia]. **29TNJ40:** Bahía de La Coruña (Las Animas), epiphyte on *Cryptopleura ramosa*, 15-November-1989, *I. Bárbara*, SANT-Algae 2954 [with spermatangia]. **29TNJ50:** Punta San Emede, Lorbé, Oleiros, Ría de Ares y Betanzos, infralittoral (-7 m), 01-September-1998, *C. López Varela*, SANT-Algae 10763; [epiphyte on *Cryptopleura ramosa,* with tetrasporangia]. **29TNJ51:** Punta San Martín, Ría de Ferrol, epiphyte on *Cryptopleura ramosa*, 20-January-1988, J. *Cremades & I. Bárbara*, SANT-Algae 1116; [with cistocarps]. **29TNJ60:** As Mirandas, Ares, Ría de Ares y Betanzos, infralittoral (-2 m), epiphyte on *Cryptopleura ramosa*, 19-August-1998, *C. López Varela*, SANT-Algae 10925 [with spermatangia]

Pontevedra: 29TNG03: Santa Tegra, A Guarda, epiphyte on *Acrosorium venulosum*, 10-April-1997, *J. Cremades & I. Bárbara*, SANT-Algae 9252 [with tetrasporangia]. **29TNG09:** Punta Canelas, San Vicente do Mar, O Grove, infralittoral (-17 m), epiphyte on *Cryptopleura ramosa,* 27-September-1997, *J. Cremades & A. J. Veiga*, SANT-Algae 9269 [with tetrasporangia]. **29TNG29:** Marín, Ría de Pontevedra, infralittoral (-7 m), epiphyte on *Cryptopleura ramosa*, 29-April-1933, *F. Miranda*, SANT-Algae 1115 [with cistocarps].

RESULTS

Gonimophyllum buffhamii was detected on the surface of the hosts forming small rosettes, which are easily observable using a magnifying glass, because of the darker pigmentation of the hemiparasite (Figs 1-2). There are usually one to three individuals of *G. buffhamii* on the host. The thalli are partly endophytic, consisting of filaments of ovoid cells that penetrate between the host cells and form secondary pit connections with them. The thallus emerges from a small stipe on which numerous pluriestromatic, rounded or lobed blades are radially developed, giving the appearance of a rosette. Plants are almost spherical, 1-4 mm in diameter; the stipe is about 2 mm in diameter and the mature blades reach 3 mm in length by 2 mm in width. The blades have a thickness that varies from a sole cell in the edges of the lamina to 6-9 cells in the middle zone, where thickness is (24) 30-100 (120) μm (Fig. 5). In surface view, the cells are apparently disordered, with circular to oval shape, (4) 6-22 (28) μm long and (4) 5-20 (28) μm wide, smaller than the cells of the host. In cross section, the cells of the middle zone are (10) 14.7-30 (40) μm long and (10) 15-37.4 (44) μm wide.

Gonimophyllum buffhamii is a dioecious species; female gametophyte presents numerous procarps and somewhat prominent spherical cystocarps that are apparent on the lamina by their darker pigmentation. Cystocarps are



Figs 1-11. Morphological features of *Gonimophyllum buffhamii*. **1.** Thallus cushion. **2.** Detail of the parasite. **3.** Tetrasporangial sori in surface view. **4.** Cross section of tetrasporangial sorus. **5.** Cross section of the pluristromatic blade. **6.** Spermatangial sorus in surface view. **7.** Detail of spermatangial sorus. **8.** Cross section of the spermatangial sorus. **9.** Plant with cystocarps. **10.** Details of carpospores. **11.** Cross section through a cystocarp. Scale bars: Figs 1, 2 = 1 mm; Figs 3, 5, 10 = 10 µm; Figs. 4, 7, 8 = 20 µm; Figs 6, 9, 11 = 100 µm.

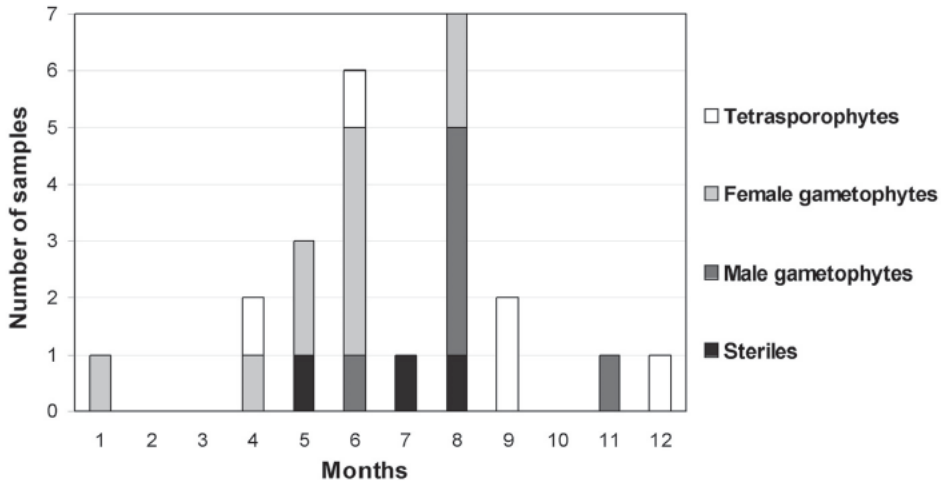


Fig. 12. Presence of *Gonimophyllum buffhamii* in the Iberian coasts throughout the year, from January (1) to December (12). Number of sterile specimens, male and female gametophytes, and tetrasporophytes are indicated. Total number of samples of *Cryptopleura ramosa* and *Acrosorium ciliolatum* = 420.

scattered, 1-6 on each lamina, located in the lower surface (Fig. 9). Cystocarps are urceolate, with a small ostiole; their size, in cross section, is 450-550 µm long and 500-600 µm wide (Fig. 11). Carpospores are numerous, ellipsoidal or pear-shaped, (16) 18-28 (40) µm long (Fig. 10). Cystocarps were found in January, April, May, June and August (SANT-Algae 1115, 1116, 10974, 11118, 11268, 11700, 11751, 15698 and 15699; MACB 5501). Male gametophytes have spermatangial sori, 300-500 × 450-800 µm, covering most of the surface, leaving an external band of 4-6 sterile cell rows (Figs 6-7). Sori occur in both faces of the lamina and are 75-100 µm thick as viewed in cross section (Fig. 8); they consist of a monostromatic layer of mother cells, 6-7 µm in diameter, which support cylindrical spermatangia 14-17 µm long by 4-6 µm wide. Spermatia are almost spherical, 4-6 µm in diameter. Spermatangia sori were found in June, August and November (SANT-Algae 2954, 10873, 10925, 10971, 10997 and 11696). Tetrasporophytes have tetrasporangial sori covering most of the blade, (300) 320-540 (640) µm in diameter, placed on both faces of the lamina (Fig. 4). Tetrasporangia are spherical, (16) 27-55 (64) µm in diameter, and contain four spores with a tetrahedral arrangement (Fig. 3). Tetrasporangial sori were found in April, June, September and December (SANT-Algae 3443, 9252, 9269, 10763 and 11108).

Of the 420 samples studied of *Cryptopleura ramosa* and *Acrosorium ciliolatum* from the Iberian Peninsula and the Balearic Islands, only in 24 of them *Gonimophyllum buffhamii* was found; mainly on *C. ramosa* (87.5%). Collections came from the lower littoral (12%) and infralittoral (88%), in localities moderately exposed to the waves. The hemiparasite was detected all over the year except in February, March and October, and was more frequent in June and August (Fig. 12).

Table 1. Summary of characters for differentiating species of *Gonimophyllum* according to the literature.

	G. africanum		*G. buffhamii*		*G. insulare*		*G. skottsbergii*
	Martin & Pocock (1953)	Stegenga *et al.* (1997)	Maggs & Hommersand (1993)	This work	Wagner (1954)	Mendoza (1970)	Setchell (1923), Wagner (1954), Abbot & Hollenberg (1976)
Parasite on	*Acrosoium spp. Botryoglossum platycarpum* (Turner) Kützing, *Neuroglossum binderianun* Kützing, *Botryocarpa prolifera* Greville	*Acrosorium spp. Botryoglossum platycarpum* (Turner) Kützing	*Acrosorium ciliolatum, Cryptopleura ramosa*	*Acrosorium ciliolatum, Cryptopleura ramosa*	*Hymenena semicostata* (J. Agardh) Kylin	*Hymenena falklandica* Kylin	*Botryoglossum farlowianum* (J. Agardh) De Toni, *Hymenena spp., Cryptopleura spp.*
Size of specimens	–	Few mm	1-4.6 mm diameter	1-4 mm diameter	5-12 mm diameter	20 mm long	15 mm diameter
Size of the lamina	–	2 mm long	0.4-3.6 × 0.5-3 mm	1-2 × 1-3 mm	3-9 × 1.6-5 mm	–	1-3 m
Number of layers of the lamina	–	Pluriestromatic	1-6 (10)	1-6 (9)	1 in marginal areas; 5 in older parts of the fronds	1 to several	Pluriestromatic, 5-7
Veins	–	Absent	Absent	Absent	Microscopic, present near the base of the blades; frequently indistinct	Microscopic and anastomosing	Microscopic veins in the lower part of the fronds
Procarps	Scattered on the lamina		Many	Many	On both surfaces of the blades	On the two surfaces of the fronds	Over both surfaces of the blades
Cystocarps (number and size)	Rounded and lobed	One to several per blade; up to 700 µm	1-4; 1000 µm	1-6; 450-600 µm	Numerous	Many	Several per blade on one side of the blade
Carposporangia	–	Terminal or in chains	24-36 × 24-30 µm	16-18 × 28-40 µm	Not possible to determine	Terminal and intermediate	Terminal

Table 1. Summary of characters for differentiating species of *Gonimophyllum* according to the literature. *(continued)*

	G. africanum		*G. buffhamii*		*G. insulare*		*G. skottsbergii*
Spermatangia	Over nearly the whole area on both surfaces, except a narrow sterile margin	Over most of the surface of the blade	In sori single with [sterile] margin 2-6 cells wide. Spermatangia 12-16 × 3-4 µm	In sori single with sterile margin 2-6 cells wide. Spermatangia 14-17 × 4-6 µm	Sori cover more than half of the blade; on both surfaces	In sori occupying 3/4 parts of the fronds except a marginal band of 60-80 µm wide	Sori cover most of both surfaces of the fronds
Tetrasporangia	Over the central part of both surfaces	Single sorus covering most of the blade, 40-50 × 15-20 µm	Covering both sides of blade except for marginal 3-6 cells, 60-95 µm in diameter	Single sorus covering most of the blade, 16-25 × 55-64 µm in diameter	Sori form a broad marginal band	In sori occupying 3/4 parts of the fronds	Absent
Polysporangia	Absent	Absent	Absent	Absent	Absent	Absent	30-50 spores
Habitat	–	–	Subtidal (2-10 m)	Low intertidal to subtidal (to 17 m)	–	Mesolittoral and infralittoral	Low intertidal to subtidal (to 7 m)
Distribution	South Africa	South Africa	British Isles, France and Spain	North of Spain	New Zealand	Argentina	Washington to California

DISCUSSION

Gonimophyllum buffhamii is not a frequent species along the Iberian coasts, in that it has been detected in less than 6 % of the samples of *Cryptopleura ramosa* and *Acrosorium ciliolatum*, most of which were from the northwest coasts of Spain. Even though the hemiparasite has not been collected in February and October, it is probably present all year round along these coasts. It is also possible that plants are fertile all year round because we observed cystocarps from January to August, spermangial sori from June to November and tetrasporangial plants from April to December. Geographical distribution of *G. buffhamii* including the east and south coasts of the British Isles (Hardy & Guiry, 2003), the French coasts of the English Channel (Dizerbo & Herpe, 2007) and the northwestern Iberian Peninsula (Escudero *et al.*, 2009), suggests that its life cycle would be controlled by the temperature of seawater in winter, between 9 and 11°C.

Although our samples of *G. buffhami* were morphologically very similar to plants from the British Isles (Maggs & Hommersand, 1993), some minor differences in size of cystocarps, carposporangia and tetrasporangia are apparent. These differences are listed in Table 1.

Morphological and reproductive characters obtained in this study have been compared with literature data for the four species of *Gonimophyllum* (Table 1). Although the four species differ in geographic distribution, the characters that allow the separation of the four species of the genus are not consistent, and differences among species are scarce. In the original description of *G. skottsbergii* Setchell (1923) indicates the presence of polysporangia, structures that had not been observed in the other species of *Gonimophyllum* and whose presence was considered as sufficient to describe the samples from California as a new species; later, other authors confirmed this observation while extending its distribution from Vancouver Island to the southern California (Kylin, 1924; Wagner, 1954; Abbott & Hollemberg, 1974). *Gonimophyllum africanum* has been reported only between Table Bay near Cape Town and the mouth of the Kei River, both of them localities mentioned by Martin & Pocock (1953). They indicate that the character that separates it from *G. buffhami* is the size of the female plants, which are larger in *G. africanum*. This species has also been collected in southern Brazil, around Cabo Frío, Rio de Janeiro (Villaça *et al.*, 2008) on *C. ramosa,* and in several localities of the coasts of Uruguay (Coll & Oliveira, 1999). For *G. insulare* only the type locality by Wagner (1954) for New Zealand (Half Moon Bay, Stewart Island) and the one report by Mendoza (1974) for the south of Argentina (Puerto Deseado) are known. *Gonimophyllum insulare* grows on *Hymenena semicostata* and it has been separated from other species of the genus by its large size, the more pronounced lobation of the female and tetrasporangial blades (Wagner, 1954) and the presence of microscopic veins, which may not be observable due to the considerably reduced vegetative apparatus (Feldmann & Feldmann, 1958). The presence of microscopic veins as taxonomic character is problematic in this tribe; in *A. ciliolatum*, a species characterized by the presence of these veins, we only observed veins in samples more than 6 mm long.

All the four species of *Gonimophyllum* grow on hosts belonging to Delesseriaceae and almost always belonging to the tribe Cryptopleureae: *Acrosorium, Cryptopleura, Botryoglossum* or *Hymenena* (Wynne, 2001). The only known exceptions are is *G. africanum* that, besides living on *Acrosorium*, has also been collected on *Neuroglossum binderianun*, belonging to the tribe Schizoserideae and

on *Botryocarpa prolifera*, of the tribe Botryocarpeae, along the South Africa coasts (Martin & Pocock, 1953). Parasitism of *Gonimophyllum* on hosts of different tribes, but of the same family, has led some authors to doubt the validity of the definition of adelphoparasite (Zuccarrello *et al.,* 2004).

Taxonomy of the genus *Gonimophyllum* is still in need of revision because the four species recognized at present show few morphological, anatomical or reproductive differences among themselves. With regard to reproductive characters, the only exception is the presence of polysporangia in *G. skottbergii,* which could be due to a local character rather than specific (Wagner, 1954). The most important criterion at present for species differentiation, with some exception, is their geographical distribution rather than the morphological characters. Molecular data will be needed to assess species boundaries more accurately.

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