

***Colaconema ophioglossum* comb. nov.
and *Liagorophila endophytica*,
two acrochaetioid algae (Rhodophyta)
from the eastern Atlantic**

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Abstract — Two species of acrochaetioid algae (Rhodophyta) are reported from the Canary Islands for the first time. Both *Colaconema ophioglossum* comb. nov., previously known from North Carolina and Puerto Rico in the Western Atlantic [as *Audouinella ophioglossa* Schneider and *Acrochaetium ophioglossum* (Schneider) Ballantine *et* Aponte], and *Liagorophila endophytica* Yamada, cited from several localities in the Pacific Ocean and with a single report from the Caribbean coast of Colombia, constitute new records for the eastern Atlantic Ocean. *Colaconema ophioglossum* was found growing epi-endophytically between the cortical fascicles of the recently described Canarian endemic *Dudresnaya multiramosa* Afonso-Carrillo, Sansón *et* Reyes, which constitutes a new host for this species. Its vegetative cells contain a single lobate parietal chloroplast with a single pyrenoid, a feature exclusive of *Colaconema*, and consequently the species is transferred to this genus. *Liagorophila endophytica* was discovered in the outer cortex of *Liagora canariensis* Børgesen. Data concerning geographical distribution and observations on vegetative and reproductive morphology, especially the development of the carposporophyte, are presented for the two species. In *C. ophioglossum*, the fertilized carpogonium divides transversely and gonimoblasts are monopodially branched. In *L. endophytica* the fertilized carpogonium divides longitudinally and the gonimoblasts are radially produced by successive longitudinal cells divisions. This distinctive type of gonimoblast development is regarded as a taxonomically significant feature, and suggests retention of *Liagorophila* as a separate genus. Conflicting reports of plastid morphology do not allow confident ordinal placement of *Liagorophila* and the genus is regarded as of uncertain affinity, but allied to the Acrochaetiales or Colaconematales.

Acrochaetiales / Canary Islands / *Colaconema ophioglossum* comb. nov. / Colaconematales / *Liagorophila endophytica* / marine algae / morphology / Rhodophyta

Résumé — *Colaconema ophioglossum* comb. nov. et *Liagorophila endophytica*, deux algues acrochaétioides (Rhodophyta) de l'Océan Atlantique oriental. Deux espèces ayant une morphologie acrochaétioides (Rhodophyta) sont signalées aux îles Canaries pour la première fois. *Colaconema ophioglossum* comb. nov., précédemment connue en Caroline du Nord et Puerto Rico dans l'Océan Atlantique occidentale [comme *Audouinella ophioglossa* Schneider et *Acrochaetium ophioglossum* (Schneider) Ballantine *et* Aponte], et *Liagorophila endophytica* Yamada, citées dans plusieurs localités de l'Océan Pacifique et avec une localisation unique sur la côte des Caraïbes de la Colombie, représentent une

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première observation dans l'Océan Atlantique oriental. *Colaconema ophioglossum* a été trouvée en épi-endophyte entre les faisceaux corticaux de l'espèce endémique des Canaries *Dudresnaya multiramosa* Afonso-Carrillo, Sansón *et* Reyes, qui constitue un nouvel hôte pour cette espèce. Ses cellules végétatives contiennent un seul chloroplaste pariétal lobé avec un pyrénnoïde, caractère exclusif de *Colaconema* ; par conséquent, l'espèce est transférée dans ce genre. *Liagorophila endophytica* a été découverte dans le cortex externe de *Liagora canariensis* Børgesen. Des données sur la répartition géographique et des observations de la morphologie végétative et reproductrice, particulièrement le développement du carposporophyte, sont présentées pour les deux espèces. Dans le *Colaconema ophioglossum*, le carpogone fécondé se divise transversalement et les gonimoblastes ont une ramification monopodiale. Dans le *Liagorophila endophytica*, le carpogone se divise longitudinalement et les gonimoblastes sont organisés radialement par des divisions longitudinales successives des cellules. Ce type exclusif de développement du carposporophyte constitue un caractère taxinomiquement significatif qui suggère de conserver *Liagorophila* comme un genre distinct d'affinité incertaine mais allié aux Acrochaetiales ou aux Colaconematales.

Acrochaetiales / Algues marines / Colaconematales / *Colaconema ophioglossum* comb. nov. / Iles Canaries / *Liagorophila endophytica* / morphologie / Rhodophyta

INTRODUCTION

Acrochaetioid algae have the simplest heterotrichous organization of the Florideophyceae (Rhodophyta), and generally constitute an inconspicuous component of many littoral and sublittoral communities in all seas (Woelkerling, 1983). Acrochaetioid plants have usually been grouped in the order Acrochaetiales, but recently Harper & Saunders (2002), based on molecular data, have suggested that two lineages occur, each representing a separate order containing a single family. Harper & Saunders (2002) considered the differences in chloroplast morphology as important diagnostic features at the generic level. In the scheme presented by these authors, the Acrochaetiales includes plants with vegetative cells characterized by one of the three following attributes: (1) multiple parietal discoid to band-shaped chloroplasts, lacking pyrenoids (*Rhodochorton* Nägeli), (2) multiple parietal lobed to discoid chloroplasts, lacking pyrenoids (*Audouinella* Bory de Saint-Vincent), and (3) single stellate chloroplast, each with a single central pyrenoid (*Acrochaetium* Nägeli). The Colaconematales, however, include plants with vegetative cells containing one to several parietal chloroplasts of varying shape (lobed to spiral to irregular, but never stellate), with or without pyrenoids (*Colaconema* Batters).

Although some acrochaetioid species occur regularly on rock, most species grow on or in a biotic substratum. Hosts with a largely loose cortex (e.g. *Liagora*, *Helminthocladia*, *Dudresnaya*) commonly support partly or entirely endophytic plants. Our studies carried out on the ephemeral spring-summer flora of the Canary Islands (Afonso-Carrillo *et al.*, 2002) and recent samplings have resulted in the collection of gelatinous or calcified red algae, containing endophytic acrochaetioid species previously unknown in the Canaries.

Present knowledge on the acrochaetioid species of the Canary Islands is mainly due to the studies of Børgesen (1927), who described new taxa and contributed valuable data on the habitats of many species. Subsequently, Afonso-Carrillo (1980), Viera-Rodríguez *et al.* (1987), Reyes *et al.* (1993) and Sansón *et al.*

(2002) added new records. In the present account, two epi-endophytic species previously unreported in the eastern Atlantic Ocean (*Audouinella ophioglossa* and *Liagorophila endophytica*) are added to the marine algal flora of the Canary Islands. Plants of *Audouinella ophioglossa* have vegetative cells with a single lobate parietal chloroplast with a single pyrenoid, a feature exclusive to the genus *Colaçonema* as recently emended by Harper & Saunders (2002). As a consequence, this species is transferred to *Colaçonema*. The occurrence of fertile gametophytes in both *C. ophioglossum* and *L. endophytica* has also provided an opportunity to examine the post-fertilization development in each species.

MATERIAL AND METHODS

Selected fragments containing acrochaetioid algae were obtained from liquid-preserved specimens of *Dudresnaya multiramosa* Afonso-Carrillo, Sansón *et* Reyes and *Liagora canariensis* Børgesen fixed in 4 % formalin in sea-water. These fragments were stained in 1% aqueous aniline blue, mounted in a 50 % Karo corn syrup solution, and squashed slightly to separate the filaments. Selected fragments of *L. canariensis* were previously decalcified in 1-5 % HCl. Drawings were prepared with the aid of a camera lucida attached to a Zeiss microscope. Herbarium abbreviations follow Holmgren *et al.* (1990).

OBSERVATIONS AND DISCUSSION

Colaçonema ophioglossum (Schneider) comb. nov. (Figs 1-11)

Basionym: *Audouinella ophioglossa* Schneider, *Smithsonian Contributions to the Marine Sciences* 22: 13, figs 3a-p. (1983).

Homotypic synonym: *Acrochaetium ophioglossum* (Schneider) Ballantine *et* Aponte, *Caribbean Journal of Science* 33: 151 (1997):

Audouinella ophioglossa was described by Schneider (1983) from plants growing in *Dudresnaya crassa* Howe in Onslow Bay, North Carolina (USA). The species was later reported from Puerto Rico (Ballantine & Wynne, 1986), Georgia (Searles, 1987), and Florida (Ballantine, 1996), always on the same host. Ballantine & Aponte (1997) transferred the species to *Acrochaetium* following the taxonomic criteria of Silva *et al.* (1996). Until now, *Dudresnaya crassa* Howe was regarded as the obligate host of *Audouinella ophioglossa*, and Schneider & Searles (1991) suggested that the distribution of this epi-endophyte was possibly linked to the distribution of *Dudresnaya crassa*.

The Canarian specimens of *Colaçonema ophioglossum* were growing as an epi-endophyte in branches of the recently described *Dudresnaya multiramosa* Afonso-Carrillo, Sansón *et* Reyes (2002) collected at a depth of 33 m. Plants are monoecious and up to 1.2 mm tall, consisting of endophytic irregularly contorted filaments with a persistent large and globose spore that is 8-11 µm in diameter (Figs 1, 2). Erect filaments are simple or branched distally, with slender cylindrical cells, 4-5 µm in diameter and 25-50 µm long, each containing a single lobate parietal chloroplast with a single pyrenoid (Fig. 3). Terminal or lateral unicellular hairs



Figs 1-11. *Colaconema ophioglossum*. Figs 1, 2. Habit of two specimens showing endophytic irregularly contorted filaments with a persistent globose spore (arrows) and simple erect filaments. Scale bar = 50 μ m. Fig. 3. Detail of an erect filament with monosporangia. Note a single lobate parietal chloroplast with a single pyrenoid in each cell. Fig. 4. Detail of an erect filament with spermatangia formed in pairs on stalk-cells arranged in whorls. Fig. 5. Detail of a carposogonium. Fig. 6. Extended base of fertilized carposogonium. Fig. 7. First transverse division of the carposogonium. Figs 8-10. Early developmental stages of carposporophytes with young gonimoblasts growing monopodially. Fig. 11. Mature carposporophyte with terminal subspherical carposporangia. Scale bar for figures 3-11 = 20 μ m.

are common (Figs 1, 3). Lateral and sessile ovoid monosporangia, 7-10 μm in diameter and 13-18 μm long, were observed singly or in pairs on plants bearing gametangia (Fig. 3). Spherical spermatangia 2-3 μm in diameter are formed in pairs on one-celled stalk-cells arranged in whorls of three or four, or in opposite pairs, or less frequently occurring one per node (Fig. 4). Carpogonia are lateral and sessile, with the bottle-shaped basal portion 3-4 μm in diameter, and a trichogyne up to 35 μm long (Fig. 5). After presumed fertilization, the base of the carpogonium extends upwards and the trichogyne is lost (Fig. 6). The first division of the carpogonium is transverse (Fig. 7). The distal cell divides again transversely once or twice, and short lateral branches are initiated from all cells of this chain (Figs 8-10). The mature carposporophyte is subglobose and up to 40 μm in diameter. It is monopodial in construction with the main axis containing four or five cells and the shorter lateral branches bearing large, terminal, subspherical carposporangia, 10-13 μm in diameter (Fig. 11). Residual carposporangial walls are not retained.

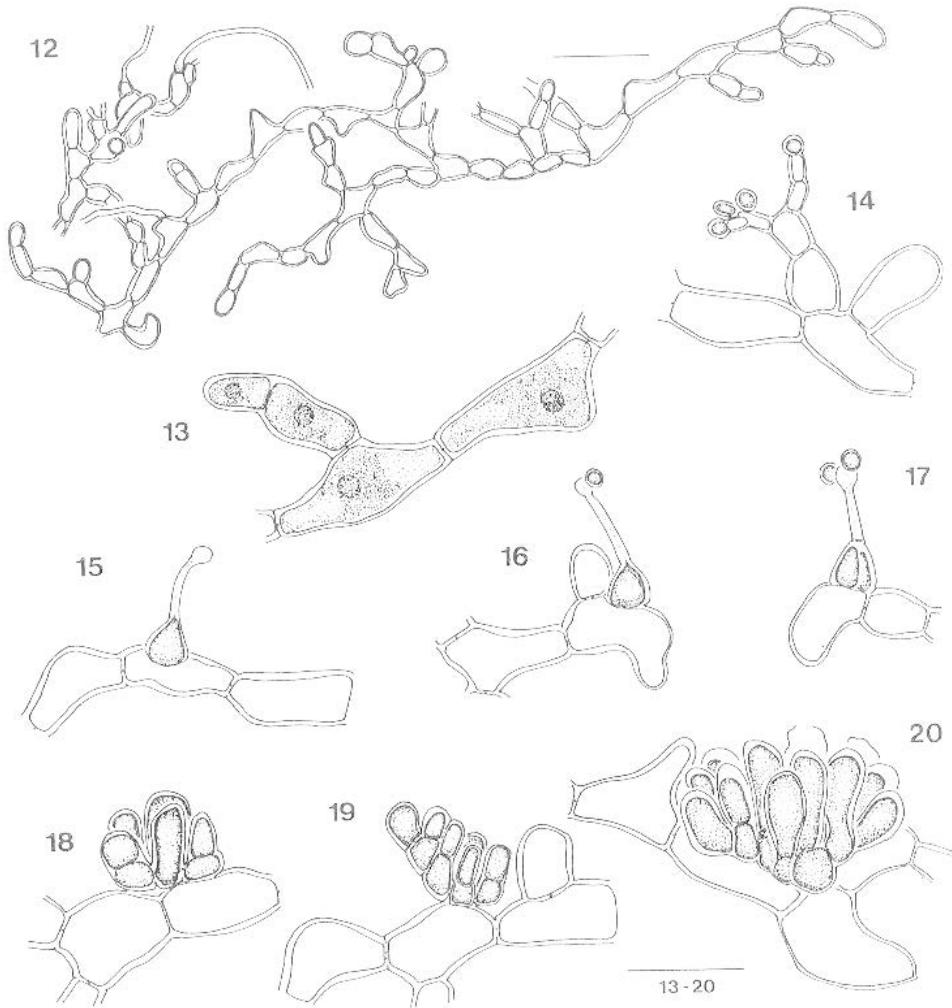
In the classification scheme presented by Harper & Saunders (2002) for acrochaetioid algae, the only genus in the Acrochaetiales and Colaconematales with species having parietal plastids each with a pyrenoid is *Colaconema*. Schneider (1983) suggested that *Colaconema ophioglossum* (as *Audouinella*) was closest in morphology to *Acrochaetium subtilissimum* (Kützing) Hamel, an epi-endophyte of *Dudresnaya verticillata* (Withering) Le Jolis and other species from the eastern Atlantic coasts of France (Hamel, 1928). However, *C. ophioglossum* can be differentiated from *A. subtilissimum* by its blunt apices, slender erect filaments 4-5 μm in diameter, conspicuous unicellular hairs, subspherical carposporangia, and the verticillate arrangement of male branches. All these attributes are present in the Canary Islands specimens. *Colaconema ophioglossum*, along with *Acrochaetium bermudense* (Vickers) Børgesen, are the only epi-endophyte species in the flora of the Canary Islands with a large basal cell remaining in the original spore wall (Afonso-Carrillo & Sansón, 1999). *A. bermudense*, however has larger vegetative and reproductive structures.

Although Schneider (1983) described female gametophytic plants bearing carpogonia and carposporophytes in the original account of *Audouinella ophioglossa*, details on the mode of development of the gonimoblast were not provided. In the present study, a transverse division of the fertilized carpogonium was observed, and the apical cell divides subsequently to form a monopodial branching system as the gonimoblast develops. Both transverse initiation and monopodial development of the gonimoblast have been previously observed in other species [e. g. *C. asparagopsis* Chemin, *C. dasyae* (Collins) Harper *et* Saunders and *C. daviesii* (Dillwyn) Stegenga] placed by Harper & Saunders (2002) in *Colaconema* (Stegenga & Borsje, 1976; Magne, 1977; Abdel-Rahman & Magne, 1990).

Material examined: TFC Phyc 10979 (14 September 1998, Playa de San Juan, Tenerife, Canary Islands, leg. J.F. González; epi-endophytic in *Dudresnaya multiramosa*).

***Liagorophila endophytica* Yamada (Figs 12-20)**

The monotypic genus *Liagorophila* was described by Yamada (1944) based on material from Taiwan that was found growing as an endophyte in *Liagora orientalis* J. Agardh [= *Izziella orientalis* (J. Agardh) Huisman *et* Schils (2002)]. Subsequently, *Liagorophila endophytica* has been reported in the East China Sea and Japan (Fan & Li, 1964; Yoshida, 1998), Hawaii and Ecuador



Figs 12-20. *Liagorophila endophytica*. Fig. 12. Habit. Scale bar = 50 μm . Fig. 13. Detail of a creeping filament with each cell containing a parietal chloroplast and a single pyrenoid. Fig. 14. Spermatangia on short erect filaments. Figs 15, 16. Details of sessile carpogonia. Fig. 17. First longitudinal division of a fertilized carpogonium. Figs 18, 19. Early developmental stages of carposporophytes with short gonimoblastic filaments formed by successive longitudinal cells divisions. Fig. 20. Mature carposporophyte with most cells elongated to form vertically oriented carposporangia. Scale bar for figures 13-20 = 20 μm .

(Abbott, 1999). In the Atlantic Ocean, *L. endophytica* has been reported only from the Caribbean coast of Colombia (Bula-Meyer, 1986).

The Canarian specimens of *Liagorophila endophytica* were discovered in the outer cortex of *Liagora canariensis* Børgesen collected at a depth of 5 m. Plants of *Liagorophila endophytica* consist of a prostrate system of irregularly branched filaments (Fig. 12) creeping within the gelatinous matrix of the host.

Cells are irregular to subcylindrical, 7-20 μm in diameter and 15-35 μm long, often widest in the middle (Figs 12, 13). Short erect filaments are occasionally formed towards terminal portions of repent filaments. Each cell contains a parietal chloroplast and a single pyrenoid (Fig. 13). Most plants were sterile, but some had gametangia. Spermatangia are sessile, subspherical, 3-4 μm in diameter, and occur 1-3 on short erect filaments (Fig. 14). Carpogonia are sessile and arise laterally on cells of prostrate filaments (Figs 15, 16). They consist of a subconical carpogonium, 7-10 μm in diameter, with a trichogyne up to 20 μm long that is distally inflated and often has several spermatia attached to it (Figs 16, 17). After presumed fertilization, the carpogonium divides longitudinally into two unequal daughter cells (Fig. 17). Both cells take part in the formation of the gonimoblast. Successive longitudinal cell divisions result in short gonimoblast filaments in which most cells elongate to form lateral and vertically oriented carposporangia (Figs 18-20). Mature gonimoblasts are subdiscoid, 25-40 μm in diameter and 28 μm high, and bear ovoid carposporangia 5-8 μm in diameter and 12-20 μm long. Residual carposporangial walls (Fig. 20) persist. Monosporangial plants were not observed.

Liagorophila was delimited primarily by the longitudinal first division of the fertilized carpogonium, in contrast to the transverse division exhibited by *Acrochaetium* (Yamada, 1944). Abbott (1966) and Lee *et al.* (1986) confirmed this feature in the type material of *Liagorophila endophytica*. Our observations on post-fertilization development confirm previous accounts of Yamada (1938), Abbott (1966) and Bula-Meyer (1986). There is no monopodial development. Gonimoblast filaments are formed laterally by successive longitudinal divisions from both cells of the divided carpogonium, and, after some radial divisions, a lateral vertically oriented carposporangium is produced from each cell.

As a consequence of the chaotic taxonomic history of acrochaetioid algae, *Liagorophila endophytica* has also been placed in both *Audouinella* Bory and *Acrochaetium*. Garbary (1980) questioned using characteristics relating to the division of the fertilized carpogonium for generic delineation within a group (the Acrochaetiaceae) where the sexual stages are not known for a majority of included taxa. Based in a broad concept of *Audouinella*, Garbary (1980) chose to recognize only one genus of Acrochaetiaceae, and consequently subsumed *Liagorophila* into *Audouinella*. He also proposed a new name, *Audouinella yamadae* Garbary, because of the prior existence of *Audouinella endophytica* (Batters) Dixon.

Subsequently, Lee & Lee (1988) and Harper & Saunders (2002) have provided different classification schemes for the acrochaetioid algae. In these schemes, differences in chloroplast morphology were considered important diagnostic features at the genus level. These authors assumed that cells of *Liagorophila endophytica* each possess a single stellate chloroplast with a central pyrenoid, and consequently they subsumed *Liagorophila* into *Acrochaetium*. Lee & Lee (1988) proposed the new combination *Acrochaetium yamadae* (Garbary) Lee *et al.*, a proposal overlooked by Harper & Saunders (2002).

In contrast, Woelkerling (1971) regarded chloroplast morphology as unreliable for distinguishing genera because in several taxa the shape of the chloroplast can differ from cell to cell, depending upon the situation or position in a plant. In fact, both Abbott (1966) and Bula-Meyer (1986) reported that *Liagorophila* cells contain a parietal chloroplast with a pyrenoid, and finally Abbott (1999) characterized the genus as having stellate to band-shaped chloroplasts, each with a pyrenoid. These conflicting reports regarding chloroplast morphology make it difficult to confidently assign the species to one or another of the two lineages identified by Harper and Saunders (2002).

While the generic placement of *Liagorophila endophytica* is still a matter for discussion, the taxon is nevertheless unique amongst the acrochaetioid algae in features as its post-fertilization development (Abdel-Rahman & Magne, 1990). In several species the absence of an initial division of the zygote has been described, but in most acrochaetioid algae in which the formation of the gonimoblast has been observed, a first transverse division of the fertilized carpogonium roughly separates it into halves (Woelkerling, 1983). We believe that the taxonomic value of this character in genus delineation should be reassessed, as it has been shown to be of value in other primitive red algae. In the Liagoraceae, for example, the presence or absence of an initial division of the zygote (= post-fertilization carpogonium), and whether that division is transverse or longitudinal, are consistent generic features (Kraft, 1989). Most commonly in the Liagoraceae the initiation of the gonimoblast follows a transverse division, but the genus *Helminthocladia* J. Agardh is unique in its oblique to longitudinal first division (O'Dwyer & Afonso-Carrillo, 2001).

These distinctive types of gonimoblast development appear to be more significant taxonomically than many vegetative characters used to delineate genera in the Acrochaetiaceae (Abbott, 1999), and supports recognizing *Liagorophila* as distinct genus. Wynne (1998) and Yoshida (1998) have also maintained the original concept of *Liagorophila*, which we also accept here. At present, however, due to the absence of molecular data and the apparent variability in chloroplast morphology, it would be appropriate to retain *Liagorophila endophytica* as a taxon of uncertain affinity but allied to the Acrochaetiales or Colaconematales.

In habit, *Liagorophila endophytica* is close to *Acrochaetium liagorae* Børgesen, a species that is relatively common as an endophyte in liagoroid plants in the Canary Islands (Reyes *et al.*, 1993; Afonso-Carrillo & Sansón, 1999). *Acrochaetium liagorae*, however, has smaller vegetative cells, usually elaborate monosporangia, spermatangia that arise in groups on differentiated stalk-cells, and gonimoblasts that are monopodially constructed from a transversally divided fertilized carpogonium (Woelkerling, 1971).

Material examined: TFC Phyc 10980 (03 September 2002, Fajana de Franceses, La Palma, Canary Islands, leg. C. Sangil; endophytic in *Liagora canariensis*).

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