

Distinctive morphological features of *Sargassum desfontainesii* (Fucales, Phaeophyceae)

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Abstract – *Sargassum desfontainesii* (Fucales, Phaeophyceae), an Atlantic species recognisable by the unusual shape of blades (filiform and several times forked, instead of the typical leaflike laterals of most species of *Sargassum*) is morphologically re-examined in populations from the Canary Islands. Previous descriptions were exclusively based on pressed dried specimens and they are inexact for several diagnostic features. Fresh specimens exhibit (1) primary and secondary branches regularly cylindrical with smooth surface (never subangular, slightly compressed or spinous), (2) blades exclusively terete (never linear or triquetrous with a central percurrent midrib), (3) vesicles mostly muticous, but vesicles ending in a short coronal blade, or supported on a forked stalk are relatively common, and (4) male receptacles longer and more slender than the androgynous receptacles. Although until now the species has been considered as a genuine member of the subgenus *Phyllotrichia*, *Sargassum desfontainesii* lacks certain distinctive features, such as the distichous and compressed primary branches, and the linear, pinnately branched lower blades. It is suggested that this species should be placed in the subgenus *Sargassum*, section *Malacocarpicae*, subsection *Cymosae*.

Canary Islands / Fucales / marine algae / morphology / Phaeophyceae / *Sargassum desfontainesii*

Résumé – **Caractères morphologiques distinctifs du *Sargassum desfontainesii* (Fucales, Phaeophyceae).** La morphologie de *Sargassum desfontainesii* (Fucales, Phaeophyceae), une espèce atlantique reconnaissable par la forme peu commune des rameaux végétatifs (filiformes et plusieurs fois bifurquées, au lieu de la forme foliacée typique de la plupart des espèces de *Sargassum*), est à nouveau examinée sur des populations des îles Canaries. Les anciennes descriptions ont été exclusivement basées sur les spécimens secs de l'herbier et elles sont inexactes quant à plusieurs caractères diagnostiques. Les spécimens frais présentent (1) des branches primaires et secondaires régulièrement cylindrique avec une surface lisse (jamais subangulaires, légèrement comprimées ou muriculées), (2) des rameaux exclusivement cylindriques (jamais linéaires ou triquètres avec une nervure percurrente centrale), (3) des vésicules qui sont majoritairement mutiques, mais celles qui finissent en une branche coronale courte, ou soutenue par un pédicelle bifurqué sont relativement communes, et (4) des réceptacles mâles plus longs et étroits que les réceptacles androgynes. Bien que jusqu'ici l'espèce ait été considérée comme appartenant au sous-genre *Phyllotrichia*, *Sargassum desfontainesii* n'en possède pas les caractères distinctifs comme les branches primaires distiques et comprimées, et les rameaux inférieurs linéaires avec une ramification pennée. Il est suggéré de placer l'espèce dans le sous-genre *Sargassum*, section *Malacocarpicae*, sous-section *Cymosae*.

Algues marines / Fucales / Iles Canaries / morphologie / Phaeophyceae / *Sargassum desfontainesii*

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INTRODUCTION

Among the 400 currently accepted species included in the brown algal genus *Sargassum* C. Agardh, at least twenty-six (plus a similar number of infraspecific taxa) are known from the North Atlantic Ocean (John *et al.*, 2004; Wynne, 2005). *Sargassum* species are characterized by an erect habit consisting of a holdfast with one to several main axes (stipes) bearing primary branches that form leaflike laterals (blades), secondary branches, globose air bladders (vesicles), and fruiting branches (receptacles) (Yoshida, 1983; Ang & Trono, 1987; Womersley, 1987; Díaz-Villa *et al.*, 2004). Species identification in *Sargassum* is quite complex, mainly due to the lack of conscientious descriptions and to the partial information obtained from thallus portions and immature individuals, without considering the intraspecific variation (Taylor, 1960; Kilar *et al.*, 1992; Díaz-Villa *et al.*, 2004). However, some species are easily recognisable by the unusual shape of the blades. *Sargassum desfontainesii* (Turner) C. Agardh (1820) [basonym: *Fucus desfontainesii* Turner (1811)], originally described from the Canary Islands, is one of these exceptional species because of its filiform, several times forked blades, unlike the more typical leaflike blades (Børgesen, 1926).

Sargassum desfontainesii is a common shallow sublittoral species that has been frequently reported from the Canary Islands (Børgesen, 1926; Afonso-Carrillo & Sansón 1999), as well as in the other eastern Atlantic islands of Azores (Neto, 1994), Madeira (Levring, 1974), and Salvage Islands (Audiffred & Weisscher, 1984). In addition, the species has also been reported from the Mediterranean coast of Morocco (González García & Conde, 1992), as well as from Venezuela (Ganesan, 1990) and Trinidad (Richardson, 1975) in the western Atlantic Ocean. Current knowledge on the morphology of *S. desfontainesii* is based on the brief and incomplete descriptions given by C. Agardh (1820), J. Agardh (1848, 1889), Grunow (1916) and the more detailed account of Montagne (1841, as *Sargassum comosum* Montagne). However, the intraspecific variation of the characters with taxonomic value is poorly documented because all these descriptive works are exclusively based on pressed, dried herbarium specimens. During the course of our recent studies on *Sargassum* species from the Canary Islands (Díaz-Villa *et al.*, 2004, 2005), we had the opportunity to examine numerous fresh collections of *S. desfontainesii*. Preliminary observations allowed us to detect a greater morphological variation than previously reported. As a detailed morphological study of mature plants was necessary, we analysed the morphological features of a population for the purpose of quantifying the morphological variability of *S. desfontainesii* from its type locality.

MATERIAL AND METHODS

Thalli of *Sargassum desfontainesii* were collected from lower eulittoral tidal pools exposed to wave activity in Punta del Hidalgo, on the north slope of Tenerife, Canary Islands. Eleven completely developed (with vesicles and receptacles) specimens were randomly collected each month from March to July 2002. Specimens were placed in plastic bags and preserved in 4-10 % formalin in seawater. All morphological characteristics related to holdfasts, stipes, branches, blades, vesicles and receptacles were recorded for each specimen. Number and shape of all vesicles were recorded, and the size of the largest vesicle of each

primary branch was measured. Size and characters related to blades were examined in all blades of two selected individuals and in the largest blade from each primary branch of each specimen. Number, diameter and arrangement of cryptostomata were obtained from two blades of each specimen. Receptacle size and number of branches were recorded from selected receptacles of mature thalli. Minimum, maximum sizes and the 95 % confidence limits were determined for all measurements. Micrographs were taken with a digital camera (Nikon Coolpix 4600), mounted on a Zeiss standard microscope. Selected specimens were deposited in the herbarium TFC (Departamento de Biología Vegetal, Universidad de La Laguna, Canary Islands) as TFC Phyc 13110, 13154, 13155, 13156 and 13157.

RESULTS

Habit

Sargassum desfontainesii is pseudoperennial with fully developed mature thalli throughout the spring. It is usually yellowish-brown in colour but becomes gradually reddish-brown when senescent, mature thalli are up to 50 cm in height (Fig. 1). Each thallus consists of a holdfast, stipes and primary branches supporting primary blades, secondary branches with their respective secondary blades, vesicles and receptacles. Throughout summer and autumn the specimens are small, reduced to the holdfast, stipes and short primary branches with few primary blades.

Holdfasts and stipes

Holdfasts are discoid to irregular, (7-)15-26(-38) mm in diameter, but they can become confluent, as a result it is difficult to separate them in dense populations. Holdfasts are dark brown in colour and exhibit a slightly rough surface. From each holdfast (1-)3-8(-15) stipes arise. Stipes are also dark brown, erect, slightly verrucose, cylindrical, from (2-)5-15(-47) mm in length and (1-)2-4 (-7) mm in diameter, simple or up to six times branched. Usually 1-6(-13) primary branches are distally and spirally arranged on each stipe, but stipes lacking primary branches occasionally occur.

Primary and secondary branches

Primary branches are erect, up to 480 mm long, yellowish-brown in colour, smooth, and cylindrical, 1(-2) mm in diameter (Fig. 1). Secondary branches arise from the axil of some primary blades. Secondary branches are similar in morphology to primary branches, although shorter, reaching up to 150 mm long, but becoming longer when replacing a damaged primary branch.

Blades

Although most blades arise from primary and secondary branches, a few blades are borne directly from the stipe (cauline blades). Cauline blades are similar in morphology to the more proximal primary blades, but longer and more branched.

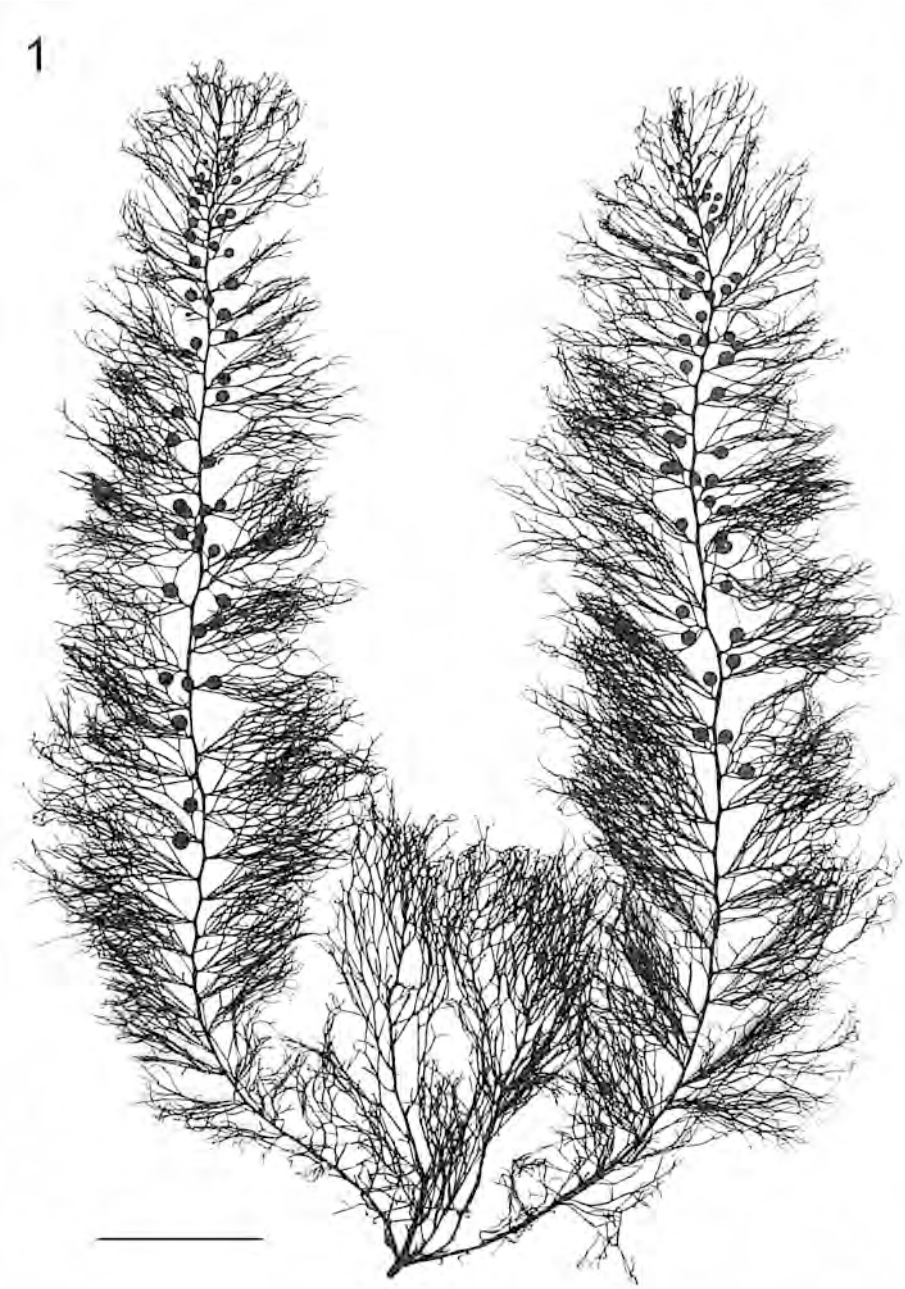


Fig. 1. Habit of a pressed specimen of *Sargassum desfontainesii* (TFC Phyc 13110). Scale = 5 cm.

Primary blades are alternately and spirally arranged on primary branches, with successive blades separated at intervals of 3-5 mm in the middle portions of the branches. Primary blades are filiform, 2-4(-8) times regularly forked with wide angles of branching, (3-)24-46(-86) mm long and 1(-2) mm wide (Figs 2-5). Blades are flattened at each bifurcation, lack midrib and end in acute apices. Secondary blades arise from secondary branches, arranged in the same way as primary branches. Secondary blades are more densely arranged than primary blades, spaced 1-2 mm, (3-)12-36(-53) mm long and 1 mm wide, 1-2(-3) times forked, although some remain unbranched (Figs 6-12).

Cryptostomata

Cryptostomata are usually absent. When present, they are scarce and scattered on the blades, but occasionally numerous cryptostomata are found at the margin of the largest blades. Cryptostomata are elliptical, 60-214 × 24-143 µm in diameter.

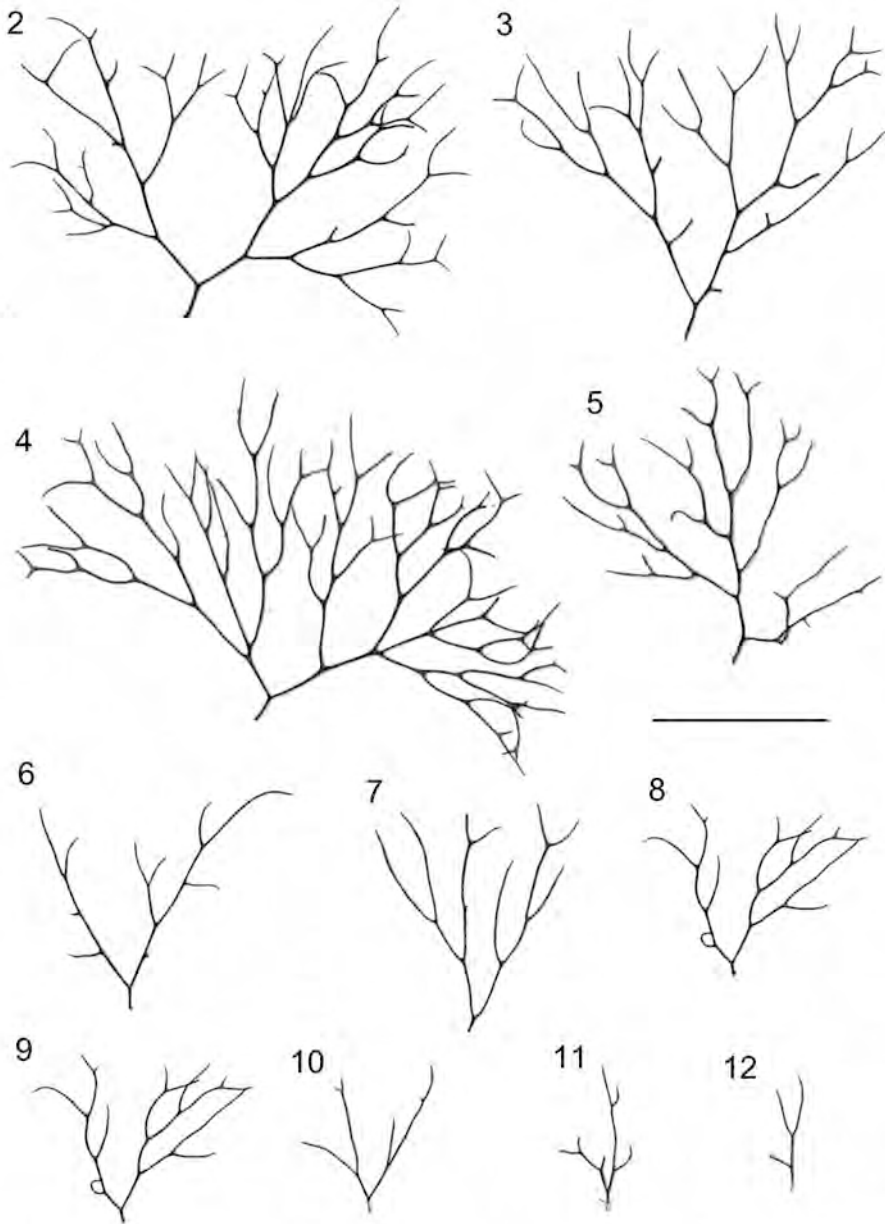
Vesicles

Vesicles are borne in axils of secondary blades or replace them (Fig. 13). Vesicles are spherical to slightly oblong, usually mucous (71% of 342 vesicles examined) or once to twice apiculate (29%), ranging from 2-5(-6) mm long and (2-)3-5(-6) mm in diameter (Figs 19-21). They are terminal in a simple (90%), rarely branched (10%) (Fig. 22), filiform stalk, (2-)3-4(-6) mm long. Double fused vesicles rarely occur (Fig. 23).

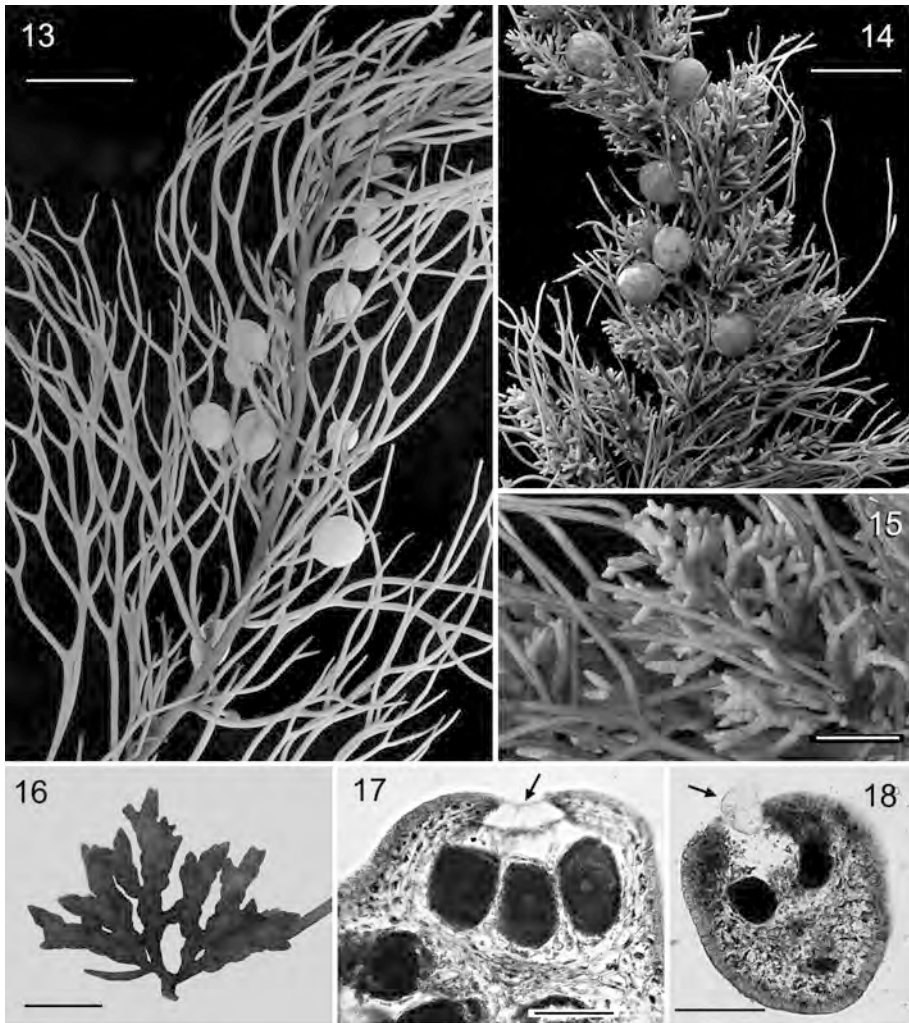
Receptacles

Thalli are androdioecious in gametangial distribution [i.e. there are male thalli and androgynous thalli (male and female gametangia in different receptacles but in the same receptacle)]. Receptacular branchlets arise from the axil of a secondary blade or a vesicle (Figs 14, 15). They can be up to 27 mm long and bear up to 12 receptacles densely arranged in an alternate-spiral sequence (Fig. 15). Androgynous receptacles are erect, initially terete, but later verrucose by receptacle growth, (3-)4(-7) mm long and (0.5-)1.0(-1.5) mm wide, but decreasing in diameter towards the acute apex (Figs 16, 24). Each receptacle forms a cymose cluster with an apparently dominant axis unbranched to 3(-6) times laterally branched. Lateral branches are simple or once to twice forked. Receptacles develop acropetally, covering the receptacle almost entirely, with only a short simple or branched pedicel in fully developed receptacles remaining sterile (Figs 16, 24). In surface view, their wide ostiole and their dark brown colour (originating from the oogonia inside) distinguish female receptacles. A hyaline to orange-coloured plug in the ostiole closes female receptacles until egg liberation (Figs 17, 18). After release, eggs are retained in mucilage around the receptacles. Male receptacles are smaller and their narrow ostiole is not apparent in surface view.

Male receptacles are erect, terete, with a slightly rough surface, clear brown in colour and are arranged in the same way as the androgynous ones (Fig. 25). They are longer and slender [(4-)5(-6) mm long and (0.5-)0.7(-1.2) mm in diameter] than androgynous receptacles. Diameter of receptacles is constant from the base towards the tips, and the number of lateral branches is slightly higher than androgynous receptacles: (2-)4(-7) times cymosely branched.



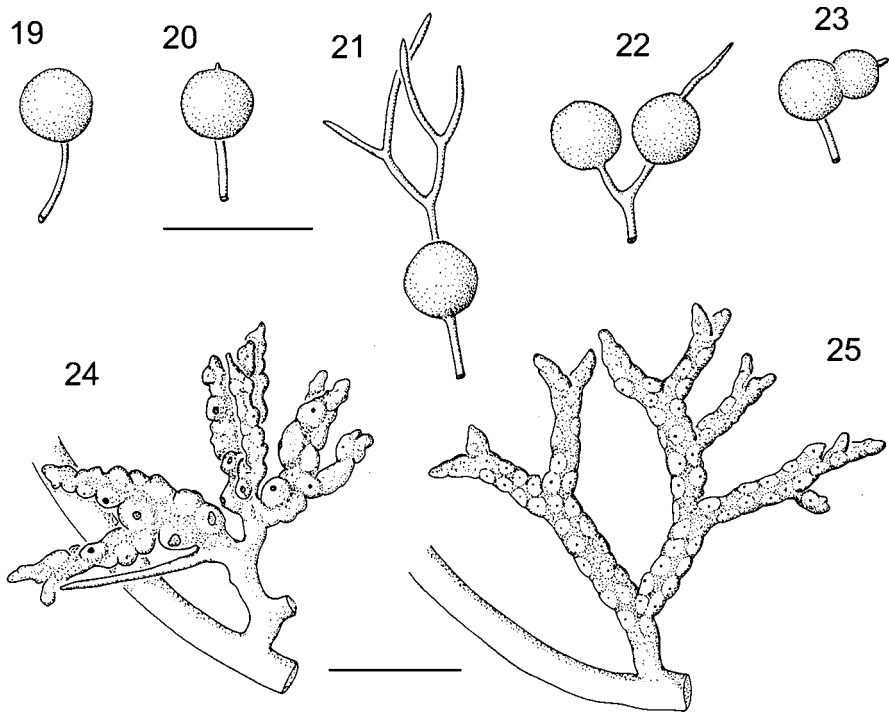
Figs 2-12. Size and shape variation of blades in *Sargassum desfontainesii*. 2-5. Primary blades. 6-12. Secondary blades. Scale = 3 cm.



Figs 13-18. Vesicles and receptacles of *Sargassum desfontainesii*. **13.** Detail of blades and vesicles in an immature liquid-preserved specimen. Scale = 1 cm. **14.** Detail of a liquid-preserved mature specimen densely furnished with fully developed receptacles. Scale = 1 cm. **15.** Secondary branch showing clusters of receptacles. Scale = 3 mm. **16.** Detail of a cluster of androgynous receptacles. Scale = 2 mm. **17-18.** Transverse sections of female conceptacles containing immature oogonia. Note that hyaline plugs (arrows) close ostioles. Scales = 200 μ m.

DISCUSSION

The detailed study of numerous fully developed, fresh specimens of *Sargassum desfontainesii* has allowed us to provide a complete description of the species based on the knowledge of the variation of the characters with taxonomic value in *Sargassum* (Yoshida, 1983; Kilar *et al.*, 1992, Díaz-Villa *et al.*, 2004).



Figs 19-25. Vesicles and receptacles in *Sargassum desfontainesii*. **19-23**. Variations in vesicles. Scale = 10 mm. **19**. Mucicous. **20**. Short apiculate. **21**. With a coronal blade. **22**. Paired in a forked stalk. **23**. Double fused. **24**. Androgynous receptacle. **25**. Male receptacle. Scale = 2 mm.

Although the distinction of species of *Sargassum* is usually quite difficult (Kilar, 1992), *S. desfontainesii* is easily recognisable by the shape of its blades. The species has been frequently reported from Eastern Atlantic localities (Levring, 1974; Audiffred & Weisscher, 1984; Neto, 1994; Afonso-Carrillo & Sansón, 1999; John *et al.*, 2004), supporting identifications on the descriptions given by phycologists of the nineteenth century (C. Agardh, 1820; Montagne, 1841; Kützing, 1861; J. Agardh, 1889). However, our observations show that some morphological characters were erroneously attributed to this species by these authors, and as no morphological re-examination had been made, this ensemble of attributes has characterized the species until now. All primary and secondary branches examined were regularly cylindrical in all their length exhibiting a smooth surface. Subangular branches, slightly compressed branches, or spinous surfaces that had been reported with occasional occurrence by C. Agardh (1820), J. Agardh (1889) and Montagne (1841), were not observed in the present study.

In a detailed description of the shape, size and branching of blades, Montagne (1841, as *S. comosum*), erroneously referred to them as triquetrous with an obvious central and percurrent midrib. In this study, we show that blades are regularly filiform (except the slightly flattened bifurcations) without midrib. Blade section was probably incorrectly described because observations of early phycologists were often exclusively made from dried, wrinkled and contracted

herbarium specimens. Montagne (1841) also reported the occurrence of broad and flat proximal blades that progressively become narrower to filiform towards the terminal portions of branches. Later, J. Agardh (1889) described spinous branches and flat basal blades, with dentate or serrate margins, in immature juvenile thalli. He assumed that these juvenile forms would evolve to adult individuals with the typical characters of *Sargassum desfontainesii*, and he attributed to this species a small immature specimen deposited in the Herbarium of Bory as *Fucus endiviaefolii* Bory. However, all these blade variations do not appear in the numerous thalli examined during this study and these forms probably belong to incomplete misidentified specimens.

Vesicles were initially characterised as muticous (C. Agardh, 1820; Kützing, 1849; J. Agardh, 1889), but Montagne (1841) showed that they were occasionally apiculate. We have observed a high proportion (30%) of apiculate vesicles, and a branched stalk, previously unreported, is relatively frequent (10% of vesicles).

Reproductively, *Sargassum desfontainesii* is an androdioecious species (i.e. with male and androgynous thalli). First information on the shape of receptacles was given by Montagne (1841, as *S. comosum*), because Turner's illustration (1811) and C. Agardh's description (1820) were made from immature specimens with only rudimentary receptacles. Kützing (1861, as *S. comosum*) drew a receptacular branchlet and later Grunow (1916) described the androdioecious condition of the species. The morphological differences between male and androgynous receptacles are presented here for the first time. In addition, the cavity of each female conceptacle is closed until egg liberation by a previously unreported ostiolar plug, in a similar way to that recently described in *S. orotavicum* Díaz-Villa, Afonso-Carrillo *et* Sansón (Díaz-Villa *et al.*, 2004).

Based on observations of herbarium specimens of *Sargassum desfontainesii* from the Canary Islands, Grunow (1916) distinguished three varieties and three formae. The var. *genuina* Grunow [including f. *chaetophylla* (Mertens) Grunow, f. *intricata* Grunow, and f. *linearis* Grunow], var. *albertisii* (Piccone) Grunow, and var. *hispida* Grunow. The var. *genuina* and the f. *chaetophylla* (both with filiform blades) represent the range of species variation, but the f. *intricata* (with furcate squarrose blades), and the f. *linearis* (with flat blades 6-7 mm wide, tapering upwards) are misidentifications of other *Sargassum* species. The var. *albertisii* [based on *S. albertisii* Piccone (1884)], and the var. *hispida* (based on *Fucus endiviaefolii* Bory in herbarium), are currently accepted as synonymous of *S. vulgare* C. Agardh (Børgesen, 1926; Prud'homme van Reine *et al.*, 1994).

Although initially J. Agardh (1848) included *Sargassum desfontainesii* in the 'sectio *Eusargassum*, tribu *Cymosae*', when he later established the *Sargassum* system of classification in five subgenera (J. Agardh, 1889), *S. desfontainesii* was considered as a genuine species of the subgenus *Phyllotrichia*, a placement that has been retained until now (Womersley, 1954; Goldberg & Huisman, 2004). Species in the subgenus *Phyllotrichia* are characterised by (1) winged primary branches, arising from the stipe as flattened to foliose pinnatifid expansions, (2) blades flattened and pinnately branched (3) vesicles spherical and muticous, and (4) terete receptacles usually simple, without spines, in racemose clusters (J. Agardh, 1889; Setchell, 1931, 1933; Yoshida, 1983; Womersley, 1954, 1987). Only three of the species reported from *Phyllotrichia* present a distribution outside the Australian region (Womersley, 1954, 1987; Phillips, 1995; Goldberg & Huisman, 2004): *S. desfontainesii* (North Atlantic), *S. piluliferum* (Turner) C. Agardh (Indian Ocean, Asia and Australia) and *S. palmeri* Grunow (Northeastern Pacific)

(Abbott & Hollenberg, 1976; Grunow, 1915, 1916). J. Agardh (1889) and Grunow (1915, 1916) placed these three species in a separate tribe (*Dimorphae* J. Agardh) in *Phyllotrichia* on the basis of the terete shape of the branches and the differences in morphology between proximal and distal blades.

Our observations show that *Sargassum desfontainesii* does not exhibit any of the features that define the subgenus *Phyllotrichia*. Primary and secondary branches are regularly cylindrical (never subangular or slightly compressed), blades are exclusively filiform (never flattened, linear, or triquetrous), vesicles are mostly mucous, but also ending in a short coronal blade, and receptacles are several times branched. Because of the ensemble of features observed, we suggest the placement of *S. desfontainesii* in the subgenus *Sargassum*, section *Malacocarpicae* (J. Agardh) Abbott, subsection *Cymosae* (J. Agardh) Tseng *et al.* (Abbott *et al.*, 1988). Further ecological and molecular studies are needed to make a final conclusion.

Recent molecular studies in *Sargassum* (Phillips & Fredericq, 2000; Stiger *et al.* 2003; Phillips *et al.*, 2005) supported many of the subgeneric to sectional levels delineated by J. Agardh (1889). However, according to the data obtained from *S. piluliferum* and *S. palmeri*, both species appear associated with the clade of the section *Malacocarpicae* of the subgenus *Sargassum* (Stiger *et al.*, 2003; Phillips *et al.*, 2005). These evidences leave empty the tribe *Dimorphae*, and the subgenus *Phyllotrichia* would include only species with Australian distribution.

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