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Taxonomy of the *Dictyota ciliolata–crenulata* complex (Dictyotales, Phaeophyceae)

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We reassessed the taxonomy of dentate *Dictyota* species formerly attributed to *D. ciliolata* and *D. crenulata*. Both taxa have long been assumed to be broadly distributed in tropical to warm-temperate seas. Recent molecular data, however, provided evidence that *D. crenulata* constituted a complex of at least four species with restricted geographical distributions. Based on those results and careful morphological examination, we split *D. crenulata sensu lato* into *D. crenulata sensu stricto* restricted to Pacific Central America, *D. jamaicensis* with a tropical amphi-Atlantic distribution and *D. canariensis* and *D. pleiacantha* sp. nov. from Macaronesia. Morphological analysis showed that these species were distinguished by subtle morphological differences. In contrast to *D. crenulata sensu lato*, the wide tropical distribution of *D. ciliolata* was confirmed by DNA data. In addition, *psb*A sequence analysis did not provide evidence to segregate *D. menstrualis* and *D. plectens* from *D. ciliolata*.

Key Words: Brown algae, *Dictyota ciliolata*, *Dictyota crenulata*, Dictyotales, Diversity, Molecular phylogenetics, Morphology, Taxonomy

INTRODUCTION

The brown algal genus *Dictyota* Lamouroux is common in marine tropical and temperate waters worldwide (Womersley 1987). Although a conspicuous component of many of these floras, species are often difficult to identify, with obvious consequences for ecological, biogeographical and physiological research. The problem of delimiting species based on their morphology reflects our inability to recognise diagnostic characters in members of the genus that are generally characterised by substantial intraspecific morphological plasticity (Hörnig *et al*. 1992a; De Clerck & Coppejans 1999; De Clerck 2003; Hwang *et al*. 2005; Tronholm *et al*. 2008, 2010a, b). As a result, many uncertainties in species-level diversity at regional and global scales persist (Hörnig & Schnetter 1988; De Clerck 2003; Tronholm *et al*. 2010b).

One of the most widely used characters to differentiate *Dictyota* species consists of the presence or absence of teeth or outgrowths from the thallus margin or surface, although it has been realized that dentation shows marked intraspecific variation (Hörnig *et al*. 1992a; De Clerck & Coppejans 1999; De Clerck 2003). Here we present a taxonomic study of tropical and warm-temperate *Dictyota* species with dentate margins. These species are often reported as *D. crenulata* J. Agardh or *D. ciliolata* Sonder *ex* Kützing. Recent molecular data demonstrated considerable conflict between traditional and DNA-based species criteria for *D. ciliolata* and *D. crenulata* (Tronholm *et al*. 2012). *Dictyota ciliolata* was shown to be a widely distributed species in the Atlantic and Indian Oceans. *Dictyota crenulata*, on the other hand, was found to constitute a complex of four morphologically similar (pseudocryptic) species with dentate margins in addition to several phylogenetically related dentate (*D. sandvicensis* Sonder) and non-dentate species [*D. implexa* (Desfontaines) Lamouroux, *D. cymatophila* Tronholm, Sansón & Afonso-Carrillo, *D. mertensii* (Martius) Kützing, and *Dictyota* cf. *caribaea*]. In contrast to the presumed wide distribution of *D. crenulata*, molecular data showed that the ranges of the four pseudocryptic species were more restricted: *D. crenulata* #1 was restricted to the Pacific Central American coast, *D. crenulata* #2 and *D. crenulata* #4 were only found in Macaronesia, and *D. crenulata* #3 had an amphi-Atlantic distribution. Phylogenetic analyses also showed that the *D. crenulata* clade was not closely related to *D. ciliolata*.

In this paper we characterise the morphologies of the dentate species in the *Dictyota ciliolata* and *D. crenulata* clades and revise their classification to reflect the natural relationships in this group of algae, based on the molecular phylogenetic results presented in Tronholm *et al*. (2012). In addition, relationships of *D. ciliolata* with *D. menstrualis*

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(Hoyt) Schnetter, Hörnig & Weber-Peukert and *D. plectens* (Allender & Kraft) Kraft are addressed.

MATERIAL AND METHODS

Specimens of *Dictyota ciliolata* and *D. crenulata* were collected from tropical and warm-temperate areas in both hemispheres. Vouchers for morphological analysis were pressed or wet-preserved in 5% formalin–seawater solution, and are deposited in the herbaria of Universidad de La Laguna, Canary Islands, Spain (TFC), Ghent University, Belgium (GENT) and University of Costa Rica, San José, Costa Rica (USJ).

The genetic variability within *Dictyota ciliolata* and the relationships of the latter with *D. menstrualis* and *D. plectens* were assessed by constructing a haplotype network of the plastid *psb*A gene using the statistical parsimony algorithm implemented in TCS v.1.21 (Clement *et al.* 2000). DNA sequencing and phylogenetic analysis were described previously (Tronholm *et al.* 2012). The analysis was based on a matrix of 37 sequences consisting of 736 nt. A summary of sequences and collecting data are provided in Table S1.

Treatments of morphology and anatomy follow Tronholm *et al.* (2008, 2010a, b). Photographs were taken with a DM2000 stereoscopic microscope and a MZ12.5 microscope with a DFC290 camera (Leica Camera AG, Solms, Germany). Herbarium vouchers of *Dictyota ciliolata* (MICH and BM), *D. crenulata* (MICH and BM), *D. crenulata* var. *canariensis* (W and B), *D. jamaicensis* Taylor (MICH and BM), *D. menstrualis* (Hoyt) Schnetter, Hörnig & Weber-Peukert (MICH), and *Dictyota kohlmeyeri* (Nizamuddin & Gerloff) Hörnig, Schnetter & Prud'homme van Reine (B) were examined for morphological comparison and taxonomic discussion. Herbaria abbreviations follow Holmgren *et al.* (1990).

RESULTS

Molecular analyses

We assessed the molecular divergence between *Dictyota ciliolata*, *D. menstrualis* and *D. plectens* using the plastid encoded *psb*A gene. A matrix of 37 sequences consisted of 736 nucleotides (nt), of which 13 positions (1.8%) were polymorphic. No insertions or deletions were observed. Statistical parsimony analysis showed that 10 haplotypes were separated by a small number of mutations (Fig. 1), which indicated a very close relationship of both *D. menstrualis* and *D. plectens* to *D. ciliolata*. The network consisted of a common haplotype, which included specimens from the Atlantic Ocean as well as the Indo-Pacific, and a number of satellite haplotypes that were separated by no more than two mutations. The haplotypes of *D. menstrualis* from North Carolina and *D. plectens* from eastern Australia did not differ by any greater extent than any of the other satellite haplotypes that were identified as *D. ciliolata*.

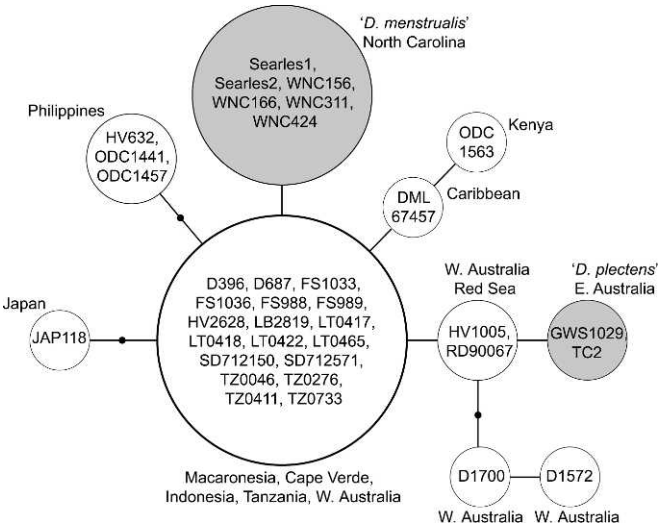


Fig. 1. Statistical parsimony network of *psb*A haplotypes within the *Dictyota ciliolata* complex. Each circle represents a haplotype. The size of the circle is proportional to the number of sampled individuals with a given haplotype. Grey circles correspond to specimens identified as *D. menstrualis* or *D. plectens*. Each line between haplotypes represents one mutation step. Missing haplotypes, indicated by small black circles, were either not sampled or extinct.

Morphological observations

We reassessed the morphology and taxonomy of the species in the *Dictyota ciliolata* and *D. crenulata* complex. The original species descriptions were not detailed; therefore, we have expanded the original descriptions with modern data to accurately separate and define each species. Diagnostic characters used to differentiate the species of the *D. crenulata* complex are summarized in Table 1. For a more comprehensive morphological comparison of all dentate *Dictyota* species, please see Table S2.

Dictyota ciliolata complex

Dictyota ciliolata Sonder *ex* Kützing 1859: 12
Figs 2–15

Dictyota ciliolata is completely erect and usually larger (up to 13.5 cm) than the other dentate species, with obvious yellow-greenish transverse banding pattern *in vivo*, which is often still visible when dried (Figs 2–3). Although the margins in this species are usually dentate (Fig. 4), some specimens have a reduced number of teeth or even entirely smooth margins (Fig. 5). Apices are acute to rounded and sometimes somewhat incurved (Figs 6–7). Sporangia are solitary; whereas, oogonia and antheridia are aggregated in sori, both being spread over both thallus surfaces; although, mainly arranged in middle and apical parts within a narrow sterile marginal border (Figs 8–10). Germinating sporangia often occur on the thallus surface (Fig. 11). The medulla is unilayered throughout (Figs 12–14); although, it can duplicate near the margins and particularly at the base of the marginal teeth (Fig. 15). Sporangia are dark brown, pyriform to subspherical, and are borne on a single stalk cell (Fig. 12). Oogonia are dark brown, subclavate to pyriform, and borne on a single stalk cell (Fig. 13). Antheridia are subcylindrical, composed of several tiers of loculi, and borne on a single stalk cell (Fig. 14). The species grows

Table 1. Relevant morphological diagnostic characters used to distinguish *Dictyota canariensis*, *D. ciliolata* , *D. crenulata, D. jamaicensis* and *D. pleiacantha*.

	D. canariensis	*D. ciliolata*	*D. crenulata*	*D. jamaicensis*	*D. pleiacantha*
Iridescence	blue-greenish; often with square dark patches in apical parts	yellow-greenish; transverse banding pattern	blue-greenish apices; broad and pale transverse banding pattern; square dark patches over the whole thallus	absent; sometimes inverted triangular dark patches in dichotomies	absent; often with inverted triangular dark patches in dichotomies, especially visible *in vivo*
Apices shape	rounded to obtuse	rounded to acute	rounded to obtuse	spathulate	rounded, elongate and spathulate
Teeth	minute, triangular	minute to ciliate	triangular to crenulate	spinose to ciliate	spinose to ciliate
Sporangia arrangement	solitary, on both surfaces	solitary, on both surfaces	solitary or grouped in small sori, on both surfaces	solitary or grouped in small sori, mainly on one surface	solitary, on both surfaces
Distribution	Canary Islands, Madeira, Cape Verde Is.	pantropical to warm temperate	Pacific coast of Central America	Caribbean Sea, Cape Verde Is.	Canary Islands

epilithically in low-intertidal pools and the shallow sublittoral, often forming extensive populations.

Dictyota crenulata complex

Dictyota crenulata J. Agardh 1847: 7
Figs 16–20

Dictyota crenulata was described by J. Agardh from San Agustín (Oaxaca) on the Pacific coast of Mexico. Based on the presence of a multilayered medulla in the basal parts of the thallus and basal proliferations, Nizamuddin & Gerloff (1979) transferred this taxon to *Dilophus*. In the absence of a holotype, these authors designated a lectotype from the Agardh herbarium (LD) but erroneously cited the specimen as LD 49042a, instead of LD 49049a (De Clerck 2003). As a result of the merger of *Dilophus* with *Dictyota* by Hörnig and co-workers (1992a, b), the species was returned to *Dictyota*.

Tronholm *et al.* (2012) found that genuine *D. crenulata* (*D. crenulata* 1) is restricted to the Pacific Central America coasts. This species is characterised by a crenulate margin of triangular teeth, rounded to obtuse blue-greenish iridescent apices, broad and pale transverse surface banding pattern and dark pigmented square patches spread over the entire thallus that are especially visible *in vivo* (Figs 16–18). Sporangia are scattered over both surfaces of the thallus, either singly or grouped in small sori (Figs 19–20). Although reported for this species (Nizamuddin & Gerloff 1979), specimens examined in this study do not possess a multilayered medulla near the base of the thallus.

Dictyota canariensis (Grunow) Tronholm *stat. nov.*
Figs 21–28

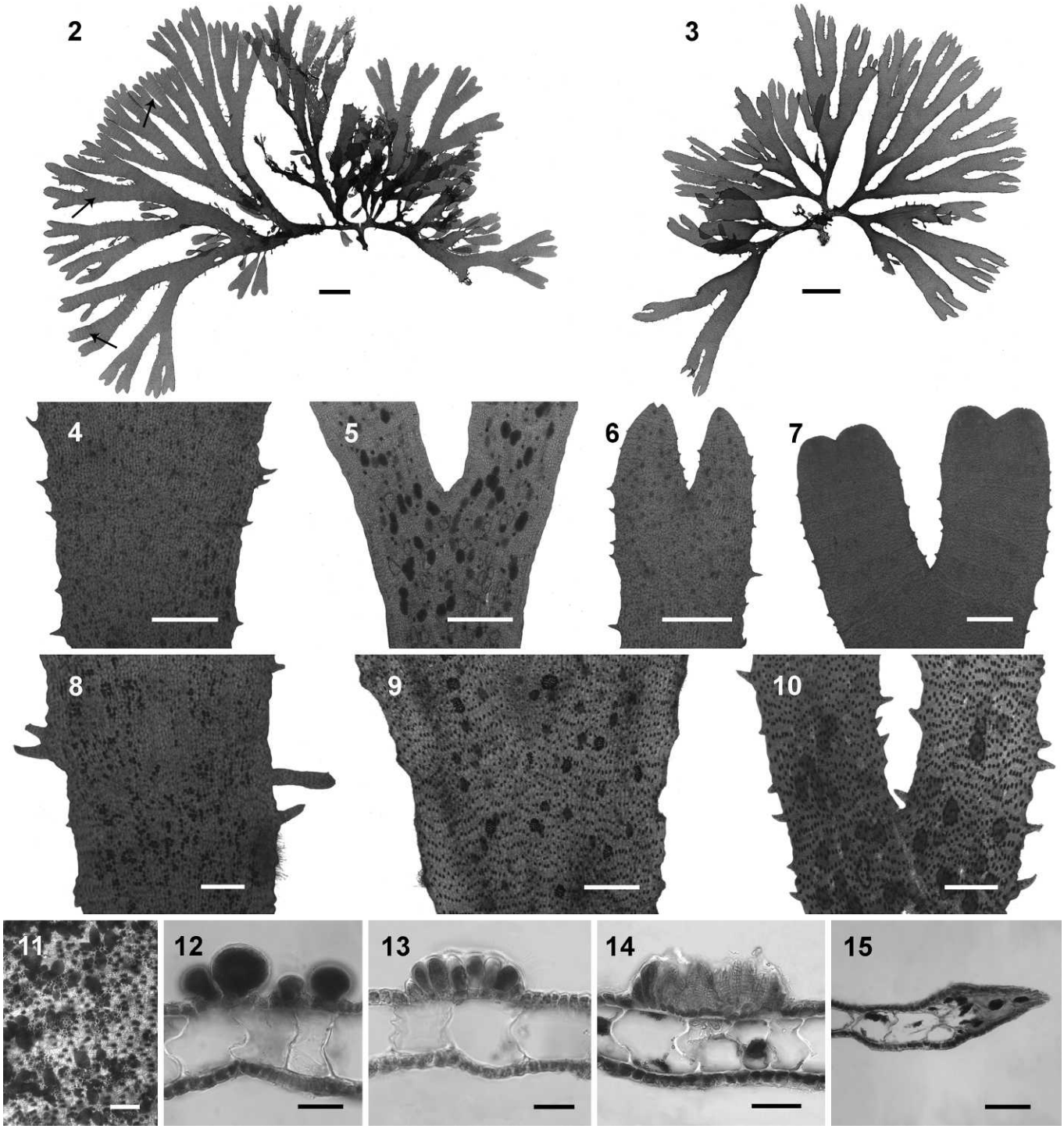
BASIONYM: *Dictyota crenulata* var. *canariensis* Grunow *in* Piccone, *Crociera del Corsaro alle Isole Madera e Canarie del Capitano Enrico d'Albertis. Alghe*. p. 54 (1884).

Dictyota crenulata var. *canariensis* Grunow was described from material collected by Liebetruth in the Canary Islands. In the absence of a holotype, a lectotype (W18753) was selected by Nizamuddin & Gerloff (1979) from the Grunow Herbarium in W. Nizamuddin & Gerloff (1979) also reported this variety from Madeira, based on a specimen collected by Liebetruth in 1863 and misidentified as *Dictyota ciliata* J. Agardh (deposited in B; No. 24708). Re-examination of the type material of *D. crenulata* var. *canariensis* (Fig. 21) and the specimen from Madeira (Fig. 22) has shown that these are morphologically similar to individuals recently collected in the Canary Islands, which were recognised as a distinct species (*D. crenulata* #2) in the DNA-based species delimitation analysis of Tronholm *et al.* (2012).

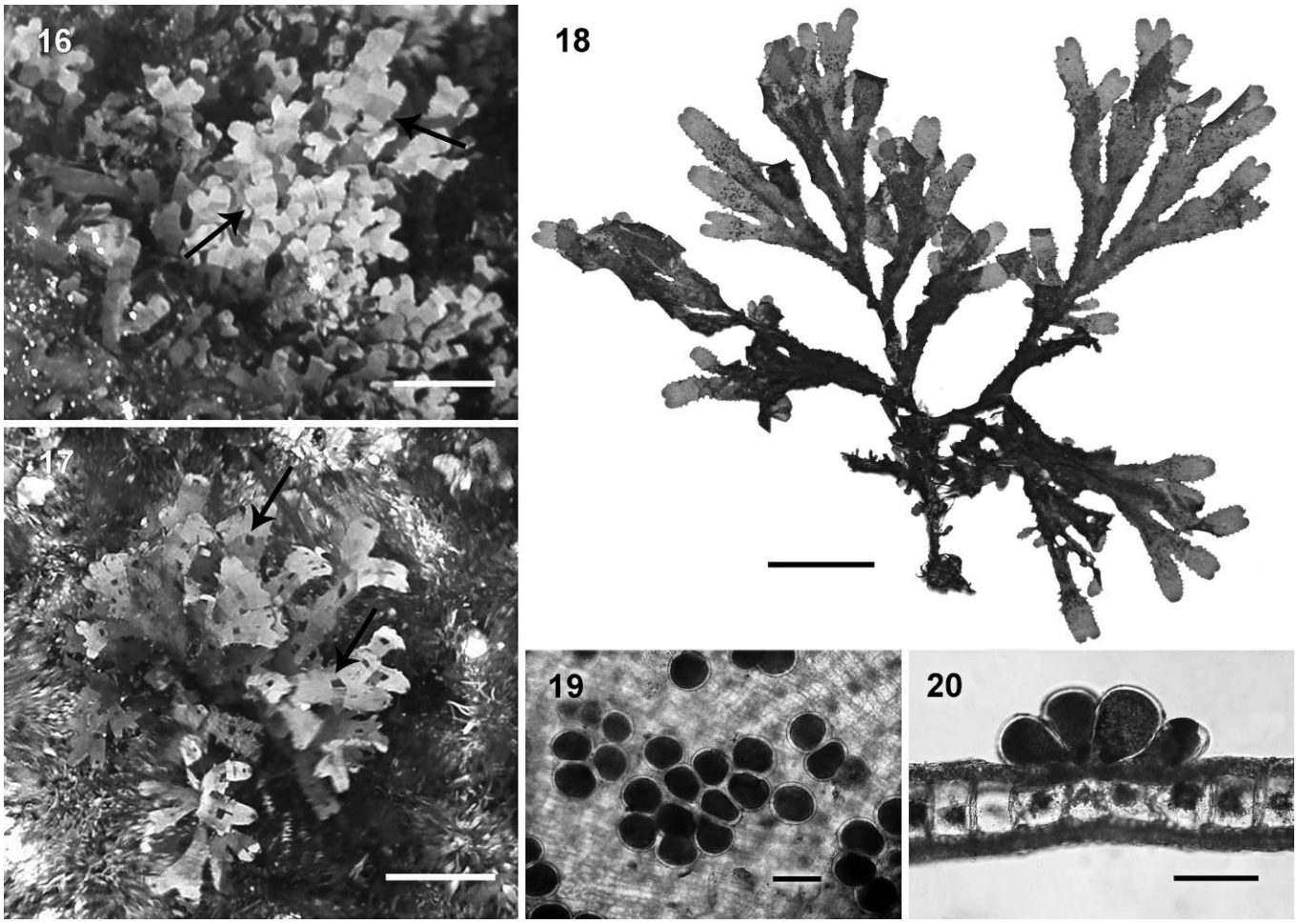
Dictyota canariensis is characterised by a blue-greenish iridescence; square or rectangular pigmented patches that are often present near the apices; regularly dentate margins with minute, triangular teeth; rounded to obtuse apices (Figs 23–25); and frequent surface proliferations (Fig. 26). The medulla is unilayered throughout, and sporangia are scattered singly on both thallus surfaces (Figs 27–28). Gametophytes have not been found so far. In general, the growth form of *D. canariensis* depends on the developmental stage, as juvenile thalli have a cushion-like habit but later develop into longer erect straps. This species grows at exposed localities in low-intertidal pools and in the shallow sublittoral, either epilithically or anchored to rock covered with coarse sand.

Dictyota jamaicensis Taylor 1960: 630–631
Figs 29–35

Dictyota jamaicensis was described by Taylor from Christopher's Cove (Drax Estates, Jamaica) to accommodate Caribbean specimens superficially resembling *D. crenulata*. Due to the morphological similarity of the two taxa, several authors have proposed that *D. jamaicensis* is a synonym of *D. crenulata* (Dawson 1962; Nizamuddin & Gerloff 1979; Hörnig *et al.* 1992a; Wysor & De Clerck 2003). According to Tronholm *et al.* (2012), however, Caribbean–Cape Verdean and the Canarian specimens previously identified as *D. crenulata* formed two lineages, *D. crenulata* #3 and *crenulata* #4 respectively, both distinct from genuine *D. crenulata*. The type material of *D. jamaicensis* (MICH 29205; Fig. 29) closely resembles the specimens from the Caribbean and Macaronesia used in our analyses in growth form, type of dentation and shape of apical segments (Figs 30–33). Although this latter character is not always present, the revision of material from W.R. Taylor's herbarium revealed that many Caribbean specimens (filed as *D. ciliolata*) show pigmented patches in their dichotomies (MICH 32709, MICH 67–833, Barbados; MICH 34059, Saint Kitts). We therefore accept *D. jamaicensis* and the amphi-Atlantic lineage *D. crenulata* #3 as the same taxonomic entity. This species is characterised by spathulate apices (Fig. 32) and spinose to ciliate teeth on the margins (Fig. 33). Sporophytes bear sporangia scattered mainly on one surface of the



Figs 2–15. *Dictyota ciliolata*.
Figs 2–3. Specimens from the Canary Islands (TFC Phyc 13052, TFC Phyc 14598, respectively), note the transverse banding pattern (arrows). Scale bar = 1 cm.
Fig. 4. Detail of an immature female gametophyte showing margins with ciliate teeth (TFC Phyc 14602). Scale bar = 2 mm.
Fig. 5. Detail of a male gametophyte showing smooth margins (TFC Phyc 14603). Scale bar = 2 mm.
Fig. 6. Detail of acutely tapering apices (TFC Phyc 14604). Scale bar = 1 mm.
Fig. 7. Detail of broadly rounded apices (TFC Phyc 14604). Scale bar = 1 mm.
Fig. 8. Surface view of solitary sporangia (TFC Phyc 14606). Scale bar = 1 mm.
Fig. 9. Surface view of female sori (TFC Phyc 14602). Scale bar = 1 mm.
Fig. 10. Surface view of male sori (TFC Phyc 14605). Scale bar = 1 mm.
Fig. 11. Detail of germinating sporangia on the thallus surface (TFC Phyc 14606). Scale bar = 400 μm.
Fig. 12. Transverse section of the thallus showing sporangia borne on a single stalk cell (TFC Phyc 14606). Scale bar = 50 μm.
Fig. 13. Transverse section of female sorus (TFC Phyc 14602). Scale bar = 50 μm.
Fig. 14. Transverse section of male sorus (TFC Phyc 14605). Scale bar = 50 μm.
Fig. 15. Transverse section of a marginal tooth (TFC Phyc 14606). Scale bar = 100 μm.



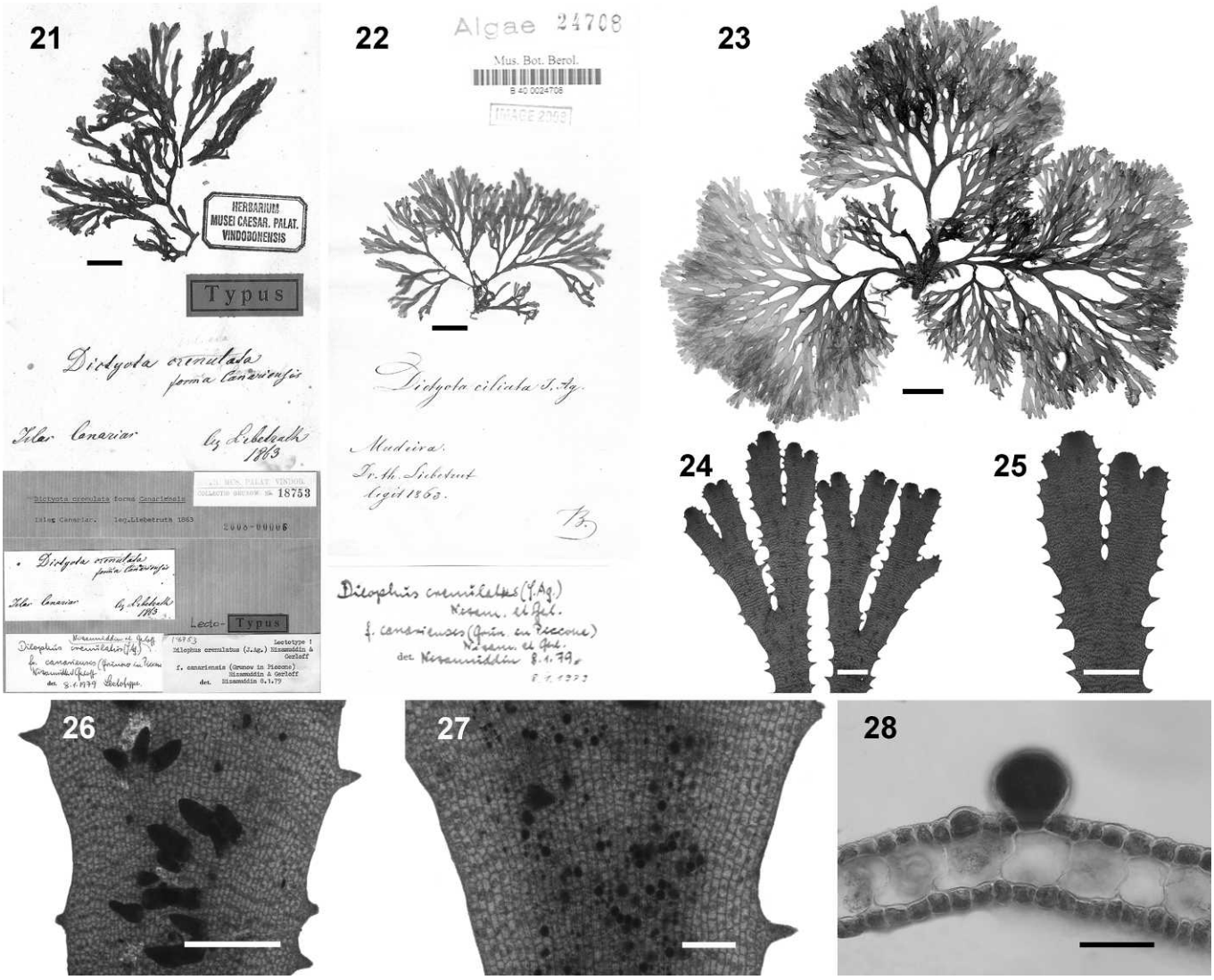
Figs 16–20. *Dictyota crenulata sensu stricto*.
Fig. 16. *In situ* habit of a specimen (CFMX-206) showing transverse banding pattern (arrows). Scale bar = 1 cm.
Fig. 17. *In situ* habit of a specimen (CFMX-321) with square-like dark patches (arrows). Scale bar = 1 cm.
Fig. 18. A typical sporophyte habit from Mexico (MX0082). Scale bar = 1 cm.
Fig. 19. Surface view of solitary and grouped sporangia (CFMX-206). Scale bar = 100 μm.
Fig. 20. Transverse section of the thallus showing sporangia borne on a single stalk cell (CFMX-206). Scale bar = 100 μm.

thallus, either singly or grouped in small sori (Figs 34–35). The medulla is unilayered throughout the thallus (Fig. 35).

The molecular analysis of Tronholm *et al*. (2012) showed that several dentate specimens from the Canary Islands formed a distinct species lineage (*Dictyota crenulata* #4). Since this lineage does not correspond to any described taxon, we describe it here as a new species, *D. pleiacantha*.

Dictyota pleiacantha Tronholm *sp. nov*.
Figs 36–46

DESCRIPTION: Thallus (8.4–)10.6–11.9(–14.5) cm long, erect, stiff, crisp, often spirally twisted in basal parts, attached to the substrate by rhizoids that form a discoid holdfast. Colour *in situ* greenish–pale brown, frequently with inverted triangular dark patches in the dichotomies. Dried specimens retaining the colour; triangular patches usually still visible. The width of the axes uniform throughout the thallus; interdichotomies (4–)10.6–11.2(–26) mm long and (2.5–)4.9–5.1(–7) mm wide. Apices rounded, elongate and spathulate, (1–)1.4–1.5(–2.5) mm wide, apical cell protruding. Branching subdichotomous, with more-or-less distinct main axes (10–)12–13(–15) times forked, the branch angles acute toward apical segments (17–)27–29(–62)°, broader in middle and basal segments (28–)54–57(–81)°. Margins dentate, the teeth spinose to ciliate orientated toward the apices; segments often with marginal proliferations. Germinating sporangia common on basal parts of the thallus. Cortex unilayered, cells (26–)41–43(–79) μm long, (12–)17–18(–29) μm wide and (12–)17–18(–26) μm high. Medulla unilayered, cells (105–)198–207(–330) μm long, (45–)81–84(–120) μm wide and (55–)103–110(–202) μm high. Sporangia scattered singly on both thallus surfaces, dark brown, (76–)92–96(–114) μm in diameter, borne on a single stalk cell (7–)15–16(–24) μm high. Oogonia grouped in dark brown oval sori, the sori (255–)351–371(–570) μm long, (165–)263–283(–405) μm wide, with (25–)61–65(–91) oogonia *per* sorus. Mature oogonia (26–)46–51(–110) μm in diameter (57–)77–81(–114) μm high, borne on a single stalk cell (7–)16–17(–24) μm high. Antheridia grouped in ellipsoidal whitish sori (270–)366–396(–495) μm long and (165–)232–245(–270) μm wide, surrounded by (1–)2(–3) rings of pigmented paraphyses, the antheridia (57–)65–68(–81) μm high, borne on a single stalk cell (12–)14–15(–17) μm high. Paraphyses unicellular (79–)90–93(–100) μm high.



Figs 21–28. *Dictyota canariensis*.
Fig. 21. Lectotype of *Dictyota crenulata* var. *canariensis* (W18753). Scale bar = 1 cm.
Fig. 22. *Dictyota crenulata* var. *canariensis* specimen from Madeira (B24708). Scale bar = 1 cm.
Fig. 23. Recently collected specimen of *D. canariensis* (TFC Phyc 14478). Scale bar = 1 cm.
Fig. 24. Subdichotomous branching of a distal segment (TFC Phyc 14600). Scale bar = 2 mm.
Fig. 25. Detail of broadly rounded apices and dentate margins with triangular teeth (TFC Phyc 14600). Scale bar = 2 mm.
Fig. 26. Surface proliferations on lower segments (TFC Phyc 14601). Scale bar = 1 mm.
Fig. 27. Surface view of solitary sporangia (TFC Phyc 14601). Scale bar = 400 μm.
Fig. 28. Transverse section showing sporangia borne on a single stalk cell, note unilayered medulla (TFC Phyc 14601). Scale bar = 50 μm.

ETYMOLOGY: *plei* (Greek) = (in compounds), many-; *acantha* (Greek) = spine, prickle

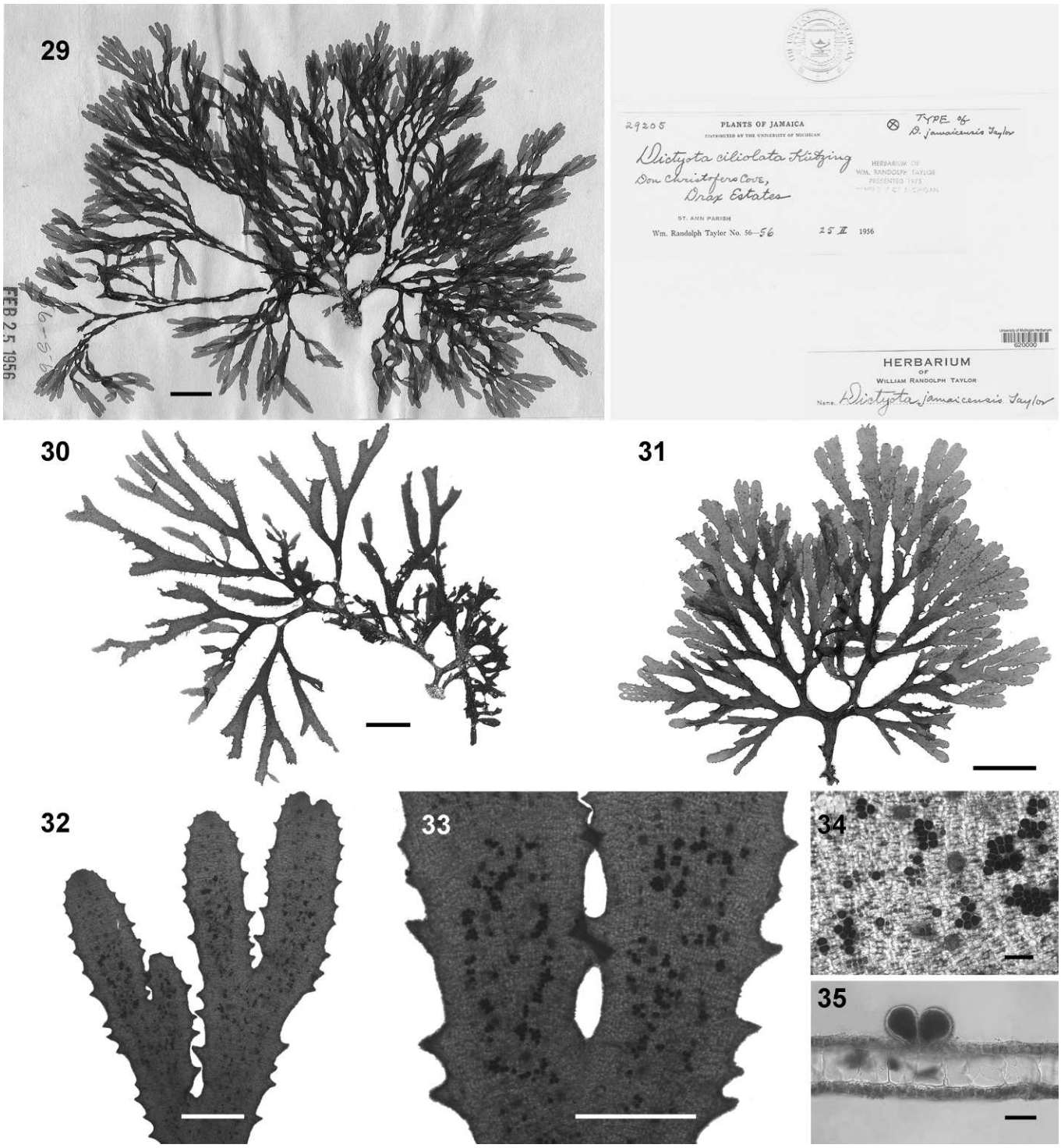
HOLOTYPE: TFC Phyc 13161 (D193), Punta del Hidalgo, Tenerife, Canary Islands (28°34′N, 16°20′W), A. Tronholm, M. Sansón & J. Afonso-Carrillo, 21 December 2005, sporophyte.

ISOTYPE: TFC Phyc 14466 (D401) in Gent.

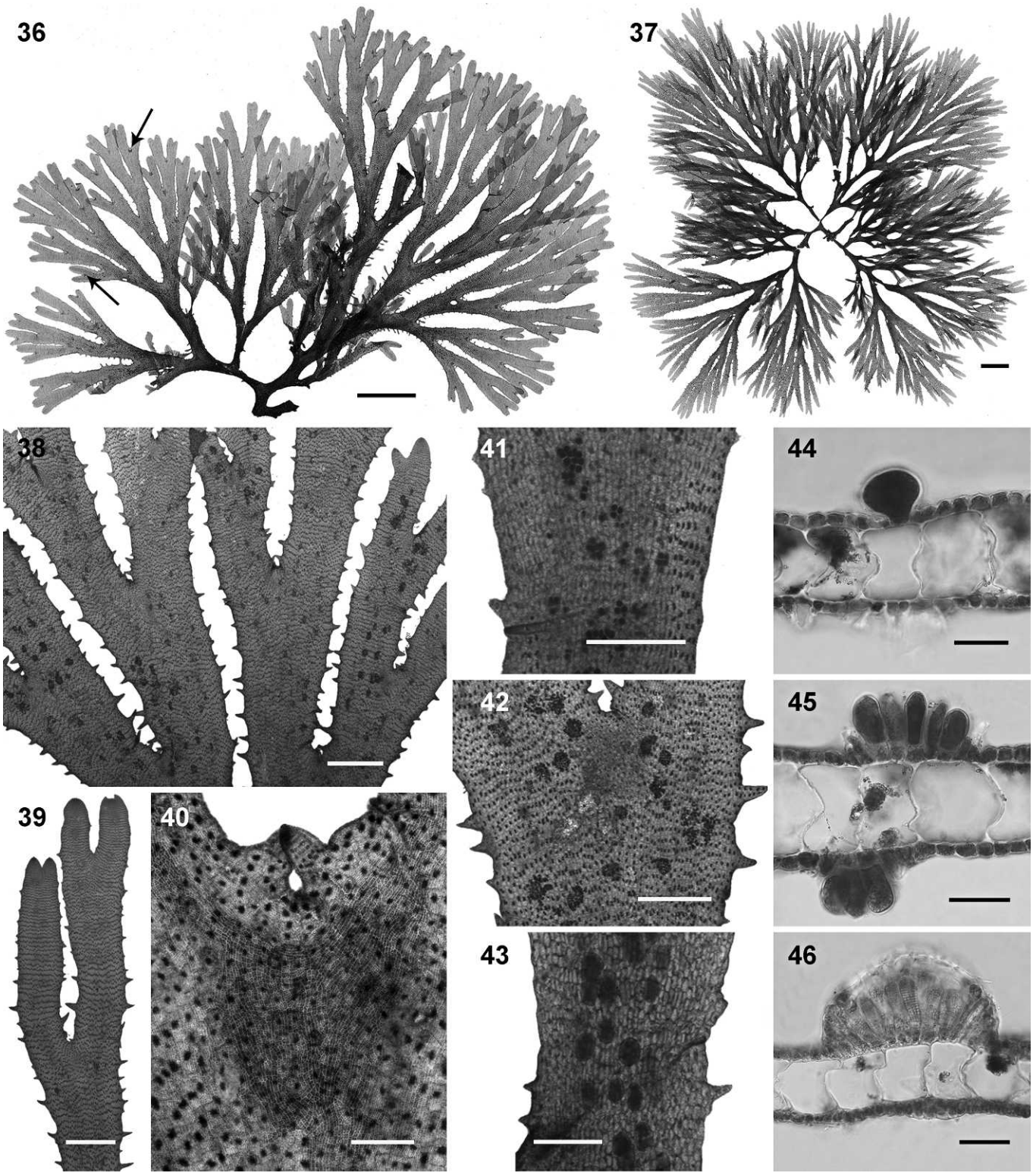
OTHER SPECIMENS EXAMINED: **Canary Islands:** Tenerife, Punta del Hidalgo, *leg*. A. Tronholm (5 June 2003, TFC Phyc 14460–14461, females; 14 January 2007, TFC Phyc 14462, sporophyte; 10 April 2007, TFC Phyc 14463, D310, sterile; 6 May 2007, TFC Phyc 14464, D335, female; 11 July 2007, TFC Phyc 14465, D400, male; 11 July 2007, TFC Phyc 14466, D401, sporophyte; 30 August 2007, TFC Phyc 14467, D402, sporophyte; 28 September 2007, TFC Phyc 14468-14469-14470, males, TFC Phyc 14471, sporophyte, TFC Phyc 14472, female; 13 March 2008, TFC Phyc 14473, sporophyte; 28 February 2009, TFC Phyc 14474, sporophyte); Playa de Las Arenas, *leg*. A. Tronholm (14 April 2007, TFC Phyc 14475, D324, sterile); El Médano, *leg*. A. Tronholm (31 August 2007, TFC Phyc 14476, D404, sporophyte); Gran Canaria, Faro de Maspalomas, *leg*. A. Tronholm (17 August 2007, TFC Phyc 14477, D394, sporophyte).

DISTRIBUTION: The species is only known from the Canary Islands.

HABITAT: This species grows epilithically at exposed localities in low-intertidal pools and the shallow sublittoral.



Figs 29–35. *Dictyota jamaicensis*.
Fig. 29. Holotype specimen (MICH 29205). Scale bar = 1 cm.
Fig. 30. Specimen from Dominican Republic (TFC Phyc 14596, DR27–28). Scale bar = 1 cm.
Fig. 31. Specimen from Cape Verde Is. (TFC Phyc 14597). Scale bar = 1 cm.
Fig. 32. Detail of spathulate apices (TFC Phyc 14597). Scale bar = 2 mm.
Fig. 33. Detail of a sporophytic medial segment showing serrate margins (TFC Phyc 14597). Scale bar = 2 mm.
Fig. 34. Surface view of solitary and grouped sporangia (TFC Phyc 14597). Scale bar = 200 μm.
Fig. 35. Transverse section of the thallus showing sporangia borne on a single stalk cell, note unilayered medulla (TFC Phyc 14597). Scale bar = 50 μm.



Figs 36–46. *Dictyota pleiacantha.*

Fig. 36. Image of a sporophyte, Punta del Hidalgo, Tenerife, Canary Islands designated as holotype (TFC Phyc 13161; D193). Note the inverted triangular dark patches at dichotomies (arrows). Scale bar = 1 cm.

Fig. 37. Sporophytic topotype (TFC Phyc 14599). Scale bar = 1 cm.

Fig. 38. Branch dichotomies in a medial segment (TFC Phyc 14607). Scale bar = 2 mm.

Fig. 39. Rounded and tapering apices of a serrate distal segment (TFC Phyc 14608). Scale bar = 2 mm.

Fig. 40. Detail of an inverted triangular dark patch at a segment dichotomy (TFC Phyc 14608). Scale bar = 400 μm.

Fig. 41. Surface view of solitary sporangia (TFC Phyc 14608). Scale bar = 1 mm.

DISCUSSION

The present study deals with the taxonomic implications derived from the findings in Tronholm *et al*. (2012) regarding the species composition of the *Dictyota ciliolata* and *D. crenulata* complex. This molecular-phylogenetic study demonstrated the existence of four lineages in the *D. crenulata* complex; although, no formal names were assigned to each of these entities. In the present paper we reinvestigated the validity of these taxa, and we now assign the following species names to the corresponding genetic lineages: *D. crenulata* #1 is considered to represent the genuine *D. crenulata*, and it is restricted to the Pacific coast of Central America; *D. crenulata* #2 is assigned to *D. canariensis*, and it is only known from Macaronesia; *D. crenulata* #3 is assigned to *D. jamaicensis*, and it has an amphi-Atlantic distribution and *D. crenulata* #4 is described as *D. pleiacantha sp. nov*., and it is known only from the Canary Islands.

As shown in Table 1, one of the most relevant morphological diagnostic characters to distinguish *Dictyota canariensis*, *D. ciliolata*, *D. crenulata*, *D. jamaicensis* and *D. pleiacantha* is the presence of iridescence and its form, a feature that is rarely mentioned in historic descriptions. Both *D. canariensis* and *D. crenulata* show blue-greenish iridescence and square dark patches, near the apices in the former and over the whole thallus length in the latter, as well as a broad and pale transverse banding pattern, which is absent in *D. canariensis*. On the contrary, iridescence in *D. ciliolata* is yellow-greenish forming a conspicuous transverse banding pattern. Neither *D. pleiacantha* nor *D. jamaicensis* seem to show iridescence; although, inverted triangular dark patches in dichotomies are frequent in the former and sometimes present in the latter. Apices are rounded to obtuse in all species, except in *D. jamaicensis* and *D. pleiacantha*, which are somewhat spathulate. Teeth in *D. crenulata* and *D. canariensis* are smaller, more regular and triangular than in the other dentate species, which are ciliate to spinose. Sporangia are solitary in all species; although, it can also been observed forming small groups in *D. crenulata* and *D. jamaicensis*. It is unclear at present if *D. ciliolata* var. *bermudensis* Taylor (1960) is synonymous with *D. jamaicensis*. Wysor & De Clerck (2003) suggested that this variety of *D. ciliolata* might actually represent a growth form of *D. crenulata* but its affinities can still not be verified in the absence of topotype material.

A morphological comparison of dentate species of *Dictyota* (Table S2) shows that two other dentate members, *D. grossedentata* and *D. sandvicensis*, are morphologically as well as phylogenetically distinct from both the *D. ciliolata* and *D. crenulata* complexes of species (Tronholm *et al*. 2012). *Dictyota grossedentata* can be easily recognised by its prostrate habit, regularly triangular teeth and right-angled branching. *Dictyota sandvicensis* typically has spathulate marginal proliferations not present in any of the other species (De Clerck 2003; Abbott & Huisman 2004). No molecular data are available for *D. hauckiana* Nizamuddin and *D. spinulosa* J. D. Hooker & Arnott but their morphological characterisations are straightforward. *Dictyota hauckiana* is one of the largest species of the genus (up to 50 cm), characterised by conspicuous and numerous ciliate teeth, infrequent branching, and sporangia grouped in sori. *Dictyota spinulosa* is distinguishable by its spinose surface proliferations in addition to marginal teeth (Harvey *in* Hooker & Arnott 1838; Kützing 1859; Okamura 1915; De Clerck 2003). Recently, another dentate species, *D. dolabellana* De Paula, Yoneshigue-Valentin & Teixeira, was described based on morphological and biochemical data (De Paula *et al*. 2007). Differences between this species and *D. ciliolata* or *D. jamaicensis* are subtle and consist in having triangular and perpendicular teeth mainly in apical parts of the thallus, instead of the ciliate or spinose dentation of the latter. Although no molecular data are available for *D. dolabellana*, chemical results appear to be conclusive, since this species is the only dentate member of *Dictyota* that produces dolabellane diterpenes.

In addition, we investigated the relationships of *Dictyota ciliolata* with *D. menstrualis* and *D. plectens*. *Dictyota ciliolata* resembles the western Atlantic *D. menstrualis* in overall morphology, and the distinctness between both taxa has been questioned previously (e.g. Earle 1969). Examination of specimens in W.R. Taylor's herbarium (MICH) reveals that many specimens from the tropical and warm-temperate western Atlantic Ocean identified as *D. menstrualis* fall completely within the morphological boundaries of *D. ciliolata*, even to the extent of showing the typical transverse banding pattern (e.g. MICH 14986, 24018, 24019, 49-287A, 49-1640, 32144). In addition, a haplotype network of *psb*A sequence data shows that specimens from North Carolina identified as *D. menstrualis* were not clearly distinct from the *D. ciliolata* haplotypes.

Dictyota plectens has also been questionably distinguished from *Dictyota ciliolata* (Kraft 2009, pp. 191, 334). This species was originally described as *Dictyota bartayresiana* ('*bartayresii*') var. *plectens* by Allender & Kraft (1983, p. 114) based on specimens from its type locality, Lord Howe Island in the southern Coral Sea. The justification for this putative species was rendered doubtful, however, by De Clerck & Coppejans (1997), who demonstrated that the name *Dictyota bartayresiana* had erroneously been used for a taxon known as *Canistrocarpus crispatus* (Lamouroux) De Paula & De Clerck. Sequence data, however, revealed that *Dictyota bartayresiana* var. *plectens* was phylogenetically distinct from both *Canistrocarpus crispatus* and *Dictyota bartayresiana*, instead coming closest to *Dictyota ciliolata* (De Clerck *et al*. 2006). Because the final disposition of the

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Fig. 42. Surface view of female sori (TFC Phyc 14607). Scale bar = 1 mm.
Fig. 43. Surface view of male sori (TFC Phyc 14609). Scale bar = 1 mm.
Fig. 44. Transverse section with a stalked sporangium (TFC Phyc 14608). Scale bar = 50 μm.
Fig. 45. Transverse section of two oogonial sori (TFC Phyc 14607). Scale bar = 50 μm.
Fig. 46. Transverse section of an antheridial sorus (TFC Phyc 14609). Scale bar = 50 μm.

entity was left unresolved, Kraft (2009) raised it to provisional species status.

Future research, using less conservative markers, could yet indicate that both *Dictyota menstrualis* and *D. plectens* are after all distinct lineages warranting species status but if that should prove the case, it is most likely that *D. ciliolata* proper will have to be subdivided into a large number of other cryptic and pseudocryptic species.

Dictyota kohlmeyeri is also similar to *D. ciliolata* in external morphology, since it too displays dentate margins (see Hörnig *et al*. 1992b; Afonso-Carrillo & Sansón 1999). This species was originally described as *Dilophus kohlmeyeri* by Nizamuddin & Gerloff (1979, p. 870) from material collected by Kohlmeyer near Puerto de la Cruz (north of Tenerife, Canary Islands). Apart from the original description, little is known about this Macaronesia-endemic species (John *et al*. 2004). Despite extensive sampling in the surroundings of Puerto de la Cruz (Sauvageau 1912; Børgesen 1926; Pinedo *et al*. 1992; Tronholm, personal observations), it seems never to have been recollected. The type material of *D. kohlmeyeri* (B 27031) consists of a collection of 10 specimens (sporophytes and gametophytes; Fig. S1 in the supplementary material). A critical examination of this material revealed that all specimens fall within the morphological limits of *D. ciliolata*, since it shows a typical banding pattern and dentation. Contrary to the claims of the original description, we found no evidence of a multilayered medulla in basal or distal parts of the thallus. We therefore consider *D. kohlmeyeri* as a taxonomic synonym of *D. ciliolata*.

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SUPPLEMENTARY DATA

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REFERENCES

Abbott I.A. & Huisman J.M. 2004. *Marine green and brown algae of the Hawaiian Islands*. Bishop Museum Press, Honolulu. 259 pp.

Afonso-Carrillo J. & Sansón M. 1999. *Algas, hongos y fanerógamas marinas de las islas Canarias. Clave analítica*. Serie Biología 2. Materiales Didácticos Universitarios. Servicio de Publicaciones de la Universidad de La Laguna, La Laguna, Tenerife. 254 pp.

Agardh J.G. 1847. Nya alger från Mexico. Öfversigt af Kongl. *Vetenskaps-Adademiens Förhandlingar, Stockholm* 4: 5–17.

Allender B.M. & Kraft G.T. 1983. The marine algae of Lord Howe Island (New South Wales): the Dictyotales and Cutleriales (Phaeophyta). *Brunonia* 6: 73–130.

Børgesen F. 1926. Marine algae from the Canary Islands especially from Teneriffe and Gran Canaria II. Phaeophyceae. *Kongelige Danske Videnskabernes Selskab, Biologiske Meddelelser* 6: 1–112.

Clement M., Posada D. & Crandall K.A. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657–1659.

Dawson E.Y. 1962. Additions to the marine flora of Costa Rica and Nicaragua. *Pacific Naturalist* 3: 375–395.

De Clerck O. 2003. *The genus Dictyota in the Indian Ocean*. Opera Botanica Belgica 13. National Botanic Garden of Belgium, Meise. 205 pp.

De Clerck O. & Coppejans E. 1997. The genus *Dictyota* (Dictyotaceae, Phaeophyta) from Indonesia in the Herbarium Weber-van Bosse, including the description of *Dictyota canaliculata* spec. nov. *Blumea* 42: 407–420.

De Clerck O. & Coppejans E. 1999. Two new species of *Dictyota* (Dictyotales, Phaeophyta) from the Indo-Malayan region. *Phycologia* 38: 184–194.

De Clerck O., Leliaert F., Verbruggen H., Lane C.E., De Paula J.C., Payo D.A. & Coppejans E. 2006. A revised classification of the Dictyoteae (Dictyotales, Phaeophyceae) based on *rbc*L and 26S ribosomal DNA sequence analyses. *Journal of Phycology* 42: 1271–1288.

De Paula J.C., Bomeny Bueno L., de Palmer Paixão Frugulhetti I.C., Yoneshigue-Valentin Y. & Teixeira V.L. 2007. *Dictyota dolabellana* sp. nov. (Dictyotaceae, Phaeophyceae) based on morphological and chemical data. *Botanica Marina* 50: 288–293.

Earle S.A. 1969. Phaeophyta of the eastern Gulf of Mexico. *Phycologia* 7: 71–254.

Holmgren P.K., Holmgren N.H. & Barnett L.C. 1990. *Index herbariorum Part I: the herbaria of the world*, ed. 8. Regnum Vegetabile 120. International Association of Plant Taxonomy, New York Botanical Garden, New York. 693 pp.

Hooker W.J. & Arnott G.A. 1838. *The botany of Captain Beechey's voyage; comprising an account of the plants collected by Messrs Lay and Collie, and other officers of the expedition, during the voyage to the Pacific and Bering's Strait, performed in His Majesty's Ship Blossom, under the command of Captain F.W. Beechey, R.N., F.R. & A.S., in the years 1825, 26, 27, and 28*. pp. 241–288. Henry G. Bohn, London.

Hörnig I. & Schnetter R. 1988. Notes on *Dictyota dichotoma*, *D. menstrualis*, *D. indica* and *D. pulchella* spec. nova (Phaeophyta). *Phyton* 28: 277–291.

Hörnig I., Schnetter R. & Prud'homme van Reine W.F. 1992a. The genus *Dictyota* (Phaeophyceae) in the North Atlantic. I. A new generic concept and new species. *Nova Hedwigia* 54: 45–62.

Hörnig I., Schnetter R. & Prud'homme van Reine W.F. 1992b. The genus *Dictyota* (Phaeophyceae) in the North Atlantic. II. Key to the species. *Nova Hedwigia* 54: 397–402.

Hwang I.-K., Kim H.S. & Lee W.J. 2005. Polymorphism in the brown alga *Dictyota dichotoma* (Dictyotales, Phaeophyceae) from Korea. *Marine Biology* 147: 999–1015.

John D.M., Prud'homme van Reine W.F., Lawson G.W., Kostermans T.B. & Price J.H. 2004. A taxonomic and geographical catalogue of the seaweeds of the western coast of Africa and adjacent islands. *Beihefte zur Nova Hedwigia* 127: 1–339.

Kraft G.T. 2009. *Algae of Australia. Marine benthic algae of Lord Howe Island and the southern Great Barrier Reef, 2. Brown algae*. Australian Biological Resources Study & CSIRO Publishing, Canberra & Melbourne. 364 pp.

Kützing F.T. 1859. *Tabulae phycologicae*. Vol. 9. Nordhausen, Germany. 42 pp.

Nizamuddin M. & Gerloff J. 1979. New species and new combinations in the genus *Dilophus* J. Ag. *Nova Hedwigia* 31: 865–879.

Okamura K. 1915. *Icones of Japanese algae, vol. III*. Kazamashobo, Tokyo. pp. 123–218.

Piccone A. 1884. *Crociera del Corsaro alle Isole Madera e Canarie del Capitano Enrico d'Albertis*. *Alghe*. Tipografia del R. Istituto Sordo-Muti, Genova. 60 pp.

Pinedo S., Sansón M. & Afonso-Carrillo J. 1992. Algas marinas bentónicas de Puerto de la Cruz (antes Puerto Orotava), Tenerife (Islas Canarias). *Vieraea* 21: 29–60.

Sauvageau C. 1912. A propos des *Cystoseira* de Banyuls et Guéthary. *Bulletin de la Station Biologique d'Arcachon* 14: 133–556.

Taylor W.R. 1960. *Marine algae of the eastern tropical and subtropical coasts of the Americas*. The University of Michigan Press, Ann Arbor. 870 pp.

Tronholm A., Leliaert F., Sansón M., Afonso-Carrillo J., Tyberghein L., Verbruggen H. & De Clerck O. 2012. Contrasting geographical distributions as a result of thermal tolerance and long-distance dispersal in two allegedly widespread tropical brown algae. *PLoS ONE* 7: e30813.

Tronholm A., Sansón M., Afonso-Carrillo J. & De Clerck O. 2008. Distinctive morphological features, life-cycles phases and seasonal variations in subtropical populations of *Dictyota dichotoma* (Dictyotales, Phaeophyceae). *Botanica Marina* 51: 132–144.

Tronholm A., Sansón M., Afonso-Carrillo J., Verbruggen H. & De Clerck O. 2010a. Niche partitioning and the coexistence of two cryptic *Dictyota* (Dictyotales, Phaeophyceae) species from the Canary Islands. *Journal of Phycology* 46: 1075–1087.

Tronholm A., Steen F., Tyberghein L., Leliaert F., Verbruggen H., Ribera Siguán M.A. & De Clerck O. 2010b. Species delimitation, taxonomy and biogeography of *Dictyota* in Europe. *Journal of Phycology* 46: 1301–1321.

Womersley H.B.S. 1987. *The marine benthic flora of Southern Australia*. *Part II*. South Australian Government Printing Division, Adelaide. 484 pp.

Wysor B. & De Clerck O. 2003. An updated and annotated list of marine brown algae (Phaeophyceae) of the Caribbean coast of the Republic of Panama. *Botanica Marina* 46: 151–160.

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