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Redefining the taxonomic status of *Laurencia dendroidea* (Ceramiales, Rhodophyta) from Brazil and the Canary Islands

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Morphological and molecular studies have been performed on *Laurencia dendroidea* derived from Brazil and the Canary Islands. This species possesses all of the characters that are typical of the genus *Laurencia*, including the production of the first pericentral cell underneath the basal cell of the trichoblast; the production of tetrasporangia from particular pericentral cells without the formation of additional fertile pericentral cells; spermatangial branches that are produced from one of two laterals on the suprabasal cell of the trichoblasts; and a procarp-bearing segment that possesses five pericentral cells. The phylogenetic position of *L. dendroidea* was inferred by analysing the chloroplast-encoded *rbcL* gene sequences of 51 taxa. Phylogenetic analyses revealed that the taxa previously identified and cited in Brazil as *Laurencia filiformis*, *L. majuscula* and *L. obtusa* and in the Canary Islands as *L. majuscula* all represent the same taxonomic entity and examination of type material allowed us to identify this entity as *L. dendroidea*, whose type locality is in Brazil. *Laurencia obtusa* from the Northern Atlantic is confirmed to represent a distinct species, which displays high genetic divergence with respect to western and eastern Atlantic samples. The phylogenetic analyses also supported the nomenclatural transfer of *Chondrophyucus furcatus* (Cordeiro-Marino & M.T. Fujii) M.T. Fujii & Senties to *Palisada furcata* (Cordeiro-Marino & M.T. Fujii) Cassano & M.T. Fujii *comb. nov.*

Key words: *Chondrophyucus furcatus*, *Laurencia dendroidea*, molecular phylogeny, *Palisada furcata comb. nov.*, *rbcL*, Rhodomelaceae, Rhodophyta, taxonomy

Introduction

The red alga *Laurencia* and related genera comprise a very diverse group of species that has undergone several taxonomic changes in recent decades, culminating in the recognition of five genera: *Laurencia* J.V. Lamouroux, *Osmundea* Stackhouse, *Chondrophyucus* (Tokida & Saito) Garbary & J.T. Harper, *Palisada* (Yamada) K.W. Nam and *Yuzurua* (K.W. Nam) Martin-Lescanne. The changes made were based on both morphological and molecular approaches and involved the resurrection of the genus *Osmundea* (Nam *et al.*, 1994); the elevation of subgenus *Chondrophyucus* to generic rank (Garbary & Harper, 1998); new delineations of the genera *Chondrophyucus*, *Laurencia* and *Osmundea* (Nam, 1999); proposal and subsequent validation by Nam (2006, 2007) of the genus *Palisada*, based on Yamada's (1931) section *Palisadae*; and the establishment of the

genus *Yuzurua*, based on Nam's (1999) subgenus *Yuzurua* (Martin-Lescanne *et al.*, 2010).

Several morphological, anatomical and reproductive characters that are used in the taxonomy of the *Laurencia* complex of genera have been shown to possess diagnostic value only at the generic level (Saito, 1967; Nam *et al.*, 1994; Garbary & Harper, 1998; Nam, 1999, 2006). Likewise, many species are poorly defined and exhibit extensive morphological plasticity, which complicates their taxonomic delimitation. This complication is reflected by the large number of species and infra-specific taxa that have been assigned to the complex: Guiry & Guiry (2011) list 430 taxa but consider only 134 to be currently accepted taxonomically. The use of molecular markers has proved to be useful in delimiting taxa and inferring their phylogenetic relationships, and has corroborated the current generic classification (Nam *et al.*, 2000; McIvor *et al.*, 2002; Abe *et al.*, 2006; Fujii *et al.*, 2006; Díaz-Larrea *et al.*, 2007;

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Cassano *et al.*, 2009; Gil-Rodríguez *et al.*, 2009; Martin-Lescanne *et al.*, 2010; Rocha-Jorge *et al.*, 2010; Senties *et al.*, 2011).

The *Laurencia dendroidea*–*obtusa* complex exemplifies the morphological plasticity of *Laurencia* species, which has led to many misidentifications. This complex includes the type species of the genus *Laurencia*, *L. obtusa* (Hudson) J.V. Lamouroux, which was described as *Fucus obtusus* by Hudson (1778). Its type locality was originally unspecified but was probably Devon or Sussex, England, according to Maggs & Hommersand (1993) and Silva *et al.* (1996). *Laurencia obtusa* has long been one of the most commonly identified *Laurencia* species and has been reported from tropical, temperate and cold seas, assuming a cosmopolitan character. Many infraspecific taxa have been described within it (37 according to Guiry & Guiry, 2011). *Laurencia dendroidea* was originally described by J. Agardh (1852) and was collected from an unspecified site in Brazil. It was later included in the Brazilian species list by Martens (1870). Crouan & Crouan (in Mazé & Schramm, 1878) proposed two varieties and one form of *L. dendroidea* from Guadeloupe, namely var. *corymbifera* Crouan P.L. & H.M. Crouan, var. *tenuifolia* Crouan P.L. & H.M. Crouan and f. *denudata* P.L. Crouan & H.M. Crouan. They provided a minimal description for each of the three names, including only a brief phrase regarding the colours of the thalli to distinguish them. These taxa are considered to be *nomina subnuda* in P.C. Silva's on line *Index Nominum Algarum* (<http://ucjeps.berkeley.edu/INA.html>).

Yamada (1931) reduced *Laurencia dendroidea* to a variety of *L. obtusa*; he separated them on the basis that var. *dendroidea* had more slender branches than other varieties, and it lacked projecting surface cells. Taylor (1931) reported *L. dendroidea* from Brazil and also questioned its validity as an independent species. Following Yamada (1931), Taylor (1960) later considered vars *corymbifera* and *tenuifolia* and f. *denudata* to be synonyms of *L. obtusa*.

Until recently, *Laurencia obtusa* has been widely reported for the Brazilian coast (Joly, 1965; Oliveira Filho, 1969, 1977; Pedrini, 1980; Yoneshigue, 1985; Paes e Mello & Pereira, 1990; Figueiredo Creed & Yoneshigue-Valentin, 1997; Pinheiro-Joventino *et al.*, 1998; Da Gama *et al.*, 2002; Paradas *et al.*, 2010). In addition, specimens have been reported from Brazil that have similar morphology to *L. obtusa* but have been identified as *L. microcladia* Kützting (Joly, 1965; Oliveira Filho, 1969; Cordeiro-Marino, 1978; Figueiredo *et al.*, 2004), *L. heteroclada* Harvey (Oliveira Filho, 1969), *L. composita* Yamada (Oliveira Filho, 1969; Paes e Mello & Pereira, 1990),

L. arbuscula Sonder (Cordeiro-Marino *et al.*, 1983; Fujii, 1990), *L. scoparia* J. Agardh (Cordeiro-Marino *et al.*, 1983; Fujii, 1990), *L. majuscula* (Harvey) A.H.S. Lucas (Széchy & Nassar, 2005) and *L. filiformis* (Fujii, 1998; Fujii & Senties, 2005).

Fujii (1990) considered that *Laurencia heteroclada sensu* Oliveira Filho (1969), *L. microcladia sensu* Joly (1965) and Cordeiro-Marino (1978) and *L. obtusa sensu* Joly (1965) represented misidentifications of *L. arbuscula* or *L. scoparia*, although the latter species has been considered to be conspecific with *L. filiformis* by Rodríguez de Ríos & Saito (1983). Fujii (1998) argued that the taxa that were named as *L. arbuscula*, *L. scoparia*, *L. filiformis* f. *filiformis*, *L. filiformis* f. *dendritica* Saito & Womersley and *L. filiformis* f. *heteroclada* Saito & Womersley from Brazil form a species complex, but nevertheless maintained them as distinct entities. Later, Fujii & Senties (2005) recognized that specimens reported from Brazil as *L. arbuscula*, *L. scoparia* and *L. filiformis* and its varieties correspond to morphological variations of a single species, with the epithet *L. filiformis* taking priority over the others. This observation was confirmed when Fujii *et al.* (2006) analysed *rbcL* gene sequences and illustrates the great difficulty of taxonomic delimitation in *Laurencia* based solely on morphological features.

In this paper, our aim was to use detailed morphological observations and molecular analyses to establish whether *L. dendroidea* is distinct from *L. obtusa* and to determine the true identities of specimens from Brazil and the Canary Islands previously referred to the various *Laurencia* species listed above. Our phylogenetic analyses also allowed us to resolve the taxonomic position of *Chondrophycus furcatus* (Cordeiro-Marino & M.T. Fujii) Senties & M.T. Fujii, supporting transfer to the genus *Palisada* (Yamada) K.W. Nam.

Materials and methods

Morphological observations

Samples of *Laurencia dendroidea* were collected from Brazil and the Canary Islands (Spain). Voucher specimens and material for morphological study were fixed in 4% formalin–seawater or pressed as herbarium sheets. Transverse and longitudinal hand sections were made with a stainless-steel razor blade and stained with 0.5% aqueous aniline blue solution, acidified with 1 N HCl (Tsuda & Abbott, 1985). Living specimens were also examined to check for presence of *corps en cerise*. Measurements are given as length × diameter. Vouchers are deposited in HRJ, SP, SPF, UAMIZ, TFC and BCM. Additional specimens from the Botanical Museum Herbarium, Lund, Sweden (LD), the State

Herbarium of South Australia (AD), Trinity College Dublin, Ireland (TCD), Nationaal Herbarium Nederland, Leiden University, the Netherlands (L), the Herbarium of the University of São Paulo, Brazil (SPF), and the Herbarium of the Botanical Garden of Rio de Janeiro, Brazil (RB), were analysed for comparison. Specimens examined morphologically are listed in Appendix S1 (Supplementary material). Photomicrographs were taken with a Sony W5 digital camera (Tokyo, Japan) coupled to a Nikon microscope. Herbarium abbreviations follow the online *Index Herbariorum* (<http://www.nybg.org/bsci/ih/ih.html>).

Molecular analyses

Samples used for molecular analysis were dried in silica gel. Total DNA was extracted, after grinding in liquid nitrogen, using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA) following the manufacturer's instructions. A total of 51 *rbcL* sequences were used in this study, including 14 newly generated sequences; the rest were obtained from GenBank (Table S1, Supplementary material). For each sequence generated a total of 1467 base pairs of the *rbcL* gene were amplified in three overlapping parts with the primer pairs: FrbcLstart–R753, F492–R1150 and F993–RrbcS (Freshwater & Rueness, 1994), using PCR master mix (Promega, Madison, WI, USA). All PCR products were analysed by electrophoresis in 1% agarose to check product size and were purified with MicroSpinTMS-300 HR Columns (GE Healthcare Life Sciences, Piscataway, USA) in accordance with the manufacturer's instructions. Sequencing was carried out with BigDye Terminator Cycle Sequencing Reaction Kits (Applied Biosystems, NJ, USA) on an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems). The primers used for sequencing were those used for the PCR amplification. The full sequence was obtained from both DNA strands. Multiple alignments for *rbcL* sequences were constructed using the computer program BioEdit 7.0.4.1 (Hall, 1999) and are given in the Supplementary file.

Phylogenetic analyses

Phylogenetic relationships were inferred with PAUP 4.0b10 (Swofford, 2002) and MrBayes v.3.0 beta 4 (Huelsenbeck & Ronquist, 2001). Maximum-parsimony trees (MP) were constructed using the heuristic search option, tree-bisection-reconnection branch-swapping, and unordered and unweighted characters. Support values for the relationships discovered in each analysis were calculated by performing bootstrap analyses (Felsenstein, 1985), as implemented in PAUP. Ten thousand heuristic search replicates were executed using the TBR branch-swapping algorithm. The model used in the Bayesian analysis was the general-time-reversible model of nucleotide substitution with invariant sites and gamma distributed rates for the variable sites (GTR + I + G). This model was selected based on maximum-likelihood ratio tests implemented in Modeltest version 3.06 (Posada & Crandall, 1998) with a

significance level of 0.01 by the Akaike Information Criterion. For Bayesian analysis, four chains of the Markov chain Monte Carlo (one hot and three cold) were used, sampling one tree every 10 generations for 1 000 000 generations starting with a random tree. Log-likelihood values stabilized at around 50 000 generations, which were discarded as 'burn in'. A 50% consensus tree (majority rule as implemented by PAUP) was computed after the 'burn in' point. The range of *rbcL* divergence values within and among species was calculated using uncorrected 'p' distances using PAUP.

Results

Molecular analyses

We sequenced the *rbcL* gene for 14 specimens: eleven of *Laurencia sensu stricto*, two of *Palisada*, and *Chondria collinsiana* M.A. Howe. By adding sequences from GenBank, an alignment of 51 sequences was assembled, including *Ceramium brevizonatum*, *Bostrychia radicans*, *Chondria collinsiana*, *C. dasphylla* and *C. californica* as outgroups (Table S1). A total of 257 nucleotides was removed from the alignment at the beginning and end, as many sequences from the GenBank were incomplete, producing a data set of 1210 base pairs (Supplementary file 3).

Specimens of *Laurencia* from Brazil and the Canary Islands collected under various names – *L. arbuscula*, *L. cf. catarinensis*, *L. filiformis*, *L. majuscula* and *L. obtusa* – showed low levels of genetic variation for the *rbcL* gene. Based on the 1210 bp alignment, the Brazilian samples exhibited 0–0.90% genetic divergence, whereas among sequences for both Brazilian and Canaries specimens, there was 0.66–0.90% divergence. In contrast, *Laurencia obtusa* from the North Atlantic (Ireland) differed from the *Laurencia* specimens from Brazil and the Canary Islands ('*L. majuscula*') by 5.6–6.0%.

The data set consisted of 751 constant characters, 366 parsimony-informative sites and 93 parsimony non-informative sites. The analyses showed that *Laurencia* and related genera comprise a monophyletic group containing five clades, each with high support and corresponding to one of the currently recognized genera (Fig. 1). Within *Laurencia sensu stricto*, *rbcL* sequences of *Laurencia* specimens from Rio de Janeiro and Bahia resembling *L. arbuscula*, *L. filiformis*, *L. majuscula* and *L. obtusa*, together with Genbank sequences under the names *L. cf. catarinensis* and *L. arbuscula* from São Paulo (Fujii *et al.*, 2006) and *L. majuscula* from Tenerife, Canary Islands, Spain (Gil-Rodríguez *et al.*, 2009), formed a fully supported clade in all of the analyses. In all analyses, *Chondrophycus*

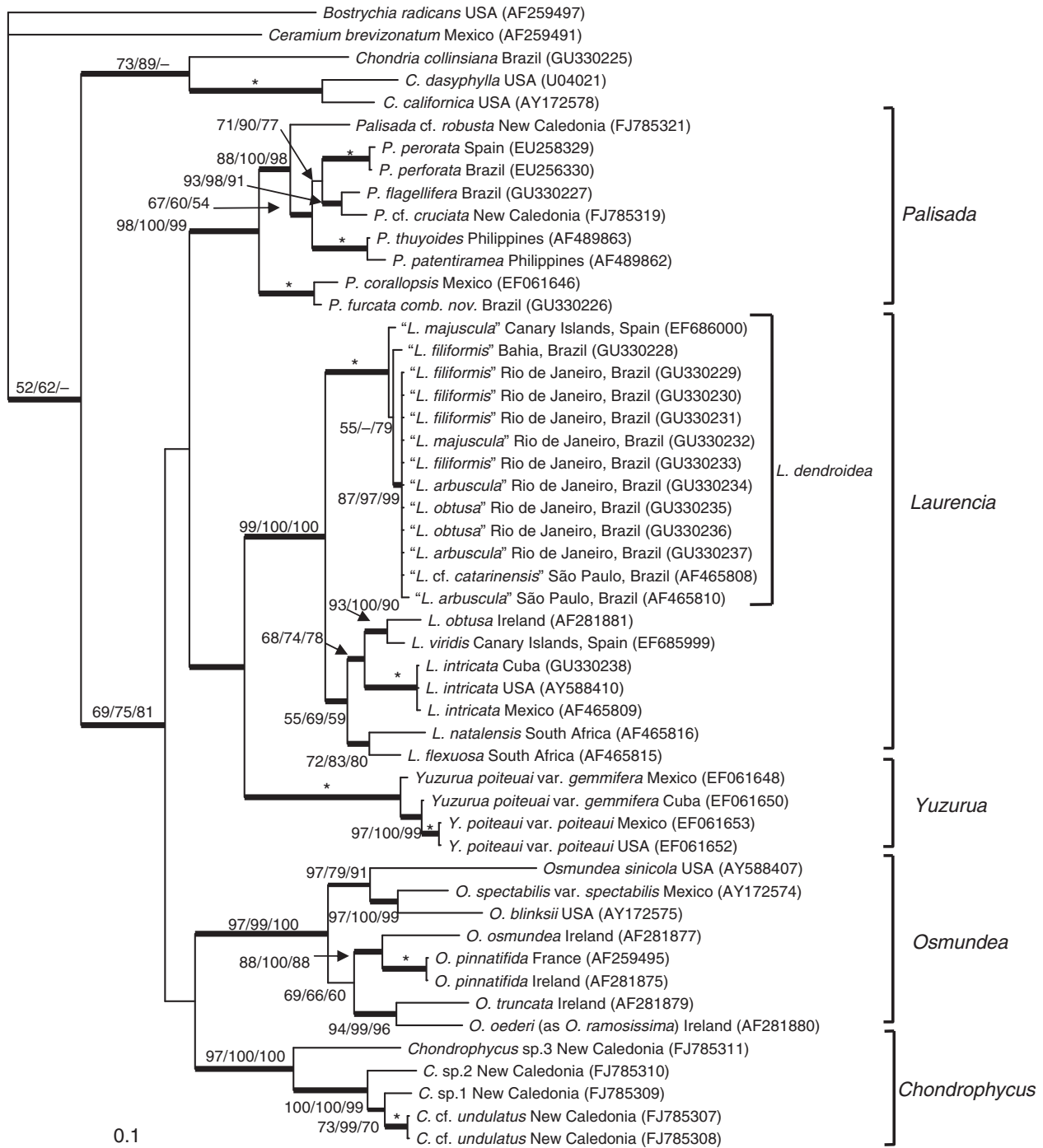


Fig. 1. Consensus tree derived from Bayesian analyses of *rbcL* sequences. The posterior probabilities (when > 95%) are shown as thicker branches. Bootstrap supports for MP/NJ (2000 replicates)/ML (100 replicates) are shown at the nodes; – indicates lack of bootstrap support; * indicates bootstrap support = 100%.

furcatus was phylogenetically distant from the genus *Chondrophycus*, and joined *Palisada* with high support.

Morphological comparisons

Given the *rbcL* evidence indicating conspecificity of Brazilian and Canaries specimens previously identified under a variety of different names, we

studied type specimens in order to discover their correct name, which proved to be *L. dendroidea*. We also re-examined herbarium specimens from Brazil and the Canaries to provide correct determinations for them and to establish the range of form within this species. Below, we give a unified, emended description for *L. dendroidea*, document its type, and make comparisons with species previously confused with it.

***Laurencia dendroidea* J. Agardh (1852, p. 753)**

(Figs 2–29)

HOMOTYPIC SYNONYM: *Laurencia obtusa* (Hudson) J.V. Lamouroux var. *dendroidea* (J. Agardh) Yamada, 1931: 224.

HETEROTYPIC SYNONYM: *Laurencia scoparia* J. Agardh, 1852: 746–747 (syntype localities: La Guaira, Venezuela; Brazil [Silva *et al.*, 1996: 509]).

LECTOTYPE: Botanical Museum Herbarium, Lund, Sweden (LD 36669)!

TYPE LOCALITY: Brazil (unspecified site).

DISTRIBUTION: Widespread in the Atlantic Ocean.

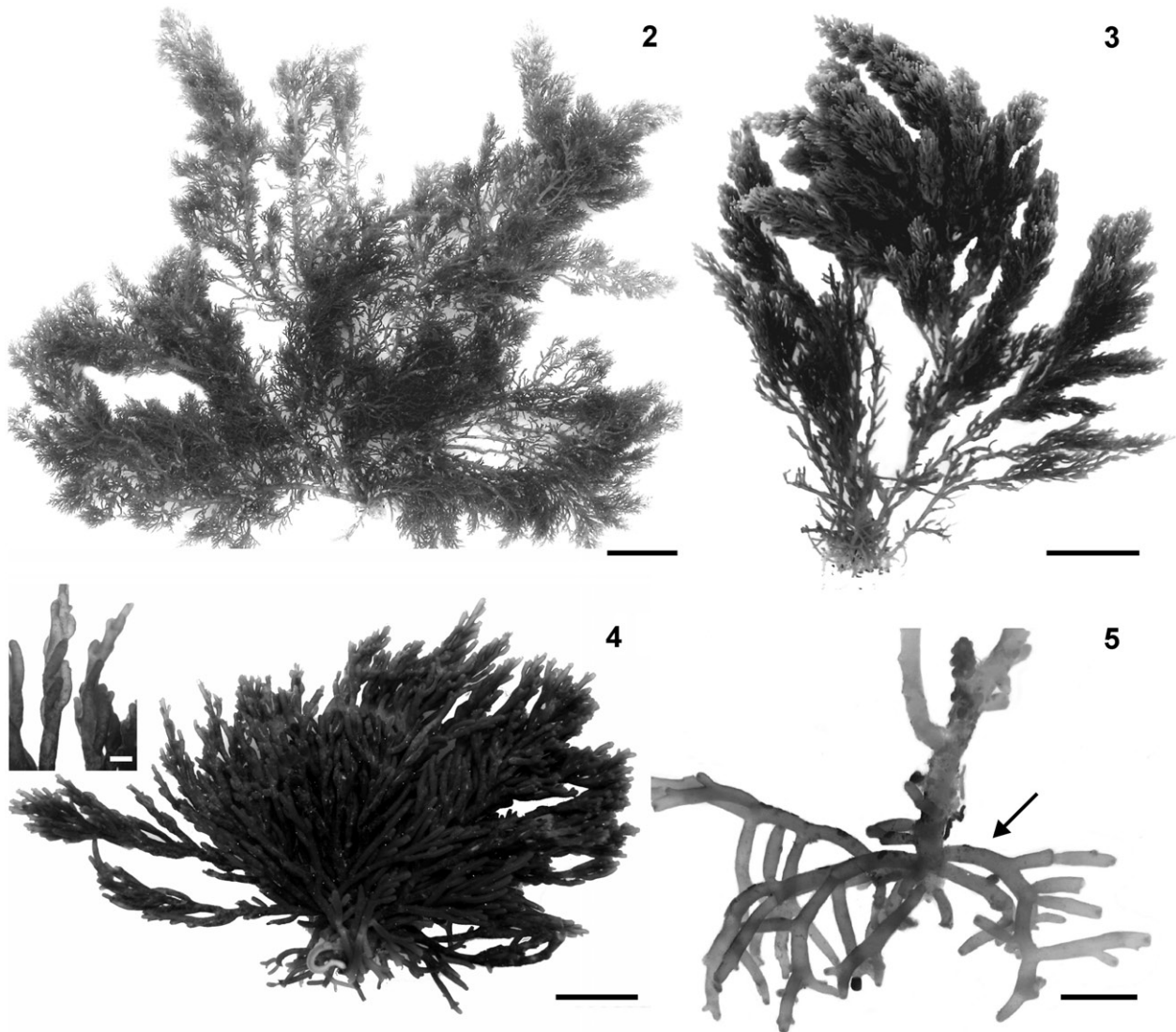
PREVIOUS MISAPPLIED NAMES FOR BRAZIL: *Laurencia filiformis sensu* Fujii (1998, pp. 26–29, figs 3–33); Pinheiro-Joventino *et al.* (1998, p. 35); Pereira *et al.* (2002, p. 122); Fujii & Senties (2005, pp. 84–85, figs 26–35); Széchy & Nassar (2005, p. 384); Pereira *et al.* (2005, p. 80); as *Laurencia* sp. 4 (Fujii 1990, pp. 101–102, figs 140–149); *Laurencia filiformis* f. *dendritica sensu* Fujii (1998, p. 29); Pereira *et al.* (2002, p. 122); Fujii & Senties (2005, p. 85); as *Laurencia* sp. 2 (Fujii 1990, pp. 87–88, figs 119–129); Széchy & Paula (1997, p. 6); *Laurencia filiformis* f. *heteroclada sensu* (Fujii, 1998, p. 29); Fujii & Senties (2005, p. 86); as *Laurencia* sp. 3 (Fujii 1990, pp. 94–95, figs 130–139); *Laurencia heteroclada sensu* Oliveira-Filho (1969, pp. 178–179, pl. 29, figs 167, 168); *Laurencia arbuscula sensu* Cordeiro-Marino *et al.* (1983, pp. 29–39, figs 1–13); Fujii (1990, pp. 36–38, figs 48–58); Figueiredo-Creed & Yoneshigue-Valentin (1997, p. 36); Gestinari *et al.* (1998, p. 73); Pedrini *et al.* (1994, p. 729); Nunes (1998, p. 13); Széchy & Nassar (2005, p. 384); *Laurencia composita sensu* Oliveira-Filho (1969, pp. 176–177, pl. D, fig. 1, *pro parte*); *Laurencia majuscula sensu* Széchy & Nassar (2005, p. 384); *Laurencia microcladia sensu* Joly (1965, p. 234, pls 56, 58, 59, figs 670, 688, 695); Oliveira Filho (1969, p. 179); Cordeiro-Marino (1978, pp. 130, figs 395, 396); Pinheiro-Joventino *et al.* (1998, p. 35); Figueiredo *et al.* (2004, p. 13); *Laurencia obtusa sensu* Joly (1965, p. 244, pl. 56, figs 671, 672, pl. 58, fig. 689, pl. 59, figs 696, 697); Pedrini (1980, pp. 232–233); Yoneshigue (1985, pp. 328–329); Figueiredo-Creed & Yoneshigue-Valentin (1997, p. 36, *pro parte*); Pinheiro-Joventino *et al.* (1998, p. 35); *Laurencia obtusa* var. *densa* [*L. densa*] *sensu* Oliveira-Filho (1969, p. 180, pl. 31, fig. 180); Pedrini (1980, p. 233).

PREVIOUS MISAPPLIED NAMES FOR THE CANARY ISLANDS, SPAIN: *Laurencia majuscula sensu* Gil-Rodríguez & Haroun (1993, pp. 114–115); Masuda *et al.* (1998, pp. 266–268, figs 1–6);

Haroun *et al.* (2002, p. 152); Haroun *et al.* (2003, p. 156); Gil-Rodríguez *et al.* (2003, p. 30); Haroun *et al.* (2008, p. 170); Haroun *et al.* (2009, p. 164).

Habit: Plants erect, forming dense tufts 4–20 cm high, brown-purple or violet-greenish in colour (usually greenish in the main axes and primary lateral branches and violet in remaining portions of the plant). The thalli are terete, are cartilaginous in texture, adhere to herbarium paper when dry, and are 0.9–2.8 mm in diameter in the middle portion of the main axis (Figs 2–4). Erect axes arise from a single discoid holdfast or from an aggregation of discoid holdfasts; stolon-like branches and descending branches are formed from the lower portions (Fig. 5) and are secondarily attached by smaller holdfasts. The branching is alternate-spiral to irregular, uniformly dense throughout the thallus to sparse, with 3–5 orders of branches. The first-order branches are long (up to 17 cm) and display the same branching pattern as the main axes; they become shorter upwards, resulting in a thallus with a pyramidal outline. The ultimate branchlets are simple or compound, and are usually cylindrical with truncated tips; however, in some populations they narrow towards the apex, which results in spine-like branchlets (Fig. 6). The branchlets are short and straight or long and sinuous and arise at a wide to very narrow angle. They can be parallel to the axis, turned slightly to markedly outwards, or curved in towards the axis, and measure (0.35–) 0.6–3.2 (–6.3) × (0.17–) 0.4–0.6 (–0.75) mm. The branchlets and second-, third- and fourth-order branches are sometimes deciduous, so that the axes display scars following detachment (Figs 7, 8). The main axes and first-order branches can bear many adventitious branchlets, which can produce tetrasporangia.

Vegetative structure: In median longitudinal sections through a branchlet, the outer cortical cell walls near the apices sometimes do not project beyond the surface, or they may project slightly or even markedly (Fig. 9). In surface view, the cortical cells are regularly arranged in longitudinal rows throughout the thalli and are connected to each other by longitudinally oriented secondary pit-connections (Fig. 10). There are one or two (or three) *corps en cerise* per cortical cell (Fig. 11) but only one in each trichoblast cell. In surface view, the cortical cells are isodiametric and polygonal in the upper portions of the thalli, rounded to longitudinally elongate in the middle portions [(28–) 43–150 (–188) × (25–) 33–62 (–83) μm] and elongate-polygonal in the lower portions. In transverse section, the thalli can be seen to possess one layer of pigmented cortical cells and four or five layers of colourless medullary cells (Fig. 12). In transverse section the cortical cells are

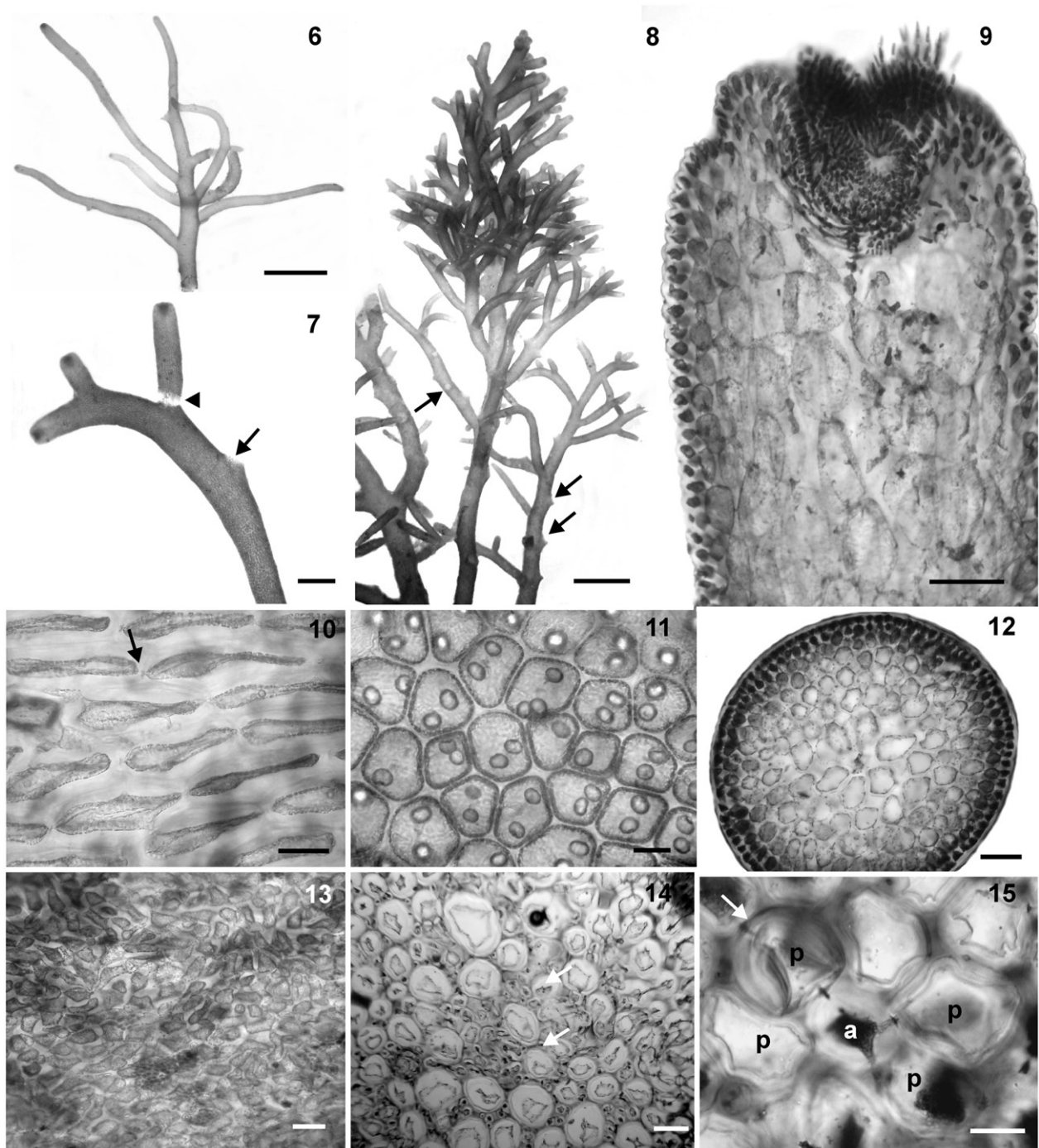


Figs 2–5. Habit of *Laurencia dendroidea*. **2, 3.** Habit of specimens from protected areas. **4.** Habit of specimen from exposed area, with detail of ultimate branchlets (inset). Note detail of ultimate branchlets markedly curved towards the axis. **5.** Detail of basal portion of the thallus showing stolon-like and descending branches formed from the lower portions (arrow). Scale bars = 2 cm (Figs 2, 3), 1 cm (Figs 4, 5), and 1 mm (Fig. 4, inset).

quadratic, cuneiform to rectangular, are neither radially elongated nor arranged as a palisade, and measure (20–) 27.5–50 (–77.5) × (20–) 30–42.5 (–65) μm in the middle portions of the thalli. Secondary cortication is present in the lower portions of the thalli (Fig. 13). Medullary cells are rounded or slightly radially elongated, measure (55–) 80–150 (–182.5) × (40–) 55–100 (–125) μm in the middle portions of the thalli, and become larger toward the thallus centre. Intercellular spaces are present in the younger portions, and many filling cells are present in the older portions of the main axes (Fig. 14). Each vegetative axial segment cuts off four pericentral cells (Fig. 15). Lenticular thickenings can be abundant, rare, or absent. When they are present, they occur in medullary cell walls of the main axes or lateral

branches (Fig. 15), and especially at the bases of the branches or cystocarps. The first pericentral cell is produced underneath the basal cell of the trichoblast.

Reproductive structures: Tetrasporangial branchlets are cylindrical, simple or compound, and measure (0.6–) 1.3–4.5 (–7.5) × 0.3–0.6 mm (Figs 16, 17). At the apex of the fertile branches, each axial segment produces only one fertile pericentral cell (the fourth) (Figs 18, 19), which cuts off two pre-sporangial cover cells distally and abaxially to the tetrasporangial initial (Figs 19, 20). Subsequently, one post-sporangial cover cell is produced (Fig. 19); it continues to divide and contributes to the production of cortication around the tetrasporangium. The pre-sporangial cover cells do not divide and display

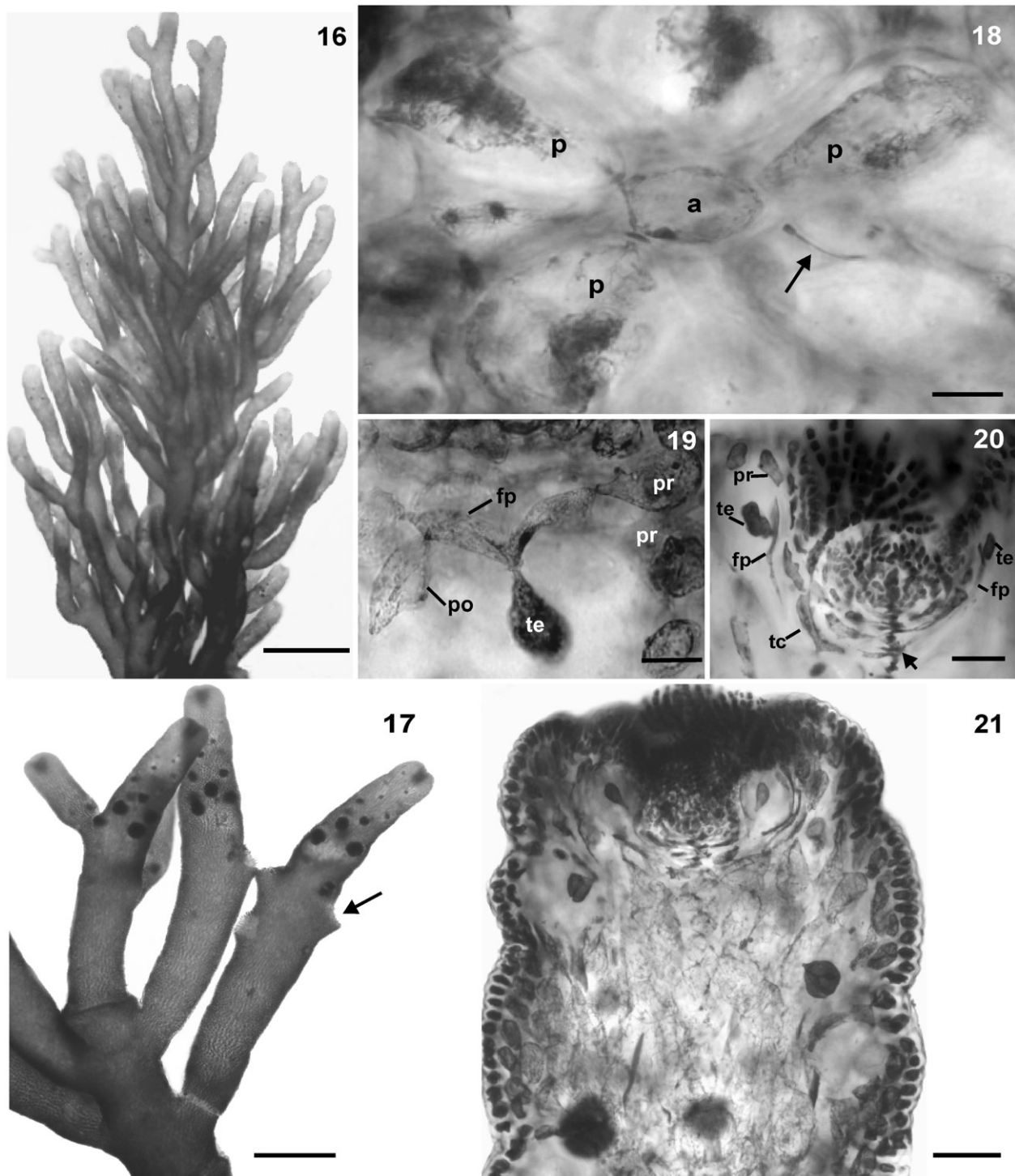


Figs 6–15. Branchlets and vegetative structures of *Laurencia dendroidea*. **6.** Detail of long and sinuous ultimate branchlets. **7.** Detail of a branch showing scar of released branchlet (arrow). Note detachment of a branchlet (arrowhead). **8.** Upper portion of the thallus showing branches with many scars of released branchlets (arrows). **9.** Longitudinal section through a branchlet showing projecting cortical cells. **10.** Cortical cells in surface view, showing a secondary pit-connection (arrow). **11.** Cortical cells in surface view, showing *corps en cerise* in living material. **12.** Transverse section of the thallus. **13.** Old portion of the thallus in surface view showing secondary cortication. **14.** Detail of medulla of older thallus in transverse section, showing filling cells (arrows). **15.** Transverse section of the upper portion of a branch showing an axial cell (a) with four pericentral cells (p). Note lenticular thickening in pericentral cell (arrow). Scale bars = 2 mm (Figs 6, 8), 500 μ m (Fig. 7), 100 μ m (Figs 9, 12, 14), 50 μ m (Figs 10, 13) and 25 μ m (Figs 11, 15).

a transverse-type alignment relative to the fertile axis in surface view. Tetrasporangial maturation occurs in a clockwise spiral, and the final arrangement is a parallel pattern with respect to the fertile branchlets (Fig. 21). Mature tetrasporangia are

tetrahedrally divided, measuring 60–170 μ m in diameter.

In the female thalli (Fig. 22), each procarp-bearing segment produces five pericentral cells (Fig. 23), the fifth of which becomes the

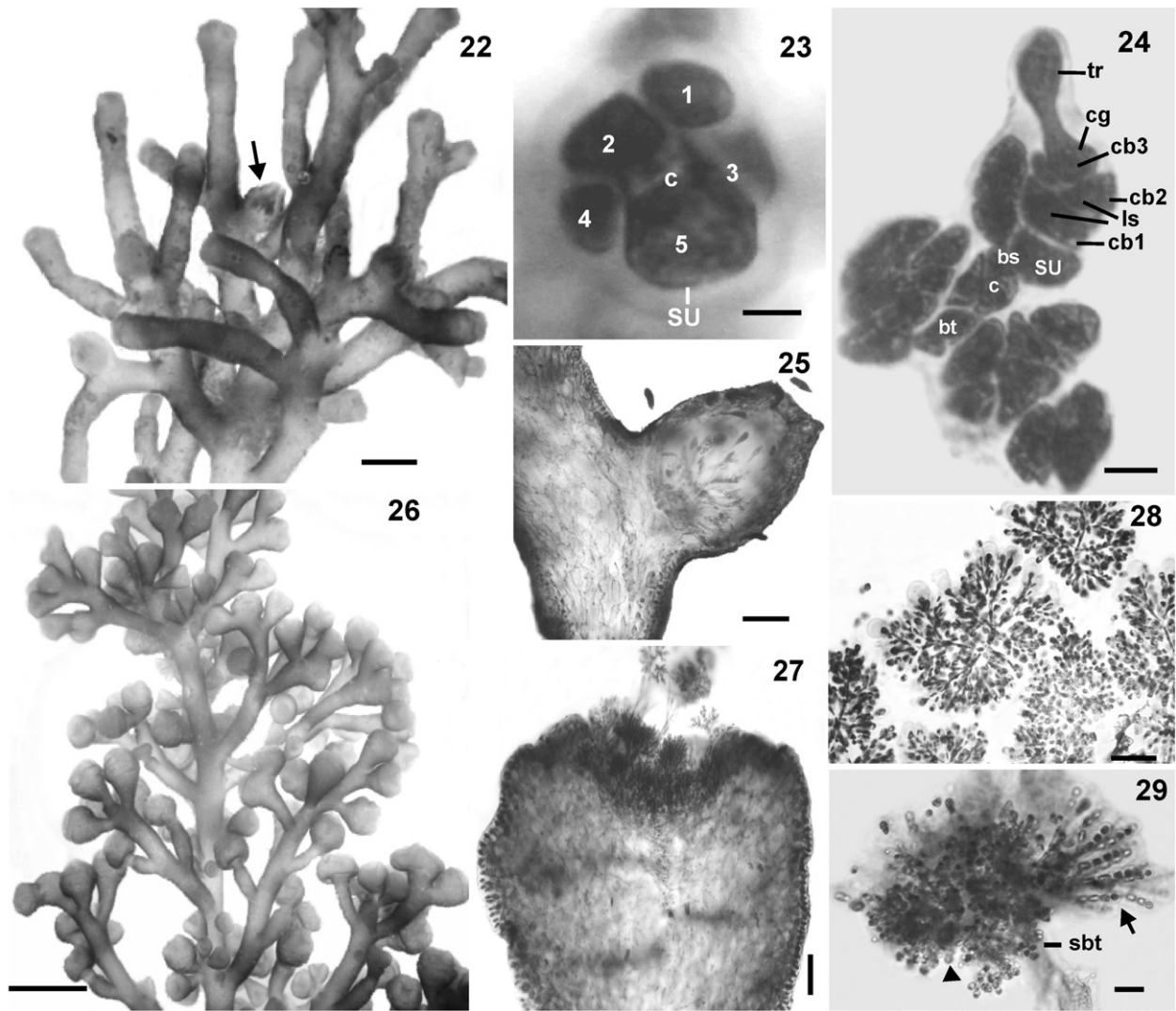


Figs 16–21. Tetrasporangial structures of *Laurencia dendroidea*. **16.** Tetrasporangial branches. **17.** Detail of tetrasporangial branchlets. Note scars of released branchlets (arrow). **18.** Transverse section of tetrasporangial axial segment showing an axial cell (a) and one fertile pericentral cell, the fourth (arrow); the other pericentral cells remain vegetative (p). **19.** Detail of a fertile pericentral cell (fp) with two pre-sporangial cover cells (pr), tetrasporangium (te) and one post-sporangial cover cell (po). **20.** Longitudinal section through an apical portion of tetrasporangial branchlet, showing origin of tetrasporangia (te) from axial cell (arrow), fertile pericentral cells (fp), and pre-sporangial cover cells (pr). Note trichoblast (tc) from an axial cell. **21.** Longitudinal section through a tetrasporangial branchlet showing parallel arrangement of the tetrasporangia. Scale bars = 2 mm (Fig. 16), 500 μ m (Fig. 17), 100 μ m (Fig. 21), 50 μ m (Figs 18, 20), and 25 μ m (Fig. 19).

supporting cell of a four-celled carpogonial branch containing two groups of sterile cells (basal and lateral) (Fig. 24). The fully developed cystocarps are conical without a protuberant ostiole; they are subapical and prominent in the thallus, and

measure 570–1120 μ m in diameter (Fig. 25). Carposporangia are clavate, 112.5–245 \times 20–80 μ m.

Male branches are clavate, characteristically swollen, and simple or compound, and measure



Figs 22–29. Female and male structures of *Laurencia dendroidea*. **22.** Female branches. Note cystocarp (arrow). **23.** Procaryp-bearing segment with five pericentral cells, the fifth becoming the supporting cell (su) of the carpogonial branch; central cell of procaryp-bearing segment (c). **24.** Procaryp before fertilization with four-celled carpogonial branch (cb), carpogonium (cg), trichogyne (tr), lateral sterile group (ls), basal sterile group (bs), supporting cell (su), central cell of procaryp-bearing segment (c), basal cell of trichoblast (bt). **25.** Longitudinal section through a female branchlet with prominent cystocarp without protuberant ostiole. **26.** Male branches. **27.** Longitudinal section through a male branchlet showing spermatangial branches in cup-shaped tips. **28.** Detail of trichoblast-type spermatangial branches with terminal vesicular sterile cells. **29.** Detail of spermatangial branches on trichoblast with two laterals, sterile (arrow) and spermatangial (arrowhead) branches on its suprabasal cell (sbt). Note spermatangia with an apical nucleus. Scale bars = 2 mm (Fig. 26), 1 mm (Fig. 22), 200 μ m (Fig. 25), 100 μ m (Fig. 27), 25 μ m (Figs 28, 29), 10 μ m (Fig. 24) and 5 μ m (Fig. 23).

(850–) 960–1280 (–1360) μ m in diameter (Fig. 26). In longitudinal section through a fertile branchlet, the spermatangial pits are cup-shaped, and an axial cell row is discernible at the base (Fig. 27). Spermatangial trichoblasts arise from the axial cell, and consist of fertile and sterile branches (Figs 28, 29); the fertile branches produce many ovoid spermatangia measuring 7.5×5 – 7.5×5 μ m, and terminate in vesicular sterile cells, of 17.5 – 30×12.5 – 22.5 μ m; each spermatium possesses an apical nucleus.

Habitat: The specimens were collected from the intertidal to subtidal zone at a 3 m depth, and

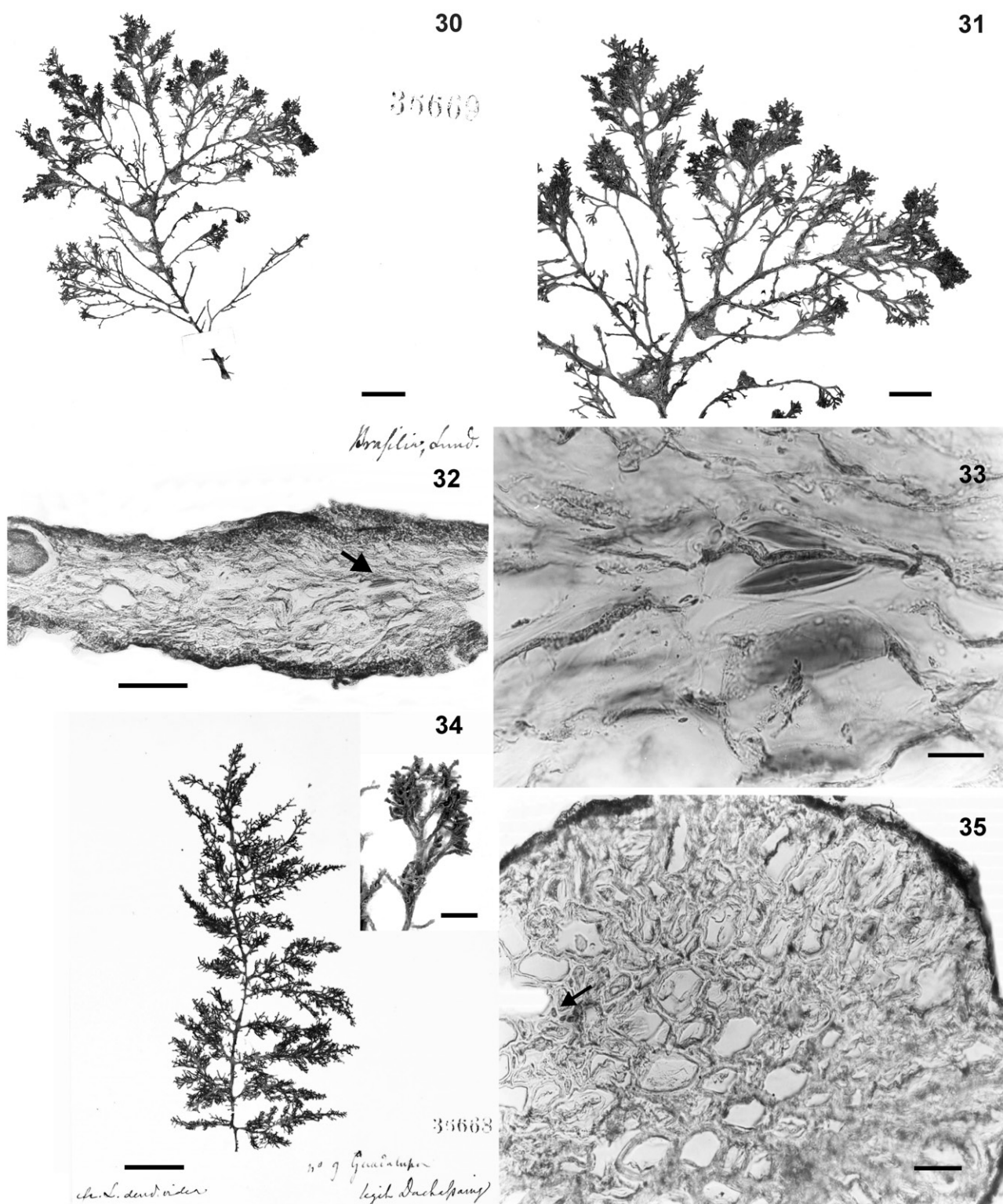
they were protected from or exposed to wave action sites.

Observations on the type of Laurencia dendroidea

LECTOTYPE: LD 36669 (Figs 30–33).

ISOLECTOTYPE: LD 36668 (Figs 34, 35).

The lectotype (LD 36669) is a tetrasporophyte *c.* 8 cm high, with irregularly spiral branching and ultimate branchlets that are short and predominantly compound (Figs 30, 31). Lenticular thickenings were sparsely observed in the ultimate branchlets (Figs 32, 33). The isolectotype specimen



Figs 30–35. Type material of *Laurencia dendroidea*. **Figs 30–33.** Lectotype (LD 36669). **30.** Habit of the thallus. **31.** Detail of branches. **32.** Transverse section of ultimate branchlet showing lenticular thickenings (arrow). **33.** Detail of lenticular thickenings. **Figs 34, 35.** Isolectotype (LD 36668). **34.** Habit of the thallus. **35.** Transverse section of old portion of the thallus showing filling cells (arrow). Scale bars = 2 cm (Fig. 34), 2 mm (Fig. 34, inset), 1 cm (Fig. 30), 5 mm (Fig. 31), 100 μ m (Fig. 35), 40 μ m (Fig. 33) and 25 μ m (Fig. 32).

(LD 36668) consists of a plant 14 cm high with dense, alternate-spiral to irregular branching (Fig. 34). In a cross-section of the thallus of the isolectotype, the basal portion contained little

secondary growth and cell filling (Fig. 35). Adventitious branches were observed to be distributed along the thallus from the base to the upper portion. Lateral branches were up to

4 cm long and were distributed throughout the plant with the same branching pattern as the main axis. The ultimate branchlets were long and mostly simple.

Comparison between Laurencia dendroidea and L. filiformis, L. arbuscula and L. obtusa

Comparison between our material and the lectotype of *L. filiformis* from the Agardh herbarium in Lund, Sweden (LD 36488), revealed that *L. filiformis* is morphologically distinct from Brazilian and Canarian *L. dendroidea*, having narrow thalli with irregular and sparse branching. *Laurencia filiformis* was originally described from Western Australia as *Chondria filiformis* C. Agardh and its great morphological plasticity was recognized by Saito & Womersley (1974), who therefore referred to it as the '*filiformis* complex'. Based on morphological and anatomical characters, especially on differences related to the habitat, Saito & Womersley (1974) recognized two other forms of *L. filiformis* in addition to the typical form, namely *L. filiformis* f. *heteroclada*, based on *L. heteroclada* Harvey, and *L. filiformis* f. *dendritica*. The typical form was characterized by Saito & Womersley (1974) as growing in protected sites with calm waters, with one or few axes arising from a small discoid holdfast, narrow thalli of up to 1 mm in diameter, and lenticular thickenings often present in the walls of the medullary cells. *Laurencia filiformis* f. *heteroclada* was characterized as growing in areas exposed to wave action; it presents numerous fastigiate axes originating from a stoloniferous base, a broader thallus (1–2 mm in diameter) than in the typical form, and lenticular thickenings are absent or occasionally present. The third form, *Laurencia filiformis* f. *dendritica*, was described as typical of deeper waters, growing in areas with moderate to strong wave action; it has a larger and more robust thallus (up to 3 mm in diameter) and lenticular thickenings are absent (Saito & Womersley, 1974). However, Masuda (1997) recognized f. *filiformis* and f. *heteroclada* as separate species, justifying this by the presence of numerous fastigiated axes from a stoloniferous base, the occasional presence of lenticular thickenings in *heteroclada*, and the production of unrelated sets of halogenated secondary metabolites by *filiformis* and *heteroclada*. His treatment was followed by Wynne *et al.* (2005) in their study of the *Laurencia* complex of the Sultanate of Oman, although Womersley (2003) did not himself recognize the forms of *L. filiformis* he had previously described (in Saito & Womersley, 1974).

Our examination of the type specimen of *L. heteroclada* (Herb. Harvey, Alg. Aust. Exsic. 210) revealed that it differs from all of the

non-fastigiate material of *L. dendroidea* from Brazil and the Canaries. Likewise, material of *L. arbuscula* from the type locality in Australia (SPF8500), previously cited by Womersley (2003, p. 467, fig. 208A) as representative of this species, proved to have a different habit from Brazilian specimens of *L. dendroidea* previously identified as *L. arbuscula*: the Australian material has long axes covered by abundant short branchlets, which are spaced at regular intervals.

Laurencia microcladia sensu Joly (1965) and *sensu* Cordeiro-Marino (1978) was placed in synonymy with *L. arbuscula* or *L. scoparia* by Fujii (1990), based on an analysis of herbarium material (SP and SPF). Later, both were regarded as *L. filiformis* in Brazil by Fujii & Senties (2005) and Fujii *et al.* (2006). The specimens of '*L. filiformis*' were proven to be *L. dendroidea* according to our results. Likewise, analysis of herbarium specimens (SPF) from Brazil identified as *L. composita* revealed that these taxa also correspond to *L. dendroidea*.

The *Laurencia obtusa* specimen that we analysed (from Guernsey, Channel Islands, off the coast of France (xi.1990, C. Maggs, SP 400.116) was morphologically distinct from *L. dendroidea*, especially regarding the habit and the very flaccid thallus, which was not cartilaginous in texture. The cortical cells projected slightly near the apex of the branches, and the specimen lacked lenticular thickenings in the walls of the medullary cells. However, lenticular thickenings were found in the type specimen ('*Fucus obtusus*': LD36708) that we examined.

Discussion

Molecular circumscription and relationships of Laurencia dendroidea

The *rbcL* sequences of *Laurencia* specimens from Rio de Janeiro and Bahia resembling *L. arbuscula*, *L. filiformis*, *L. majuscula* and *L. obtusa*, were compared with each other and with Genbank sequences under the names *L. cf. catarinensis* and *L. arbuscula* from São Paulo (Fujii *et al.*, 2006) and *L. majuscula* from Tenerife, Canary Islands, Spain (Gil-Rodríguez *et al.*, 2009). The twelve Brazilian populations (Rio de Janeiro, São Paulo and Bahia) and the Canarian population formed a fully supported clade in all of the analyses, with intraclade divergences ranging from 0 to 0.90%. The results confirm that all of the morphological variants belong to a single, extremely plastic taxonomic entity, and they corroborate the results obtained by Fujii *et al.* (2006) for *L. arbuscula*, *L. filiformis* and *L. scoparia* from Brazil.

Comparisons of the Brazilian specimens with the type material of *L. filiformis* and reference material

from the type locality show that these taxa are morphologically distinct, especially with respect to the habit of the plants. However, the characteristics of our specimens are consistent with the characteristics of *L. dendroidea*, which is a species that was originally described from Brazil. Therefore, based on morphological and molecular studies, we confirmed that the species that were previously attributed to the Brazilian coast as *L. arbuscula*, *L. filiformis*, *L. majuscula* and *L. obtusa* must all be identified as *L. dendroidea*. The phylogenetic analysis that was performed in this study and the analysis by Fujii *et al.* (2006) using the *rbcL* gene sequences showed that *L. obtusa* from the North Atlantic (Ireland, a region near the type locality) is a distinct species that is not grouped with any *L. dendroidea* samples from Brazil and the Canary Islands. Therefore, *L. dendroidea* should not be treated as a variety of *L. obtusa* and should instead be treated as an independent species.

The characteristics of *Laurencia dendroidea*

Laurencia dendroidea possesses all of the characters that are typical of the genus, such as the production of the first pericentral cell underneath the basal cell of the trichoblast, the production of tetrasporangia from particular pericentral cells, without the formation of additional fertile pericentral cells, spermatangial branches that are produced from one of two laterals on the suprabaasal cell of the trichoblasts, and a procarp-bearing segment with five pericentral cells. The species is recognizable primarily by its thallus, which is usually densely branched from the base to the upper portions, pyramidal in outline, and contains one fertile pericentral cell (the fourth) in its tetrasporangial segments.

Studies of the type material and/or reference materials of *L. dendroidea*, *L. filiformis*, *L. majuscula* and *L. obtusa* from different herbaria were made by Fujii (1990) and again in this study. Our examination of the type specimen of *L. dendroidea* (LD 36669) revealed the presence of lenticular thickenings, which were not observed by Yamada (1931). Yamada treated *L. dendroidea* as a variety of *L. obtusa* and characterized it as lacking lenticular thickenings and surface cell projections, and having branches that are thinner than in other varieties of *L. obtusa*.

Relationship between *Laurencia dendroidea*, *L. majuscula* and *L. filiformis*

Laurencia dendroidea is closest morphologically to *L. majuscula*. This was noted long ago by J. Agardh (1876), who considered the species to

be a synonym of *L. dendroidea*. Saito & Womersley (1974) considered *L. majuscula* to be clearly different from other Australian species. It is readily recognized by its habit, is densely branched, has a relatively soft texture, contains distinctly projected cortical cells (especially near the apices of the axes and branches) and lacks lenticular thickenings. The isotype (MEL 1006997) and additional material of *L. majuscula* that were examined in this study revealed specimens that are morphologically close to some Brazilian and Canarian *L. dendroidea* plants, with (1) a thallus that is pyramidal in outline, (2) dense branching, (3) development of adventitious branchlets, and (4) projecting cortical cells. However, due to the broad morphological and habit plasticity displayed in many of the populations we examined, further judgement regarding the relationship between *L. dendroidea* and *L. majuscula* must await molecular studies of the latter. Likewise, sequence data are needed for *L. filiformis* to clarify its taxonomic position and phylogenetic relationships.

Morphological plasticity of *Laurencia dendroidea* and causes of confusion with other *Laurencia* species

Morphological variation of *L. dendroidea* with regard to the basal system, the presence or absence of lenticular thickenings, and the degree of projection of the cortical cell walls, and also differences in habitat, have misled previous research and led to incorrect citation of this taxon under different names for the Brazilian coast, such as *L. arbuscula* (Cordeiro-Marino *et al.*, 1983), *L. composita* (Oliveira Filho, 1969), *L. filiformis* f. *filiformis*, *L. filiformis* f. *heteroclada*, *L. filiformis* f. *dendritica* (Fujii & Senties, 2005), *L. majuscula* (Széchy & Nassar, 2005), *L. microcladia* (Joly, 1965; Cordeiro-Marino, 1978; Pinheiro-Joventino *et al.*, 1998; Figueiredo *et al.*, 2004) and *L. obtusa* (Joly, 1965; Pedrini, 1980; Yoneshigue, 1985; Figueiredo-Creed & Yoneshigue-Valentin, 1997). In our study, specimens with the characteristics of these other taxa showed morphological features that can be related to environmental conditions. For example, specimens that grew in the intertidal zone and the fringe of the subtidal zone in moderately exposed areas or areas exposed to high-energy wave action had smaller thalli (4–7 cm high) and several erect axes arising from a basal portion consisting of an aggregation of discoid holdfasts; lenticular thickenings were absent or rare, sometimes found only in the bases of cystocarps. Specimens from Brazil with such characteristics (though some may have longer thalli) have previously been referred to *L. arbuscula* or *L. filiformis* f. *dendritica* (Fujii, 1990, 1998). However, some specimens with the same characters but completely lacking lenticular

thickenings have previously been identified as *L. obtusa* (Joly, 1965), or *L. obtusa* var. *densa* if the branches were densely arranged, covering the axes (Oliveira Filho, 1969); both authors followed Yamada (1931), the main monographic study of *Laurencia sensu lato* available at that time. Specimens growing in the subtidal zone down to 3-m depth in calm areas, such as bays and inlets, had longer thalli (up to 20 cm), a basal portion consisting of a single discoid holdfast, stolon-like branches, and lateral descending branches formed from the lower portions, and abundant to rare or absent lenticular thickenings. These specimens have previously been identified as the typical form of *L. filiformis*. Similar plants growing in the lower intertidal zone in areas with high water movement and always possessing lenticular thickenings have been identified as *L. filiformis* f. *heteroclada* (Fujii, 1998), or even as *L. majuscula*, if the cortical cell walls projected markedly near the apices (Széchy & Nassar, 2005).

Since Yamada published his 1931 analysis, morphological characters, such as the projection of the cortical cell walls, and the presence, absence and frequency of lenticular thickenings, have been considered to be valuable for separating sections, species and varieties in *Laurencia sensu lato*. However, in *L. dendroidea*, the degree of projection of the cortical cell walls was extremely variable in all of the populations we studied, and varied among individuals within the same population. Similarly, the presence, absence and frequency of lenticular thickenings varied among different populations; they are found more frequently at the bases of the cystocarps or younger lateral branches. In some populations, the plants displayed many vegetative or tetrasporangial deciduous branches and branchlets, which left scars on the axes following detachment. The specimens presented characteristically long, sinuous and spiny-like branchlets. These deciduous branchlets may function in the vegetative propagation of the species.

Transfer of Chondrophyucus furcatus to Palisada

Chondrophyucus furcatus was described as *Laurencia furcata* Cordeiro-Marino & M.T. Fujii from Brazil (Cordeiro-Marino *et al.*, 1994) and transferred to *Chondrophyucus* by Fujii & Senties (2005), primarily due to the presence of two pericentral cells per vegetative axial segment. The authors commented that due to the presence of fertility at the second pericentral cells in the tetrasporangial segments, this species was more closely related to species currently assigned to the genus *Palisada* rather than *Chondrophyucus*. Our phylogenetic analyses strongly support transfer of *C. furcatus* to

Palisada and the nomenclatural change is proposed here:

***Palisada furcata* (Cordeiro-Marino & M.T. Fujii) Cassano & M.T. Fujii, comb. nov.**

BASIONYM: *Laurencia furcata* Cordeiro-Marino & M.T. Fujii in Cordeiro-Marino *et al.*, (1994, p. 374, figs 1–19).

HOMOTYPIC SYNONYM: *Chondrophyucus furcatus* (Cordeiro-Marino & M.T. Fujii) M.T. Fujii & Senties (2005, p. 109, figs 69–77).

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Supplementary material

The following supplementary material is available for this article, accessible via the Supplementary Content tab on the article’s online page at <http://dx.doi.org/10.1080/09670262.2011.647334>.

TEJP 647334 supplementary material.docx

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