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> Yola METTI, Giovanni FURNARI & Donatella SERIO

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Vitor VASCONCELOS

Faculdade de Ciências da Universidade do Porto and CIIMAR, Rua do Campo Alegre, s/n, 4169-007 Porto (Portugal)

COUVERTURE / COVER:

Natural habitat of Corynecladia mediterranea from its type locality in Golfo di Monte Cofano, Trapani, Sicily, Italy.

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Molecular analyses reveal the presence of *Corynecladia* J.Agardh (Rhodophyta, Rhodomelaceae) in the Mediterranean Sea with two new species, *C. millarii* sp. nov. and *C. mediterranea* sp. nov.

Yola METTI

Australian Institute of Botanical Science, Botanic Gardens of Sydney, 362 Narellan Rd, Mount Annan NSW 2567 (Australia) yola.metti@botanicgardens.nsw.gov.au (corresponding author)

Giovanni FURNARI Donatella SERIO

Department of Biological, Geological and Environmental Sciences, University of Catania, Via Empedocle, 58 – 95128 Catania (Italy)

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ABSTRACT

The findings of this study expanded the geographic distribution of the genus *Corynecladia* J.Agardh, thought to be endemic to Australia. It is recorded for the first time as present in Europe, with two newly proposed species: *C. millarii* sp. nov. and *C. mediterranea* sp. nov. New collections belonging to the *Laurencia* complex were sampled from the Sicilian coasts of Italy. Examination of this material was carried out using both morphological comparisons and phylogenetic analyses of chloroplast (*rbcL*) and mitochondrial (COI-5P) nucleotide sequences. The resulting phylogenetic trees divided the Mediterranean specimens into two supported, separate branches, within the genus *Corynecladia*. Morphological analysis supported placement of these species within *Corynecladia* and as distinct from other congeners. Specifically, the two new species were conspicuous in the absence of a secondary cortex which is typical of other *Corynecladia* taxa. Included in this study is a detailed dichotomous key to the *Laurencia* complex taxa of the Mediterranean.

Mediterranean, *Corynecladia*, *Laurencia*, dichotomous keys, new species.

KEY WORDS

RÉSUMÉ

Des analyses moléculaires révèlent la présence de Corynecladia J.Agardh (Rhodophyta, Rhodomelaceae) en Méditerranée avec deux nouvelles espèces, C. millarii sp. nov. et C. mediterranea sp. nov.

Les résultats de cette étude ont élargi la répartition géographique du genre *Corynecladia* J.Agardh que l'on croyait endémique à l'Australie. Il est signalé pour la première fois comme présent en Europe, avec deux espèces nouvellement proposées: *C. millarii* sp. nov. et *C. mediterranea* sp. nov. De nouvelles collections appartenant au complexe *Laurencia* ont été échantillonnées sur les côtes siciliennes d'Italie. L'examen de ce matériel a été réalisé à l'aide de comparaisons morphologiques et d'analyses phylogénétiques de séquences nucléotidiques chloroplastiques (*rbcL*) et mitochondriales (COI-5P). Les arbres phylogénétiques résultants ont divisé les spécimens méditerranéens en deux branches distinctes et supportées, au sein du genre *Corynecladia*. L'analyse morphologique a confirmé le placement de ces espèces se distinguaient par l'absence d'un cortex secondaire typique des autres taxons de *Corynecladia*. Cette étude comprend une clé dichotomique détaillée des taxons du complexe *Laurencia* de la Méditerranée.

MOTS CLÉS Méditerranée, Corynecladia, Laurencia, clés dichotomiques, espèces nouvelles.

INTRODUCTION

The Laurencia complex contains 231 accepted taxa at specific and infraspecific levels (Guiry & Guiry 2023). Currently the complex contains the following genera: Laurencia J.V.Lamouroux (1813), Chondrophycus (Tokida & Saito) Garbary & J.T.Harper (Garbary & Harper 1998), Corynecladia J.Agardh reinstated by Nam (2006), Laurenciella Cassano, Gil Rodríguez, Sentíes, Díaz-Larrea, M.C.Oliveira & M.T.Fujii (Cassano et al. 2012b), Ohelopapa F.Rousseau, Martin-Lescanne, Payri & L. Le Gall (Rousseau et al. 2017), Osmundea Stackhouse (1809) resurrected by Nam et al. (1994), Palisada (Yamada) K.W.Nam (2007) and Yuzurua (K.W.Nam) Martin-Lescanne (Martin-Lescanne et al. 2010). These are widely distributed throughout the world, from sub-Arctic waters to tropical coasts, and from littoral to sublittoral to depths of 65 m.

In the Mediterranean Sea, taxa belonging to the *Laurencia* complex recorded to date include: *Laurencia* (with eight species and one subspecies), *Laurenciella* (one species), *Osmundea* (seven species) and *Palisada* (five species). Previous to this study *Corynecladia* was not recorded in the Mediterranean.

Corynecladia was first described by Agardh (1876) to encompass his own newly described species C. umbellata, and an unusual Laurencia species, Laurencia clavata described by Sonder (1853), both of which were described from Australian material. However, many later researchers agreed with Sonder (1853) and considered *Corynecladia clavata* (Sonder) J.Agardh to belong within Laurencia (Yamada 1931; Saito & Womersley 1974; Nam & Choi 2001). Nam (2006) reinstated Corynecladia to contain L. clavata after his cladistic analysis based on 49 morphological features showed L. clavata to consistently group outside of Laurencia. In 2015, the genus Coronaphycus Metti (Metti et al. 2015) was proposed during a study on the Laurencia of Australia and included two species: C. elatus (C.Agardh) Metti and C. novus Metti. Identifying features of the genus included in particular the presence of a secondary cortex. Coronaphycus was then found to be congeneric with the previously disused Corynecladia based on new molecular data of the generitype C. clavata collected from Australia (Cassano et al. 2019). Corynecladia was amended with three species, all of which were found only in Australia, and included Corynecladia clavata, C. elata (C.Agardh) Cassano, M.C.Oliveira & M.T. Fujii, and C. nova (Metti) Cassano, M.C.Oliveira & M.T.Fujii.

A study was undertaken recently in the Mediterranean to collect and examine plants morphologically similar to *Laurenciella marilzae* (Gil-Rodríguez, Sentíes, Díaz-Larrea, Cassano & M.T.Fujii) Gil-Rodríguez, Sentíes, Díaz-Larrea, Cassano & M.T.Fujii. Specimens were collected from along the Sicilian coast (Fig. 1) but, some of them, when examined using molecular analyses, were not *L. marilzae* but instead aligned within *Corynecladia* (Serio *et al.* 2000: figs 1-8; Furnari *et al.* 2001: figs 32-34; Serio *et al.* 2020: fig. 1). Therefore, in this study the Mediterranean specimens were carefully examined using both molecular and traditional morphological observation, resulting in the proposal of two novel species of *Corynecladia*.

MATERIAL AND METHODS

MORPHOLOGICAL OBSERVATIONS

Specimens were collected from 2007 to 2021 by snorkelling at various Sicilian marine stations (Italy). Morpho-anatomical observations were carried out on both living material and material preserved in a solution of 4% formalin-seawater. For microscopic observations, some specimens were stained with 1% aqueous aniline blue acidified with diluted HCl, which enhances visualization of pit connections, and observed by Zeiss Axioplan (Göttingen, Germany). Sections were made by razor blade under a stereoscopic Zeiss microscope. Photographs were made using a Zeiss Axiocam 208 color, Zeiss Axiocam ICc1 digital camera and Nikon D2X digital camera (Nikon Corporation, Tokyo, Japan). Underwater photographs were made with a Gopro Hero8 black (San Mateo, California, United States). Herbarium specimens are held at the Herbarium of the Department of Biological, Geological and Environmental Science, Plant Biology Section of the University of Catania (CAT). Herbarium abbreviations follow Thiers (2022). Examined specimens and their collection locations are reported in the Appendix.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

The Qiagen DNEasy Plant Mini Kit (Qiagen, Valencia, CA, United States) was used to extract total genomic DNA from silica dried material. Two gene regions were targeted for analyses; the chloroplast *rbc*L gene, which codes for the large subunit of RuBisCO, and the 5' end of the mitochondrial cytochrome c oxidase I gene (COI-5P). The two gene regions were amplified separately by polymerase chain reaction (PCR) using a Veriti 96-well thermal cycler (Thermo Fisher Scientific, Applied Biosystems, Australia). The rbcL gene was amplified in either one fragment using the primer pair FrbcL start sh (ATGTCTAACTCTGTAGAAG) with RrbcS_start (GTTC-CTTGTGTTAATCTCAC) or in two pieces using F645 (ATGCGTTGG AAAGAAGAATTCT) with RrbcS_start, and FrbcL_st_sh with R749 (GCTCTTTCATACATATCTTC-CATTG) (Freshwater & Rueness 1994; Showe-Mei et al. 2001; Metti et al. 2013; Metti 2017). PCR amplifications were undertaken for the COI-5P gene region using the primer pair GAZF1 and GAZR1 (Saunders 2005). The amplification programs that were used are detailed in Freshwater & Rueness (1994) for *rbcL* and in Saunders (2005) for COI-5P. The PCR mixture was made to 20 µL, using the following concentration of reagents: 11.8 µL of dH20, 2 µL of 10x reaction buffer (Bioline Ltd.), 1 µL of MgCl2 at 25 mM (Promega, Madison, United States), 2 µL of 4x dNTPs at 2.5mM each, 0.2 µL of BioTaq DNA polymerase (Bioline Ltd.), 0.5 µL of the forward primer at 20 μ M, 0.5 μ L of the reverse primer at 20 μ M, and 2 μ L of the genomic DNA. The amplified DNA concentrations were visualized on a 1.5% agarose gel using 4 µL of PCR product. Amplified products were sent to Macrogen Korea (Seoul, South Korea) to be purified and sequenced. The same primers were used for both DNA sequencing and amplification. The resulting raw sequences were cleaned using the program Geneious 10.2.5 (https://www.geneious.com).

The sequences were aligned using the ClustalW Multiple Alignment program (Thompson *et al.* 1994), an accessory application within BIOEDIT v7.2.0 for PC (Hall 1999). The alignments were manually adjusted.

Phylogenetic analysis

A total of 69 sequences were included for the *rbc*L alignment, ten of which were newly generated through this study. The remainder 59 sequences were downloaded from GenBank (www.ncbi.nlm.nih.gov/nucleotide/). The final length of the *rbc*L alignment was 1185 base pairs. For the COI-5P alignment a total of 66 COI-5P sequences were included with 14 being newly generated. The final length for the COI-5P alignment was 568 base pairs. Phylogenetic trees for both gene regions were rooted using Rhodomelaceae and Ceramiaceae species as outgroups (including *Chondria* C.Agardh, *Vertebrata* S.F.Gray and *Ceramium* Roth species). Newly generated sequences were deposited in GenBank (http://www.ncbi.nlm. nih.gov). All sequences included in this study were detailed in the Appendix.

For the *rbc*L gene region two analyses were run: Maximum Likelihood (ML) and Bayesian (BI). Both were undertaken on the online CIPRES Gateway (Miller et al. 2010). For ML analyses, RAxML v8.2.12 (Stamatakis 2014) was used to infer phylogenies. Node support was estimated using 1000 bootstrap replicates. The evolutionary model was set to a GTR substitution model, including a gamma-distributed rate variation, as set by RAxML. The substitution rate matrix was (A-C) = 2.172104, (A-G) = 7.258084, (A-T) = 2.061828, (C-G) = 1.209311, (C-T) = 16.498996, and (G-T) = 1.000000. The assumed nucleotide frequencies were freqA = 0.317280, freqC = 0.155187, freqG = 0.212861, and freqT = 0.314672. For the BI analyses the program MrBayes 3.2.2 (Ronquist et al. 2012) was used. Four chains of the Markov chain Monte Carlo (one hot and three cold) were set. All analyses started with a random tree and were calculated for 500 000 generations, with one tree sampled every 1000 generations. The first 25% of trees were discarded as a burn in. A 50% majority rule consensus tree was determined from the remaining trees. Posterior probabilities were calculated.

A separate Neighbour Joining (NJ) analysis was run for the COI-5P region. The software PAUP for PC (v.4.0a152, Swofford 2017) was used to run the NJ analyses, as well as to calculate pairwise distances using uncorrected p distances. Two thousand bootstrap replicates were run to estimate node support.

RESULTS

MOLECULAR (*RBC*L)

The *rbcL* consensus tree of the ML analysis (Fig. 2) showed the *Laurencia* complex to be highly supported (ML bootstrap (boot) = 98%, BI posterior probability (pp) = 1.00) and all generic clades within it to be monophyletic. The *rbcL* tree showed the following clades to be fully supported at a generic level: *Laurencia, Laurenciella, Yuzurua, Chondrophycus*, and



FIG. 1. — Distribution of *Corynecladia* J.Agardh in the Mediterranean Sea. White arrow indicates the type locality of *Corynecladia millarii* sp. nov.; black arrow indicates the type locality of *Corynecladia mediterranea* sp. nov.; and the black circle indicates the other station where the latter was collected.

Osmundea. Palisada was highly supported (ML boot = 98%, BI pp = 1.00) and *Ohelopapa* had only one sequence. The *Corynecladia* clade was moderately to highly supported (ML boot = 93%, BI pp = 0.99). This was within the same range of support as previously reported (Cassano *et al.* 2019; Serio *et al.* 2020; Metti 2022).

The *Corynecladia* clade was comprised of 11 taxa, including two topotype sequences (*C. nova*, and the generitype *C. clavata*) (Fig. 2). Intrageneric pairwise distances (p) within this clade ranged from 0.18% to 9.38%. Five species-level clades were seen, including one with only a single sequence (*C. elata*). The Mediterranean sequences formed two individual, fully supported clades (ML boot = 100%, BI pp = 1.00) as did *C. clavata*, and *C. nova*. Pairwise distances between the two Mediterranean taxa ranged from 5.64% to 6.34%.

The pairwise distances between the two Mediterranean taxa and the generitype C. clavata were within commonly accepted intrageneric limits (up to 7.36% for both), supporting their placement within Corynecladia. The proposed Mediterranean taxa Corynecladia millarii sp. nov. and C. mediterranea sp. nov. showed as sister taxa, which formed a fully supported clade. This Mediterranean clade itself resulted as sister to a clade containing both the generitype C. clavata, and C. elata (ML boot = 98%, BI pp = 1.00). Pairwise distances between these two larger clades ranged from 6.38% to 4.36%. The largest distances within the *rbc*L phylogeny were seen between C. nova from the east coast of Australia, and the proposed C. millarii sp. nov. from the Mediterranean (9.38%). Intraspecific pairwise distances within species-level clades were 0.00% except for the proposed C. mediterranea sp. nov. where the p values ranged from 0.00% to 0.18%, well within the generally accepted intraspecies value of 2%.

MOLECULAR (COI-5P)

The NJ analyses for the COI-5P loci showed the eight *Laurencia* complex genera as monophyletic clades (*Ohelopapa* was a single sequence), with only *Laurencia* moderately supported (NJ bootstrap = 91%) and *Laurenciella* weakly supported (NJ bootstrap = 80%). The *Laurencia* complex itself was unsupported, as were the other clades, including *Corynecladia*. Intrageneric pairwise distances within the *Corynecladia* assemblage



Fig. 2. — The RaxML maximum likelihood (ML) tree inferred from *rbcL* sequence data showing both ML bootstrap values (1000 replicates) and Bayesian posterior probabilities. Values greater than 65/0.65 are shown. **Bold lines** and * indicate full support of values greater or equal to 99/0.99. Sequences in **bold** are newly generated from this study; sequences from topotype material are indicated by ^; and the generitype sequences indicated by †. GenBank accession numbers follow taxa names.

ranged from 5.11% to 10.21%. The *Corynecladia* assemblage showed two primary groupings. One was the Mediterranean group containing newly generated sequences, including *C. millarii* sp. nov. and *C. mediterranea* sp. nov., which was weakly

supported (NJ bootstrap = 71%). The other group was the Australian group, including *C. clavata* and *C. elata*, which was supported (NJ bootstrap = 95%). Clades at the species level were fully supported (NJ bootstrap = 100%) except for *C. elata*

which contained only one sequence. Intraspecific pairwise distances within the proposed *C. millarii* sp. nov. clade were 0.00 to 0.53%, within the proposed *C. mediterranea* sp. nov. were 0.70 to 0.78% and within *C. clavata* 0.18 to 0.35%.

Family RHODOMELACEAE Horaninow Genus *Corynecladia* J.Agardh

Corynecladia millarii sp. nov. (Figs 3-5)

Plants red in colour, soft in texture, forming tufts up to 7 cm high; thalli terete up to 1 mm in diameter, arising from a discoid holdfast with secondary stoloniferous branches; branching irregularly alternate, usually with 2(3) orders of branches; ultimate branchlets are cylindricalclavate; four periaxial cells per vegetative axial segment. Secondary pit-connections between cortical cells localized in middle to inner part of the cells. Cortical cells with one (rarely two) corps en cerise. No lenticular thickenings. Tetrasporangia in parallel arrangement cut-off abaxially from the third and fourth periaxial cells. It differs from other species of *Corynecladia* in showing neither secondary cortication nor starch grains in medullary cells and from genera *Laurencia* and *Laurenciella* in the occurrence of deep secondary pit connections between cortical cells. It differs from the related *C. mediterranea* mainly in different molecular sequences.

TYPE MATERIAL. — Italy • Sicily, Syracuse, Capo Murro di Porco; 37°00'37"N, 15°18'28"E; epilithic; 0.1 m depth; 13.III.2021; D. Serio; holotype (tetrasporophyte): CAT[CAT 2721]; Gen-Bank: OQ738957, OQ738958 • *ibid.*; isotypes: CAT[CAT 2722, CAT 2723]; GenBank: OQ738959, OQ738960, OQ738961, OQ738962 • *ibid.*; 15.III.2007; paratype (tetrasporophyte): CAT[CAT 2063]; GenBank: OQ738952 • *ibid.*; 25.IV.2021; paratype (tetrasporophyte): CAT[CAT 2727].

TYPE LOCALITY. — Italy, Sicily, Syracuse, Capo Murro di Porco.

ETYMOLOGY. — The specific epithet is in honor of the late friend and colleague Dr Alan Millar from Sydney, Australia.

DISTRIBUTION. — Type locality and probably more widely distributed.

HABITAT. — Plants epilithic in upper subtidal up to 1 m depth.

DESCRIPTION

Plants epilithic, soft, red and up to 7 cm high. Terete throughout, attached to substrate by a discoid holdfast with stolon-like branches and smaller discoid holdfasts (Fig. 3A, B). Erect axes, 1 mm in diameter in the middle portion of the thallus, irregularly alternately branched, usually with 2(-3) orders of branches. Branchlets with slight epidermal cell projection near the apex (Fig. 4A). Cortical cells with one (rarely two) corps en cerise (Fig. 4B). In transverse section cortical cells quadratic to rectangular, not radially elongated nor arranged as a palisade, measuring $20-25 \times 15-20 \,\mu\text{m}$ in the middle portions of the plant (Fig. 4C). Cortical cells connected to each other by thin secondary pit-connections. In longitudinal section these secondary pit-connections localized in the middle to inner part of the cells (Fig. 4D) making them hardly visible in surface view. Medullary cells rounded, 35-40 × 25-30 µm in the middle portions of the thallus, larger toward the centre. Walls of medullary cells without lenticular thickenings



Fig. 3. – *Corynecladia millarii* sp. nov.: **A**, plant habit of holotype CAT 2721; **B**, plant in natural habitat. Scale bar: 1 cm.



Fig. 4. — *Corynecladia millarii* sp. nov., holotype CAT 2721: **A**, branchlet showing epidermal cells slightly projecting near the apex; **B**, epidermal cells in surface view showing one corps en cerise per cell (**white arrows**); **C**, transverse section of the thallus; **D**, longitudinal section showing secondary pit connections between epidermal cells located in median part of the cells (**white arrow**). Scale bars: A, C, 100 μm; B, D, 50 μm.

(Fig. 4C). Each vegetative axial segment cuts off four periaxial cells (Fig. 5B). Tetrasporangial initials cut off abaxially from the third and fourth periaxial cells (Fig. 5A, B). No additional tetrasporangial periaxial cells produced. Mature tetrasporangia tetrahedrally divided, measuring 60-70 μ m in diameter. Tetrasporangia in a parallel arrangement along the axis of the stichidium (Fig. 5C). Gametangia unknown.

Corynecladia mediterranea sp. nov. (Figs 6-8)

Plants red-yellowish in colour, soft in texture, forming tufts up to 8 cm high; thalli terete up to 2 mm in diameter, arising from a discoid holdfast with secondary stoloniferous branches; branching irregularly alternate, usually with 2(3) orders of branches; ultimate



Fig. 5. — Corynecladia millarii sp. nov., holotype CAT 2721: **A**, longitudinal section of a tetrasporic branch showing a tetrasporangium cut off abaxially from a fertile pericentral cell; **B**, transverse section of a tetrasporic branch near the apex showing the axial cell (**a**) with two sterile (**p**) and two elongate fertile (**fp**) pericentral cells; **C**, tetrasporangial branchlet showing parallel arrangement of tetrasporangia. Scale bars: A, B, 50 µm; C, 200 µm.

branchlets are cylindrical-clavate; four periaxial cells per vegetative axial segment. Secondary pit-connections between cortical cells localized in middle to inner part of the cells. Cortical cells with one corps en cerise. No lenticular thickenings. Tetrasporangia in parallel arrangement cut-off abaxially from the third and fourth periaxial cells. It differs from other species of *Corynecladia* in showing neither secondary cortication nor starch grains in medullary cells and from genera *Laurencia* and *Laurenciella* in the occurrence of deep secondary pit connections between cortical cells. It differs from the related *C. millarii* mainly in different molecular sequences.

TYPE MATERIAL. — Italy • Sicily, Trapani, San Vito Lo Capo, Golfo di Monte Cofano; 38°06'21"N, 12°41'36"E; epilithic; 0.5 m depth; 9.VII.2017; D. Serio; holotype (tetrasporophyte): CAT[CAT 2724]; GenBank: OQ738971 • *ibid.*; Porto Palo di Capo Passero; 36°39'03.8"N, 15°04'37.4"E; epilithic; 0.2 m depth; 8.V.2021; D. Serio; paratype (tetrasporophyte): CAT[CAT 2726]; GenBank: OQ738950, OQ738951.

TYPE LOCALITY. — Italy, Sicily, Trapani, San Vito Lo Capo, Golfo di Monte Cofano.

ETYMOLOGY. — The specific epithet indicates the Sea in which the species was found.

DISTRIBUTION. — Type locality, Golfo di Monte Cofano (Trapani, Sicily); Porto Palo di Capo Passero (Syracuse, Sicily); and probably more widely distributed.

HABITAT. — Plants epilithic in upper subtidal up to 1 m depth.

DESCRIPTION

Plants epilithic, soft, red yellowish, up to 8 cm high, terete throughout, attached to substrate by a discoid holdfast with stolon-like branches and smaller discoid holdfasts (Fig. 6A, B). Erect axes, 1-2 mm in diameter in the middle portion of the thallus, irregularly alternate, usually with 2(-3) orders of branches. Epidermal cells with slight projection near the apex (Fig. 7A). One corp en cerise per cortical cells (Fig. 7B). Cortical cells showing thin secondary pit-connections. In longitudinal section they appeared localized in the middle to inner part of the cells (Fig. 8A). In transverse section, cortical cells quadratic to rectangular, neither radially elongated nor arranged as a palisade, measuring $25-30 \times 30-35$ µm in the middle portions of the plant (Fig. 8B). Medullary cells rounded, $40-50 \times 35-45$ µm in the middle portions of the plant, larger toward the center of the axes. Walls of medullary cells without lenticular thickenings (Fig. 8B). Each vegetative axial segment cuts off four periaxial cells (Fig. 8D). Tetrasporangial initials cut off abaxially from the third and fourth periaxial cells (Fig. 8D). No additional tetrasporangial periaxial cells produced. Mature tetrasporangia tetrahedrally divided, 90-100 µm in diameter. Tetrasporangia forming a parallel arrangement along the axis of the stichidium (Fig. 8C). Gametangia unknown.

DISCUSSION

The purpose of this study was to determine the taxonomy of Mediterranean thalli with both habit and gross morphology similar to *Laurenciella marilzae* as reported by Serio *et al.* (2000: figs 1-8), Furnari *et al.* (2001: figs 32-34) and Serio *et al.* (2020: fig. 1). In both *rbcL* and COI-5P analyses the above studied specimens grouped as two separate taxa within the *Corynecladia* clade, and not in either the *Laurencia* or *Laurenciella* clades.

The type species of *Corynecladia* is *C. clavata*, described from southern Australia. In the *rbc*L molecular results of this study both Mediterranean taxa nested in the same clade as *C. clavata*, supporting their placement in this genus. *Corynecladia millarii* sp. nov. and *C. mediterranea* sp. nov. each showed to be fully supported clades within the genus. Also, they were separated from each other by large interspecific pairwise distances, indicating two separate species.

Corynecladia itself was a moderately supported genus with large intrageneric distances. However, although intrageneric distances within *Corynecladia* were large, these large distances were only due to C. nova, which had a maximum pairwise distance from C. millarii sp. nov. of 9.38%, and from C. mediterranea sp. nov. of 9.28%. On the resulting phylogenetic tree C. nova is alone on a branch basal to the other Corynecladia taxa. These results could be support for recognizing C. nova at a generic level. However, these two distances were the only values that were outside of the generally accepted value of 8% for intrageneric distances. The next largest pairwise distance between C. nova and any other Corynecladia taxa was 6.59% (C. clavata), which was less than between C. clavata and either of the new Mediterranean taxa. All other interspecific distances between C. nova and other Corynecladia taxa were again below commonly accepted intrageneric distance limits, supporting C. nova as best belonging within Corynecladia. Perhaps future discoveries and more molecular sampling of this genus will help to further elucidate its placement and Corynecladia intrageneric relationships overall.

COI-5P results were congruent with *rbc*L results although *Corynecladia* was unsupported. In this case COI-5P was





FIG. 6. — Corynecladia mediterranea sp. nov.: A, plant habit of holotype CAT 2724; B, plant in natural habitat. Scale bar: 5 mm.

not enough to resolve the genus. Most genera within the complex were also unsupported, except for *Laurencia* (ML bootstrap = 91%) and *Laurenciella* (ML bootstrap = 80%). Both *C. millarii* sp. nov. and *C. mediterranea* sp. nov. resulted within *Corynecladia*, defined by the presence of the generitype *C. clavata* within the clade. And again the Mediterranean sequences formed two, well separated taxa.

The genus *Corynecladia* has been considered a synonym of *Laurencia* (Yamada 1931; Kylin 1956) until Nam (2006: 693) reached the conclusion that "*Corynecladia* should be reinstated for the type species *L. clavata*". Nam based this move on particular characters of *Laurencia clavata* Sonder (now *C. clavata* (Sonder) J. Agardh), specifically the marked constriction at the base of the ultimate branchlets, as well as its unique verticillate branching structure. In that paper, Nam, after having reported Womersley's (2003: 460) opinion that in *L. clavata* "tetrasporangia seem to be abaxially produced from outer cortical cells" stated that "a critical examination of their (tetrasporangia) origin is needed". This observation



FIG. 7. — *Corynecladia mediterranea* sp. nov., holotype CAT 2724: **A**, apical part of a branch showing epidermal cells slightly projecting near the apex; **B**, epidermal cells in surface view showing one corps en cerise per cell. Scale bars: A, 150 μ m; B, 100 μ m.

of Womersley led some researchers (Cassano et al. 2019: 13) to consider the possibility that sporangia in Corynecladia, in addition to originating from particular periaxial cells, could also be produced from subcortical cells. In support of this latter possibility, they refer to observations made by Agardh (1876) and Womersley (2003). However, Womersley's (2003) statement "... Tetrasporangia... in parallel arrangement cut off abaxially from outer cells..." appears to be unreliable. The parallel arrangement of sporangia is derived from their production from particular periaxial cells. When sporangia are produced from outer cortical cells the result is a random arrangement of sporangia. From both Womersley's and Harvey's illustrations tetrasporangia clearly appear in a parallel arrangement which is incompatible with an outer subcortical cell origin (Harvey 1862: pl. CLXXXIX, as Chondria clavata (Sonder) Harvey; Womersley 2003: fig. 206D). Observations recorded by Agardh (1876) state that in both Corynecladia and Laurencia: "Sphaerosporae infra apicem

TABLE 1. — Comparison of morphological features within Corynecladia J.Agardh. Asterisk indicates the paper, reported in the references below, where the corresponding character was observed.

		Corynecladia millarii sp. nov.	Corynecladia mediterranea sp. nov.	Corynecladia nova (Metti) Cassano, M.C.Oliveira & M.T.Fujii	<i>Corynecladia clavata</i> (Sonder) J.Agardh	Corynecladia elata (C.Agardh) Cassano, M.C.Oliveira & M.T.Fujii
	Height of the thallus	Up to 7 cm	Up to 8 cm	Up to 2-3 cm	10-15 cm or higher	Up to 40 cm
	Colour	Red	Red yellowish	Various shades of pink	Reddish-brown	Reddish-brown
	Thallus	Terete	Terete	Compressed except near the base	Terete	Compressed except near the base
	Texture	Soft	Soft	Sturdy but not strictly cartilaginous	Subcartilaginous	Rigid
Vegetative structure	Type of attachment	Discoid holdfast and stolon-like branches	Discoid holdfast and stolon-like branches	Few thick rhizoids that grow along the substrate	Discoid holdfast	Discoid holdfast or creeping branches
	Corps en cerise per cell	1 (occasionally 2) in cortical cells	1 in cortical cells	Absent	Not detectable	Not detectable
	Epidermal cells (projection)	Present	Present (slightly)	Present (slightly)	Absent	Absent
	Secondary pit connections	Present	Present	Present	Present	Present
	Secondary cortication	Absent	Absent	Present	Present	Present
	Refractive discoid starch grains	Absent	Absent	Absent?	Present	Absent
	Lenticular thickenings	Absent	Absent	Absent	Absent	Present
	Pericentral cells	4	4	4	4	4
Tetrasporangial	Additional	Absent	Absent	_	-	Absent
stichidium	Tetrasporangia (position)	3rd, 4th	3rd, 4th	_	-	3rd, 4th
	Tetrasporangia (arrangement)	Parallel	Parallel	Parallel	Parallel*	Parallel
Female	Procarp-bearing segment	-	-	-	-	5
structure	Cystocarp shape	-	-	Ovoid with ostiole not protuberant	Conical to hemispherical with rounded to truncated apex	Ovoid with ostiole not protuberant
Male structure	Origin of spermatangial branches	-	-	From one of two lateral on suprabasal cell of the trichoblast	From one of two lateral on suprabasal cell of the trichoblast	From one of two lateral on suprabasal cell of the trichoblast
	Type locality	Capo Murro di Porco, Syracuse, Sicily Mediterranean sea	Porto Palo di Capo Passero, , Syracuse, Sicily Mediterranean sea	Plantation Point, Jervis Bay, , NSW, Australia	Lefevre Peninsula South Australia	, King Island, Bass Strait, Australia
	Habitat	Up to 1m depth	Up to 1m depth	Up to 9 m depth	Up to 30 m depth	Up to 25 m depth
	References	This study	This study	Metti <i>et al.</i> (2015); Cassano <i>et al.</i> (2019)	Womersley (2003) Cassano <i>et al.</i> (2019); *Saito & Womersley (1974)	;Nam & Choi (2001); Cassanc <i>et al.</i> (2019)

ramulorum sine ordinem in zonam transversalem aggregatae in cellulis infra-corticalibus formatae, rotundate tringule divisae" (Sporangia within apices of branches with any order in transversal zones arranged forming in subcortical cells, rounded and triangularly divided) (Agardh 1876: 642, 644 for *Corynecladia* and *Laurencia*, respectively). More recently, in both genera parallel arrangement of tetrasporangia and their pericentral cell origins are consistently observed (Saito 1967; Saito & Womersley 1974; Metti *et al.* 2015; Cassano *et al.* 2019). Therefore, we conclude that in *Corynecladia* the tetrasporangia are produced only from particular periaxial cells.



Fig. 8. — Corynecladia mediterranea sp. nov., holotype CAT 2724: **A**, longitudinal section showing secondary pit connection between epidermal cells located in median part of the cells, white arrows indicate secondary pit connections between epidermal cells; **B**, transverse section of the thallus near the base; **C**, tetrasporangial branchlet showing parallel arrangement of tetrasporangia; **D**, transverse section of a tetrasporic branch near the apex showing an axial cell (**a**) with two sterile (**p**) and two elongate fertile (**fp**) pericentral cells. Scale bars: A, 40 µm; B, 100 µm; C, 200 µm; D, 20 µm.

At the time of this study, in the Mediterranean were 22 Laurencia complex species recognized. This included nine Laurencia and one Laurenciella species, which share the characteristic of four pericentral cells with Corynecladia. The two newly proposed taxa differ from both Laurencia and Laurenciella genera in the visibility of secondary pitconnections, in particular, Corynecladia secondary pit connections are thin, deep and hardly visible from surface view. The three Laurencia taxa that are most similar to C. millarii sp. nov. and C. mediterranea sp. nov. include: Laurencia obtusa which mainly differs by the irregular ramification of both branches and branchlets; L. microcladia which primarily differs by the presence of lenticular thickenings and displaying a whorled branching structure; and L. glandulifera which differs from the proposed Corynecladia species by the presence of very short, wart-like ultimate branchlets. A dichotomous key was developed and included in this study to explain in detail the differences between all the Mediterranean Laurencia complex taxa, and includes the two newly proposed Corynecladia species.

Finally, it's noteworthy that, apart from molecular affinity, *C. millarii* sp. nov. and *C. mediterranea* sp. nov. in both vegetative and reproductive characters seem closer to *Lau*- *rencia* and *Laurenciella*, from which they mainly differ in the occurrence of deep secondary pit connections between cortical cells, than to *Corynecladia* from which they differ in showing neither secondary cortication nor starch grains in medullary cells. Thus, *Corynecladia* is a very morphologically variable genus (Table 1) including species with a secondary cortication (wider in *C. elata* and *C. nova* [Metti *et al.* 2015], less wide in *C. clavata* [Nam & Choi 2001], absent in Mediterranean species [this study]), starch grains in medullary and subcortical cells (rather evident only in *C. clavata*, absent in Mediterranean species), and with secondary pit connections between cortical cells localized in the middle to inner part of the cells (the last character present in Mediterranean species and in *C. nova* [see Metti *et al.* 2015: fig 6C]).

Based on the above considerations, the following further amendment of the genus *Corynecladia* is proposed:

Corynecladia J.Agardh gen. emend.

Species genera et ordines algarum, seu descriptiones succinctae specierum, generum et ordinum, quibus algarum regnum constituitur 3: 642 (Agardh 1876).

Key to the Mediterranean species of the *Laurencia* complex

1.	Thalli throughout compressed or with only ultimate branchlets cylindrical. Two pericentral cells per axial seg- ment, spermatangial branches of filament-type and tetasporangia produced from epidermal cells
2.	Secondary pit connections between epidermal cells present
3.	Axes arising from a spreading basal crust. Spermatangial depressions cup-like, but slightly sunken. Species living in the littoral zone
4.	Epidermal cells in surface view very elongated longitudinally. Spermatangial depressions cup-shaped. Cystocarps urceolate. Species living in the lower littoral zone to upper sublittoral zone
	<i>Osmundea truncata</i> (Kützing) K.W.Nam & Maggs Epidermal cells in surface view very elongated longitudinally in the basal and median parts of the thallus, isodiametric in the subapical parts. Spermatangial depressions cup-shaped, but slightly sunken, located at the bifurcation of the branches. Cystocarps ovoid. Species living in the upper sublittoral zone (up to 7 m depth) Osmundea gederi (Gunnerus) G. Furnari
	Epidermal cells in surface view polyhedral. Spermatangial depressions pocket-shaped. Cystocarps ovoid. Species living in the lower sublittoral zone or if in shallower water in shaded habitats
5.	Axes arising from a thick spreading crust. Epidermal cells, in transverse section, radially elongated and palisade- like. Medullary cells without lenticular thickenings. Spermatangial depressions cup-shaped. Species living in the
	Axes arising from a stoloniferous holdfast. Epidermal cells, in transverse section, obconic and not palsade-like. Medullary cells with lenticular thickenings. Spermatangial depressions pocket-shaped. Species living in the lit- toral zone
	(Its occurrence in the Mediterranean sea should be confirmed.)
6.	Secondary pit connections between epidermal cells present. Four pericentral cells per axial segment
7.	Adult thalli not taller than 20 mm8Thalli up to 15 cm or more high9
8.	One to three (rarely four) erect axes, arising from a discoid holdfast. Axes simple or with one short subapical branchlet. Epidermal cells slightly projecting near the apex. Medullary cells with lenticular thickenings. Species epiphytic on both seagrasses leaves and macroalgae
	One (occasionally two or three) erect axes arising from a discoid holdfast. Axes to four orders of ramification. Epidermal cells not projecting near the apex. Species epiphytic only on seagrasses leaves
9.	Thalli more or less densely entangled10Thalli erect not entangled11
10.	Thalli densely entangled forming compact tufts. Branching irregularly spiral. In transverse section the axial cell not distinguishable in median portions of the thallus. Species living in the lower littoral to upper sublittoral zones.
	Thalli prostrate flexuous and frequently entangled. In transverse section, the axial cell is readily distinguishable in median portions of the thallus. Branching sparse, irregular with branches and branchlets often inserted nearly at a right angle. Branchlets with apices obtuse. Species living in the lower sublittoral zone or if in shallower water in shaded habitats
11.	Presence of deciduous branchlets formed abundantly near branches. Species living in the sublittoral zone Laurencia caduciramulosa Masuda & Kawaguchi
	Absence of deciduous branchlets 12
12.	Axes radially ramified. Branches and branchlets spirally ramified giving a pyramidal outline to the thallus 13 Axes irregularly or whorled ramified

DESCRIPTION

Apical cell sunk in an apical pit of branchlet; central axis recognisable only near apical cell; forming extensive cortex; four periaxial cells on vegetative axial segments; the first periaxial cell underneath the trichoblasts; secondary pit connections between cortical cells present; secondary cortication present or not (according to species); medullary and subcortical cells with numerous refractive discoid starch grains (according to species); spermatangial development of trichoblast type; spermatangial branches produced from one of two laterals on suprabasal cell of trichoblasts; procarp-bearing segments with five periaxial cells; tetrasporangial in parallel arrangement; tetrasporangial production only from particular periaxial cells. Differs from *Laurencial Laurenciella* also in molecular sequences.

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APPENDIX

APPENDIX. - A list of species used for molecular work in this study, including newly generated rbcL and COI-5P sequences, and downloaded GenBank sequences.

Species	Accession number	Location and collecting data	Reference	Marker
Ceramium kondoi Yendo	DQ350388	Japan, Niigata, Itoigawa, E.C.Yang, G.Y.Cho,	GenBank	rbcL
Chondria californica (Collins) Kylin	AY172578	K.Kogame, S.M.Boo, C1315 United States, California, San Diego County, Beach Club Reef (La Jolla Shores), 1.VII.1996,	McIvor et al. (2002)	rbcL
Chondria capillaris	MG255052	Ireland, Frinavarra, 17.VIII.2004, SAP106295	Sutti <i>et al.</i> (2018)	rbcL
Chondria capillaris	MF094021	United Kingdom, England, Swanage, 7.VI.2015, PD2129	Díaz-Tapia <i>et al.</i> (2017)	COI-5P
Chondria collinsiana M.A.Howe	GU330225	Prazil, Rio de Janeiro, Armação dos Búzios, Praia Rasa, 13.I.2005, V.Cassano, J.C.De-Paula, SP399 865	Cassano et al. (2012b)	rbcL
Chondria crassicaulis Harvev	GU223872	Japan, Niigata Pref., Kashiwazaki, Kujira-nami, 03 V2008, Kashiwazaki-A4	Kurihara et al. (2010)	COI-5P
Chondria dangeardii E.Y.Dawson	GU223879	United States, Hawaii, Molokai, 21.III.2008, ARS03592	Kurihara <i>et al.</i> (2010)	COI-5P
Chondria decipiens Kylin	MG272232	United States, California, San Nicolas Island, 14.XI.2012, UC2025838	Sutti <i>et al.</i> (2018)	COI-5P
Chondria scintillans G.Feldmann	KF492717	France, Brittany, Roscoff-Theven, 05.XII.2002, F.Rousseau, JML0048	Machín-Sánchez et al. (2014)	COI-5P
Chondria succulenta (J.Agardh) Falkenberg	KY120336	Australia, NSW, Batehaven, 30.V.2005, Y.Metti, YM309, NSW879470	Metti <i>et al.</i> (2015)	rbcL
Chondrophycus dotyi (Y.Saito) K.W.Nam	HQ423050	United States, Hawaii, Oahu, Waikiki Natatorium, 27.IV.2007, K.Shultz, BISH669750 (#00693)	Sherwood et al. (2010)	COI-5P
Chondrophycus dotyi	KX815263	United States, Hawaii, Oahu, Sandy Beach, 31.V.2015, E.Stein, SP 469.710	Sentíes et al. (2016)	rbcL
Chondrophycus sp.	FJ785311	New Caledonia, Loyalty Islands, Beautemps/ Beaupré, 06.IV.2005, C.Payri, IRD112	Martin-Lescanne et al. (2010)	rbcL
Chondrophycus sp.	GU223885	United States, Hawaii, Richardson Beach Park, 23.I.2008, A.Kurihara, K.Conklin, ARS 03326	Sherwood et al. (2010)	COI-5P
Chondrophycus sp.	KX146174	New Caledonia, Loyalty Islands, Beautemps/ Beaupré, C.Pavri, 06.IV.2005, JML0250	Rousseau <i>et al.</i> (2017)	rbcL
Chondrophycus sp.	KX815262	Mexico, Quintana Roo, Isla Mujeres, Garrafon de Castilla, 12.II.2007, A.Sentíes, M.C.Gil.Bodríguez, IJAMIZ1240	Sentíes <i>et al.</i> (2016)	rbcL
Chondrophycus sp.	KY120337	Australia, Norfolk Island, Collins Head, intertidal, 21.III.2005, Y.Metti, A.Millar, YM296, NSW900770	Metti <i>et al.</i> (2015)	rbcL
Chondrophycus sp.	KY927795	South Africa, 09.VI.2010, R.J.Anderson, J.J.Bolton, CMF-2017	Francis et al. (2017)	rbcL
Chondrophycus succisus (A.B.Cribb) K.W.Nam	GU223884	United States, Molokai, 11.II.2007, ARS02583	Kurihara <i>et al.</i> (2010)	COI-5P
Chondrophycus tronoi (E.Ganzon-Fortes) K.W.Nam	AF489864	Philippines	GenBank	rbcL
Chondrophycus cf. undulatus (Yamada) Garbary & Harper	FJ785307	New Caledonia, Maré, Loyalty Is., 22.III.2005, C.Payri, IRD100	Martin-Lescanne et al. (2010)	rbcL
Chondrophycus undulatus	HQ422752	United States, Hawaii, Maui, Ahihi Bay (Site 2), 25 VI 2007, A Kuribara, #02493	Sherwood et al. (2010)	COI-5P
Chondrophycus undulatus	HQ422996	United States, Hawaii, Oahu, Hauula Beach Park, 18 IX 2007 A Kuribara #02922	Sherwood et al. (2010)	COI-5P
Corynecladia clavata (Sonder) I Agardh	MF094079	Australia, Victoria, Walkerville, 20.1.2015, P.Díaz- Tania, M.Brookes, PD1300	Díaz-Tapia <i>et al.</i> (2017)	rbcL
Corynecladia clavata	MH704453	Australia, Victoria, The Caves, 20.1.2015, P.Díaz-	GenBank	rbcL
Corynecladia clavata	MH704456	Australia, Victoria, The Caves, 20.1.2015, P.Díaz- Tania M Brookes, SPE58163	GenBank	COI-5P
Corynecladia clavata	MK260194	Australia, Victoria, Point Lonsdale, Town Beach, 18.V.2010, G.T.Kraft, R.Kraft, B.Dog jr., GWS017395	GenBank	COI-5P

Species	Accession number	Location and collecting data	Reference	Marker
Corynecladia elata	KY120339	Australia, Western Australia, Rottnest Island,	Metti et al. (2015)	rbcL
(C.Agardh) Cassano,		subtidal, 15.XI.2008, James Eu, JE01,		
M.C.Oliveira & M.T.Fujii	0000000	NSW900764		
Corynecladia elata	OR046643	Australia, Western Australia, Rottnest Island,	This study	COI-5P
Convocladia moditorranea	00738971	IS.XI.2008, J.EU, JEUT, NSW900764 Italy Sicily Tranani San Vito Lo Cano, Golfo	This study	rbcl
Metti, G.Furnari & Serio.	00100011	di Monte Cofano (38°06'21"N, 12°41'36"E).	This study	IDCL
Sp. nov.		09.VII.2017. D.Serio. MCZ2. CAT2724		
Corynecladia mediterranea	OQ738951	Italy, Sicily, Syracuse, Porto Palo di Capo Passero	This study	rbcL
sp. nov.		(36°39'03.8"N, 15°04'37.4"E), 08.V.2021,		
		D.Serio, 4CPm21, CAT2726		
Corynecladia mediterranea	OQ738950	Italy, Sicily, Syracuse, Porto Palo di Capo Passero	This study	COI-5P
sp. nov.		(36°39′03.8″N, 15°04′37.4″E), 08.V.2021,		
Convocladia mediterranea	OB046646	Greece Grecia Peloponneso Gerolimenas	This study	COI-5P
SD. NOV.	01040040	(36°28'45"N, 22°24'02"F), 31 VIII.2009, D.Serio.	This study	001 01
op:		GR1		
Corynecladia mediterranea	OR046647	Italy, Sicily, Trapani, San Vito Lo Capo, Castelluzzo	This study	COI-5P
sp. nov.		(38°06'21"N, 12°41'36"E), 01.VII.2009, D.Serio,		
		MC4		
Corynecladia mediterranea	OR046648	Italy, Sicily, Trapani, San Vito Lo Capo, Castelluzzo	This study	COI-5P
sp. nov.		(38°06'21"N, 12°41'36"E), 09.VII.2017, D.Serio,		
Corvnecladia mediterranea	OB046645	Italy Favignana Cala San Nicola 01 IX 2017	This study	COI-5P
Sp. nov.		D.Serio. FV5	The study	00101
Corynecladia millarii Metti,	OQ738952	Italy, Sicily, Syracuse, Cap Murro di Porco,	This study	rbcL
G.Furnari & Serio,		15.III.2007, D.Serio, CAT 2063		
sp. nov.				
Corynecladia millarii	OQ738962	Italy, Sicily, Syracuse, Cap Murro di Porco	This study	rbcL
sp. nov.		(37°00′37″N, 15°18′28″E), 13.III.2021, D.Serio,		
Corvnecladia millarii	00738961	Italy Sicily Syracuse Can Murro di Porco	This study	COI-5P
SD, NOV.	00100001	(37°00'37"N, 15°18'28"F), 13.III.2021, D.Serio.	This Study	001 01
0011011		CMPR4, CAT 2723		
Corynecladia millarii	OQ738960	Italy, Sicily, Syracuse, Cap Murro di Porco	This study	rbcL
sp. nov.		(37°00'37"N, 15°18'28"E), 13.III.2021, D.Serio,		
	0.0700050	CMPR2, CAT 2722		
Coryneciadia millarii	OQ738959	Italy, Sicily, Syracuse, Cap Murro di Porco	This study	COI-5P
sp. nov.		(37 00 37 N, 13 18 28 E), 13.111.2021, D.Serio,		
Corvnecladia millarii	00738958	Italy, Sicily, Syracuse, Cap Murro di Porco	This study	rbcl
sp. nov.		(37°00'37"N, 15°18'28"E), 13.III.2021, D.Serio,		
·		CMPR1, CAT 2721		
Corynecladia millarii	OQ738957	Italy, Sicily, Syracuse, Cap Murro di Porco	This study	COI-5P
sp. nov.		(37°00'37"N, 15°18'28"E), 13.III.2021, D.Serio,		
Convocladia millarii		CMPR2, CAI 2722	This study	
sp. nov	UN040044	15 III 2007 D Serio CAT 2063	This study	COI-5F
Corvnecladia nova (Metti)	KY120340	Australia, NSW, Jervis Bay, Plantation Pt,	Metti e <i>t al.</i> (2015)	rbcL
Cassano, M.C.Oliveira &		subtidal, 15.II.2005, Y.Metti, A.Millar, YM194,		
M.T.Fujii		NSW900767		
Corynecladia nova	OQ738973	Australia, NSW, Jervis Bay, Plantation Pt,	This study	rbcL
		subtidal, 15.II.2005, Y.Metti, A.Millar, YM195,		
Laurancia aldingansis	IE810351	NSWI 130351 Brazil Rio de Janeiro, Arma ção dos Búzios, Braja	Cassano et al. (2012b)	rbcl
Y Saito & Womerslev	51 610551	Basa 1312005 V Cassano J C De-Paula	, Cassallo et al. (2012b)	IDCL
Laurencia caduciramulosa	JF781525	Spain, Canary Islands, Tenerife, Punta del	Machín-Sánchez et al. (2012)	rbcL
Masuda & S.Kawaguchi		Hidalgo, 6.V.2008, M.C.Gil-Rodríguez, M.T.Fujii,		
0		V.Cassano, J.Díaz-Larrea,		
Laurencia catarinensis	KF492781	Spain, Canary Islands, Tenerife, Punta del Hidalgo,	Machín-Sánchez et al. (2014)	rbcL
Cordeiro-Marino & Fujii		22.VI.2012, M.C.Gil-Rodríguez, M.Machín-		
Lauronaia dandraidaa		Sanchez, MMS0151 Brazil Sao Baulo, Ubatuba, Ilba dao Couves	Fuiii at al. (2006)	rhal
.1 Agardh	AL402000	1912001 M T Fuili	i ujii et al. (2000)	IDCL
Laurencia dendroidea	HQ422746	United States, Hawaii, ARS02549	GenBank	COI-5P

Species	Accession number	Location and collecting data	Reference	Marker
Laurencia dendroidea	KF492725	Spain, Canary Islands, La Gomera, Punta de La Dama, 21.IX.2009, Eva Aylagas, M.Machín-	Machín-Sánchez et al. (2014)	COI-5P
Laurencia dendroidea	KF492726	Sánchez, MMS0183 Spain, Canary Islands, La Gomera, Charco del Conde, 23.IX.2009, Eva Aylagas, M.Machín-	Machín-Sánchez et al. (2014)	COI-5P
Laurencia dendroidea	KF492785	Sánchez, MMS0182 Spain, Canary Islands, Tenerife, El Pris, 13.V.2011, M.C.Gil-Rodríguez, M.Machín-Sánchez,	Machín-Sánchez et al. (2014)	rbcL
Laurencia dendroidea	KX258827	MMS0082 Oman, Dohfar (17°27'36.0"N, 55°14'24.0"E),	Rousseau <i>et al.</i> (2017)	COI-5P
Laurencia dendroidea	MH388711	Venezuela, Falcon, Playa Buchuacos, 06.X.2012,	Garcia-Soto & Lopez-	COI-5P
Laurencia dendroidea	OR046643	Australia, WA, Rottnest Island, 15.XI.2008, J.Eu,	This study	COI-5P
Laurencia dendroidea	MT822855	Australia, NSW, Batehaven, 30.V.2005, Y.Metti,	Metti 2017	COI-5P
Laurencia intricata	MG004181	United States, Florida, Key Biscayne, Crandon	Collado-Vides et al. (2018)	rbcL
Laurencia nidifica J.Agardh	HQ422750	United States, Hawaii, Oahu, Laie, 08.IV.2007,	Sherwood et al. (2010)	COI-5P
Laurencia nipponica	GU223874	Russia, Sakhalin Island, Tangi, 23.VI.2003, T.Abe,	Kurihara <i>et al.</i> (2010)	COI-5P
Laurencia obtusa (Hudson)	AF281881	Ireland, Co. Donegal, Fanad Head (intertidal pool),	Nam et al. (2000)	rbcL
Laurencia obtusa	OQ738953	Italy, Syracuse, MPA Plemmirio, Capo Murro	This study	COI-5P
Laurencia obtusa	OQ738955	Italy, Syracuse, MPA Plemmirio, Capo Murro di Porco 13 III 2021 D Serio CMPA2	This study	COI-5P
Laurencia obtusa	OQ738965	Italy, Favignana, Cala Faragloioni, 02.IX.2017, D Serio, EV8	This study	rbcL
Laurencia obtusa	OQ738969	Italy, Sicily, San Vito Lo Capo, Castelluzzo, 08 J 2011 D Serio MCA5	This study	rbcL
Laurencia obtusa	OQ738970	Italy, Sicily, San Vito Lo Capo, Castelluzzo,	This study	rbcL
Laurencia obtusa	OQ738946	Italy, Syracuse, MPA Plemmirio, Capo Murro di Porco, 08 V2021, D.Serio, 2CPm2021	This study	COI-5P
Laurencia obtusa	OQ738948	Italy, Syracuse, MPA Plemmirio, Capo Murro di Porco, 08 V 2021, D.Serio, 3CPm2021	This study	COI-5P
Laurencia obtusa	KX258828	France, Languedoc-Roussillon, Pyrenees- Orientales, Cap Beart, Banyuls-sur-Mer, 11 VII 2007 L Bitther LBC0053	Rousseau <i>et al.</i> (2017)	COI-5P
Laurencia oliveirana Yoneshigue-Valentin,	JF810352	Brazil, Ponta da Cabeca, Arraial do Cabo, Rio de Janeiro, 2008, V.Cassano, J.C.De-Paula, SP300 857	Cassano <i>et al.</i> (2012b)	rbcL
Laurencia pacifica Kylin	HQ544189	United States, 20.V.2010, B.Clarkston, K.Hind, S.Toews, GW/S022084	GenBank	COI-5P
Laurencia pyramidalis Bory	KF492756	Spain, Canary Islands, Fuerteventura, Garcey, 10 IX 2012 M Machin-Sánchez, MMS0154	Machín-Sánchez et al. (2014)	COI-5P
Laurencia pyramidalis	KF492793	Spain, Canary Islands, Fuerteventura, Garcey, 10 IX 2012 M Machin-Sánchez, MMS0154	Machín-Sánchez et al. (2014)	rbcL
Laurencia viridis Gil- Rodríguez & Haroun	KF492760	Portugal, Azores, Santa Maria, Boca de ribeira seca, 02.VII.2011, M.T.Fujii, A.Neto, J.Pombo, M.Machín-Sánchez, MMS0038	Machín-Sánchez et al. (2014)	COI-5P
Laurencia viridis	KF492794	Portugal, Azores, Santa Maria, Boca de ribeira seca, 02.VII.2011, M.T.Fujii, A.Neto, J.Pombo,	Machín-Sánchez et al. (2014)	rbcL
Laurenciella marilzae (Gil- Rodríguez, Sentíes, Díaz-Larrea, Cassano & M.T.Fujii) Gil-Rodríguez, Sentíes, Díaz-Larrea, Cassano & M.T.Fujii	EF686002	Spain, Punta del Hidalgo Tenerife, Canary Islands, 12.VII.2006, Gil-Rodríguez, TFCPhyc.N#13129	Gil-Rodríguez <i>et al.</i> (2009)	rbcL
Laurenciella marilzae	GU938189	Brazil, Laje de Santos Marine State Park, Parcel do Sul, Sao Paulo, 2007, R.Rocha-Jorge, SP399814	Rocha-Jorge et al. (2010)	rbcL

Species	Accession number	Location and collecting data	Reference	Marker
Laurenciella marilzae	HQ115065	Mexico, Isla Mujeres, Quintana Roo, 2008,	Sentíes et al. (2011)	rbcL
Laurenciella marilzae	KF492762	A.Sentíes, M.T.Fujii, UAMIZ1019 Spain, Canary Islands, Lanzarote, Pechigueras, 15.I.2013, M.C.Gil Rodriguez, M.Machín- Sánchez, MMS0174	Machín-Sánchez et al. (2014)	COI-5P
Laurenciella marilzae	KX146186	Croatia, Scedro, 11.VI.2007, J.Utge, L. Le Gall,	Rousseau <i>et al.</i> (2017)	rbcL
Laurenciella marilzae	KX258829	Croatia, Scedro, 11.VI.2007, J.Utge, L. Le Gall,	Rousseau <i>et al.</i> (2017)	COI-5P
Laurenciella marilzae Laurenciella marilzae	MF093987 MT822847	Spain, Pta Hidalgo, Tenerife, 10.VI.2015, HV1501 Italy, Sicily, San Vito Lo Capo (Trapani), 09.VII.2017, MCZ6	Díaz-Tapia <i>et al.</i> (2017) This study	COI-5P COI-5P
Laurenciella marilzae Laurenciella mayaimii L.Collado-Vides,	MT822850 MG004176	Italy, Sicily, Brucoli (Siracusa), 18.VII.2017, BZ1 United States, Florida, Biscayne Bay, Deering Estate, 12.VIII.2013, SPF58079	This study Collado-Vides <i>et al.</i> (2018)	COI-5P COI-5P
Laurenciella mayaimii	MG004177	United States, Florida, Biscayne Bay, Deering	Collado-Vides et al. (2018)	COI-5P
Laurenciella mayaimii	MG004178	United States, Florida, Key Largo, 14.VIII.2013, FTG167920	Collado-Vides et al. (2018)	COI-5P
Laurenciella mayaimii	MG004182	United States, Florida, Biscayne Bay, Deering Estate, 12,VIII,2013, SPF58079	Collado-Vides et al. (2018)	rbcL
Laurenciella mayaimii	MG004183	United States, Florida, Key Largo, 14.VIII.2013, FTG167920	Collado-Vides et al. (2018)	rbcL
<i>Laurenciella</i> sp.	MF094082	Australia, Twen Reef, Victoria, intertidal, 19.I.2015, PD1524	Díaz-Tapia et al. (2017)	rbcL
Laurenciella namii Popolizio, C.W.Schneider &	MG004179	United States, Florida, Key Biscayne, Crandon Park, 12.VIII.2013, SPF57893	Popolizio et al. (2022)	COI-5P
Laurenciella namii	MG004184	United States, Florida, Key Biscayne, Crandon Park, 12 VIII 2013, SPE57893	Popolizio et al. (2022)	rbcL
Ohelopapa flexilis (Setchell F.Rousseau, Martin- Lescanne, Payri &) KX146187	French Polynesia, Tahiti, Tahara reef, 24.III.2007, A.Apham, 01A07	Rousseau <i>et al.</i> (2017)	rbcL
Ohelopapa flexilis	KX258830	French Polynesia, Tahiti, Tahara reef, 24.III.2007, A Anham 01A07	Rousseau <i>et al.</i> (2017)	COI-5P
Osmundea blinksii (Hollenberg & I.A.Abbott) K.W.Nam	AY172575	United States, California, San Mateo Co., Ano Nuevo, Greyhound Rock, 17.VII.1996, C.A.Magos	McIvor <i>et al.</i> (2002)	rbcL
Osmundea oederi (Gunnerus) G.Furnari	KU566532	Portugal, Azores, Sao Miguel, Ferraria, 27.VI.2011, E.Nogueira, V.Cassano, A.Sentíes, MMS0010	Machín-Sánchez et al. (2016)	COI-5P
Osmundea oederi	KU566558	Portugal, Azores, Sao Miguel, Ferraria, 27.VI.2011, E.Nogueira, V.Cassano, A.Sentíes, MMS0010	Machín-Sánchez et al. (2016)	rbcL
Osmundea oederi	KX258833	France, Normandy, Manche, Grand Colomier nord, îles Chausey (48°52'48.0"N, 1°49'58.8"W) 16 W 2008 L Le Gall LI G1116	Rousseau <i>et al.</i> (2017) ,	COI-5P
Osmundea osmunda (S.G.Gmelin) K.W.Nam & Maggs	AF281877	Ireland, Co. Donegal, St. John's Point, 12.X.1999, #1038	Nam et al. (2000)	rbcL
Osmundea osmunda	KJ960860	France, Brittany, Le Loup, 30.VIII.2011, L.Couceiro, M.Robuchon, RMAR2969	GenBank	COI-5P
Osmundea pinnatifida (Hudson) Stackhouse	KF492771	Portugal, Azores, Pico, Santa Cruz Ribeiras- Piscinas, 29.VI.2011, M.T.Fujii, A.Neto, M.Machín-Sánchez, MMS0034	Machín-Sánchez et al. (2014)	COI-5P
Osmundea pinnatifida Osmundea prudhommevanreinei Machín-Sánchez & Gil- Bodríguez	KU647694 KU566546	Portugal, 29.VI.2011, MMS0034 Spain, Canary Islands, Tenerife, Playa Paraiso, 08.V.2012, M.C.Gil-Rodríguez, M.Machín- Sánchez, MMS0144	Machín-Sánchez et al. (2016) Machín-Sánchez et al. (2016)	<i>rbc</i> L COI-5P
Osmundea prudhommevanreinei	KU566568	Spain, Canary Islands, Tenerife, Playa Paraiso, 08.V.2012, M.C.Gil-Rodríguez, M.Machín- Sánchez, MMS0144	Machín-Sánchez et al. (2016)	rbcL
Osmundea spectabilis (Postels & Ruprecht) K.W.Nam	KM254320	United States, California, McAbee Beach, Monterey, 21.V.2010, B.Clarkston, K.Hind, S.Toews, GWS022243	Saunders (2014)	COI-5P

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Osmundea spectabilis	KM254469	United States, California, Bird Rock, Pacific Grove	, Saunders (2014)	COI-5P
		GWS022314		
Osmundea spectabilis var. spectabilis	AY172573	United States, California, Cambria, San Luis Obispo, 10.VII.1996	McIvor et al. (2002)	rbcL
Osmundea splendens (Hollenberg) K.W.Nam	KM254322	United States, California, Santa Cruz (Four Mile), 19.V.2010, B.Clarkston, K.Hind, S.Toews, GWS021984	Saunders (2014)	COI-5P
Osmundea truncata (Kützing) K.W.Nam & Magas	JF781523	Spain, Islas Canarias, Tenerife, Barranquera, 2008, TFCPHYC14650	Cassano <i>et al.</i> (2012b)	rbcL
Palisada cf. robusta K W Nam	FJ785321	New Caledonia, Lifou, C.Payri, 23.III.2005, IRD92	Martin-Lescanne et al. (2010)	rbcL
Palisada crustiformans (K.J.McDermid) A.R.Sherwood, A.K.wibara & K.W.Nam	KX146195	United States, Hawaii, Isaac Hale Beach, 24.I.2008, A.Kurihara, ARS3327	Rousseau <i>et al.</i> (2017)	rbcL
Palisada crustiformans	KX258840	United States, Hawaii, Isaac Hale Beach, 24 J 2008, A Kuribara, ABS3327	Rousseau <i>et al.</i> (2017)	COI-5P
Palisada flagellifera (J.Agardh) K.W.Nam	EF685998	Spain, Canary Islands, Tenerife, Playa Paraiso, 12.VII.2006, M.C.Gil-Rodríquez, M.T.Fujii, A.Sentíes, TFC Phyc. N#13127	Gil-Rodríguez <i>et al.</i> (2010)	rbcL
Palisada flagellifera	KF492772	Spain, Canary Islands, Tenerife, Punta del Hidalgo, 13.I.2012, M.C.Gil-Rodríguez, M.Machín- Sánchez, MMS0095	Machín-Sánchez et al. (2014)	COI-5P
Palisada furcata (Cordeiro- Marino & M.T.Fujii) Cassano & M.T.Fujii	GU330226	Brazil, Praia de Tambau, Paraiba, 24.II.2004, M.T.Fujii, SP399.928	Cassano <i>et al.</i> (2012a)	rbcL
Palisada parvipapillata (C.K.Tseng) K.W.Nam	GU223895	United States, Hawaii, Oahu, 18.IX.2007, ARS02921	Kurihara <i>et al.</i> (2010)	COI-5P
Palisada perforata (Bory) K.W.Nam	EU256325	Spain, Canary Islands, Tenerife, Playa Paraiso, 14.VII.2006, M.C.Gil-Rodríguez, A.Sentíes, G. & M T Euiii, TEC Phys. 13134	Cassano <i>et al.</i> (2009)	rbcL
Palisada perforata	EU256326	Brazil, Rio de Janeiro, Rio das Ostras, Areias Negras, 3.VIII.2005, V.Cassano, M.B.B.Barreto, HB.I 10838	Cassano <i>et al.</i> (2009)	rbcL
Palisada perforata	EU256327	Spain, Canary Islands, Tenerife, Bahia Izquierda, Faro, Punta del Hidalgo, 6.X.2005, M.C.Gil- Bodríguez, TFC Phyc. N#13068	Cassano <i>et al.</i> (2009)	rbcL
Palisada perforata	EU256331	Brazil, Rio de Janeiro, Parati, Praia Vermelha, 30.XII.2005, V.Cassano, HRJ 10840	Cassano <i>et al.</i> (2009)	rbcL
Palisada perforata	KF492773	Spain, Canary Islands, Tenerife, Punta del Hidalgo, 13.I.2012, M.C.Gil-Rodríguez, M.Machín- Sánchez, MMS0093	Machín-Sánchez et al. (2014)	COI-5P
Palisada perforata	MH388710	Venezuela, Falcon, Playa Buchuacos, 6.X.2012, G. Garcia-Soto, GGS012	Garcia-Soto & Lopez- Bautista (2018)	COI-5P
Palisada rigida (J.Agardh) Metti	OM328131	Australia, Queensland, Redcliffe (27°13'59.7"S, 153°07'03.7"E), 30.V.2013, A.J.K.Millar & P.Ooilvie, NSW1114937, Q014	Metti 2022	rbcL
Palisada tenerrima (Cremades) Serio, Cormaci, G.Furnari & Boisset	MF544099	Italy, Torre Faro, Messina, 08.X.2009, V.Fiore, PhL686	Manghisi <i>et al.</i> (2019)	COI-5P
Palisada tenerrima Palisada yamadana (M.A.Howe) K.W.Nam	MG030782 HQ422794	Tunisia, Chebba, 22.VI.2014, R. Miladi, RM0081 United States, Hawaii, ARS03490.	Manghisi <i>et al.</i> (2019) Sherwood <i>et al.</i> (2010)	COI-5P COI-5P
Vertebrata foetidissima (Cocks ex Bornet) Díaz- Tapia & Maggs	JQ653283	Portugal, Algarve, Olhos d'Aqua (37°05'20"N, 8°11'27"W), 20.II.2011, P.Díaz & I.Barbara, OLHOS	Díaz-Tapia <i>et al.</i> (2012)	rbcL
Yuzurua poiteaui (J.V.Lamouroux) Martin- Lescanne var. gemmifera (Hanren) M. L.Wumpe	EF061649	Mexico, Yucatan, Cancun, Playa del Carmen, 2004, J.Díaz-Larrea, A.Sentíes	Díaz-Larrea <i>et al.</i> (2007)	rbcL
Yuzurua poiteaui var. gemmifera	EF061650	Cuba, Rincon de Guanabo, La Havana, 2005, J.Díaz-Larrea, A.A.Mallea	Díaz-Larrea et al. (2007)	rbcL
Yuzurua poiteaui var. gemmifera	EF061652	United States, Florida, Long Key, Ovan Side, 1998, S.Frederik	Díaz-Larrea et al. (2007)	rbcL

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Yuzurua poiteaui var. gemmifera	EF061653	Mexico, Yucatan, Cancun, Playa del Carmen, 2005, J.Díaz-Larrea, A.Sentíes	Díaz-Larrea et al. (2007)	rbcL
<i>Yuzurua</i> sp.	KX146198	Guadeloupe, Antilles, Carribean, Chenal ilet Colas, Grand Cul-de-Sac Marin, 03.V.2012, F.Rousseau, Y.Buske, J.Espinosa, M.Snyder, G.Dirberg, FRA1041	Rousseau <i>et al.</i> (2017)	rbcL
<i>Yuzurua</i> sp.	KX258843	Guadeloupe, Antilles, Carribean, Chenal ilet Colas, Grand Cul-de-Sac Marin, 03.V.2012, F.Rousseau, Y.Buske, J.Espinosa, M.Snyder, G.Dirberg, FRA1041	Rousseau <i>et al.</i> (2017)	COI-5P