

Article

Taxonomic Insights into *Caulerpa* (Bryopsidales, Chlorophyta) Species in French Polynesia: Confirmation of 13 Species and Reinstatement of *C. pickeringii* Harvey & Bailey

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Abstract: *Caulerpa* J.V. Lamouroux is a genus of green macroalgae belonging to the family Caulerpaceae in the order Bryopsidales. The genus comprises 104 currently accepted species, of which 51 have been recorded from Pacific Islands. Among these islands, French Polynesia is found in the middle of the South Pacific Ocean and includes five archipelagos (i.e., the Austral, Gambier, Marquesas, Society, and Tuamotu Islands) where seaweed inventories have reported a total of 16 *Caulerpa* species so far based on morphology. Here, based on a sampling covering the five archipelagos of French Polynesia, we attempt to (i) verify the taxonomy of *Caulerpa* species present in these regions based on phylogeny, (ii) describe in more detail the specific diversity between the five archipelagos, and (iii) provide a morphological identification tool for these species. We successfully obtained 134 new *tufA* sequences for phylogenetic analyses, which corresponded to 13 species. We propose to resurrect *C. pickeringii* Harvey & Bailey for representatives of *C. webbiana* var. *pickeringii* and classify it in the *Caulerpa* subgenus *Araucarioideae*. We also transfer *C. seuratii* to *C. pickeringii* based on genetic results. A new morphological identification key is provided as well as an updated distribution of *Caulerpa* species across French Polynesia.

Keywords: *Araucarioideae*; biodiversity; *C. seuratii*; *C. pickeringii*; *C. holmesiana*; DNA barcoding; macroalgae; *tufA*



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1. Introduction

Caulerpa J.V. Lamouroux is a genus of green macroalgae belonging to the family Caulerpaceae in the order Bryopsidales. Anatomically, *Caulerpa* species are characterised by a coenocytic organization, meaning that they are composed of a giant multinucleated cell called a siphon. The genus *Caulerpa* is distinguished from other Bryopsidales by the presence of inward projections of the cell forming a network in the lumen of siphons called trabeculae. Externally, *Caulerpa* species consist of a creeping stolon from which upright fronds arise with a vertical axis (rachis) that can bear branchlets (ramuli). The thallus is anchored to the substratum by rhizoids.

The genus comprises 104 currently accepted species (including two fossil taxa), of which 51 have been recorded from Pacific Islands [1]. *Caulerpa* species are subdivided into six subgenera and seven sections (subgenus *Charoideae* section *Charoideae*, subgenus *Cliftonii* section *Cliftonii*, subgenus *Hedleyi* section *Hedleyi*, subgenus *Caulerpella* section *Caulerpella*, subgenus *Araucarioideae* section *Araucarioideae*, subgenus *Caulerpa* section *Sedoideae*, and subgenus *Caulerpa* section *Caulerpa*) [2]. *Caulerpa* species are distributed worldwide in tropical and warm-temperate seas, with contrasting species ranges [3]. While the genus is well-known for some of its invasive species, such as *C. taxifolia* (M.Vahl) C. Agardh [4], it is also of economic interest with some high-value species consumed in certain countries as “green caviar” [5].

Caulerpa species taxonomy is hampered by morphological plasticity that can be due to environmental variations (see for example [6–9]). This plasticity resulted in the placement of several species as synonyms and the creation of forms, varieties, or ecads to accommodate the different or intermediate forms of species (e.g., *C. cupressoides* comprises eight forms and nine varieties). This proliferation of taxonomic ranks has highlighted the need for DNA barcodes for reliable identification [2,9,10].

French Polynesia is composed of five archipelagos (the Austral, Gambier, Marquesas, Society, and Tuamotu Islands) located in the middle of the South Pacific Ocean (Figure 1). A total of 118 emerged islands composes the five archipelagos, ranging from high islands (e.g., Tahiti) to atolls (e.g., Rangiroa), and spread over an area of 4,800,000 km² [11]. The five archipelagos also differ by climate, from equatorial to sub-tropical conditions in the Marquesas and the Austral Islands, respectively [12]. Despite the isolation of French Polynesia at the eastern end of the decreasing gradient of biodiversity from the Coral Sea region, its latitudinal extent and diversity of geomorphological structures contribute to its relatively diverse biodiversity with 702 species of macroalgae [13].

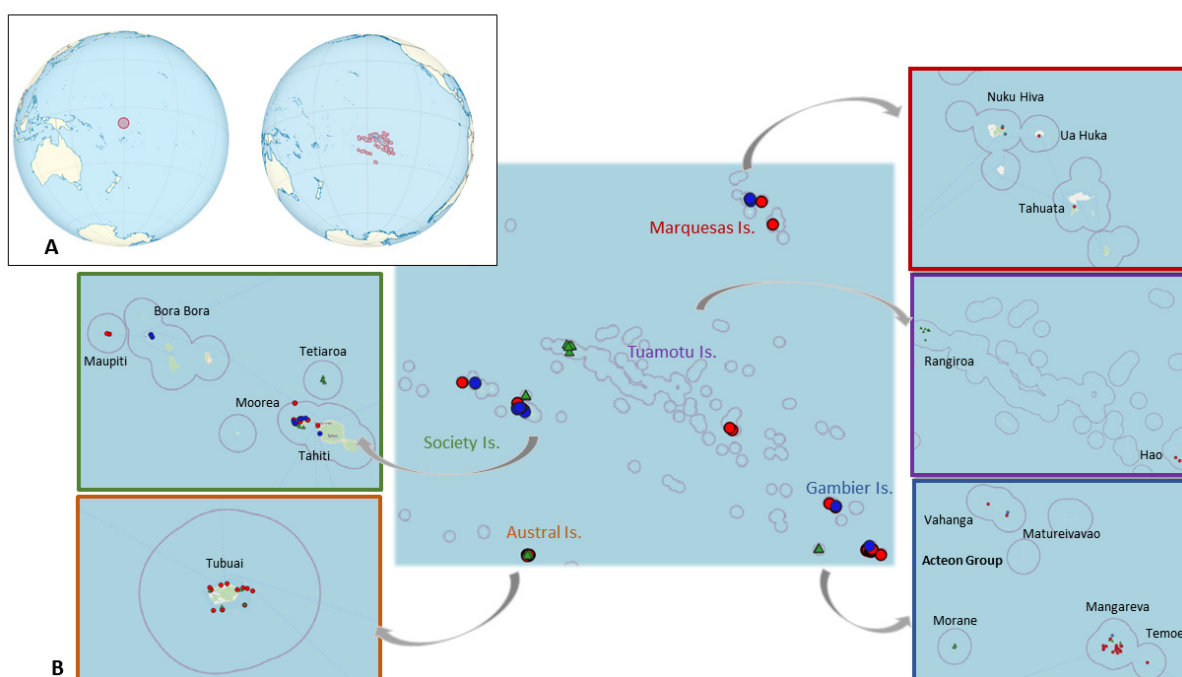


Figure 1. (A): Position of Tuvalu islands (left) and French Polynesia archipelagos (right) in the Pacific Ocean (source: TUBS from CC BY-SA 3.0, https://commons.wikimedia.org/wiki/Main_Page, accessed on 25 January 2024); (B): Distribution maps of samples from French Polynesia used in this study, with a zoom to the five archipelagos. Red dots are samples successfully sequenced, blue dots are specimens for which DNA was not available, and green triangles are samples from GenBank, including specimens from [13].

The genus *Caulerpa* in French Polynesia was first mentioned by Montagne (1842), who described *C. mamillosa* (currently considered as *C. cupressoides* var. *mamillosa* (Montagne) Weber-van Bosse) from the Gambier archipelago [14]. Harvey and Bailey (1851) described *C. pickeringii* (currently considered a variety of *C. webbiana* Montagne) from Wilson’s Island (Manihi Atoll), Tuamotu Archipelago [15]. Later, Weber-van Bosse (1910) described *Caulerpa seuratii* from Tokaai atoll (Tuamotu) [16], a toponym which does not appear on any map, and which is probably Tikei atoll, located in the King George Islands (Tuamotu). Subsequently, various seaweeds inventories reported several *Caulerpa* species from this area (e.g., six species from Tahiti [17]; 11 species from Moorea and Takapoto [18]; 12 or 15 species all archipelagos included [12,19]). Overall, a total of 16 species have been reported by these previous investigations based on morphology [1], including seven varieties and one form (see Table 1). Vieira et al. (2023) reassessed the species diversity of *Caulerpa* using DNA barcoding with the *tufA* marker, confirming 12 species in their recent marine flora species inventory [13].

Table 1. Overview of the *Caulerpa* species documented in French Polynesia with the references of the first record and whether or not confirmed by [19], and by DNA barcoding with *tufA* in [13] (v: confirmed; x: not confirmed).

| Species | Reference | [19] | [13] |
|---|---|------|------|
| <i>Caulerpa bikinensis</i> W.R.Taylor | [18] | v | v |
| <i>Caulerpa chemnitzia</i> (Esper) J.V. Lamouroux | [19] (as <i>C. racemosa</i> var. <i>peltata</i>) | v | v |
| - incl. <i>C. chemnitzia</i> var. <i>turbinata</i> (J. Agardh) Fernández-García and Riosmena-Rodríguez | - [20] (as <i>C. racemosa</i> var. <i>turbinata</i>) | v | x |
| <i>Caulerpa cupressoides</i> (Vahl) C. Agardh | [17] | v | v |
| - incl. <i>C. cupressoides</i> var. <i>lycopodium</i> Weber-van Bosse | - [21] | v | x |
| - and <i>C. cupressoides</i> var. <i>mamillosa</i> (Montagne) Weber-van Bosse | - [22] | v | x |
| <i>Caulerpa nummularia</i> Harvey ex J. Agardh | [17] (as <i>C. peltata</i> f. <i>imbricata</i>) | v | v |
| <i>Caulerpa oligophylla</i> Montagne | [13] | x | v |
| <i>Caulerpa prolifera</i> (Forsskål) J.V. Lamouroux | [12] | x | x |
| <i>Caulerpa racemosa</i> (Forsskål) J. Agardh | [17] | v | v |
| - incl. <i>C. racemosa</i> var. <i>macrophysa</i> (Sonder ex Kützinger) W.R.Taylor | - [13] | x | v |
| <i>Caulerpa sedoides</i> C. Agardh | [12] | x | x |
| <i>Caulerpa selago</i> (Turner) C. Agardh | [12] | x | x |
| <i>Caulerpa serrulata</i> (Forsskål) J. Agardh | [23] | v | v |
| - incl. <i>C. serrulata</i> var. <i>boryana</i> (J. Agardh) Gilbert | - [12] | x | x |
| - and <i>C. serrulata</i> var. <i>pectinata</i> (Weber Bosse) W.R. Taylor | - [12] | x | x |
| <i>Caulerpa sertularioides</i> (S.G.Gmelin) M.Howe | [21] | v | v |
| <i>Caulerpa seuratii</i> Weber-van Bosse | [18] | v | x |
| <i>Caulerpa taxifolia</i> (Vahl) C. Agardh | [21] | v | v |
| - incl. <i>C. taxifolia</i> f. <i>tristichophylla</i> Svedelius) | - [19] | v | x |

Table 1. Cont.

| Species | Reference | [19] | [13] |
|--|------------------------------------|------|------|
| <i>Caulerpa urvilleana</i> Montagne | [21] | v | v |
| <i>Caulerpa verticillata</i> J. Agardh | [18] | v | v |
| <i>Caulerpa webbiana</i> Montagne | [17] | v | v |
| - incl. <i>C. webbiana</i> var. <i>pickeringii</i> (Harvey & Bailey) Eubank | - [24] (as <i>C. pickeringii</i>) | v | x |

Based on sampling covering the island of Funafuti (Tuvalu) and the five archipelagos of French Polynesia, we aim to extend the study of [13] by (i) verifying the taxonomy of *Caulerpa* species present in these regions based on phylogeny, (ii) describing in more detail the specific diversity between the five archipelagos, and (iii) providing a morphological identification tool for these species.

2. Materials and Methods

2.1. Sampling

A total of 161 specimens were included in this study, which were collected by SCUBA opportunistically or during marine flora surveys between 2008 and 2019 in the five archipelagos of French Polynesia (FP): The Austral islands (Tubuai), the Society islands (Moorea, Tahiti, Bora Bora, Maupiti, Tetiaroa), the Marquesas islands, the Gambier islands (Mangareva, Morane, and Temoe), and the Tuamotu islands (Hao, Matureivavao, Rangiroa, and Vahanga) (see Supplementary Table S1). We also added 20 samples from Funafuti Island, belonging to Tuvalu, a distant archipelago 3500 km to the northwest of French Polynesia). Samples were preserved in 95% ethanol and/or silica gel for DNA analyses and in 5% sea water formaldehyde solution for morphological analyses. Herbarium vouchers were also pressed and dried on paper. The specimens from this study are deposited in NOU and UPF (herbarium abbreviations follow Thiers (2023, continuously updated) [25]).

2.2. DNA Extraction, Amplification, and Sequencing

Total genomic DNA was extracted from ethanol, silica, or herbarium fragments using the cetyl trimethyl ammonium bromide (CTAB) extraction protocol [26]. The *tufA* gene (encoding the elongation factor Tu) was amplified with the primers *tufA*-F (TGA AAC AGA AMA WCG TCA TTA TGC) and *tufA*-R (CCT TCN CGA ATM GCR AAW CGC) [27] or *HtufA*-F (ATG ATW ACN GGH GCN GCW CAA ATG G) and *HtufA*-R (TTG TTC KAA CAT AAA ATT GWG GTC) [28]. The Polymerase Chain Reaction (PCR) mix contained 2 µL of DNA (1–20 ng/µL), 1 µL each of forward and reverse primer, 8.5 µL of Milli-Q water, and 12.5 µL of AmpliTaq Gold 360 Master Mix (Applied Biosystems, Foster City, CA, USA) for a total volume of 25 µL. PCRs were performed with the following program: a first denaturation step at 94 °C for 4 min, then 40 cycles of denaturation (94 °C for 45 s), primer annealing (46 °C for 1 min for *tufA* and 1.5 min for *HtufA*), and extension (72 °C for 1.5 min), and a final extension cycle at 72 °C for 5 min. The efficiency of the PCR was checked by electrophoresis. PCR products were sent to GenoScreen (Lille, France) for Sanger sequencing. Sequences were then edited, assembled, and aligned with the Geneious 7.0.6 software (<http://www.geneious.com>, accessed on 11 October 2023, ref. [29]).

2.3. Sequence Dataset

At the French Polynesia scale, in addition to the sequences from the samples collected and presented above, we enriched our dataset with all the sequences released from [13] and two existing *Caulerpa* sequences from French Polynesia available in GenBank, representing 68 *tufA* sequences (see Table S1). We also added four new sequences from collaborators because they were the first for either a given species or locality.

To complete our dataset at a broader phylogenetic scale, we also selected one reference sequence per accepted species clade from GenBank. Firstly, we have added holotype sequences (i.e., four sequences) and *tufA* references sequences proposed by Belton et al. (2014, 2019 [10,30]; i.e., 35 sequences) (See Table S1). Then, the selection for unrepresented species among the sequences available from GenBank was as follows: selection of sequence from a sample collected from the type locality of the species, and if not, near the type locality of the species. Finally, sequences of the bryopsidaleans *Avrainvillea lacerata* J. Agardh, *A. nigricans* Decaisne, *Bryopsis plumosa* (Hudson) C. Agardh, *Codium duthieae* P.C. Silva, and *C. platylobium* Areschoug were added as outgroup taxa.

After a preliminary phylogenetic analysis, the species clades with representatives from FP were further supplemented with additional sequences from a wider geographic range. These sequences were from our own collection or GenBank (see Table S1).

2.4. Phylogenetic Reconstructions

Maximum Likelihood (ML) and Bayesian Inference (BI) trees were reconstructed through the CIPRES web portal [31]. The best partition scheme and evolutionary models associated were identified with PartitionFinder v. 1.1.0 [32] under the Akaike Information Criterion (AIC) and resulted in: GTR+G, GTR+I+G, and GTR+I+G for, respectively, 1st, 2nd, and 3rd codon positions. The ML tree was reconstructed with RAxML [33] with the “rapid bootstrapping and search for the best-scoring ML tree” algorithm, the GTR GAMMA model, and 1000 replicates of bootstraps (bs) on the three-partitioned dataset. BI tree was carried out in MrBayes 3.1.2 [34], with two independent runs of 20 million generations, sampled every 1000 generations, on the three-partitioned dataset with indicated evolutionary models. The software Tracer 1.7.13 [35] was used to check for the convergence of the Markov Chains Monte Carlo (MCMC) and the effective sample size (ESS) values of each run. The first 10% generations were discarded as burn-in before the consensus topology and the posterior probabilities (PP) were computed. The ML and BI trees were then visualised using FigTree [36].

2.5. Morpho-Anatomical Observations

The morpho-anatomical observations were made for species needing identification confirmation. The anatomical structures were observed under a LEICA M165C stereo microscope (LEICA, Wetzlar, Germany) equipped with a LEICA EC3 camera (LEICA, Wetzlar, Germany). The observations focused on the external morphology, stolons (appearance), upright assimilators (number, appearance, branching), and ramuli (number, appearance, branching, and appearance of the tips).

3. Results

3.1. Phylogeny and Species Identification

A total of 344 sequences were included in our phylogenetic analyses, including 134 newly produced sequences (110 from French Polynesia specimens, 20 from Tuvalu specimens, and four from other localities), of which 47 (unique haplotypes) were deposited in the GenBank database (OR891689-OR891717 and PP313086-PP3130103). The general tree topology (Figure 2a–c) is globally consistent with previous publications (except that no outgroup and no subgenus *Charoideae* representatives were used in [30] and except for the subgenus *Charoideae* position in [2]), although here the subgenus *Cliftonii* is the first to diverge from the rest of the *Caulerpa* species, albeit only weakly supported in the ML tree (bs = 54). There are then two strongly supported clades, one consisting of the subgenera *Caulerpella*, *Hedleyi*, and *Araucarioideae* (bs = 97; PP = 1), and a second consisting of the subgenera *Charoideae* and *Caulerpa* (bs = 97; PP = 0.99). A total of 69 species have been represented in our phylogenetic analyses, of which 13 are found in French Polynesia. From these 13 species, nine are strongly supported (bs \geq 90; PP \geq 0.98): *C. bikinensis*, *C. chemnitzia*, *C. nummularia*, *C. oligophylla*, *C. racemosa*, *C. sertularioides*, *C. taxifolia*, *C. verticillata*, and *C. webbiana*., *C. urvilleana* is moderately supported (bs = 0.79; PP = 0.94). *C. serrulata* (bs < 80)

is not monophyletic in the BI tree (cf. Supplementary Figure S1) and *C. cupressoides* is not monophyletic in both trees. Finally, *C. seuratii* is not monophyletic and closely related to sequences assigned to '*C. webbiana* var. *pickeringii*' in [13].

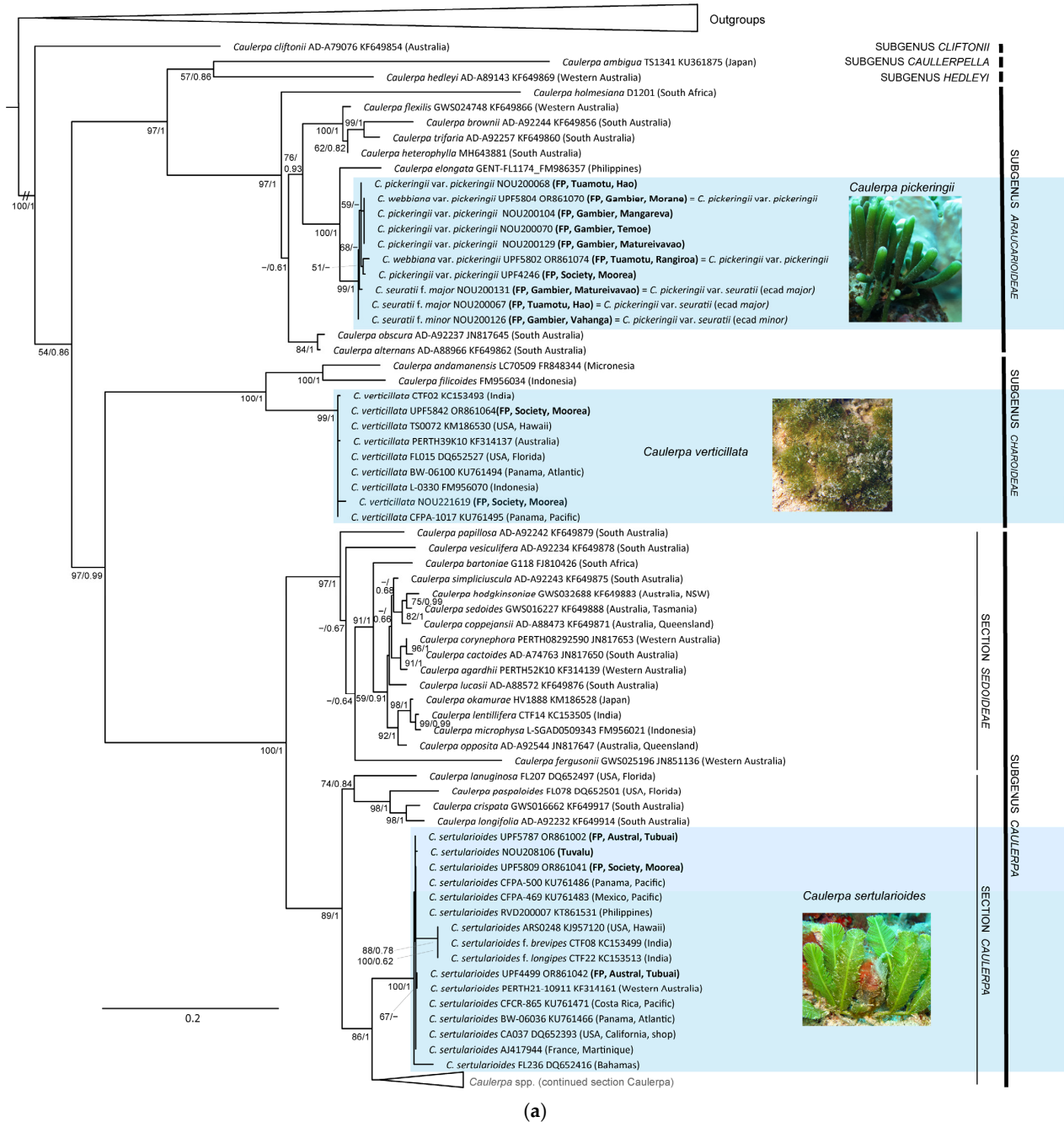
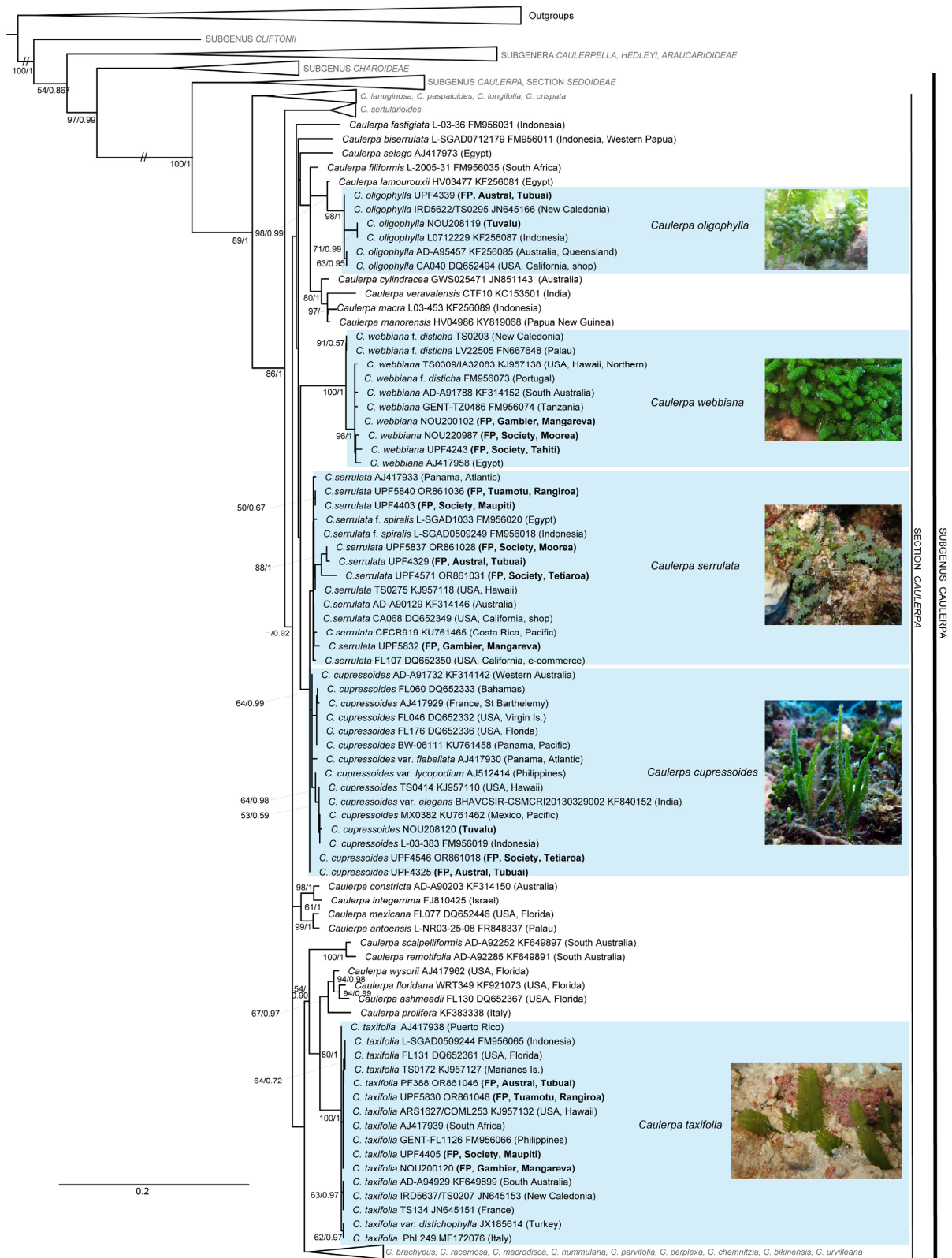


Figure 2. Cont.



(b)

Figure 2. Cont.

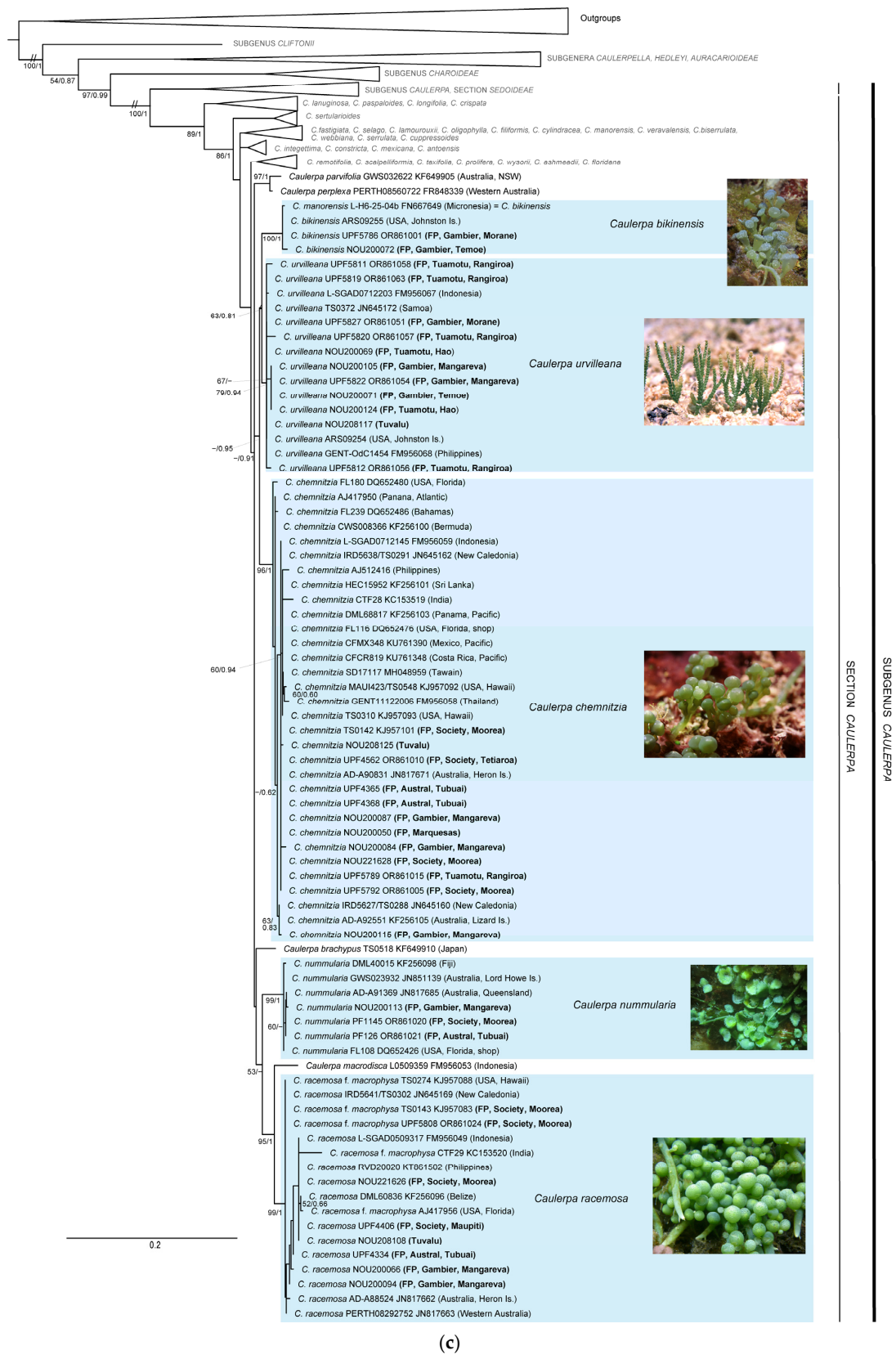


Figure 2. ML phylogeny of *Caulerpa* species for the *tufA* gene. Geographic origin of sequences integrated in the phylogeny are indicated at the country level, and at sub-level when relevant. The species presented in French Polynesia and Tuvalu are highlighted in blue and sample localities are indicated in bold. ML bs/BI PP values are reported at nodes if >50% and >0.50, respectively.

Abbreviations: FP: French Polynesia, NSW: New South Wales (Australia), USA: United States of America. Example images by Claude Payri, Mayalen Zubia, Orempuller J., and Menou Jean-Louis. (a): first part: *Caulerpa* subgenera *Cliftonii*, *Hedleyi*, *Araucarioideae*, *Caulerpella*, and *Charoideae* and subgenus *Caulerpa* section *Sedoideae* and part of section *Caulerpa* (see b,c for detail of the prune clade). (b): second part: Subgenus *Caulerpa*, section *Caulerpa* (see a,c for detail of the prune clade). (c): third part: Subgenus *Caulerpa*, section *Caulerpa* (see a,b for detail of the prune clades).

Sequences from our dataset clustering with '*C. webbiana* var. *pickeringii*' are from specimens collected in Rangiroa, Matureivavao, and Hao islands in the Tuamotu Archipelago, not far from the type locality (Manihi Atoll (Wilson's Island), Tuamotu Archipelago). '*C. webbiana* var. *pickeringii*' is a distinct monophyletic clade in our tree (Figure 2a), which branches remotely, in a different clade than *C. webbiana* (Figure 2b). The closely related *C. seuratii* has been sequenced in this study from specimens from the Acteon group located in the northern part of the Gambier archipelago and from the Tuamotu archipelago (Hao), which is the type locality of the species. The two forms of *C. seuratii* do not form a monophyletic group in our trees. When comparing genetic distances from the different sequences, intraspecific similarities within '*C. webbiana* var. *pickeringii*' range from 99.504% to 100% and from 99.858% to 100% within *C. seuratii*. Interspecific similarities were 99.380%–99.876% between both species. Maximal interspecific similarity was higher than minimal intraspecific similarity found among these species. Therefore, we can assume that all these sequences may correspond to a single species. We thus decide to resurrect *C. pickeringii* Harvey & Bailey (described in 1851 and thus taking authority over *C. seuratii* described in 1910), and transfer *C. seuratii* to *C. pickeringii*. The two forms of *C. seuratii* can be considered as ecads, i.e., morphologies influenced by environmental conditions, until we have sufficient genetic data to consider them as forms. Therefore, *C. pickeringii* as redefined here based on molecular data with strong support (bs = 99; PP = 1) presents three distinct morphologies (*C. pickeringii*, *C. pickeringii* var. *seuratii* ecad major, and *C. pickeringii* var. *seuratii* ecad minor).

3.2. Geographical Range of Species in FP and Tuvalu

A total of 13 species (and seven varieties) of *Caulerpa* were identified in French Polynesia (see Figure 3 for their illustrations): 11 *Caulerpa* species have been found in the Society Islands, ten in Gambier and in Austral, nine in the Tuamotu islands, and four species in the Marquesas (Table 2). In Tuvalu, we report for the first time the five following *Caulerpa* species: *C. urvilleana*, *C. oligophylla*, *C. chemnitzia*, *C. racemosa*, and *C. cupressoides*.

The *Caulerpa* species found in French Polynesia showed a contrasting distribution among the archipelagos. Two species were restricted to one archipelago (*C. verticillata* in Moorea, Society Is., and *C. oligophylla* in Tubuai, Austral Is.), while three others were retrieved in all five archipelagos (*C. chemnitzia*, *C. serrulata*, and *C. taxifolia*).

3.3. Taxonomic Treatment

Caulerpa pickeringii is currently regarded as a synonym of *C. webbiana* var. *pickeringii* (Harvey & Bailey) Eubank [1]. Eubank (1946) considered that the differences between the two species were not of sufficient magnitude to consider them distinct, and reduced *C. pickeringii* to a variety of *C. webbiana* [7]. Nevertheless, in this study, the *tufA* data confirm that these two species are indeed distinct. We therefore propose the reinstatement of *C. pickeringii* and consider the characters distinguishing them as discriminant.

***Caulerpa pickeringii* Harvey & Bailey 1851 (Figure 4).**

Original publication: Harvey, W.H. and Bailey, J.W. (1851) [15]. [Dr. Gould presented, on behalf of Professors W.H. Harvey of Trinity College, Dublin, and J.W. Bailey of West Point, descriptions of seventeen new species of Algae collected by the United States Exploring Expedition...]. Proceedings of the Boston Society of Natural History 3: 370–373.

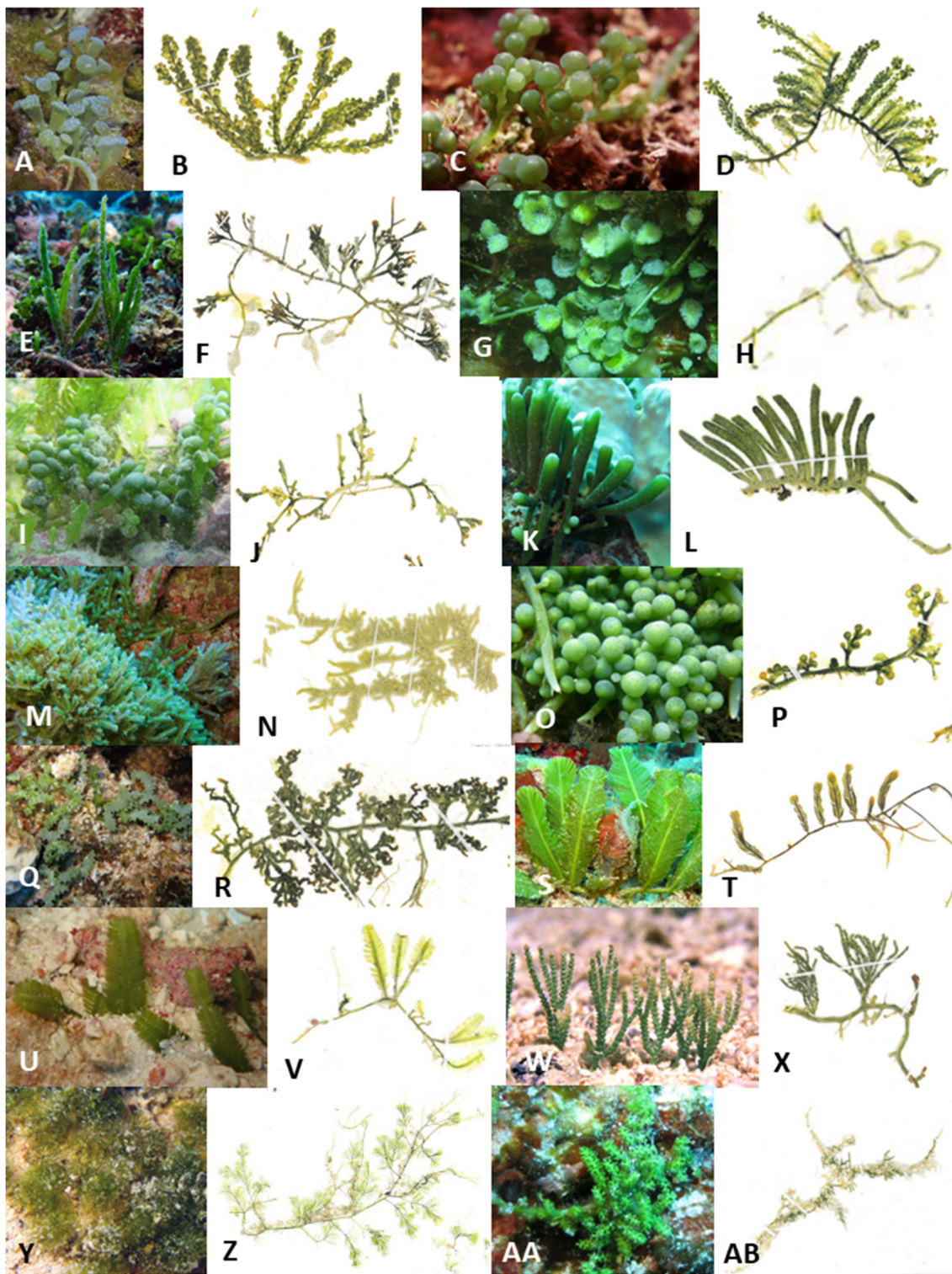


Figure 3. Illustrations of *Caulerpa* species found in French Polynesia. (A,B): *Caulerpa bikinensis*; (C,D): *Caulerpa chemnitzia*; (E,F): *Caulerpa cupressoides*; (G,H): *Caulerpa nummularia*; (I,J): *Caulerpa oligophylla*; (K,L): *Caulerpa pickeringii* var. *pickeringii*; (M,N): *Caulerpa pickeringii* var. *seuratii*; (O,P): *Caulerpa racemosa*; (Q,R): *Caulerpa serrulata*; (S,T): *Caulerpa sertularioides*; (U,V): *Caulerpa taxifolia*; (W,X): *Caulerpa urvilleana*; (Y,Z): *Caulerpa verticillata*; (AA,AB): *Caulerpa webbiana*.

Table 2. *Caulerpa* species distribution among the French Polynesian archipelagos. For each archipelago, the islands where the species have been collected are also indicated. * Localities confirmed by DNA sequences; supplementary localities reported from: ¹ specimens of our collection but without DNA data available; ² [16]; ³ [17]; ⁴ specimen collected by Vasseur in 1974; ⁵ [18]; ⁶ [12]; ⁷ [19] (if not previously cited).

| Species/Archipelagos | Gambier (incl. Acteon Is.) | Society | Austral | Tuamotu | Marquesas |
|--------------------------|---|---|--|---|--|
| <i>C. bikinensis</i> | Temoe *, Morane *, Matureivavao ¹ , Vahanga ¹ | | | Hao ¹ , Takapoto ⁵ , Raroia ⁶ , Paraoa ⁶ , Taiaro ⁶ , Kauehi ⁶ , Nihiru ⁶ , Haraiki ⁶ , Marokau ⁷ , Nengo Nengo ⁷ , Fangatau ⁷ , Vairaatea ⁷ , Vahitahi ⁷ , Tatakoto ⁷ , Tikehau ⁷ | |
| <i>C. chemnitzia</i> | Mangareva *, Akamaru ⁷ | Moorea *, Tetiaroa *, Bora Bora ¹ , Tahiti ³ | Tubuai *, Rapa ⁷ , Rurutu ⁷ | Rangiroa *, Takapoto ⁶ , Mataiva ⁶ , Nengo Nengo ⁷ | Nuku Hiva *, Ua Huka *, Tahuata * |
| <i>C. cupressoides</i> | Mangareva *, Marutea ² , Taravai ⁷ | Moorea *, Tetiaroa ¹ , Tahiti ³ , Bora Bora ⁷ | Tubuai *, Rapa ⁷ | Hao ² , Hikueru ² , Moruroa ⁶ , Haraiki ⁷ , Hikueru ⁷ | |
| <i>C. nummularia</i> | Mangareva *, Makapu ² , Akamaru ⁷ | Moorea *, Maka Pou ⁶ , Tahiti ⁷ | Tubuai * | | Nuku Hiva ¹ |
| <i>C. oligophylla</i> | | | Tubuai * | | |
| <i>C. pickeringii</i> | Mangareva *, Matureivavao *, Morane *, Temoe *, Vahanga *, Marutea ² , Aukena ⁶ | Moorea *, Bora Bora ¹ , Tahiti ⁶ | Tubuai * | Rangiroa *, Hao *, Tookai ² , Takapoto ⁴ , Kauehi ⁶ , Manihi ⁶ , Raroia ⁶ , Moruroa ⁶ , Makatea ⁶ , Mataiva ⁶ , Tikehau ⁶ , Nihiru ⁶ , Hiti ⁷ , Hikueru ⁷ , Marokau ⁷ , Nengo ⁷ , Reka Reka ⁷ | |
| <i>C. racemosa</i> | Mangareva *, Marutea ² , Aukena ⁶ , Motu Taraururoa ⁷ | Moorea * Maupiti *, Bora Bora ¹ , Tahiti ³ , Motu Tapu ⁶ | Tubuai *, Rapa ⁷ , Raivavae ⁷ | Moruroa ⁶ , Takapoto ⁵ , Mataiva ⁶ , Tikehau ⁶ , Rangiroa ⁶ , Marokau ⁷ | |
| <i>C. serrulata</i> | Mangareva *, Aukena ² , Taravai ⁷ | Moorea *, Maupiti *, Tetiaroa *, Tahiti ¹ , Bora Bora ⁷ | Tubuai * | Rangiroa *, Anna ² , Tookai ² , Raroia ⁶ , Moruroa ⁶ , Mataiva ⁶ , Tikehau ⁶ , Haraiki ⁷ , Vairaatea ⁷ | Tahuata ¹ |
| <i>C. sertularioides</i> | | Moorea *, Tahiti ³ , Bora Bora ⁷ | Tubuai *, Raivavae ⁷ | | |
| <i>C. taxifolia</i> | Mangareva *, Taravai ² Aukena ⁶ | Maupiti *, Moorea ¹ , Tahiti ⁷ | Tubuai *, Rapa ⁷ | Rangiroa *, Tookai ² | Fatu Hiva ¹ , Ua Huka ¹ , Ua Pou ¹ |
| <i>C. urvilleana</i> | Mangareva *, Morane *, Temoe * Marutea ² | Mopelia ⁶ | | Rangiroa *, Hao *, Hikueru ² , Takapoto ⁵ , Raroia ⁶ , Moruroa ⁶ , Kauehi ⁶ , Makatea ⁶ , Makatea ⁶ , Taiaro ⁶ , Tikehau ⁶ , Puka Puka ⁷ , Nengo Nengo ⁷ , Vairaatea ⁷ | |
| <i>C. verticillata</i> | | Moorea * | | | |
| <i>C. webbiana</i> | Mangareva * | Moorea *, Tahiti * | Rapa ⁷ | Tekokota ⁷ | |
| Total number of species | 10 | 11 | 10 | 9 | 4 |

Lectotype: # 37, collected by J. W. Bailey (1 January 1896) in Wilson’s Island, Tuamotu group (ABRU0000462). Note: When they first described the species in 1851, Harvey and Bailey did not assign a type specimen to *C. pickeringii*. We therefore decided to designate a lectotype on this specimen (# 37, ABRU0000462) of *C. pickeringii* collected by J. W. Bailey on 1st January 1896 from the type locality “Wilson’s Island, Poumouta group” (Tuamotu archipelago) deposited at the University of New Hampshire herbarium.

Type locality: Wilson’s Island (Manihi Atoll), Tuamotu Archipelago, French Polynesia.
tufA reference sequence: OR891699 from NOU200068 (GAM13-CP597) collected in the Tuamotu Archipelago (Hao), not far from type location.

Description (emended from Harvey and Bailey, 1851): Thallus prostrate composed of upright assimilators on a stolon densely covered till the apex with (pseudo)dichotomous branched squama or ramuli. Upright assimilators branched or unbranched, covered with horizontal ramuli, radial, tri-, or multiseriate. Ramuli branched or unbranched, with dichotomous, simple, forked or mucronated tips.

Caulerpa pickeringii var. *pickeringii* (autonym)



Figure 4. *C. pickeringii*. (a–h): *C. pickeringii* var. *pickeringii*. (a,b): in situ habit; (c,d): herbarium specimens (c: NOU200104; d: NOU200068); (e): cross-section of stolon (NOU200104); (f): close-up on the verticillate ramuli of the stolon (NOU200104); (g): verticillate ramuli around the uprights (NOU200068); (h): dichotomously divided ramuli with dichotomous and mucronate tips (NOU200104); (i–o): *C. pickeringii* var. *seuratii*; (i): in situ habit; (j): *C. pickeringii* var. *seuratii* ecad *major* herbarium specimen (NOU200067); (k): *C. pickeringii* var. *seuratii* ecad *minor* herbarium specimen (NOU200126); (l): cross-section of stolon with squama (NOU200126); (m): close-up on the mucronate tips of squama (NOU200126); (n): triseriate ramuli on uprights (NOU200067); (o): undivided branchlets with trichotomous tips (NOU200067). Scale bars: (a): 1.25 cm; (b): 1.10 cm; (c,d): 1 cm; (e,f): 1 mm; (g): 0.3 mm; (h): 0.25 mm; (i): 2.5 cm; (j,k): 1 cm; (l–n): 1 mm; (o): 2 mm.

Thallus prostrate composed of spongy assimilators (Figure 4a–d) on a stolon densely covered with (pseudo)dichotomously branched ramuli till near the growing tip of the

stolon (Figure 4e,f). Assimilators long, densely covered with horizontal verticillate and short ramuli (Figure 4g), several times dichotomously branched (6–12 or more), with forked or bimucronate tips (Figure 4h).

Distribution: *Caulerpa pickeringii* var. *pickeringii*: French Polynesia [12,21,24]. The species was also reported in the Philippines [37] based on field identification but not confirmed genetically. Littler and Littler (2003) have recorded the species in Fiji [38]. However, a careful observation of the illustration (p. 227) suggests that it is more likely *C. webbiana*.

Specimens examined: *Caulerpa pickeringii* var. *pickeringii*: French Polynesia, Society Is., Moorea, 2008: NOU221616 (CP08-924), NOU221009 (CP08-925), PF244, PF479, PF1377; French Polynesia, Gambiers Is., Matureivavao, 2013: NOU200129 (GAM13-CP003); French Polynesia, Gambiers Is., Mangareva, 2013: NOU200104 (GAM13-CP191); French Polynesia, Gambiers Is., Temoe, 2013: NOU200070 (GAM13-CP553); French Polynesia, Tuamotu Is., Hao: NOU200068 (GAM13-CP597).

Additional *tufA* sequences: OR891704 (NOU200129), OR891702 (NOU200104), OR891698 (NOU200070), OR891699 (NOU200068), OR861071 (UPF4246), OR861044 (UPF4509), OR861045 (PF384), OR861072 (UPF4483), OR861047 (UPF5829), OR861074 (UPF5802), OR861067 (UPF5805), OR861068 (UPF5801), OR861069 (UPF5803), OR861070 (UPF5804).

Notes: *Caulerpa pickeringii* var. *pickeringii* is similar to *C. webbiana* in its radially attached ramuli around the uprights, but it is distinguished from *C. webbiana* by the presence of ramuli on the entire stolon, while it is partly covered by ramuli in the latter.

***Caulerpa pickeringii* var. *seuratii* (Weber-van Bosse) Lagourgue and Payri comb. nov. and stat. nov.**

Basionym: *Caulerpa seuratii* Weber-van Bosse 1910: 2, pl. I: Figures 5–9; pl. II: Figure 1 [16].

Lectotype: NOU200067. No type specimen was designated by Weber-van Bosse, 1910; we therefore designated a lectotype for this variety on a specimen collected in Hao (Tuamotu Is.), which is the locality closest to the type locality.

Type locality: Tokaai (probably Tikei), Tuamotu Archipelago, French Polynesia

tufA reference sequence: PP313094 (from NOU200067).

Description: Thallus composed of creeping stolon covered with squama, from which assimilators arise (Figure 4i–k). Squama bifurcated or quadrifurcated, with forked and mucronated tips (Figure 4l,m), scattered, surrounding the stolon but also at the base of assimilators, but as they ascend, they lengthen and become simple ramuli. Numerous assimilators, thick or long and thin, densely covered with tri- (Figure 4n) or multiseriate ramuli, with simple, dichotomous, or trichotomous tips (Figure 4o).

Distribution: French Polynesia (14, 34), Palau [39]. It was also reported in Fiji [38,40], but the illustration (p. 233) in [38] rather seems to correspond to *C. webbiana*.

Specimens examined: French Polynesia, Gambiers Is., Matureivavao: NOU200131 (GAM13-CP001), NOU221620 (GAM13-CP001B); French Polynesia, Tuamotu Islands, Hao: NOU200123 (GAM13-CP009), NOU200067 (GAM13-CP009B); French Polynesia, Gambier Is., Vahanga: (NOU200126 (GAM13-CP006).

Additional *tufA* sequences: PP313098 (NOU200131); OR891696 (NOU200126).

Notes: *C. pickeringii* var. *seuratii* presents two distinct forms that we propose to consider as ecad here. *C. pickeringii* var. *seuratii* ecad *minor* distinguishes from *C. pickeringii* var. *seuratii* ecad *major* by longer and thinner assimilators (thick in ecad major), multiseriate ramuli (triseriate in ecad major), and tips that can be simple or bifurcated while they are always bifurcated or trichotomous in ecad major.

We propose the following dichotomous key for morphological determination of *Caulerpa* species from French Polynesia (updated from [19]):

- 1a. Ramuli usually swollen, spherical, or peltate9
- 1b. Ramuli not swollen, spherical, or peltate2
- 2a. Ramuli strap-like, sub-dichotomous, dentate, or spirally twisted.....*C. serrulata*
- 2b. Ramuli opposite, radial, or in multiple rows3
- 3a. Ramuli spiny4

- 3b. Ramuli filamentous, plumose, or furry5
- 4a. Ramuli straight, not basally compressed, spiniform, generally arranged on three to five opposite rows of densely ranked, sometimes inflated ramuli *C. cupressoides*
- 4b. Ramuli angular, slightly compressed at the bases, radially arranged in three rows with thorn-like, never inflated ramuli *C. urvilleana*
- 5a. Ramuli in two or three opposite rows, stolons naked6
- 5b. Ramuli radially or arranged in whorls7
- 6a. Ramuli cylindrical and of the same diameter throughout. *C. sertularioides*
- 6b. Ramuli compressed, basally constricted, with tapered tips. *C. taxifolia*
- 7a. Ramuli slender, in whorls, stolons naked. *C. verticillata*
- 7b. Ramuli radial, not in whorls, stolons covered with ramuli (or squama).8
- 8a. Ramuli forming a continuous, uniform covering on fronds and stolons . . . *C. pickeringii*
- 8b. Ramuli forming a non-continuous covering, stolons partly naked, especially at apical part. *C. webbiana*
- 9a. Ramuli stalked and spherical or vesicule-like, vesicules10
- 9b. Ramuli clavate, peltate, disc-like, or of variable form.11
- 10a. Ramuli inflated, spherical to subspherical, or pyriform, laxly or radially arranged. . .
..... *C. racemosa*
- 10b. Ramuli elongate, club-shaped, flattened or slightly convex, alternate or distichous
..... *C. bikinensis*
- 11a. Ramuli clavate to subpherical, distantly spaced, sometimes completely lacking
..... *C. oligophylla*
- 11b. Ramuli peltate, disc-like, mushroom-like, or of variable forms12
- 12a. Ramuli distinctly peltate, with smooth and/or renulated margins, singly or new peltate discs arising from the margin or centre of parent disc. *C. nummularia*
- 12b. Ramuli of highly variable shape, clavate to turbinate or peltate, usually very crowded and radially arranged. *C. chemnitzia*

4. Discussion

4.1. Species Diversity in French Polynesia

This study is the first to provide genetic confirmation of the presence of 13 species in French Polynesia (including seven varieties/ecads), following the recent results of Vieira et al. [13], which confirmed 12 *Caulerpa* species. This work completes the latter study with (1) a taxonomic revision of the species *C. pickeringii* (resurrected) and *C. seuratii* (synonym); (2) an update of the species distribution within the five archipelagos; and (3) the creation of a dichotomous key to facilitate the identification of *Caulerpa* species present in French Polynesia.

Despite an intensive survey of Gambier Island in 2013, we could not find *C. prolifera* and *C. selago* recorded by Montagne (1845) from Mangareva [41], nor could we obtain DNA data from GenBank. Their presence in French Polynesia is questionable; if *C. selago* could have been confused in previous surveys, based on the plumose aspect, with *C. taxifolia* (which is present around Mangareva), *C. prolifera* does not resemble any form observed on this island. Finally, this study provided the first genetic sequences for *C. pickeringii* var. *seuratii* (including ecads *minor* and *major*).

While previous studies of floristic diversity in FP have reported the greatest species richness in the Society, Tuamotu, and Austral groups (74, 50, and 48% of the total flora, respectively [19]), in this study we also found a high *Caulerpa* species diversity in the Gambier archipelago (11 species). The Marquesas islands are less rich, which could be explained by the lack of reef habitats, as previously highlighted [19]. The geographical extent of Polynesia and the variety of habitats and climates that characterize the archipelagos of French Polynesia would require additional sampling effort to properly reassess species diversity.

Another interesting thing is that the Austral or Society archipelagos seem to harbour unique species, found only there and in none of the other archipelagos. Conversely, species

found in the Tuamotu, Gambier, or Marquesas are also present in at least one of the other archipelagos. This pattern could be verified by a more in-depth phylogeographic analysis of the French Polynesian archipelagos to check whether there is a real difference in *Caulerpa* species diversity, or whether this is due to a different sampling effort, or to species that are more difficult to sample (small and cryptic) and whose distribution is underestimated.

4.2. *Caulerpa* Subgenus *Araucarioideae*

With the reinstatement of *C. pickeringii*, the *Araucarioideae* clade has been enriched by another species with stolons covered with squamules and/or ramuli-like structure, like *C. elongata*.

We also provide for the first time a sequence of *C. holmesiana*, a southern hemisphere species endemic to South Africa. According to our phylogenetic analyses, this species receives strong support as an early branching species of the *Araucarioideae* clade. The *Caulerpa* subgenus/section *Araucarioideae* is characterized by stolons that are mainly squamiferous or covered with ramuli, with the exception of *C. alternans*, which has glabrous stolons [2]. *Caulerpa holmesiana* also has glabrous stolons. This species also has plumose ramuli, with a constricted pedicel and an annulated rachis, which is common in species of the *Caulerpa* subgenus *Caulerpa*. Hence, *C. holmesiana* was tentatively classified in the subgenus *Caulerpa* by [2]. Nevertheless, based on its phylogenetic position, we believe that *C. holmesiana* should be included in the subgenus *Araucarioideae*, which could be subdivided into distinct sections in the future.

4.3. French Polynesia Species with Contrasted Geographical Ranges at Global Scale

In this study, we only have genetic data from French Polynesia for *C. pickeringii* var. *pickeringii*, and its other report locality (Philippines) may have to be confirmed genetically before we can assume that this species may be endemic to the Polynesian archipelago. *C. pickeringii* var. *seuratii* has only been undoubtedly observed outside French Polynesia in Palau [39].

The *Caulerpa* species confirmed from French Polynesia in the present study show contrasting geographical ranges, including cosmopolitan species distributed in the three tropical and subtropical oceans (e.g., *C. chemnitzia*, *C. cupressoides*, *C. racemosa*, *C. serrulata*, *C. sertularioides*, *C. taxifolia*, or *C. verticillata*) to species restricted to a single oceanic basin (e.g., *C. bikinensis*, *C. nummularia*, and *C. pickeringii* in the Pacific Ocean, based on molecular record). Thus, we may speculate that the *Caulerpa* species diversity has been shaped by species colonisation (for cosmopolitan ones), but also enriched with diversification due to the isolation of FP islands (for native species).

In this study, we also provide the first sequences of *C. bikinensis* and *C. urvilleana* from Johnston atoll (Hawaii, USA), which were previously reported in this locality by [42,43], respectively. The only sequence of *C. bikinensis* available in GenBank was from Micronesia and wrongly assigned to *C. manorensis* (FN667649 from [2]).

4.4. Need for a Reference Databank of *Caulerpa* Species Sequences

During the selection of representative sequences for each species to build our phylogeny, we noticed errors or misidentifications in the sequence names available in GenBank. We have tried as far as possible to integrate reliable sequences that can be considered as good references for the species in question. In particular, we relied on the reference sequences proposed by previous studies [9,10,30], but for the vast majority of *Caulerpa* species, these have not yet been proposed. It would therefore be necessary to start creating a database of reference sequences for all existing *Caulerpa* species, in order to eliminate doubtful sequences and select the most reliable and accurate ones for each species. Among other things, it would be appropriate to set up a selection system for the creation of this database, for example, following the criteria set out here, i.e., sequence from type specimen; if not available: sequence of a specimen from type locality; if not available: sequence from a specimen collected near the type locality (but with an increase in uncertainty).

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d16040243/s1>. Table S1: List of the specimens and sequences included in this study, with sample IDs, species identification, location of sampling, BOLD ID, and GenBank accession numbers. Figure S1: Bayesian inference tree of *Caulerpa* species for the *tufA* gene. Geographic origin of sequences integrated in the phylogeny are indicated at the country level, and at sub-level when relevant. Localities in French Polynesia and Tuvalu are indicated in bold. PP values are reported at nodes if >0.50. Abbreviations: FP: French Polynesia, NSW: New South Wales (Australia), USA: United States of America.

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Data Availability Statement: Genetic data generated for this article can be found in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>), under the following accession numbers: OR891689-OR891717 and PP313086-PP3130103. In addition, all specimen data are available on the BOLD online platform (<http://bins.boldsystems.org/>).

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