Caulerpa brachypus and *Caulerpa parvifolia* (*Caulerpaceae, Ulvophyceae*) in New Zealand

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In late June, 2021 a photograph of a specimen of *Caulerpa* from Aotea/Great Barrier Island, New Zealand, was uploaded to I-Naturalist (https://www.inaturalist.org/observations/84272350). The first author was notified about this record and immediately recognised it to be a species non-native to New Zealand. The macroalgal flora of north eastern New Zealand is well documented and this species was recognised by a member of the community as something he had never seen in the region where he had grown up. Following standard protocols in New Zealand, the Marine Invasives Taxonomic Service at NIWA (National Institute of Water & Atmospheric Research—now Earth Sciences New Zealand) and Biosecurity NZ (MPI-Ministry for Primary Industries) were immediately informed. A field team from NIWA under instructions from MPI collected samples from Blind Bay, Aotea/Great Barrier Island, and *tuf*A and *rbc*L sequence data confirmed the identification as *Caulerpa brachypus* Harvey.

A second introduced species, *Caulerpa parvifolia* Harvey, was discovered in September 2021 during a delimitation survey for *Caulerpa brachypus* (Middleton & al. 2021). Although these species are morphologically similar, this second *Caulerpa* species was recognised in the field by the first author as differing from *C. brachypus*, and sequence data subsequently confirmed the identification as *C. parvifolia*.

Caulerpa brachypus was described by Harvey (1860a: 333) from "Tanegasima" [Tanega-shima, Kagoshima Prefecture, Japan], at a latitude of ca. 30˚ N. He described the species as having stout and glabrous stolons [surculis], subsessile fronds that were "*elliptic-oblong at base and very obtuse at apex, flat, with very entire veins, now here and there constricted or proliferating*". Harvey (1860b: pl. CLXXII [172]) described *Caulerpa parvifolia* from samples collected in crevices of tidal rocks in Kiama, New South Wales, Australia. This species was described as also having glabrous stolons, "*erect fronds simple or forked, linear-strapshaped, very entire, obtuse or emarginate, tapering at base to very short stipes*". Harvey noted the fronds were membranous and glossy, and "*tolerable soft and in drying the frond adheres to paper texture*". Harvey noted that a faint medial line "*simulating a nerve, is more or less visible especially in dried specimens*". In the comments following the description of *C. parvifolia*, Harvey noted "*C. brachypus from Japan has broader shorter and thicker, nearly sessile fronds and a much stouter surculus* [a shoot arising from the base] *with longer roots*".

One variety and two forms of *Caulerpa brachypus* have been described: *Caulerpa brachypus* var. *mauritiana* (Børgesen) Børgesen, *Caulerpa brachypus* f. *exposita* Børgesen, and *Caulerpa brachypus* f. *parvifolia* (Harvey) A.B.Cribb. In reducing *C. parvifolia* to a form of *C. brachypus* Cribb (1958) noted that the separation of these species had been based on the smaller size, thinner stolons, and more linear blade of *C. parvifolia*. Based on *tuf*A gene analysis Belton & al. (2015)

reinstated *Caulerpa parvifolia*. Subsequently, Belton & al. (2019) described a new species from Western Australia, *Caulerpa perplexa* Huisman, Belton, Draisma, Gurgel & Prud'homme, for material previously identified as *C. parvifolia*. The new species was sister to *C. parvifolia* from eastern Australia (New South Wales, Norfolk Island, and Lord Howe Island, Australia) in molecular analyses (Belton & al. 2019).

Sequences were obtained from 38 samples (10 of *C. brachypus* and 28 of *C. parvifolia*). The identity of both *Caulerpa* species was initially confirmed by sequencing the plastid elongation factor *tuf*A gene and the plastid-encoded large subunit of the rubisco gene (*rbc*L). Subsequently, *tuf*A was selected, as suggested by Saunders & Kucera (2010) as a DNA barcode for green macroalgae (except for the Cladophorales). DNA was extracted following a modified CTAB protocol (Zuccarello & Lokhorst 2005) or Chelex extraction (Goff & Moon 1993). The plastid elongation factor *tuf*A gene was amplified using primers tufGF4 and tufAR (Famà & al. 2002). PCR cycling conditions were: 1 min at 95 °C, followed by 34 cycles of 30 sec at 95 °C, 30 sec at 50 °C, and 45 sec at 72 °C, with a final 72 °C extension for 5 min. PCR products were cleaned using ExoSAP-IT (ThermoFisher Scientific Inc. Waltham, USA) and commercially sequenced in both directions (Macrogen Inc., Korea). Sequences were assembled, edited, and aligned using Geneious Prime 2025.0.3. (https://www.geneious.com). Phylogenetic analyses were performed using maximum likelihood (ML) implemented in IQ-TREE3 (Wong & al. 2025); genes and codons were partitioned and the best fit model selected using ModelFinder (Kalyaanamoorthy & al. 2017) also implemented in IQ-TREE3. Support for nodal branches was determined by non-parametric bootstrap (500 replicates) (Felsenstein 1985). The trees were visualized and modified with FigTree v.1.4.4. (Rambaut & al. 2018) and edited in Inkscape v. 1.4.2. Haplotype analysis of *C. brachypus* included 34 sequences (10 from NZ) – *C. parvifolia* (52 sequences (28 from NZ). A statistical parsimony network was implemented in PopART v1.7 (http://popart.otago.ac.nz/). Locality information, GenBank accession numbers and voucher numbers are given in Supplementary Table 1.

The *C. brachypus* haplotype is seemingly unique to New Zealand the closest haplotypes being from Malaysia, Papua New Guinea, Madagascar and Australia. All the New Zealand sequences of *C. brachypus* are the same (Fig. 1). *Caulerpa parvifolia* haplotypes in New Zealand are the same as an Australian haplotype from Coffs Harbour (New South Wales; sequences KF649904, KF649905, KF649906) (Fig. 2), plus two haplotypes only reported from New Zealand.

The morphology of specimens from New Zealand confirmed to be *C. brachypus* and *C. parvifolia* differ from some of the published descriptions of the species elsewhere in their ranges. The presence of marginal dentation was reported in *C. brachypus* by Belton & al. (2015) and Meñez & Calumpong (1982) but was not observed in New Zealand material or described by Harvey (1860b). *Caulerpa parvifolia* collected in New Zealand matches Harvey's description in its size, frond shape and the presence of a faint medial line but differs in having minute spines along the margins. The teeth/spines have been noted by some authors (e.g. Cribb 1958, Coppejans & Beeckman 1990 as *C. brachypus* f. *parvifolia*, Belton & al. 2015 although only occasionally, and Ballantine & al. 2023 as *C. parvifolia*).

Caulerpa brachypus Harvey

Description (of New Zealand material): Fronds firm, blade-like, usually unbranched, with a short stipe less than 1 mm long (occasionally up to 3 mm) (Figs 4–6). Fronds 20–60 mm in height and 3–5 mm wide, oblong, with uniform width, narrowed towards the base; larger individuals branched, up to 120 mm in height and 7 mm wide (Fig. 7). Margins smooth, apices rounded or slightly notched, (Figs 8–9). Colour olive, yellow green, texture membranous. Stolons terete,

stout, usually pigmented, 1–3 mm in diameter, attached by rhizoids originating from pillars (Fig. 10).

Caulerpa parvifolia Harvey

Description (of New Zealand material): Fronds delicate, blade-like, unbranched with a short terete stipe 1–3 mm long (occasionally up to 5 mm) (Figs 11–15). Fronds 15–40 mm in height and 2–4 mm wide, oval/elliptical or with uniform width, gradually tapering distally, sometimes irregularly constricted (Fig. 15) and often with visible medial line (Figs 11–12); larger individuals up to 110 mm in height and 5 mm wide (Fig. 12). Margins usually with minute spines (Fig. 16), apices notched (Figs 17–18). Colour bright green, texture soft. Stolons terete, often glossy, unpigmented, about 0.5 mm in diameter, bearing clusters of rhizoids (Figs 19–20).

These two exotic species in New Zealand may be distinguished by the thickness of the blade and stolon—*C. brachypus* is robust while *C. parvifolia* is thinner (although juvenile specimens of the two species could be easily confused), and the presence of medial lines and marginal teeth in *C. parvifolia*, which are absent in *C. brachypus.* The shape of the fronds is oval/elliptical in *C. parvifolia* and oblong in *C. brachypus*, although there is overlap in the frond shape in these species. See Table 1 below for a detailed comparison.

Table 1. Morphological characteristics of New Zealand (NZ) and Australian (AU) specimens of *Caulerpa brachypus* and *Caulerpa parvifolia*

Feature	**NZ** ***C. brachypus***	**AU** ***C. brachypus***	**NZ** ***C. parvifolia***	**AU** ***C. parvifolia***
Frond height	20–60 up to 120 mm	up to 90 mm	15–40 up to 110 mm	up to 15 mm
Frond width	3–5, up to 7 mm	5–18 mm	2–5 mm	3–4 mm
Margins	Smooth	Usually with minute widely spaced spines	Usually with minute spines	Smooth margins, occasionally with spines
Apices	Rounded, occasionally slightly notched	Notched	Notched occasionally tapering	Rounded or notched apices
Stipe length	<1 – 1– 3 mm	up to 7 mm	1–3 up to 5 mm	to 1 mm long
Stolonthickness	1–3 mm	2–3 mm	0.5 mm	0.5 mm
Rhizoids	Pillars with rhizoids	Pillars bearing dense rhizoidal clusters	Clusters of rhizoids	Clusters of rhizoids, with small or inconspicuous pillars
Source	This study	Belton & al. 2015	This study	Belton & al. 2015

Caution has to be exercised when interpreting the published records of the ranges of *C. brachypus* and *C. parvifolia*. Some authors referred to a *Caulerpa* species that was reported as invasive in Florida as *C. brachypus* when in fact it was *Caulerpa parvifolia* (as C. *brachypus* f. *parvifolia*) (e.g.

Schrope 2003, Jacoby & al. 2004, Glardon & al. 2008). As *C. brachypus* it was reported displacing native flora and fauna (Schrope 2003, Jacoby & al. 2004) in Florida.
Caulerpa brachypus is considered to be a widespread tropical and subtropical species native to the Indo-Pacific and has been reported from Africa to the Philippines and Australia, in Brazil, the Caribbean Sea and Florida (Guiry & Guiry 2026), but caution needs to be exercised with some of these records. The native range of *C. parvifolia* has been reported to be 'tropical and warm seas of the Indian and Western Pacific Ocean' (Belton & al. 2015), and in AlgaeBase as Lord Howe Island, New South Wales, Norfolk Island, Queensland, Fiji, Philippines, China, Japan, Taiwan, Kenya, South Africa, tropical and subtropical Western Atlantic, Puerto Rico (Guiry & Guiry 2026).

This work was supported through funding provided by Biosecurity New Zealand under response and delimitation contracts undertaken between 2021 and 2026, the Marine Invasives Taxonomic Service (Contracts C0037873 and C0031244) and C0038880 with Earth Sciences New Zealand (and our predecessor the National Institute of Water and Atmospheric Research).

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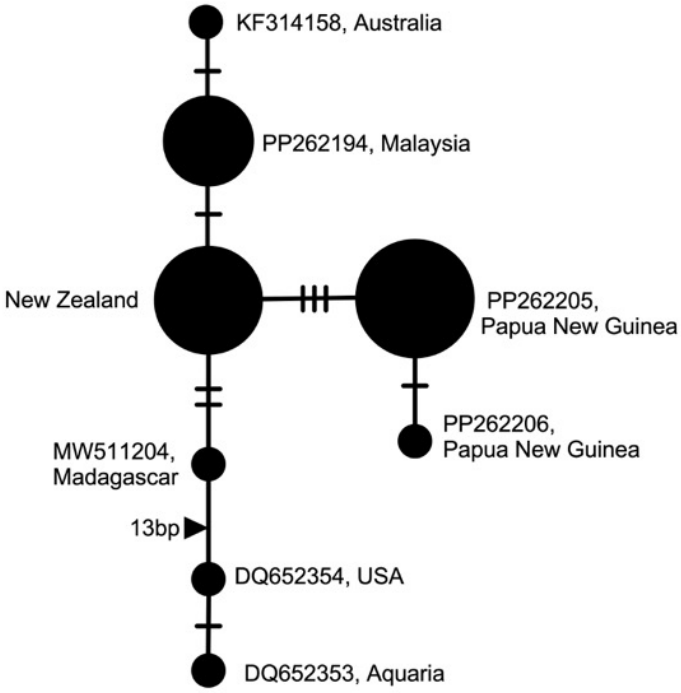


Fig. 1. Haplotype analysis (*tuf*A) of *Caulerpa brachypus* including 34 sequences (10 from New Zealand).

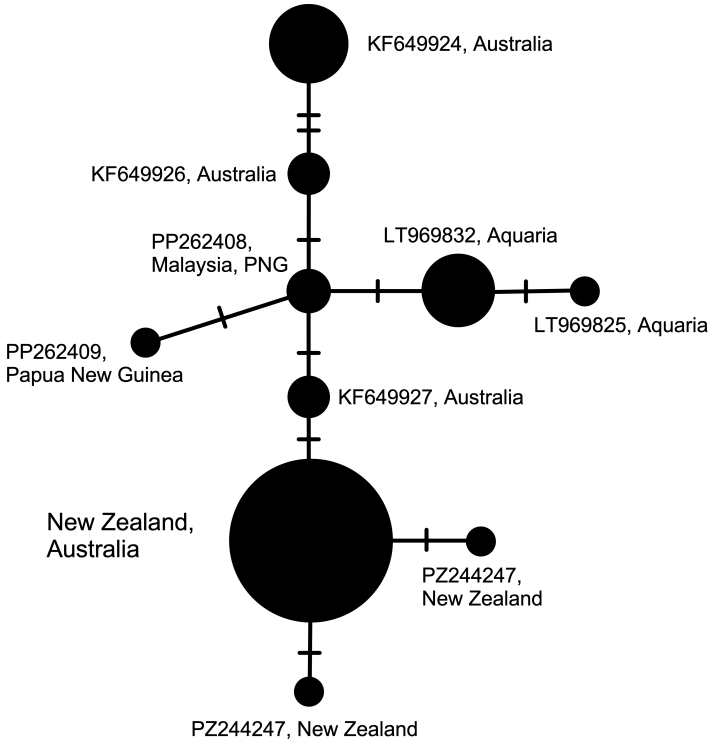


Fig. 2. Haplotype analysis (*tuf*A) of *Caulerpa parvifolia* including 52 sequences (28 from New Zealand).

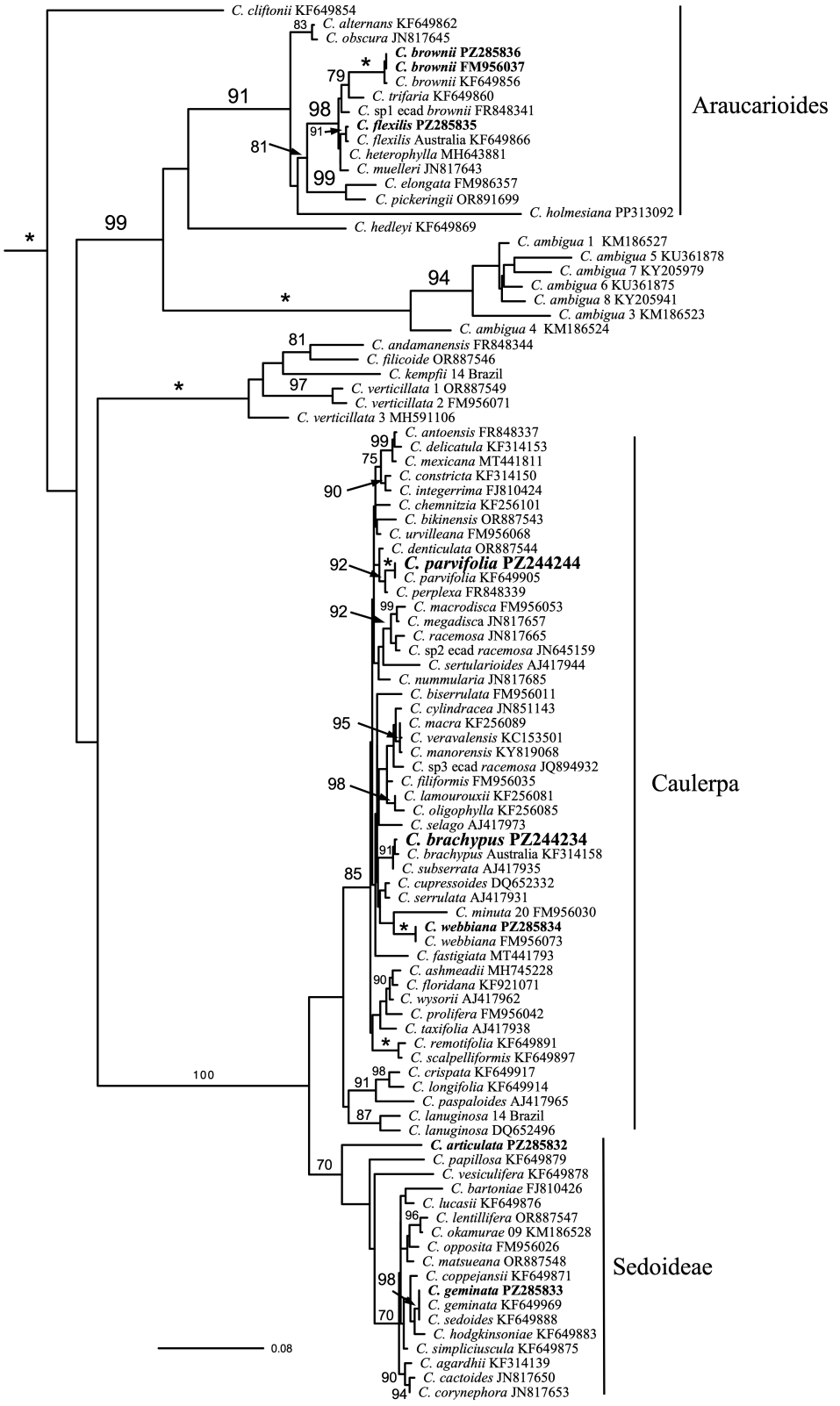
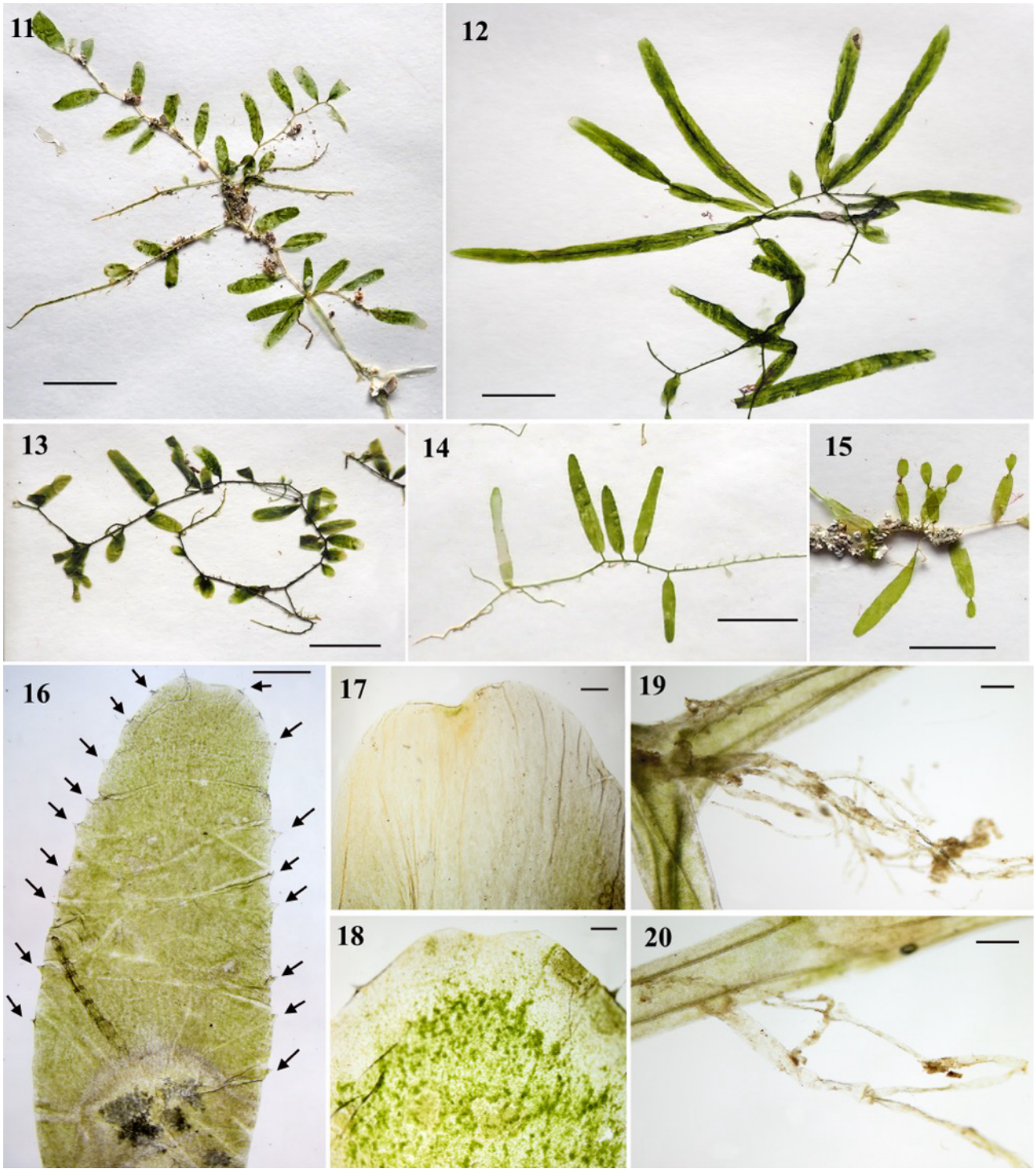


Fig. 3. Maximum likelihood phylogeny based on a 813 nucleotide *tuf*A alignment of 101 *Caulerpa* taxa, and nine outgroup *Pseudochlorodesmis* spp. (removed for clarity). Scale bar = substitutions per site. *Caulerpa* subgenera that contain New Zealand samples marked. Relevant ML bootstrap (500 replicates) values ≥70% shown. New Zealand specimens in **bold**.

Figs 4–10. *Caulerpa brachypus.* Fig. 4 . AK392640, Blind Bay. Fig. 5. AK392657, Tryphena. Fig. 6. AK392649, Great Mercury Island. Fig. 7. WELT A036579, Blind Bay. Fig. 8. Frond with smooth margins and rounded apex (AK392639). Fig 9. Slightly notched apex (AK392639). Fig 10. Conspicuous pillar with rhizoids (AK392657). Scales bars: Figs 4–7 = 2 cm; Figs 8–10 = 200 µm.



Figs 11–20. *Caulerpa parvifolia.* Fig. 11. WELT A036594, Tryphena; Fig.12. AK392664, Whangaparapara; Fig. 13. WELT A036599, Mokohinau I.; Fig. 14. WELT A036591, Tryphena; Fig.15. AK392651, Great Mercury Island; Fig. 16. Fronds with minute lateral spines (arrows), (WELT A036594). Figs 17-18, Notched apices (WELT A036594); Figs 19-20.Cluster of rhizoids (WELT A036581). Scales bars: Figs 11–15= 2 cm; Fig.16 = 1 mm; Figs; 17–20= 200 µm.

Supplementary Table 1. Voucher numbers, GenBank Accession numbers, collection date and locality information of the *Caulerpa* specimens.

Species	Museum #	GenBank	Date	Locality	Latitude S	Longitude E
C. articulata	A036606	**PZ285832**	30/10/2020	Akitio,Wairarapa	40.61911	176.41533
C. brachypus	AK392639	**PZ244235**	23/08/2021	Tryphena, Aotea	36.31871	175.48698
C. brachypus	AK392640		20/08/2021	Blind Bay, Aotea	36.26141	175.42594
C. brachypus	AK392642		06/12/2021	Blind Bay, Aotea	36.26253	175.42896
C. brachypus	AK392649	**PZ244237**	29/03/2022	Great Mercury I.	36.62783	175.78614
C. brachypus	AK392650	**PZ244239**	31/03/2022	Great Mercury I	36.62684	175.78562
C. brachypus	AK392657	**PZ244240**	6/03/2023	Tryphena, Aotea	36.30775	175.4761307
C. brachypus	AK392658	**PZ244242**	19/05/2023	Omakiwi Cove	35.241972	174.244406
C. brachypus	A036580	**PZ244243**	19/05/2023	Omakiwi Cove	35.241972	174.244406
C. brachypus	A036573/A,B	**PZ244236**	10/07/2021	Blind Bay, Aotea	36.259855	175.43601
C. brachypus	A036574		22/08/2021	Blind Bay, Aotea	36.27887	175.41988
C. brachypus	A036575		21/08/2021	Blind Bay, Aotea	36.27805	175.43228
C. brachypus	A036578		06/12/2021	Blind Bay, Aotea	36.29235	175.43188
C. brachypus	A036576	**PZ244238**	31/03/2022	Great Mercury I.	36.62684	175.78562
C. brachypus	A036577	**PZ244234**	05/03/2023	Blind Bay, Aotea	36.26301695	175.4265301
C. brachypus	A036579	**PZ244241**	7/03/2023	Blind Bay, Aotea	36.26694135	175.4376706
C. brownii	A034433	**PZ285836**	22/08/2020	Wellington	41.34262	174.79192
C. flexilis	A036604	**PZ285835**	07/03/2023	Tryphena, Aotea	36.308171	175.47584
C. geminata	A036605	**PZ285833**	22/03/2023	Army Bay, Auckland	36.6	174.81
C. parvifolia	AK392637		24/09/2021	Whangaparapara, Aotea	36.24985	175.39074
C. parvifolia	AK392638		24/09/2021	Whangaparapara, Aotea	36.25075	175.39252
C. parvifolia	AK392641		21/08/2021	Blind Bay, Aotea	36.26901	175.42417
C. parvifolia	AK392643		12/2021	Tryphena, Aotea	36.318375	175.48789
C. parvifolia	AK392644		12/2021	Whangaparapara, Aotea	36.25113	175.3916
C. parvifolia	AK392645		12/2021	Whangaparapara, Aotea	36.25113	175.3916
C. parvifolia	AK392646		19/01/2022	Whangaparapara, Aotea	36.2511	175.3916
C. parvifolia	AK392647	**PZ244248**	19/01/2022	Tryphena, Aotea	36.3184	175.4879
C. parvifolia	AK392648	**PZ244249**	15/03/2022	Great Mercury I.	36.62693	175.7849
C. parvifolia	AK392651	**PZ244252**	31/03/2022	Great Mercury I.	36.62684	175.78562
C. parvifolia	AK392652		20/03/2022	Whangaparapara, Aotea	36.25158	175.3943
C. parvifolia	AK392653	**PZ244251**	20/07/2022	French Bay, Aotea	36.255742	175.384302
C. parvifolia	AK392654		20/07/2022	Walter Hill, Aotea	36.23168	175.350944
C. parvifolia	AK392655	**PZ244254**	6/03/2023	Tryphena, Aotea	36.30924684	175.4490365
C. parvifolia	AK392656	**PZ244255**	6/03/2023	Tryphena, Aotea	36.30924684	175.4490365
C. parvifolia	AK392659	**PZ244256**	19/05/2023	Omakiwi Cove	35.241972	174.244406
C. parvifolia	AK392660	**PZ244257**	06/07/2023	Kawau I.	36.39655	174.8184
C. parvifolia	AK392661	**PZ244259**	23/04/2024	Kawau I.	36.39821	174.82029

C. parvifolia	AK392662	**PZ244245**	28/04/2024	Mokohinau I.	35.9089033	175.1073107
C. parvifolia	AK392663		28/04/2024	Mokohinau I.	35.9089033	175.1073107
C. parvifolia	AK392664		08/06/2024	Mokohinau I.	35.90878	175.106337
C. parvifolia	AK392665	**PZ244264**	08/06/2024	Leigh Harbour	36.289848	174.811118
C. parvifolia	AK392666	**PZ244268**	26/11/2024	Waiheke I.	36.76626	175.05621
C. parvifolia	AK392667		27/11/2024	Kawau I.	36.44792	174.86476
C. parvifolia	AK392668	**PZ244270**	27/11/2024	Kawau I.	36.44401	174.86447
C. parvifolia	A036581	**PZ244247**	24/09/2021	Whangaparapara, Aotea	36.24985	175.39074
C. parvifolia	A036582	**PZ244246**	24/09/2021	Whangaparapara, Aotea	36.25075	175.39252
C. parvifolia	A036583	**PZ244260**	22/09/2021	Tryphena, Aotea	36.31898	175.48623
C. parvifolia	A036584		06/12/2021	Blind Bay, Aotea.	36.27687	175.43135
C. parvifolia	A036585		12/2021	Whangaparapara, Aotea	36.25113	175.3916
C. parvifolia	A036586		12/2021	Whangaparapara, Aotea	36.25113	175.3916
C. parvifolia	A036587		19/01/2022	Whangaparapara, Aotea	36.2511	175.3916
C. parvifolia	A036588		19/01/2022	Whangaparapara, Aotea	36.2524	175.3943
C. parvifolia	A036589	**PZ244250**	15/03/2022	Great Mercury I.	36.62693	175.7849
C. parvifolia	A036590	**PZ244253**	31/03/2022	Great Mercury I.	36.62684	175.78562
C. parvifolia	A036591		17/03/2022	Tryphena, Aotea	36.30599	175.46805
C. parvifolia	A036592		20/07/2022	Beacon Point, Aotea	36.263729	175.397705
C. parvifolia	A036593		20/07/2022	Mangati Bay, Aotea	36.251897	175.373586
C. parvifolia	A036594	**PZ244244**	6/03/2023	Whangaparapara, Aotea	36.25673752	175.4000308
C. parvifolia	A036595		08/03/2023	Smiths Bay, Aotea	36.29246	175.431857
C. parvifolia	A036596	**PZ244258**	06/07/2023	Kawau I.	36.39655	174.81840
C. parvifolia	A036597	**PZ244261**	28/04/2024	Mokohinau I.	35.9089033	175.1073107
C. parvifolia	A036598	**PZ244262**	28/04/2024	Mokohinau I.	35.9089033	175.1073107
C. parvifolia	A036599	**PZ244263**	06/06/2024	Mokohinau I.	35.908791	175.107006
C. parvifolia	A036600a	**PZ244265**	24/06/2024	Rakino I.	36.718192	174.955366
C. parvifolia	A036600b	**PZ244266**	24/06/2024	Rakino I.	36.718192	174.955366
C. parvifolia	A036601	**PZ244267**	26/11/2024	Waiheke I.	36.76772	175.05933
C. parvifolia	A036602	**PZ244269**	27/11/2024	Kawau I.	36.44979	174.86494
C. parvifolia	A036603	**PZ244271**	27/11/2024	Kawau I.	36.44504	174.8707
C. webbiana	AK391740	**PZ285834**	19/11/2021	Rangitāhua/ Kermadec I.	29.28472	177.95360