DE GRUYTER Botanica Marina 2015; 58(6): 511–521

John M. Huisman*, Rainbo R.M. Dixon, Felicity N. Hart, Heroen Verbruggen
and Robert J. Anderson

The South African estuarine specialist *Codium tenue* (Bryopsidales, Chlorophyta) discovered in a south-western Australian estuary

DOI 10.1515/bot-2015-0058
Received 21 July, 2015; accepted 30 September, 2015; online first 5 November, 2015

Abstract: *Codium tenue*, previously known reliably only from estuarine habitats in South Africa, is recorded from a similar habitat in the Walpole and Nornalup Inlet system, on the south coast of Western Australia. The Australian *C. tenue* has a repeatedly divaricately dichotomously branched thallus to 11.5 cm in height, with markedly compressed axes up to 1 cm in width at branch dichotomies, but distally attenuating to terete branch apices. Structurally, thalli have cortices with distinctive cuneate utricles up to 1310 μm long and 650 μm in diameter. Both the habit and structural morphology essentially agree with *C. tenue* as known in South Africa. Sequences generated from the Australian specimens are also wholly comparable with those of South African specimens newly generated in this study. While similarly disjunct South African/Western Australian distributions are known for other algae, that of *C. tenue* is particularly remarkable in that the species is apparently an estuarine specialist.

Keywords: Australia; Codiaceae; *Codium tenue*; disjunct distribution; South Africa.

Introduction

The genus *Codium* (Chlorophyta, Bryopsidales) is globally distributed and is one of the most diverse green algal genera in the world, with over 100 currently recognised species (Chang et al. 2002, Oliveira-Carvalho et al. 2010). It occurs in a wide variety of habitats, ranging from estuarine waters to marine rocky coasts, calm and sheltered waters to deeper waters in all climates around the world (Verbruggen et al. 2007). The genus is particularly well represented in Western Australia, with some 21 species recorded (Hart and Huisman 2010).

During a 2010 survey of the marine benthic algae of the Walpole and Nornalup Inlets Marine Park, in southwest Western Australia (see Huisman et al. 2011), one of the most frequently encountered algae was a species of *Codium*. This inlet system comprises two discrete water bodies connected by a narrow channel. The southern Nornalup Inlet is open to the Southern Ocean and has a strong marine influence. The more northern Walpole Inlet, however, is further removed from the ocean and is more estuarine, with considerable freshwater input during winter. These conditions were reflected in the differing algal diversities recorded for the two inlets, with that of Walpole much reduced relative to that of Nornalup (Huisman et al. 2011). *Codium* was very common at several sites in Nornalup Inlet, but was also present at the southern end of Walpole Inlet, where it was the only large alga recorded. In both inlets it grew attached to rock and was typically covered in silt. The species would appear, therefore, to be highly tolerant of variable environmental conditions.

Despite being within the geographical bounds of a major *Codium* monograph (Silva and Womersley 1956) and Womersley's later monograph of the green algae of southern Australia (Womersley 1984), this *Codium* could not be identified as any of the known Australian species. Our goal in the present study, therefore, was to clarify the identity of this *Codium* using morphological and molecular data, and discuss the taxonomic and biogeographic implications.

***Corresponding author: John M. Huisman,** School of Veterinary and Life Sciences, Murdoch University, Murdoch, 6150 WA, Australia; and W.A. Herbarium, Science Division, Department of Parks and Wildlife, Locked Bag 104, Bentley Delivery Centre, 6983 WA, Australia, e-mail: J.Huisman@murdoch.edu.au
Rainbo R.M. Dixon and Felicity N. Hart: School of Veterinary and Life Sciences, Murdoch University, Murdoch, 6150 WA, Australia
Heroen Verbruggen: School of BioSciences, The University of Melbourne, 3010 Victoria, Australia
Robert J. Anderson: Fisheries Research, Department of Agriculture, Forestry and Fisheries, Private Bag X2, 8012 Roggebaai, South Africa; and Department of Biological Sciences, University of Cape Town, 7701 Rondebosch, South Africa

Materials and methods

Specimens were collected from shallow silt-laden subtidal waters in Nornalup and Walpole Inlets, located on the south coast of Western Australia (Table 1). Samples were either pressed onto herbarium sheets or preserved in 4% formalin/seawater solution; subsamples for DNA were dried in silica gel. Specimens were deposited in the Western Australian State Herbarium (PERTH). The *in situ* photograph (Figure 1) was taken with a Canon G9 (Canon Inc., Tokyo, Japan) in a housing. Camera lucida drawings were prepared with a drawing tube attached to a Nikon Eclipse 80i (Nikon Corporation, Tokyo, Japan).

Molecular data

DNA extraction, PCR and sequencing of Australian samples followed Dixon et al. (2012) for Australian samples (excluding the DNA purification step) and Verbruggen et al. (2007) or Verbruggen et al. (2012) for South African samples. Voucher information and GenBank accession numbers are given in Table 1. The *rbc*L, *tuf*A and *rps*3–*rpl*16 (UCP6) regions were amplified with primers from Verbruggen et al. (2007), Famà et al. (2002) and Provan et al. (2004), respectively. Three *rbc*L sequences with between 614 and 729 base pairs, three *tuf*A sequences of 905 base pairs and five *rps*3–*rpl*16 sequences between 345 and 383 base pairs long were generated. The relative positioning of *Codium tenue* (Kützing) within the broader *Codium* genus was sought using 244 *rbc*L sequences downloaded from Genbank. These were derived from the studies of Shimada et al. (2004), Verbruggen et al. (2007, 2012), Oliveira-Carvalho et al. (2012) and Verbruggen and Costa (2015). The full Bayesian Inference (BI) *rbc*L tree is presented in Supplemental Figure 1, with the clade including the newly generated sequences of *C. tenue* enlarged for clarity as Figure 18. Sequences were aligned in Geneious Pro v.5.5.6 (http://www.geneious.com; Drummond et al. 2011) and manually corrected. After trimming, the *rbc*L alignment was 750 base pairs. The model of evolution and parameters were obtained from jModelTest (http://darwin.uvigo.es/; Guindon and Gascuel 2003, Posada 2008), which selected the GTR+I+Γ substitution model. Bayesian inference analysis was performed with BEAST v.1.7.1 (http://beast.bio.ed.ac.uk/; Drummond et al. 2006, Drummond and Rambaut 2007) using estimated base frequencies, 4 Γ categories to model among-site rate heterogeneity, a relaxed log-normal molecular clock at a fixed rate of 1.0, a coalescent tree prior with a randomly generated starting tree, and run for 10 million generations, sampled every 1000th, and tree files were calculated with branch lengths in substitutions. The analysis was monitored in Tracer (http://tree.bio.ed.ac.uk/software/tracer/; Drummond and Rambaut 2007), the consensus tree created in TreeAnnotator (http://beast.bio.ed.ac.uk/treeannotator) with a burn-in of 10%, then visualised in FigTree (http://tree.bio.ed.ac.uk/software/figtree; Drummond and Rambaut 2007).

Results

Our morphological and DNA sequence data indicate that the estuarine *Codium* entity from Nornalup and Walpole corresponds to *C. tenue*, a species known from South Africa.

Codium tenue (Kützing) Kützing 1856: 33, pl. 95: fig. I

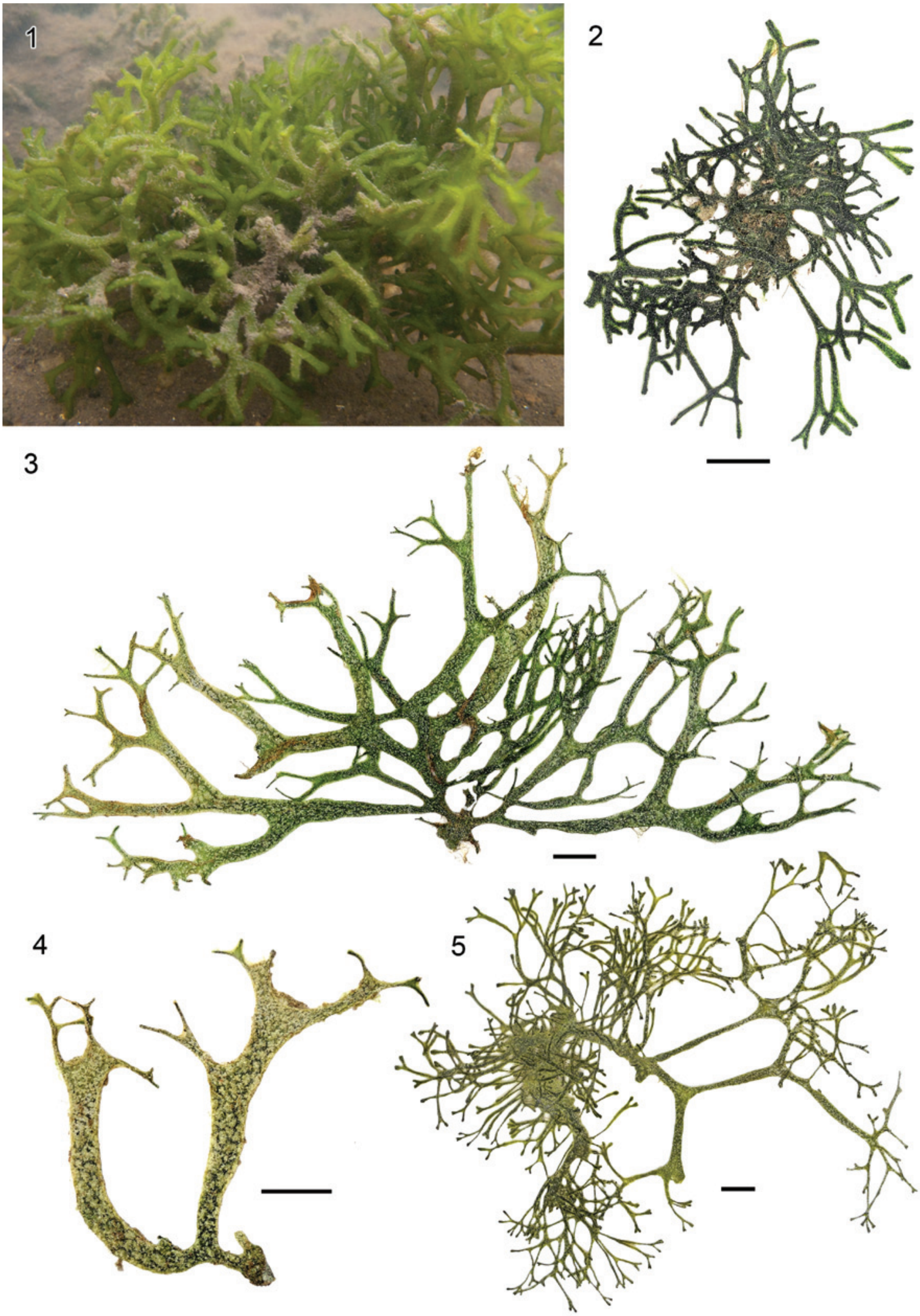
Codium sp. in Huisman et al. (2011: 35, fig. 3B)

Type locality

Caput bonae spei (eastern Cape Province, South Africa).

Table 1: Specimens of *Codium tenue* (Kützing) sequenced in this study.

GenBank accession					
Voucher	**Locality**	**Collector**	***rbc*L**	***tuf*A**	***rps*3-*rpl*16**
PERTH 08243441	Nornalup Inlet, Western Australia, 20/4/2010	J.M. Huisman			KT751242
PERTH 08243425	Nornalup Inlet, Western Australia, 20/4/2010	J.M. Huisman	KT751236		KT751241
PERTH 08243433	Nornalup Inlet, Western Australia, 20/4/2010	J.M. Huisman			KT751240
PERTH 08243492	Walpole Inlet, Western Australia, 21/4/2010	J.M. Huisman	KT751237	KT751243	KT751239
G.302	Knysa Estuary, South Africa, 7/4/2008	R.J. Anderson	KP685979	KP685771	KT751238
G.841	Kleinemonde, South Africa, 9/7/2009	R.J. Anderson		KP685785	



Figures 1–5: *Codium tenue*. (1) Habit *in situ*, Nornalup Inlet. (2) Specimen showing mostly terete branches, PERTH 08243433. (3) Pressed specimen, PERTH 08243441. (4) Specimen with flattened lower branches and terete upper branches, PERTH 08243425. (5) Specimen from South Africa, BOL 46243. All scale bars=1 cm.

Description (Australian specimens)

Thallus medium green, firm, erect to 11.5 cm high, repeatedly divaricately dichotomously branched, with rounded axils, branches tomentose and compressed to 1 cm in width at the dichotomies, attenuating and becoming terete at branch apices (Figures 2–4). Utricles squat, highly variable in size and shape in any given specimen: juvenile utricles (Figures 6–10) cylindrical, clavate; mature utricles swollen, most commonly cuneate, also clavate, obpyriform to suborbiculate (Figures 11–14). Utricles from branch apices 310–625 µm long, (160–) 200–350 (–440) µm in diameter shortly below apices tapering to 80–200 (–260) µm in diameter basally; utricles from medial and basal branches (Figures 15–17) larger, (310–) 500–700 (–1310) µm long, (145–) 250–550 (–650) µm in diameter shortly below apices, tapering to (80–) 150–350 (–550) µm basally. Utricular wall generally consistently thin over entire utricles, utricle apices broadly rounded to subtruncate, occasionally very slightly thickened to 9 µm on mature utricles. Hairs and/or hair scars occasional to common on utricles from branch apices and medial branches, whilst infrequent on utricles from basal branches, 0–2 (–4) per utricle, borne 55–150 µm below utricle apices. Medullary filaments 20–65 (–90) µm in diameter, 1–3 (–4) per utricle, with variable filament plug positions, most commonly closely adjacent to the utricle base, but rarely up to 120 µm from the utricle base on mature utricles. Gametangia not observed.

Specimens examined

Western Australia: Nornalup Inlet, 20 April 2010, *J.M. Huisman* (PERTH 08243484); East Coalmine, Nornalup Inlet, 20 April 2010, *J.M. Huisman* (PERTH 08243441; PERTH 08243425; PERTH 08243433; PERTH 08243441); Coalmine, Nornalup Inlet, on the base of old wood pilings near the boat ramp at 1.5 m depth, 1 April 2015, *J.M. Huisman* (PERTH); Walpole Inlet, 21 April 2010, *J.M. Huisman* (PERTH 08243492).

South Africa: Kowie, on submerged rocks, *W. Tyson* (BOL 15685); Cape Morgan, *H.G. Hanagan* (BOL 147127); The Kowie, 1870, *H. Becker* (BOL 147122); West Kleinemonde Estuary, 1.5 km from mouth, 9 July 2009, *R. Anderson D478* (BOL 46243).

Distribution and habitat

In Australia, *Codium tenue* is known only from Nornalup and Walpole Inlets, Western Australia, where it has been collected from shallow, silt-laden subtidal waters (Figure 1). The species is known from similar habitats in South Africa. Given the markedly different sequence derived from a specimen of *C.* cf. *tenue* from the Philippines (HV608; Genbank: EF108091, EF107942), records of this species from elsewhere are possible misidentifications and require confirmation using molecular methods.

Molecular phylogenetics

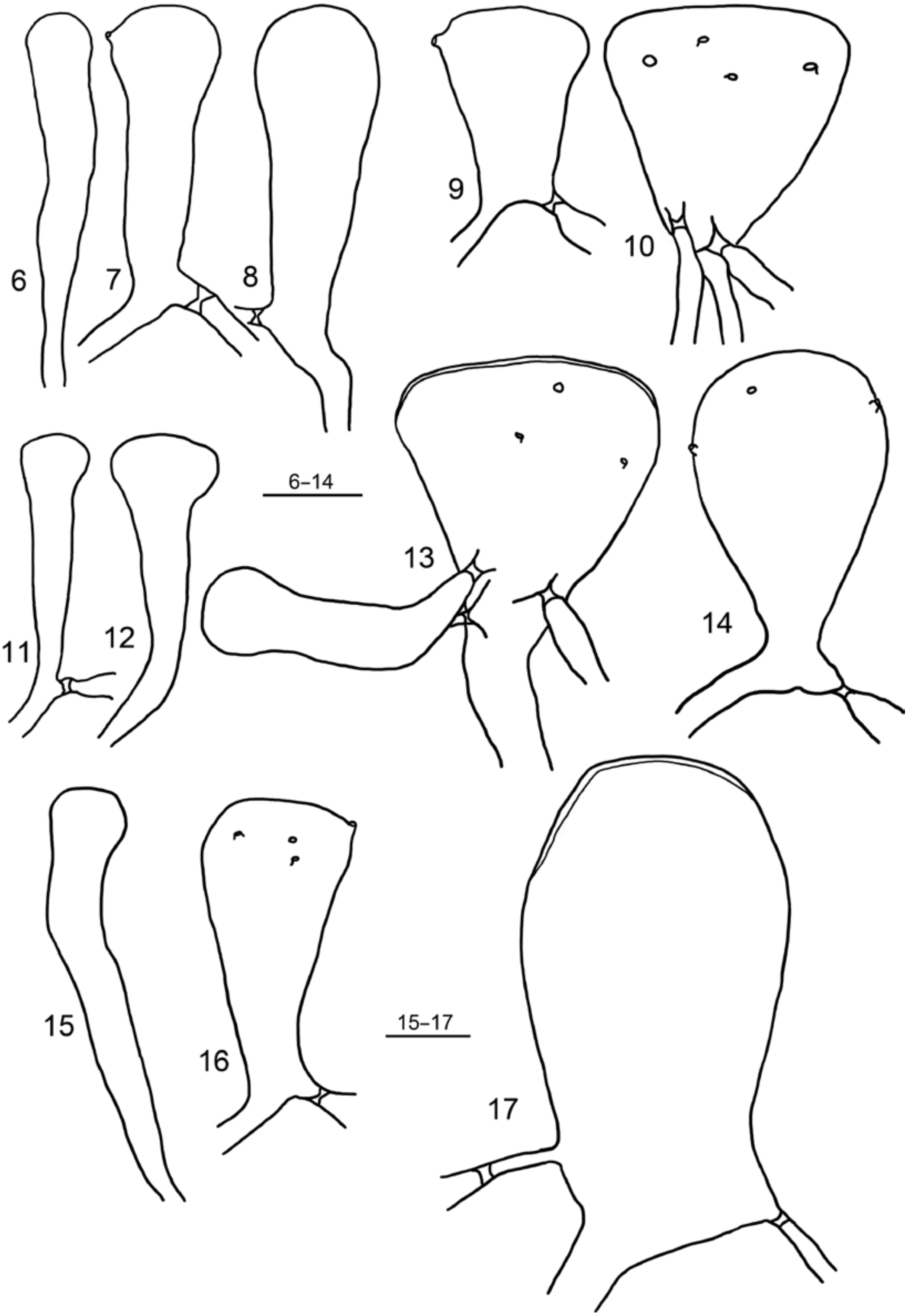
DNA sequences of the South African and Australian specimens of *Codium tenue* differed at most by one base pair in the loci investigated. In *tuf*A the most divergent sequences were 99.9% similar (1 nt polymorphism), in *rbc*L 99.8% similar (1 nt polymorphism) and in *rps*3-*rpl*16 99.8% similar (1 nt polymorphism). In *rps*3-*rpl*16 the four Australian sequences were identical except for PERTH 08243433, which included a single degenerate/ambiguous nucleotide. In *rbc*L the Australian samples were identical and differed from the South African specimen by one base pair. In *tuf*A the sequence generated for PERTH 08243492 was identical to the South African sequence for G.841 and these two differed from the second South African sequence (G.302) by one base pair.

Phylogenetic trees of the three different loci led to identical conclusions with regards to species relationships. A portion of the *rbc*L BI tree is presented here (Figure 18) and in full as a supplemental figure (Supplemental Figure 1).

Discussion

Codium tenue is distinctive in thallus habit and utricular anatomy in addition to the unique subtidal, silt-laden habitat in which it occurs. The Australian specimens showed considerable morphological variability (Figures 1–4), with seemingly immature specimens consisting entirely of narrow, terete branches (Figure 2), while axes of mature specimens were mostly compressed with terete branches found only near the apices (Figures 3 and 4). South African plants showed a similar morphology (Figure 5).

As noted by Silva (1959: 143), "*C. tenue* is very distinctive, both morphologically and ecologically. The light green colour, divaricately dichotomous branching, regular infra-axillary dilations, and attenuated tips are outstanding features". The Australian specimens conform to this description and agree in gross morphology with South African *C. tenue*, as illustrated in Silva (1959: pl. IIB) and observed here, and their utricle shapes and dimensions are also comparable. The two entities also share similar habitats, with South African *C. tenue* occupying what was



Figures 6–17: *Codium tenue*, all PERTH 08243441. (6–10) Utricles from branch apices. (6) Slender, juvenile utricle. (7) Capitate utricle, with rounded apical wall and hair scar. (8) Clavate utricle. (9) Squat, cuneate utricle, with truncated apical wall and hair scar. (10) Swollen cuneate utricle, with truncated apical wall and numerous hair scars. (11–14) Medial branch utricles. (11) Capitate juvenile utricle. (12) Capitate utricle. (13) Cuneate utricle with slightly thickened apical wall, few hair scars and budding, capitate utricle. (14) Broadly rounded clavate utricle with few hair scars, with the plug a short distance from the utricle base. (15–17) Basal branch utricles. (15) Slender, elongated juvenile utricle. (16) Clavate utricle with numerous hair scars. (17) Inflated clavate utricle, with slightly thickened apical wall, with filament plugs variably distant from utricle base. Scale bars=200 µm.

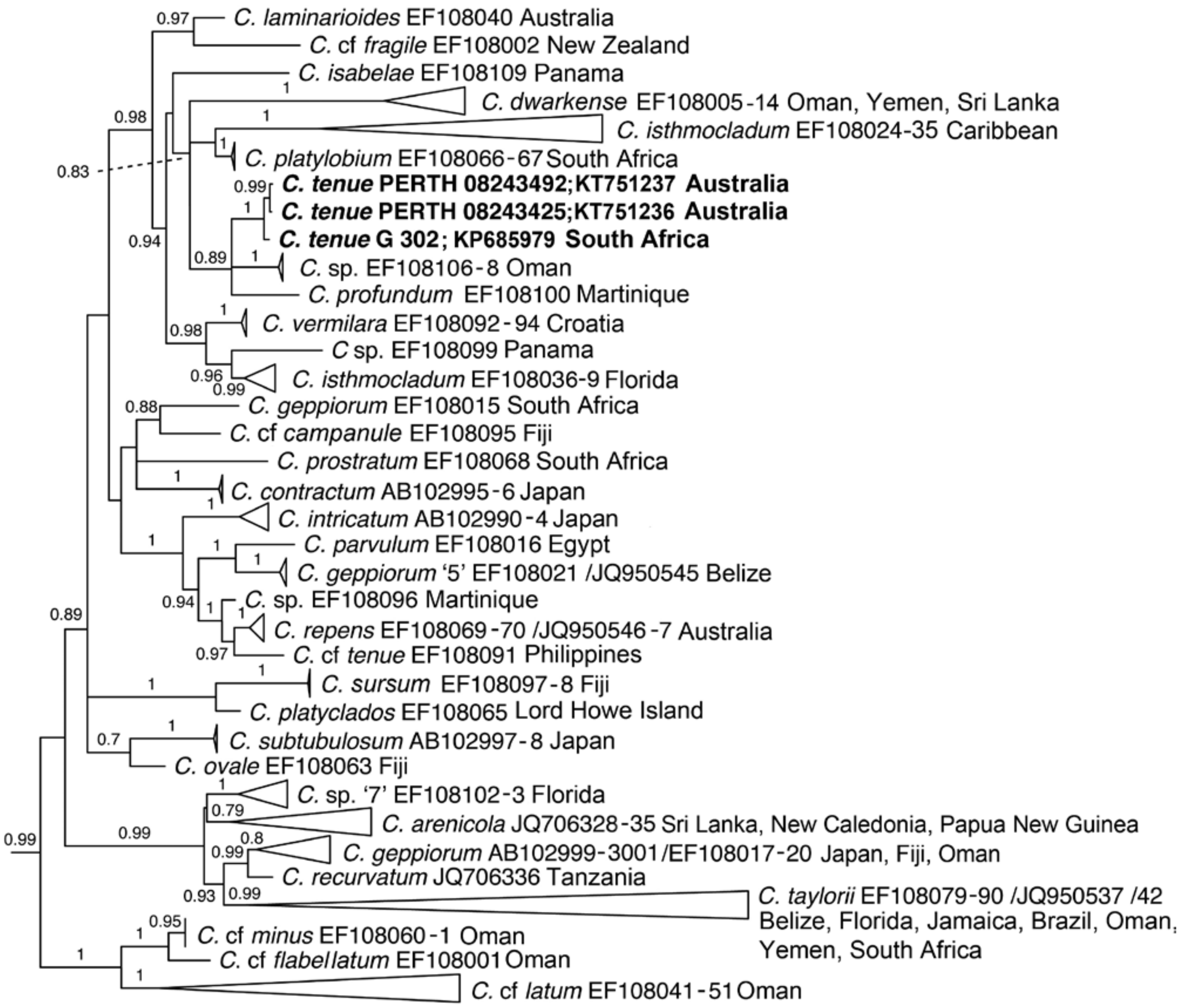


Figure 18: Phylogenetic hypothesis of *Codium* species inferred from the *rbc*L alignment of *Codium* sequences using Bayesian analysis. Sequences in bold were newly generated in this study, all others were downloaded from GenBank. This figure presents the portion of the tree that includes the newly generated sequences of *Codium tenue*, enlarged for clarity. The full *rbc*L tree is available in Supplemental Figure 1. Posterior probability branch values <0.70 are removed. Scale bar indicates the number of substitutions per site.

described by Silva (1959: 143) as "a unique habitat, growing on silt-covered rocks and shells and on concrete or wood jetty piles in river mouths (estuaries and lagoons)". This description applies precisely to the habitat of the species as found in Nornalup Inlet. Silva (1959: 143) also mentions the only recorded exception to this estuarine habitat, that of a high tide pool at Second Beach, Port St. Johns, but accounts for this exception by acknowledging a fresh water input, as "the stream from the marsh above this part of the beach enters the sea through this pool".

The utricle morphology of Australian *C. tenue* differed slightly in maximum dimensions to those described for South African specimens (see Table 2), but these larger utricles were from median and basal regions of the thalli. An examination of South African specimens showed utricles agreeing with Silva's description, but also rarely up to 1000 μm long, close to the sizes recorded for Australian utricles. Utricles from similar branch positions on Australian and South African specimens were virtually identical. Unfortunately the Australian specimens were not reproductive and the morphology of gametangia could not be compared to those described for South African specimens (Silva 1959: 142, fig. 15). However, based on habitat, morphology and molecular analyses, the Australian plants conformed to *C. tenue* and unquestionably represent the first authenticated record of this species outside of South Africa.

If we accept that *C. tenue* is thus far known reliably only from estuarine habitats in South Africa and

Table 2: Comparison of the utricular anatomical features of Australian and South African *Codium tenue*.

Feature	*C. tenue*	*C. tenue*[a]
Utricle length (max.)	To 1310 μm	To 800 (-1000) μm long
Utricle diameter (max.)	To 650 μm	To 700 μm
Plug distance from utricle base	Mostly adjacent to utricle base, but up to 120 μm distant	Adjacent to utricle base (mostly adjacent but up to 80 μm distant)
Hair position below apices	55–150 μm	70–120 μm

[a][from Silva 1959 with observations of present authors on a South African specimen (BOL 46243) in parentheses].

south-western Australia, the perplexing question is: how did this rather unlikely distribution pattern arise? How does a seemingly habitat-specific species come to occupy estuarine habitats on two widely separate continents? Several possible scenarios might be invoked.

A recent introduction

The discovery of *Codium tenue* in Australia, in a well-studied region included in a relatively recent account of the green algal flora of southern Australia (Womersley 1984) and, prior to this, a *Codium* monograph (Silva and Womersley 1956), might initially suggest a recent introduction. However, despite Womersley's contribution, there remains much to be discovered on the Australian south coast, this evinced by the recent description of the new species *Codium apiculatum* Silva, Chacana *et* Womersley (Silva and Chacana, 2012) from southern and south-western Australia. Moreover, the algae of the Walpole/Nornalup Estuary have been collected only on rare occasions, with the first relatively detailed study that of Huisman et al. (2011), when the initial discovery of *C. tenue* was made (reported as *Codium* sp. in Huisman et al. 2011). It would appear that the southern Australian algal flora will continue to yield new species and records. As such, the absence of *C. tenue* from 20th century records cannot be taken as evidence of a recent introduction. A recent introduction of *C. tenue* would also appear unlikely as Walpole/Nornalup is a relatively small inlet system, supporting only recreational boating, and its small oceanic entrance channel seemingly precludes any potential for international traffic. The only possible vector might be small sail craft, but this would again appear an unlikely scenario.

Aquaculture

There has never been any aquaculture undertaken in the Walpole/Nornalup inlet system and it is therefore unlikely that *Codium tenue* could have been accidentally introduced. However, the mussel *Mytilus edulis planulatus* Lamarck is used for aquaculture in Albany (approximately 110 km to the east) (Huisman et al. 2008). This subspecies was first described from the Albany region based on material collected during the early French expeditions; it is possibly an introduction but one that could then date to the 16th century (Hewitt 2003). Linking this mussel species to the presence of *C. tenue* would be highly speculative. In 1947 an unsuccessful attempt was made to introduce the Pacific oyster *Crassostrea gigas* (Thunberg) to Albany, however the specimens originated in Japan, well outside of the known range of *C. tenue*.

A nineteenth century introduction

It is known that the Walpole/Nornalup Inlet was visited by whalers and sealers during the 1800s. The first substantial use of the inlets occurred following the settlement of Albany in 1826, when Nornalup Inlet was used as a base for sealers hunting New Zealand fur seals (Fernie and Fernie 1989). Sailing vessels from Europe would undoubtedly have taken the usual route of heading south along the western Atlantic before rounding the Cape of Good Hope and heading eastward in the Southern Ocean, taking advantage of favourable winds. Presumably these vessels would have entered sheltered estuarine habitats along the route for supplies or to avoid bad weather, including those of southern Africa, and *Codium tenue* may have become attached to a ship's hull. It is unlikely that larger vessels travelling from Europe would have entered Nornalup Inlet due to the small oceanic entrance and generally rough seas, but it is documented that smaller landing boats and whaleboats certainly did (Fernie and Fernie 1989). Although highly speculative, support for a possible 19th century introduction includes the absent or low sequence divergence and close molecular relationship of South African and Australian specimens, indicating that the timing of their separation was unlikely to have been millions of years before present. The likelihood of a South Africa to Australia introduction, rather than the reverse, is supported by the limited distribution of *C. tenue* in Australia, but this does not preclude an Australia to South Africa introduction.

Natural causes

The close relationship of the seaweed floras of South Africa and Australia is well-documented, with numerous species (or sister species) found in the two regions (see Hommersand 1986, Verbruggen et al. 2007, De Clerck et al. 2008, Dixon et al. 2014). Hommersand (1986, 2007) has suggested that species that originally evolved in warm-temperate environments in western and southern Australia may have descendants that migrated through the Indian Ocean by way of the North Equatorial current as far as the east coast of South Africa and beyond into the Atlantic, during the Miocene and Pliocene during periods when the temperature decreased markedly. Dixon et al. (2014) invoked a similar scenario when discussing the presence of *Sargassum* subgenus *Halochoa* in both the south-western and eastern Indian Ocean. However (as mentioned above), the nearly identical DNA sequences of the *Codium tenue* populations from South Africa and Australia do not support a scenario involving millions of years of divergence.

We should also consider the possibility of more recent natural long distance dispersal to explain the disjunct distribution. There are several examples of species shared between the coasts of South Africa and southern Australia that seem to have made their way across the Indian Ocean in relatively recent times. Among these examples, the kelp species *Ecklonia radiata* (C. Agardh) J. Agardh, which is distributed in South Africa, southern Australia and New Zealand, also has a likely South African origin based on its close relationship with the South African endemic *Ecklonia maxima* (Osbeck) Papenfuss (Rothman et al. 2015) and appears to have dispersed across the Indian Ocean in relatively recent times. A similar scenario may be applicable to *Pseudocodium devriesii* Weber-van Bosse, which has an endemic South African sister species (*P. natalense* De Clerck, Coppejans *et* Verbruggen) and has populations in South Africa, Western Australia and the Arabian Sea with nearly identical *rbc*L and *tuf*A sequences (De Clerck et al. 2008, Payri and Verbruggen 2009). The estuarine nature of *C. tenue* would appear to reduce the likelihood of successful long-distance dispersal and establishment from one estuary into another estuary across the Indian Ocean. However, estuarine seaweed species are usually euryhaline and can tolerate fully marine conditions (Lüning 1990). So it is not unthinkable that, following a period of establishment in marine conditions, the species is outcompeted in this environment and maintains populations only in estuaries where it faces less competition. We thus cannot discount the possibility that *C. tenue* arrived by natural means as many other species have done, and (perhaps following a period in marine conditions) established in Australian estuarine habitats. Its absence from similar estuaries in south-western Australia would suggest that this is not the case, but these habitats have not been studied in enough detail.

Based on the available evidence, we cannot come to a definitive conclusion regarding the origin of *C. tenue* in the Walpole-Nornalup inlet, and the species should be regarded as cryptogenic.

We therefore recognise *C. tenue* as a new addition to the Australian algal flora. In the local Western Australian, let alone southern Australian flora, no other *Codium* species resembles *C. tenue*. Despite the region being included in recent monographs of southern Australian algae (e.g. Womersley 1984), vast tracts of the southern Australian coast remain unstudied or barely studied by phycologists and further exploration will undoubtedly yield new taxa and records. Documenting this flora, and the often subtle differences between species, is particularly important in light of the recent discovery of the invasive *Codium fragile* subsp. *fragile* in Albany harbour, southwestern Australia (Zeller 2008, as *C. fragile* subsp. *tomentosoides*; Hart and Huisman 2010; McDonald et al. 2015).

Codium tenue from elsewhere

Silva (1959: 142–143) noted that the nature of this species "has long been subject to much conjecture", with a consequence that "the name has been applied to unrelated species from various parts of the world". The large molecular divergence between authentic *Codium tenue* and a specimen tentatively identified as *C.* cf. *tenue* from the Philippines (Specimen: HV608; Genbank: EF108091, EF107942) clearly supports Silva's opinion, and most records not buttressed by sequence analyses should be regarded as suspect. This doubt is reinforced by marked differences in habitat. In South Africa the known distribution of *C. tenue* is from Knysna Lagoon (Western Cape Province) across the entire Eastern Cape Province coast and only just into KwaZulu-Natal, a coastal distance of about 800 km (Silva 1959, R. Anderson, pers. obs.). This region experiences mean monthly water temperatures ranging from 15–17°C in winter to 22–23°C in summer, depending on location (Smit et al. 2013), and is classified as warm temperate. This range is virtually identical to that of the

Walpole and Nornalup Inlets, with the winter temperatures 12–17°C and summer temperatures 20–22°C (DEC 2009). However, the majority of records of *C. tenue* from elsewhere are from tropical regions such as the Philippines and the Marshall Islands (see Guiry and Guiry 2015; http://www.algaebase.org). In fact, at least some of these records can be excluded based on the information provided by the recording authors. Dawson (1957: 107) mentioned that Paul Silva had examined the Eniwetok Atoll *C. tenue* and considered it an undescribed species. Taylor (1950: 94) does not mention the infra-axillary dilations (the increase in breadth below branching points) in specimens from Bikini Atoll, a feature regarded as distinctive of the species.

Acknowledgements: We thank Alan Kendrick and Michael Rule (Western Australian Department of Parks and Wildlife) for organising the Walpole expedition and collection assistance. Peter Spencer (Murdoch University) kindly provided laboratory facilities for the molecular analyses. We also thank the BOLUS Herbarium for the loan of specimens. JMH thanks the "Australian Biological Resources Study" for funding support. HV received funding from the Australian Biological Resources Study (RFL213-08) and the Australian Research Council (FT110100585).

References

Chang, J-S., C-F. Dai and J. Chang. 2002. A taxonomic and karyological study of the *Codium geppiorum* complex (Chlorophyta) in southern Taiwan, including the description of *Codium nanwanense* sp. nov. *Bot. Bull. Acad. Sin. 43*: 161–170.

Dawson, E.Y. 1957. An annotated list of marine algae from Eniwetok Atoll, Marshall Islands. *Pacific Sci. 11*: 92–132.

De Clerck, O., H. Verbruggen, J.M. Huisman, E. Faye, F. Leliaert, T. Schils and E. Coppejans. 2008. Systematics and biogeography of the genus *Pseudocodium* (Bryopsidales, Chlorophyta), including the description of *P. natalense* sp. nov. from South Africa. *Phycologia 47*: 225–235.

DEC. 2009. *Walpole and Nornalup Inlets Marine Park Management Plan 2009–2019*. Department of Environment & Conservation, Perth, Western Australia.

Dixon, R.R.M., J.M. Huisman, J. Buchanan, C.F. Gurgel and P. Spencer. 2012. A morphological and molecular study of austral *Sargassum* (Fucales, Phaeophyceae) supports the recognition of *Phyllotricha* at genus level, with further additions to the genus *Sargassopsis*. *J. Phycol. 48*: 1119–1129.

Dixon, R.R.M., L. Mattio, J.M. Huisman, C.E. Payri, J.J. Bolton and C.F. Gurgel. 2014. North meets south – Taxonomic and biogeographic implications of a phylogenetic assessment of *Sargassum* subgenera *Arthrophycus* and *Bactrophycus*. *Phycologia 53*: 15–22.

Drummond, A.J. and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol. 7*: 214.

Drummond, A.J., S.Y.W. Ho, M.J. Phillips and A. Rambaut. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biol. 4*: 88.

Drummond, A.J., B. Ashton, S. Buxton, M. Cheung, A. Cooper, J. Heled, M. Kearse, R. Moir, S. Stones-Havas, S. Sturrock, T. Thiererand and A. Wilson. 2011. *Geneious* v5.5, Available from http://www.geneious.com.

Famà, P., B. Wysor, W.H.C.F. Kooistra and G.C. Zuccarello. 2002. Molecular phylogeny of the genus *Caulerpa* (Caulerpales, Chlorophyta) inferred from chloroplast *tuf*A gene. *J. Phycol. 38*: 1040–1050.

Fernie, L. and G. Fernie. 1989. *In praise of a National Park*. Privately published, Lee and Geoff Fernie, Walpole. 88 pp.

Guindon, S. and O. Gascuel. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Syst. Biol. 52*: 696–704.

Guiry, M.D. and G.M. Guiry. 2015. *AlgaeBase*. Worldwide electronic publication, National University of Ireland, Galway. http://www.algaebase.org.

Hart, F. and J.M. Huisman. 2010. The taxonomy and pest potential of the genus *Codium* in Western Australia. Australasian Society for Phycology and Aquatic Botany Conference, Rottnest Island, Western Australia, 15–18 November 2010.

Hewitt, C.L. 2003. The diversity of likely impacts of introduced marine species in Australian waters. *Rec. South Aust. Mus. Monogr. Ser. 7*: 3–10.

Hommersand, M.H. 1986. The biogeography of the South African marine red algae: a model. *Bot. Mar. 29*: 257–270.

Hommersand, M.H. 2007. Global biogeography and relationships of the Australian marine macroalgae. *In*: (P.M. McCarthy and A.E. Orchard, eds) *Algae of Australia: Introduction*. Australian Biological Resources Study, Canberra and CSIRO Publishing, Melbourne, pp. 511–542.

Huisman, J.M., D.S. Jones, F.E. Wells and T. Burton. 2008. Introduced marine biota in Western Australian waters. *Rec. West. Aust. Mus. 25*: 1–44.

Huisman, J.M., A.J. Kendrick and M.J. Rule. 2011. Benthic algae and seagrasses of the Walpole and Nornalup Inlets Marine Park, Western Australia. *J. Roy. Soc. West. Aust. 94*: 29–44.

Kützing, F.T. 1856. *Tabulae phycologicae; oder, Abbildungen der Tange.* Vol. VI. Gedruckt auf kosten des Verfassers (in commission bei W. Köhne), Nordhausen. pp. i–iv, 1–35, 100 pls.

Lüning, K., 1990. *Seaweeds. Their Environment, Biogeography and Ecophysiology*. Wiley Interscience, New York. pp. [i]–xii, 1–527.

McDonald, J., J.M. Huisman, F.N. Hart, R.R.M. Dixon and J.A. Lewis. 2015. The first detection of the invasive macroalga *Codium fragile* ssp. *fragile* in Western Australia. *Bioinvasion Rec.4*: 75–80.

Oliveira-Carvalho, M.F., S.M.B. Pereira and F.F. Pedroche. 2010. Taxonomy and distribution of the green algal genus *Codium* (Bryopsidales, Chlorophyta) in Brazil. *Nova Hedwigia 91*: 87–109.

Oliveira-Carvalho, M.F., M.C. Oliveira, S.M.B. Pereira and H. Verbruggen. 2012. Phylogenetic analysis of *Codium* species from Brazil, with the description of the new species *C. pernambucensis* (Bryopsidales, Chlorophyta). *Eur. J. Phycol. 47*: 355–365.

Payri, C.E. and H. Verbruggen. 2009. *Pseudocodium mucronatum*, a new species from New Caledonia, and an analysis of the evolution of climatic preferences in the genus (Bryopsidales, Chlorophyta). *J. Phycol. 45*: 953–961.

Posada, D. 2008. jModelTest: Phylogenetic Model Averaging. *Mol. Biol. Evol. 25*: 1253–1256.

Provan, J., S. Murphy and C.A. Maggs. 2004. Universal plastid primers for Chlorophyta and Rhodophyta. *Eur. J. Phycol. 39*: 43–50.

Rothman, M.D., L. Mattio, T. Wernberg, R.J. Anderson, S. Uwai, M.B. Mohring and J.J. Bolton. 2015. A molecular investigation of the genus *Ecklonia* (Phaeophyceae, Laminariales) with special focus on the Southern Hemisphere. *J. Phycol. 51*: 236–246.

Shimada, S., M. Hiraoka, Y. Serisawa and T. Horiguchi. 2004. Phylogenetic studies in the genus *Codium* (Chlorophyta) from Japan. *Jap. J. Phycol. 52(Supplement):* 137–141.

Silva, P.C. 1959. The genus *Codium* (Chlorophyta) in South Africa. *J. S. Afr. Bot. 25*: 103–165.

Silva, P.C. and M.E. Chacana. 2012. *Codium apiculatum* (Codiaceae, Chlorophyta), a new species from southern and southwestern Australia. *Cryptog. Algol. 33*: 35–40.

Silva, P.C. and H.B.S. Womersley. 1956. The genus *Codium* (Chlorophyta) in southern Australia. *Aust. J. Bot. 4*: 261–289.

Smit, A.J., M. Roberts, R.J. Anderson, F. Dufois, S.F.J. Dudley, T.G. Bornman, J. Olbers and J.J. Bolton. 2013. A coastal seawater temperature dataset for biogeographical studies: large biases between *in situ* and remotely-sensed data sets around the coast of South Africa. *PLoS ONE 8*: e81944.

Taylor, W.R. 1950. *Plants of Bikini and other northern Marshall Islands*. University of Michigan Press, Ann Arbor. pp. xv+227.

Verbruggen, H. and J.F. Costa. (2015). Molecular survey of *Codium* species diversity in southern Madagascar. *Cryptog. Algol. 36*: 171–187.

Verbruggen, H., F. Leliaert, C.A. Maggs, S. Shimada, T. Schils, J. Provan, D. Booth, S. Murphy, O. De Clerck, D.S. Littler, M.M. Littler and E. Coppejans. 2007. Species boundaries and phylogenetic relationships within the green algal genus *Codium* (Bryopsidales) based on plastid DNA sequences. *Mol. Phylogenet. Evol. 44*: 240–254.

Verbruggen, H., K. Pauly and O. De Clerck. 2012. The new species *Codium recurvatum* from Tanzania. *Eur. J. Phycol. 47*: 216–222.

Womersley, H.B.S. 1984. *The marine benthic flora of southern Australia. Part I.* Government Printer, Adelaide, South Australia. pp. 329.

Zeller, M. Van. 2008. *Codium* confirmed in Albany Harbour. *Western Fisheries 2008*: 13.

Supplemental Material: The online version of this article (DOI: 10.1515/bot-2015-0058) offers supplementary material, available to authorized users.

Bionotes

John M. Huisman
School of Veterinary and Life Sciences,
Murdoch University, Murdoch, 6150 WA,
Australia; and W.A. Herbarium, Science
Division, Department of Parks and Wildlife,
Locked Bag 104, Bentley Delivery Centre,
6983 WA, Australia,
J.Huisman@murdoch.edu.au

John M. Huisman is a research fellow at Murdoch University in Perth, Western Australia. He earned his PhD at the University of Melbourne, where he developed his interests in the taxonomy of marine macroalgae. After moving to Perth he embarked on an ambitious lifelong project to document (by description and photographically) the seaweeds of Australia's west coast, an undertaking disrupted briefly in 2002–2003 when he spent a rewarding sojourn at the University of Hawaii. John has authored several books, including *Marine Plants of Australia* and *Hawaiian Reef Plants*, and is presently writing a book on the marine flora of tropical Western Australia.

Rainbo R.M. Dixon
School of Veterinary and Life Sciences,
Murdoch University, Murdoch, 6150 WA,
Australia

Rainbo R.M. Dixon completed undergraduate studies in Science at the University of Melbourne in 2005 with an honours project on the ethnobotany of marine plants in Vanuatu, supervised by Dr. Gerry Kraft. She undertook PhD studies at Murdoch University under the supervision of Dr. John Huisman looking at taxonomy and phylogenetics in the brown algal genus *Sargassum*, completing in 2015. Rainbo currently work in the research group of Professor Andrew Lowe at the University of Adelaide on DNA timber tracking.

Felicity N. Hart
School of Veterinary and Life Sciences,
Murdoch University, Murdoch, 6150 WA,
Australia

Felicity N. Hart completed her BSc (Hons.) at Murdoch University in 2010, her research topic assessing the diversity and pest potential of *Codium* in Western Australia. She currently works as a botanical consultant.

Heroen Verbruggen
School of BioSciences, The University of
Melbourne, 3010 Victoria, Australia

Heroen Verbruggen is a senior lecturer in the School of Biosciences at the University of Melbourne. Research in his lab focuses on the evolutionary diversification of marine algae, using molecular phylogenetics to explore their diversification and answer specific questions about their evolution. Systematic research is also a focus, including the question how molecular and morphometric data can complement one another in algal species delimitation.

Robert J. Anderson
Fisheries Research, Department of
Agriculture, Forestry and Fisheries, Private
Bag X2, 8012 Roggebaai, South Africa;
and Department of Biological Sciences,
University of Cape Town, 7701 Rondebosch,
South Africa

Robert J. Anderson obtained his PhD at the University of Cape Town in 1982 and since then has been employed as a seaweed biologist by the Fisheries Department of the South African government, where he is responsible for research on seaweed resources. He is also an honorary Associate Professor at UCT. He is interested in most aspects of seaweed biology, including ecology, biogeography and taxonomy.