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DNA sequencing and anatomy demonstrate that Pacific *Codium simulans* is a genetically variable species found in the floras of Bermuda and Florida

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SUMMARY

When DNA sequences from Bermuda plants described as *Codium isthmocladum* ssp. *clavatum* and a recent collection from Florida originally thought to be *C. decorticatum* were analyzed, they were found to be a genetic match to the Pacific Mexican species *C. simulans*. Historical voucher collections assigned to *C. isthmocladum* ssp. *clavatum* show that this Pacific lineage has been present in Bermuda (Atlantic) waters for over a century, thus precluding a very recent introduction from the Pacific. We hypothesize that *C. simulans* may have hitched a ride on the ballast rocks of early commercial ships plying their trade between the Pacific and Atlantic Oceans.

Key words: Alien species, *Codium isthmocladum* ssp. *clavatum*

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When Collins and Hervey (1917) described their new variety, *Codium decorticatum* v. *clavatum* Collins *et* Hervey, based upon specimens collected in Bermuda, they distinguished their firm, light green plants from the nominate variety by their sturdy texture and short club-shaped (clavate) utricles. In his monograph of the genus *Codium* in the tropical western Atlantic, Silva (1960) proposed that the Collins and Hervey taxon was more closely allied to *C. isthmocladum*

Vickers than *C. decorticatum* (Woodward) M. Howe. He proposed the new status and combination, *C. isthmocladum* ssp. *clavatum* (Collins *et* Hervey) P.C. Silva, and cited inshore *C. tomentosum* Stackhouse collections made by Collins and Hervey (1917) and Howe (1918), as well as Collins and Hervey's (1917) specimens identified as *C. decorticatum* (see Schneider 2003). Sporangiate plants from Hungry Bay, Bermuda, that were distributed in the exsiccata *Phycotheca Boreali-Americana* by Collins *et al.* (1912, no. 1869 as *C. tomentosum*) were likewise included by Silva (1960) as *C. isthmocladum* ssp. *clavatum.* In his treatment, Silva (1960) suggested that the nominate subspecies of *C. isthmocladum* did not occur in Bermuda, thus all early records of this species in the islands (Collins & Hervey 1917; Howe 1918; Tandy 1936) would be referred to the new subspecies. Due to these early collections and work on *Codium*, specimens of *C. isthmocladum* ssp. *clavatum* can be linked to Bermuda waters for more than a century. Silva (1960) also included under the new subspecies some historical *C. tomentosum* specimens collected on the 19th century H.M.S. *Challenger* expedition from deep waters offshore of Bermuda (Hemsley 1884, Murray 1889). But offshore Bermuda specimens with similar utricle shapes and sizes considered closely related to *C. isthmocladum* ssp. *clavatum* have of late been shown to be the genetically distinct *C. profundum* P.C. Silva *et* Chacana (Chacana *et al.* 2003; Silva & Chacana 2010). These deep-water specimens are not nearly as robust in habit and dimensions as the inshore specimens and could represent some of the early deep-water *Challenger* collections identified as *C. tomentosum* by Hemsley (1884) and Murray (1889). As these specimens have not been observed here, their identities need verification.

As part of the ongoing DNA barcoding study of the benthic flora of Bermuda (Cianciola *et al*. 2010), *Codium isthmocladum* ssp. *clavatum* was collected from its type locality and sequenced (Table S1). To our surprise, the specimens aligned with *C. simulans* Setchell *et* N.L. Gardner (1924), a species with its type locality in the Gulf of California at Isla San Marcos off the coast of Baja California Sur, Mexico. At present, Guiry and Guiry (2018) report this species' distribution from California to Pacific Mexico, Juan Fernandez I., Korea and the Arabian Gulf. Both the Korean and Arabian Gulf records are highly unlikely as indicated by extensive molecular surveys of *Codium* completed in these areas (Verbruggen *et al.* 2007; Lee & Kim 2015), suggesting that the actual Pacific distribution might be limited to the Americas. The molecular work presented here, based on our extensive sampling in Pacific Mexico, shows extensive haplotype diversity in samples identified as *C. simulans* (Table S2), suggesting that this is a genetically variable species. In fact, several species including *C. cuneatum* Setchell *et* N.L. Gardner, *C. conjunctum* Setchell *et* N.L. Gardner, *C. unilaterale* Setchell *et* N.L. Gardner were synonymized with *C. simulans* by Pedroche *et al.* (2002). Clearly, further work integrating morphological and molecular data will be needed to fully understand the variable nature of this species and ultimately how it should be treated taxonomically.

As *Codium simulans* has not previously been known in the Atlantic Ocean, one could speculate that the species may have been introduced historically to Bermuda. If the specimens were naturally distributed to the Atlantic Ocean they would have crossed the present location of the Isthmus of Panama prior to when plate tectonic activity closed the interocean connection and raised the present-day isthmus approximately 2.8 Mya (O'Dea *et al.* 2016). In their recent analysis, O'Dea *et al.* (2016) showed that prior to the formation of the land bridge connecting North and South America, the Panama Arc existed as a semi-emergent island chain through which abundant seawater flowed from the Pacific into the Caribbean for at least 30 Ma. Our DNA data show perfect sequence identity between the Bermudian and some of the Pacific samples, suggesting that these populations did not diverge millions of years ago, in fact they haven't diverged at all. Instead, these data are suggestive of a human-influenced introduction to the Atlantic from a diverse set of Pacific haplotypes, with some native Pacific and introduced Atlantic populations sharing identical haplotype sequences.

The long historical record of *Codium isthmocladum* ssp. *clavatum* in Bermuda rules out the possibility that *C. simulans* is a very recent introduction to the islands. In a study of historical invasions of the northwestern Atlantic Ocean, Brawley *et al.* (2009) analyzed microsatellite markers to estimate the time of the arrival for the European rockweed *Fucus serratus* Linnaeus and cytochrome *b* haplotypes for the periwinkle *Littorina littorea* Linnaeus in Pictou, Nova Scotia as between 1824 and 1858. They were able to access shipping records and noted 882 European ships from ports in Scotland, Ireland and England entering Pictou Harbor from 1773–1862 for commerce and immigration, and they speculated that discharged rock ballast was "almost certainly" the source of the alien *F. serratus* invasion in North America (Brawley *et al.* 2009). We do not know for certain when *C. simulans* was first introduced to Bermuda, but Collins' *P.B.-A.* shallow water specimens from 1912 are representative of this species. Before that time, as suggested by Silva (1960), the 19th century *Challenger* Expedition specimens identified as *C. tomentosum*, however unlikely, may still represent *C. simulans*. Whenever the introduction occurred, it seems logical that *C. simulans* could have followed a similar dispersal vector as *F. serratus*, but in this case, crossing from the Pacific to the Atlantic Ocean.

Prior to the work of Collins and Hervey (1917), only a few non-systematic collections of marine algae were made in Bermuda. As specimens of *Codium simulans* were collected in the islands since at least the early 20th century, is it possible that it was distributed to the Atlantic Ocean as far north as Bermuda in early ships along with their rock ballast? A well-known marine archeologist and treasure hunter in Bermuda, Teddy Tucker (2011) recounted his discovery of Pacific shells on an unidentified Spanish shipwreck known as the “Tankard wreck” sunk in the mid-1600s: “Later, while excavating deeper into the aft end of the ballast, we uncovered the remains of what could only have been a very comprehensive collection of shells from the Atlantic and Pacific Oceans. Judging by the way the shells were dispersed among the ballast, they must have been originally stored in various containers. There were clamshells from the northwest coast of North America, abalone shells from California, spider conchs and money cowries from the southwest Pacific islands. From the east coast of Brazil there were giant pink conchs and a type of limpet indigenous to that region, as well as a quantity of Caribbean shell and pieces of coral.” While Tucker’s account in no way implies that the marine organisms inhabiting the shells were alive when this vessel sank off Bermuda, it does suggest that ships as early as the 17th century had been in Pacific waters during a time prior to visiting the remote islands of Bermuda on their return journeys to Europe. Might one or more of these ships have wrecked in Bermuda while harboring living holdfasts of *Codium* from the Pacific Ocean on their ballast rocks? Is it possible that *Codium* plants, or just their holdfasts, attached to their hulls? The most probable mechanism for the arrival of another *Codium*, the invasive Asian *C. fragile*, on the Atlantic coast of North America was thought to be the hulls of ships from Europe to New York in the mid-20th century (Carlton & Scanlon 1985), similar to the earlier ship transport vector posited here for *C. simulans*. Should this have been the vector for the Pacific to Atlantic arrival of *C. simulans*, the specimens would likely have been exposed to the frigid waters in or off the Strait of Magellan, an environment unlikely to be agreeable to a tropical species.

Both *Codium isthmocladum* ssp. *isthmocladum* and *C. isthmocladum* ssp. *clavatum* have historically been reported from Florida, USA (Dawes & Mathieson 2008), and the nominate variety has been reported as the species recently overgrowing coral reefs in southeastern portions of the state (Lapointe *et al.* 2005a, 2005b). Unfortunately, specimens from those blooms more than a decade ago were not preserved on herbarium sheets or silica gel for molecular analysis (Lapointe, pers. comm.). An isolate of *Codium* from the Indian River Lagoon, Florida, in 2014, originally identified as *C. decorticatum* (Woodward) M. Howe, was sequenced, and, like the specimens from Bermuda, discovered to join the genetically variable *C. simulans*. Is it possible that the specimens reported by Lapointe *et al.* (2005a, 2005b) that fouled southeastern Florida reefs and beaches as “invasive *C. isthmocladum*” may be, or include, specimens of *C. simulans*? Lacking genetic analysis of specimens from southern Florida, that remains to be determined.

MOLECULAR EVIDENCE

Specimens used in genetic analysis are recorded in Table S1. A UPGMA tree based on *tufA* sequences generated as in Verbruggen and Costa (2015) shows extensive haplotype diversity among Mexican collections of *Codium simulans*, separating out into four main clusters, and suggesting that it is a genetically variable species (Fig. 1). The samples from Bermuda are situated in cluster III, with two samples (C.0208, C.0209) sharing haplotypes with Pacific Mexican samples and another sample (H.1014) branching on its own but clearly nested within the Mexican cluster III. The sequence from Florida formed a haplotype lineage of its own (cluster IV).

CODIUM SIMULANS IN THE ATLANTIC

Citing it as the most common species of *Codium* in the northern Gulf of California, Norris (2010) provided a list of 20th century synonyms for *C. simulans*, as well as a detailed description of its habit and anatomy. Silva (1951, as *C. cuneatum*) carefully explained the difficulties of distinguishing a number of morphologies and species previously considered distinct from *C. simulans* in Pacific Mexico. Beginning with Dawson (1944), similar species from the Gulf with variable morphologies were combined under the epithet *C. simulans*, although initially the taxonomy was not accepted by all workers (see Silva 1951). By the latter part of 1900s and prior to the use of molecular evidence, *C. simulans* was known as a widespread and variable species in

California and Pacific Mexico. In their morphological study of *Codium* from Pacific Mexico, Pedroche *et al.* (2002) reported that this species comprised a wide variety of morphologies (many of which were previously considered separate species) from cylindrical throughout, mostly cylindrical but compressed at the dichotomies, or mostly compressed with only the stipe and ultimate branches cylindrical.

Presently, occasional plants are found in shallow water surrounding the islands of Bermuda, including the inlet to Harrington Sound at the site of the former Frascati Hotel, the type locality of *Codium isthmocladum* ssp. *clavatum* (Collins & Hervey 1917). Over the past quarter century, Schneider and Flook (2017) monitored a persistent population of *C. simulans* in Walsingham Pond, a sheltered inland collapsed limestone sinkhole with underground connection to the sea, a population grazed by a solo resident green sea turtle where there are otherwise few herbivorous fish or invertebrates.

As an alien species in Bermuda waters for over a century, *Codium simulans* has not exhibited the massive populations often associated with an invasive species. At the northern range for warm temperate waters and with its cool winter water temperatures (18.3˚–20.9˚C, https://www.seatemperature.org), Bermuda is unlikely as an ideal location for such invasive growths of *C. simulans*, rather small populations appear in various locations of the small archipelago, the largest plants being found in the cool months of February and March. Alternatively, *C. simulans* in Bermuda could be well past its initial invasive period and, over time in its new environment, grazers and/or disease agents have adapted to this species, making it at present a low-abundance species like many native species. This would be similar to what has been followed recently for some invasive populations of seaweeds at other locations (Montefalcone *et al*. 2015, Cecere *et al*. 2016).

Specimens of *Codium simulans* from Bermuda (Table S3) fit well into the morphology of the broad concept of the species as described by Norris (2010). We have collected large specimens measuring 30 cm across in the field, but such plants are only occasional and in locations where they cannot be grazed by a large resident green sea turtle population. Isolates range from very tight and regularly dichotomous (Fig. 2a) to cervicorn specimens and large open dichotomous plants (Fig. 2b), to older plants beset with adventitious branches obscuring the overall dichotomous habit (Fig. 2c). We have not found any plants in Bermuda that approach the broader branch diameters (4–15 mm) reported for *C. simulans* in the Gulf of California (Norris 2010). Bermuda specimens have branches that range from 2–10 mm diam., the broadest points just below dichotomies, the only portions of axes that are compressed. The utricles of Bermuda specimens are short clavate (Fig. 2d) or inverted campanulate and turbinate to long clavate (Fig. 2e) with utricles intermediate between these extremes. Various shaped and sized utricles can be found on an individual in close proximity to each other in both young and old individuals though more commonly in the latter. As such, in Bermuda specimens there is a great range in utricle dimensions, from 240–700 µm long and 100–550 µm diameter at their swollen heads, similar to those listed for *C. isthmocladum* ssp. *clavatum* by Collins and Hervey (1917), and somewhat shorter in length and broader at the apices than the dimensions given for Pacific specimens of *C.*

simulans by Norris (2010). Collins and Hervey (1917) noted that the longest utricle they observed reached 980 µm, but we have not found any specimens with such long utricles in our more recent collections.

Our genetic analysis demonstrates that Pacific and Atlantic specimens of *Codium simulans* are identical or very closely related, and that specimens from Bermuda fit well into the pattern of variable morphologies and anatomies as cited for plants in Pacific Mexico (Pedroche *et al*. 2002; Norris 2010). How this species was distributed to the Atlantic Ocean remains as a conjecture, but based on the fact that identical haplotypes are shared between the Atlantic and Pacific populations, the distribution must have been historically aided by man. As such, *C. simulans* can be treated as an alien in Bermuda.

TAXONOMIC CONCLUSION

As we have sequenced and examined plants of *Codium isthmocladum* ssp. *clavatum* from the type locality in Bermuda, and they were shown to represent the same taxon as *C. simulans* from the Pacific, this variety is formally relegated as a taxonomic synonym of the latter. Despite being described as a variety earlier (Collins & Hervey 1917) than the species *C. simulans* (Setchell & Gardner 1924), a varietal name has no priority outside the rank at which it was published (ICN Art. 11.2, *Shenzhen Code*, Turland *et al.* 2018).

The disposition for our Florida *Codium simulans* isolate is more uncertain. Although the haplotype is distinct from all of the other isolates that were sampled (Fig. 1, cluster IV), it remains firmly nested in a larger clade of eastern Pacific species including *C. simulans*, *C. isabelae* W.R. Taylor and *C. giraffa* P.C. Silva (data for latter not shown). Might this be a haplotype that we simply haven't sampled from the Pacific yet? Clearly, this question cannot be answered without additional isolate sampling in Pacific Mexico and the western Atlantic and further analysis on this genetically variable species.

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Figure/Table Captions

Fig. 1. UPGMA clustering tree of *C. simulans* and C. *isabelae tufA* sequences with specimen and GenBank numbers, and collection locations. Bootstrap values are shown at branches (if >50%).

Fig. 2. *Codium simulans* from Bermuda. (a) Habit of a tight, dichotomous young plant, *CWS* 08-30-2. (b) Habit of a dichotomous mature plant, *CWS* 03-6-4. (c) Habit of an older plant with adventitious branching, *CWS/CEL* 09-18-1. (d) Truncate utricles, *CWS/CEL* 10-18-7. (e) Elongated clavate utricles, *CWS* 03-6-4.

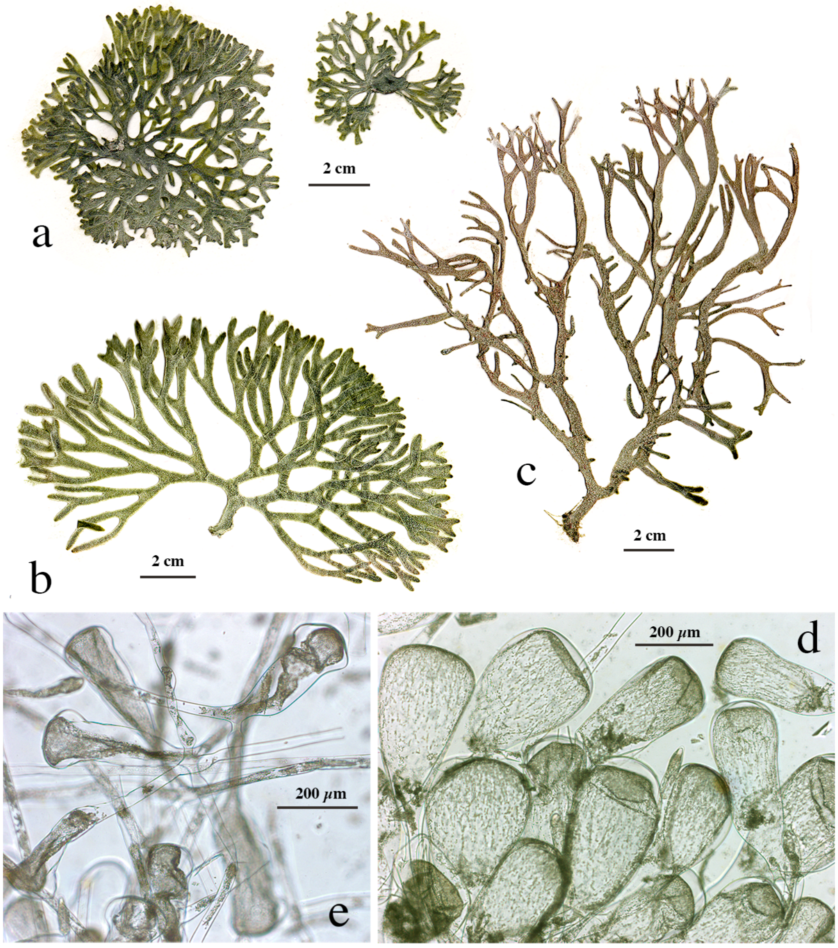
SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Collection details for *Codium* isolates included in the molecular analyses of this study with newly generated GenBank accession numbers in bold type.

Table S2. Matrix of pairwise distances (p-distance) of tufA sequences. Boxes correspond to the clusters in Fig. 1, and cluster numbers are indicated in front of the specimen identifications.

Table S3. Atlantic *Codium* specimens observed in the study.



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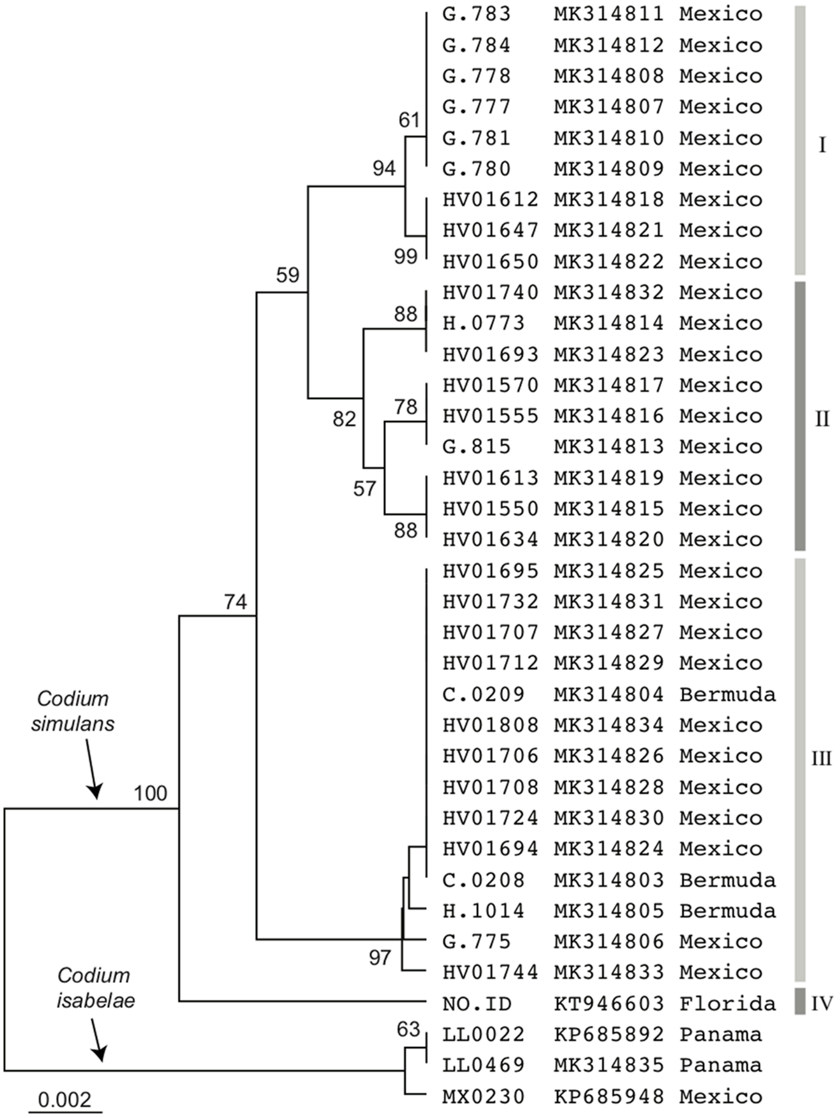

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