DNA sequencing resolves species of *Spongites* (Corallinales, Rhodophyta) in the Northeast Pacific and South Africa, including *S. agulhensis* sp. nov.

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ABSTRACT: DNA sequence data from a 296 base pair variable region of the plastid encoded *rbcl* gene was obtained from 19th century type material of *Spongites decipiens* and of *Lithophyllum tumidum* (= *Pseudolithophyllum neofarlowii*) and matched to field-collected material, confirming the application of these specific epithets in the northeast Pacific. Phylogenetic analyses of separate and concatenated *rbcl* and *psba* gene sequences show that both species belong in *Spongites*. Based on DNA sequences, the distribution of *S. decipiens* is confirmed from Haida Gwaii, British Columbia, Canada, south to its type locality at San Pedro, Los Angeles County, California, whereas, *Spongites tumidum* is distributed from near Sitka, Alaska, to Monterey County, California. Sequence data from *S. decipiens* and South African specimens called *Spongites yendoi* confirm anatomical studies that these two species are distinct but that a previously undescribed, cryptic species, *Spongites agulhensis*, is also present in South Africa. Anatomically and morphologically *S. agulhensis* is very similar to both northeast Pacific *S. decipiens* and South African *S. yendoi*, differing from the former by a single anatomical character and from the latter by two anatomical characters. Anatomy, ecology and distributions are useful in separating the South African species of *Spongites*, as well as the northeast Pacific species. Sequence divergence values align with biogeographic patterns and not with anatomical similarities for these *Spongites* species. We question the practice of placing into synonymy geographically widely separated non-geniculate coralline algal species based solely on anatomical features that likely have resulted from convergent evolution.

KEY WORDS: *psba*, *rbcl*, *Spongites decipiens*, *Spongites tumidum*, *Spongites yendoi*, Sequencing type material

INTRODUCTION

Molecular sequencing of coralline algae is revolutionizing our understanding of this important and ubiquitous group of benthic marine rhodophytes at all taxonomic ranks. Significant findings already have resulted in revisions at higher taxonomic ranks with the family Sporolithaceae elevated to ordinal rank (as Sporolithiales, Le Gall et al. 2009) and, in the family Corallinaceae, support for a previously proposed subfamily (Lithophylloideae, Bailey & Chapman 1998) and recognition of several new subfamilies (Hydrolithoideae, Neogoniolithoideae and Porolithoideae, Kato et al. 2011). At the genus and species ranks progress has been slower, owing to the difficulty of obtaining genotypes with wide geographic distributions needed to molecularly confirm morphologically and anatomically defined genera and of linking specific epithets, based on type specimens, with more recently collected field specimens (Adey et al. 2015).

In the northeast Pacific, we have begun defining genera molecularly as well as anatomically/morphologically by sequencing genotypes and related species (Gabrielson et al. 2011; Martone et al. 2012) and confirming the application of specific epithets by comparing DNA sequences of type and recently collected specimens (Hind et al. 2014a, b). Species of *Spongites* Kützing present an ideal test of this latter methodology, since historically morpho-anatomically similar specimens from different localities worldwide were identified as belonging to the same species. Thus, for example, *Spongites decipiens* (Foslie) Y.M. Chamberlain (type locality San Pedro, Los Angeles County, California) was reported from southern South America (as *Lithophyllum decipiens* (Foslie) Foslie – Foslie 1900c and as *Hydrolithon decipiens* (Foslie) W.H. Adey – Mendoza & Cabioch 1986), from Juan Fernandez Island (as *L. decipiens* – Levring 1943), from Japan (as *L. decipiens* – Masaki 1968), from India (as *L. decipiens* – Krishnamurthy & Jayagopal 1985), from eastern Russia (Perestenko 1996), from the Gulf of California (as *L. decipiens* – Dawson 1944) and from south of the type locality along the Pacific coast of both Mexico and Panama (as *L. decipiens* – Dawson 1960).

Similarly, *Spongites yendoi* (Foslie) Y.M. Chamberlain (type locality: Shimoda Harbor, Shizuoka Prefecture, Japan) was first reported from Japan and Monterey, California (as *Goniolithon yendoi* Foslie 1900a) and later from Indonesia (as *Lithophyllum yendoi* (Foslie) Foslie – Foslie 1900c), South Africa (Chamberlain 1993), Pacific Mexico (Chamberlain 1993), southern Australia (Penrose 1996), Korea (Lee & Kang 2001), New Zealand (Harvey et al. 2005) and Atlantic Mexico (Mendoza-Gonzalez et al. 2007). Moreover, throughout their histories *Spongites decipiens* and *S. yendoi* were thought to possibly be conspecific (Foslie 1901a, 1904, 1906, 1907; Dawson 1960; Masaki 1968) until Chamberlain (1993), comparing type specimens, showed that *S. decipiens* has a dimerous thallus construction, whereas *S. yendoi* is apparently uniseriate.
monomerous. Herein we present DNA sequence data confirming that *S. decipiens* is a distinct species, that some specimens from South Africa morphologically similar to *S. yendoi* and morphologically and anatomically similar to northeast Pacific *S. decipiens* are a new species, and that northeast Pacific *Lithophyllum tumidum* Foslie (=*Pseudolithophyllum neofarlowii* (Setchell & L.R. Mason) W.H. Adey) also belongs in *Spongites*. Furthermore, sequence divergence values for species morphologically and anatomically distinct but whose distribution ranges overlap are genetically more similar than morphologically and anatomically similar species from different parts of the world. The implications of these results are discussed for *Spongites* species reported to be widely geographically distributed and disjunct either within an ocean basin or across ocean basins based on morpho-anatomical characters.

**MATERIAL AND METHODS**

Freshly collected specimens were removed from the bedrock with a geology hammer and cold chisel; for specimens on pebbles, cobble or gastropod shells the substratum along with the coralline was removed. These specimens were air dried and/or placed in silica gel and/or were initially fixed in neutralised 10% commercial formalin seawater (4% formaldehyde) and stored in a 70% ethanol:10% glycerol:20% distilled water solution. Specimens were examined from the following herbaria: TRH, UC and UWC; voucher specimens were deposited in either L, NCU, UNB or UWC; herbarium acronyms follow Thiers (2015, continuously updated).

Specimens for microscopy were prepared following Maneveldt & van der Merwe (2012). For scanning electron microscopy (SEM), air-dried material was fractured using forceps, diagonal cutters or a small hammer and cold chisel. Fractured pieces were mounted on stubs, using adhesive tabs (Agar Scientific Ltd., Stansted, Essex, UK), stored in a desiccator for at least 24 h prior to examination, coated with carbon in a single cycle for 3 s in an Emitech K950X Carbon Evaporator, and examined with a Hitachi X650 scanning electron microscope at an accelerating voltage of 25 kV.

For light microscopy, formalin preserved specimens were first decalcified in 10% nitric acid. Thereafter, specimens were immersed in 70%, 90% and 100% ethanol solutions for a minimum of 60 min each in order to displace any water and acid in the specimens. Thereafter, each specimen was removed from the 100% ethanol solution and allowed to air dry for no more than a few seconds. Specimens were then immersed in Leica Historesin filtration medium for several hours until completely infiltrated. A hardening solution was added to the infiltration medium, and the specimens were orientated in this final solution until set. Gelling of the hardener usually occurred within 30–45 min; for more rapid hardening, specimens were placed immediately in an oven at 60°C for approximately 10–20 min.

Specimens were sectioned at 6–8 μm thickness using a Bright 5030 microtome. Sequential sections were removed from the microtome blade using a fine sable hair brush and transferred to a slide covered with distilled water. In this way, multiple sections were orientated on a single slide. Slides were then left to air dry for at least 24 h so that sections could stick. These slides were stained with toluidine blue (0.25 g borax 100 ml–1 and 0.06 g toluidine blue 100 ml–1), again left to air dry, and later covered with cover slips using DPX Mountant for microscopy (BDH Laboratory Supplies, East Grinstead, West Sussex, UK).

In cell measurements, length is the distance between primary pit connections, and diameter the maximum width of the cell lumen at right angles to this. Conceptacle measurements follow Adey & Adey (1973); thallus anatomical terminology follows Chamberlain (1990); and morphological (growth forms) terminology follows Woelkerling et al. (1993).

Specimens that were sequenced are listed in Table S1. Specimen preparation, extraction amplification and sequencing for rbcL followed Gabrielson et al. (2011) and for psbA followed Adey et al. (2015). The forward rbcL primer used for amplifying DNA from type specimens is given in Sissini et al. (2014).

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rbcL and psbA sequences of two species said to belong to *Spongites*, *S. decipiens* from the northeast Pacific and *S. yendoi* from South Africa, were analysed along with sequences of South African specimens initially identified as *S. yendoi* as well as specimens of *Lithophyllum tumidum* (=*Pseudolithophyllum neofarlowii*) from the northeast Pacific. Species of three genera belonging to subfamily Lithophyllidoideae were used as the outgroup (Fig. 1; Table S1) based on the sister taxon relationship of this subfamily to *Spongites* (Kato et al. 2011). The rbcL sequences for the phylogenetic
analyses were 1387 bp long; psbA sequences were 851 bp long. The two loci were combined into a single concatenated dataset with two data partitions (rbcl and psbA). Maximum likelihood (ML) analyses were performed using the default parameters of RAxML BlackBox (Stamatakis et al. 2008) with a mixed partition model until 1000 bootstrap replications were amassed.

RESULTS

In the absence of sequences from the generitype of Spongites, Spongites fruticulosa Kützing, specimens from the northeast Pacific confirmed by sequencing type material to belong to Spongites yendoi, all resolved as a single genus (Fig. 1) but as four distinct species with interspecific sequence divergence values ranging from 2.9% to 7.6% for psbA and from 5.0% to 9.8% for rbcl (Table 1). Each of these species is treated below. Of the three species of Lithophyloideae (the outgroup), two (Lithothrix aspergilllum J.E. Gray and Amphiroa zonata Yendo) were represented by sequenced topotype material (Gabrielson et al. 2011) and one (Lithophyllum incurustans Phillipi) by sequenced type material (Hernandez-Kantun et al. 2015).

**Spongites yendoi** (Foslie) Y.M. Chamberlain, 1993: 113

Figs 2–11

**BASIONYM:** Lithothamnion decipiens Foslie, 1897: 20

**LECTOTYPE:** TRH (A2-97), W.A. Setchell 1482, leg. 5.xii.1895 (Fig. 2).

**ISOLECTOTYPE:** UC 736372; thallus on fragment of the same stone as the lectotype.

**TYPE LOCALITY:** San Pedro, Los Angeles, California.

**HOMOTYPIC SYNONYMS:**

Lithophyllum decipiens (Foslie) Foslie, 1900b: 19 (see also Foslie 1900a: 21)

Hydrolithon decipiens (Foslie) W.H. Adey, 1970: 11

Pseudolithophyllum decipiens (Foslie) Steneck & R.T. Paine, 1986: 237

**ETYMOLOGY:** decipiens is Latin for deceiving (Stearn 1973). Foslie (1897) did not explain the origin of the epithet but presumably it makes reference to this species closely resembling another.

**DNA SEQUENCES:** The rbcl sequences varying in length from 296–1387 base pairs (bp) were obtained from six specimens, one (1387 bp) from Crescent City, Del Norte County, California; one (1387 bp) from Pacific Grove, Monterey County, California; three (702–1387 bp) from Shell Beach, San Luis Obispo County, California, and one (296 bp) from the isolectotype specimen (UC 736372) from San Pedro, Los Angeles County, California (Table S1). All sequences were identical over their comparable lengths except for the isolectotype that had one single nucleotide polymorphism (SNP). The psbA sequences (851 bp) were obtained for four of the same specimens for which rbcl sequences were obtained, one from Crescent City, one from Pacific Grove, and two from Shell Beach, California, and all of these sequences were identical to each other and to two sequences provided by Dr Gary Saunders from northern British Columbia, Canada (Table S1).

**HABIT:** Thalli were non-geniculate, encrusting with smooth surfaces and epithecid on primary bedrock or cobble, where they were firmly adherent and conformed to the substratum. Individual thalli were discernible from one another and did not appear to fuse together with abutting margins clearly visible under a dissecting microscope (Fig. 3).

**VEGETATIVE ANATOMY:** Thalli were dorsiventrally organised and dimerous, and haustoria were absent (Fig. 4). The single basal layer comprised cells that varied greatly in shape and size in radial and tangential view (along the filament) from squarish to rectangular to shoe-shaped (Figs. 4, 5); whereas, in tangential view (across the filament) basal layer cells were rectangular to palisade-like (Fig. 6). Fusions between basal layer cells of contiguous filaments were abundant in tangential view and frequently occupied much of the adjoining cell wall (Fig. 6). Basal cells gave rise to erect filaments that made up the bulk of the thallus. The first one or two cells appearing from basal layer cells were often large and dichotomously divided dichotomously to produce two rows of filaments that combined occupied more or less the same volume as the basal cells from which they were derived (Fig. 4). Where these cells were smaller, neither divided dichotomously (Fig. 5). Dichotomously dividing erect cells were irregularly square to rectangular with rounded corners (Fig. 4); non-dichotomously dividing erect cells were oval to square to rectangular with rounded corners, often forming bead-like filaments (Fig. 5). Fusions between cells of contiguous erect filaments were abundant and frequently occupied most of the adjoining cell wall. Secondary pit connections were not observed. Subepithallial initials were oval to square to rectangular with rounded corners and had cell lumens that stained no differently to cells of erect filaments (Fig. 7). Epithallial cells varied in shape from rounded to oval to domed, were dark-staining and occurred mostly in a single layer but may be up to three cell layers when shedding (Fig. 7). Individual bottle-shaped trichocytes (Fig. 8) were occasionally observed at the thallus surface and did not become buried in the thallus.

**REPRODUCTIVE ANATOMY:** Thalli with neither carpogonial nor carposporangial conceptacles were observed; thus this species likely was dioecious. Spermatangial (male) conceptacles were domed, raised above or occasionally flush with the surrounding thallus surface, and their chambers were rounded to transversely elliptical (Fig. 9). No conceptacle primordia were observed but, based on the orientation of the basal roof filaments (parallel to the roof), it appeared that the roof was formed from filaments that arose peripheral to the fertile area, the terminal initials of which were more elongated than their inward derivatives. These cells projected into the pore canal as papillae and were orientated more or less parallel to the conceptacle roof surface in fully developed conceptacles (Fig. 9). Unbranched (simple) spermatangial filaments developed only across the floor of the male conceptacle (Fig. 9). Senescent male conceptacles appeared to be shed, as no buried conceptacles were observed.

Tetrarosporangial thalli were morphologically similar to male thalli but their conceptacles were larger. Their
conceptacles were uniporate, domed, mostly raised above the surrounding thallus surface but occasionally were sunken with raised roofs (Figs 10, 11). Their chambers were transversely elliptical to rounded with a roof 3–6 (mostly 4) cells thick that was formed from filaments that arose peripheral to the fertile area, the terminal initials of which were more elongated than the surrounding cells (Fig. 10). These cells projected into the pore canal as papillae and were orientated more or less parallel or at a sharp angle to the conceptacle roof surface in fully developed conceptacles (Fig. 11). Throughout early development, a protective layer of epithallial cells surrounded the conceptacle primordium (Fig. 10); this protective layer was shed once the pore canal was fully developed. Mature conceptacles had floors that were sunken 12–16 cells (including the epithallial cell) below the surface. Zonately arranged tetrasporangia developed across the conceptacle floor; a central columella was absent (Fig. 11). Senescent tetrasporangial conceptacles appeared to be shed, as no buried conceptacles were observed. See Tables 2 and 3 for a summary of the morphological and anatomical features.

**REPRESENTATIVE SPECIMENS EXAMINED:** NCU 591663, NCU 596899, NCU 596901, NCU 596902 (see Table S1 for specimen data).

**DISTRIBUTION:** By DNA sequence, confirmed from northernmost California, Del Norte County, south to San Pedro, Los Angeles County, California with a disjunct population in Haida Gwaii, British Columbia, Canada.

*Spongites yendoi* (Foslie) Y.M. Chamberlain, 1993: 13

**BASIONYM:** *Goniolithon yendoi* Foslie 1900a: 25–26

**LECTOTYPE:** TRH (A1-53), Yendo 66

**TYPE LOCALITY:** Shimoda Harbor (Shizuoka Prefecture), Japan

**HOMOTYPIC SYNONYMS:**

*Lithophyllum yendoi* (Foslie) Foslie 1900b: 20

*Pseudolithophyllum yendoi* (Foslie) W.H. Adey, 1970: 14

**ETYMOLOGY:** yendoi named after its collector, K. Yendo.

**DNA SEQUENCES:** The *rbcL* (1387 bp) and *psbA* (851 bp) sequences were obtained from two specimens (Table S1). The *rbcL* sequences were identical to each other, as were the *psbA* sequences. These DNA sequences showed that *Spongites yendoi* from South Africa was a unique species compared with all other named *Spongites* specimens sequenced to date, including the Broom *et al.* (2008) specimen from New Zealand called *S. yendoi* (Table 1).

**HABIT:** Thalli were non-geniculate, encrusting and firmly adherent to substrate, epiphytic on the primary bedrock and epizoic on live molluscs, smooth to lumpy to knobly with pillar-like protuberances to 3 mm tall. Individual thalli with margins entire, thick and white-edged but thalli frequently fusing and covering large expanses in the low-intertidal but also were present in the mid-intertidal and shallow subtidal (see also Chamberlain 1993; Maneveldt & Keats 2008).

**VEGETATIVE AND REPRODUCTIVE ANATOMY:** The observations of Chamberlain (1993) are summarised in Table 3. The observations of Masaki (1968) on Japanese material are not included in Table 3, as we have sequenced only material from South Africa.

**DISTRIBUTION:** Reported to occur all along the coast of South Africa but more common along the south and southwest coasts (Maneveldt *et al.* 2008). Confirmed by DNA sequence data from the Western Cape Province (Table S1) but possibly more widespread in South Africa.

*Spongites agulhensis* Maneveldt, E. van der Merwe & P.W. Gabrielson *sp. nov.*

**Figs** 12–24

**HOLOTYPE:** L 0820786, 21.x.2011, leg. *G.W. Maneveldt*, epiphytic on shale platform in the high intertidal zone, Fig. 12.

**ISOTYPE:** UWC 11/53.

**TYPE LOCALITY:** South Africa. Western Cape Province, Cape Agulhas: L’Agulhas, Stinkbaai (34°49’26.26”S; 20°01’0.69”E).

**ETYMOLOGY:** *agulhensis* making reference to the type locality at L’Agulhas, Cape Agulhas.

**DIAGNOSIS:** Uniformly encrusting (smooth) thalli that do not become secondarily thick and discoid with orbicular protrusions, nor warty, nor wrinkled; individuals usually easily discernible, not coalescing (fusing); colour of living thalli brownish-pink; thallus construction dimerous, with cells of basal layer characteristically large and book-shaped; central columella present in tetrasporangial conceptacles; *rbcl* and *psbA* sequences unique.

**DNA SEQUENCES:** The *rbcl* gene sequences (1387 bp) from two specimens, one toptype, the other paratype (Table 1) were identical to each other, as were *psbA* sequences (851 bp) obtained from the same two specimens. These DNA sequences showed that *Spongites*...
*Spongites agulhensis* was different from all other named species of *Spongites* sequenced to date (Fig. 1; Table 1).

**Habit:** Thalli were encrusting (smooth), firmly adherent, and brownish-pink when freshly collected (Figs 13, 14). Individual thalli were discernible, not fusing together, on average 10 mm in diameter and rarely more than 20 mm with abutting margins clearly visible (Figs 12, 13). Thalli were epiphytic on shale or quartzitic sandstone platforms in high and mid-intertidal zones (Figs 13, 14).

**Vegetative Anatomy:** Thalli were dorsiventrally organised and dimerous, and haustoria were absent (Fig. 15). The single basal layer comprised cells that were irregularly square and had the appearance of an upright book (Fig. 15). In radial section ('cover view' i.e. along the filament) cells were non-palisade (Fig. 16); whereas, in tangential section ('spine view' i.e. across the filaments) they appeared palisade-like (Fig. 17). In tangential view fusions between cells of contiguous basal filaments were abundant and frequently occurred most of the adjoining cell wall. Basal cells gave rise to erect filaments that comprised the bulk of the thallus (Fig. 15). Erect filaments consisted of cells that were square to rectangular with rounded corners (Figs 15–17). Fusions between cells of contiguous erect filaments were abundant and frequently also occupied most of the adjoining cell wall (Fig. 17). Secondary pit connections were not observed in either basal or erect filaments. Subependial initials were square to rectangular with angular corners and cell lumens that stained differently to cells of an upright book (Fig. 15). In radial section ('cover view' i.e. along the filament) cells were non-palisade (Fig. 16); whereas, in tangential section ('spine view' i.e. across the filaments) they appeared palisade-like (Fig. 17). In tangential view fusions between cells of contiguous basal filaments were abundant and frequently occupied most of the adjoining cell wall (Fig. 17). As they divided, the newly forming filaments curved inward to form the roof and pore, with the terminal initials along the pore canal (Fig. 22). Roof formation appeared similar to that of male conceptacles. A discontinuous central fusion cell was present that was free from and raised above the chamber floor (Fig. 22). Arising peripherally from the fusion cell were gonimoblast filaments that were 4–7 cells long, each including a terminal carposporangium (Fig. 22).

The remains of unfertilised carpogonia persisted across the dorsal surface of the fusion cell (Fig. 22). Senescent female conceptacles appeared to be shed from the thallus surface, as no buried conceptacles were observed.

Tetrasporangial thalli were morphologically similar to gametangial thalli. Tetrasporangial conceptacles were uniporate, low-domed and raised above the surrounding thallus surface (Fig. 23). Their chambers were transversely elliptical to flattened, with the roof 4–8 cells thick. Similar to spermatangial conceptacles, the roof was formed from filaments that arose peripheral to the fertile area, the terminal initials of which were more elongate than the surrounding cells (Fig. 24). As they divided, the newly forming filaments curved inward to form the roof and pore, with the terminal initials along the pore canal becoming papillate (Fig. 24). These cells projected into the pore canal and were orientated more or less parallel or at a sharp angle to the conceptacle roof surface in fully developed conceptacles. Throughout the early development a protective layer of epithallial cells surrounded the conceptacle primordium; this protective layer was shed once the pore canal was nearly fully developed. Mature conceptacles had floors that were sunken 10–15 cells (including the epithallial cell) below the surrounding thallus surface. Zonately arranged tetrasporangia at maturity were peripherally arranged around an extensive central columella (Fig. 23). Only the lower cells of the central columella appeared to be calcified, often giving the conceptacle chamber a dumbbell-shaped appearance. Senescent tetrasporangial conceptacles appeared to be shed from the thallus surface, as no buried conceptacles were observed. See Tables 3 and S2 for a summary of the morphological and anatomical features.

**Representative Specimens Examined:** Six samples represented our entire collection for this taxon: South Africa: Western Cape Province: Cape Agulhas, L’Agulhas, Stinkbaai, L 0820786 (holotype); UWC 11/36 (isotype); UWC 10/142, 34°49’26.44”S; 20°01’1.61”E, 16.vi.2010, G. W. Maneveldt & E. van der Merwe, epiphytic on shale platform, high intertidal; UWC 11/23, 34°49’26.24”S; 20°01’0.74”E (Table S1); Struisbaai, UWC 11/24, 34°48’49.91”S; 20°03’2.74”E (Table S1); UWC 11/55, 34°48’36.85”S; 20°03’26.49”E, 21.x.2011, G. W. Maneveldt, epiphytic on quartzitic sandstone platforms in the high to upper mid-intertidal.  

**Distribution:** Known only from South Africa; Western Cape Province, Struisbaai westward to L’Agulhas (Cape Agulhas). The species has a remarkably limited distribution.
Table 2. Comparison of historical data for *S. decipiens* and *S. tumidum*. Mason’s (1953) data on *S. decipiens* is not included, as her concept of this species included at least two other species.

<table>
<thead>
<tr>
<th>Character</th>
<th>Foslie (1897, as <em>Lithophyllum decipiens</em>)</th>
<th>Steneck &amp; Paine (1986, as <em>Pseudolithophyllum decipiens</em>)</th>
<th>Chamberlain (1993, as <em>Spongites decipiens</em>)</th>
<th>Foslie (1901, as <em>Lithophyllum neofarlowii</em>)</th>
<th>Mason (1953, as <em>Lithophyllum neofarlowii</em>)</th>
<th>Steneck &amp; Paine (1986, as <em>Pseudolithophyllum neofarlowii</em>)</th>
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<tr>
<td>Substratum</td>
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<td>epilithic</td>
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<td>encrusting with smooth surfaces to 250 µm dimerous</td>
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<td>1 mm to 300 (500) µm monomerous</td>
<td>to 2 mm monomerous and dimerous</td>
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<td>Perithallial cell length × width</td>
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<td>4–13 × 4–10</td>
<td>5–10–(12) × 4–7–(9)</td>
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<td>5–15 × 5–12</td>
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<td>Spermatangial conceptacles</td>
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<td>156 ± 23</td>
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<td>90–100</td>
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<td>(external diameter) (µm)</td>
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<td></td>
<td>to 300</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetrasporangial conceptacle</td>
<td>raised (mostly) to slightly sunken</td>
<td>flush to slightly raised</td>
<td>flush to slightly raised to slightly sunken</td>
<td>raised</td>
<td></td>
<td></td>
</tr>
<tr>
<td>elevation</td>
<td>200</td>
<td>156 ± 23</td>
<td>220</td>
<td>sunken</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetrasporangial conceptacle</td>
<td></td>
<td>to 300</td>
<td></td>
<td>raised</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(external diameter) (µm)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tetrasporangia length × width</td>
<td>ND</td>
<td>55–75 × 30–50</td>
<td>90–100 × 50–60</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Old conceptacles buried/shed</td>
<td>ND</td>
<td>buried</td>
<td>90–100 × 50–60</td>
<td>shed (see plate 40, fig. b)</td>
<td>ND</td>
<td></td>
</tr>
</tbody>
</table>

1 Earlier researchers such as Foslie (1897, 1901a), Mason (1953) and Steneck & Paine (1986) did not recognise monomerous vs dimerous constructions. We have applied these terms based on their anatomical descriptions.
2 The holotype and isotype of *S. decipiens* also show a dimerous construction with large basal cells Chamberlain (1993).
3 ND, no data.
4 Mason (1953) states that hypothallial cells are multilayered (monomerous) but her plate 40, fig. C clearly shows dimerous construction.
5 Mason (1953) reports immersed (sunken) sporangial conceptacles probably in reference to conceptacle chambers because plate 40, fig. C shows flush to slightly raised conceptacle roofs.
<table>
<thead>
<tr>
<th>Character</th>
<th>S. agulhensis (This study, SA)</th>
<th>S. decipiens (This study, USA)</th>
<th>S. hyperellus (Penrose 1996, AUS)</th>
<th>S. impar (Chamberlain 1994, SA)</th>
<th>S. tumidum (This study, USA)</th>
<th>S. tunicatus (Penrose 1996, AUS)</th>
<th>S. yendoi (Chamberlain 1993, SA)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Substrate</td>
<td>epilithic</td>
<td>epilithic, epizoic</td>
<td>epilithic, epizoic</td>
<td>epilithic, epizoic</td>
<td>epilithic, epizoic</td>
<td>epilithic, epizoic</td>
<td>epilithic, epizoic</td>
</tr>
<tr>
<td>Habitat</td>
<td>high intertidal</td>
<td>mid-low intertidal</td>
<td>low intertidal</td>
<td>intertidal</td>
<td>mid-to high, rarely</td>
<td>intertidal</td>
<td>encrusting, smooth to</td>
</tr>
<tr>
<td>Growth form</td>
<td>encrusting, smooth</td>
<td>encrusting, smooth</td>
<td>encrusting to fruticose</td>
<td>encrusting, becoming cresting</td>
<td>encrusting to warty</td>
<td>encrusting to warty</td>
<td>encrusting, smooth</td>
</tr>
<tr>
<td>Habit</td>
<td>no fusion of individual thalli</td>
<td>dimerous</td>
<td>dimerous</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>encrusting, smooth</td>
</tr>
<tr>
<td>Thallus construction</td>
<td>dimerous</td>
<td>dimerous</td>
<td>monomerous</td>
<td>monomerous</td>
<td>dimerous</td>
<td>dimerous</td>
<td>monomerous</td>
</tr>
<tr>
<td>Trichocyte arrangement</td>
<td>none observed</td>
<td>solitary</td>
<td>none observed</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>solitary to paired</td>
</tr>
<tr>
<td>No. of epithallial cell layers</td>
<td>1–3</td>
<td>1–3 (mostly 1)</td>
<td>1–7</td>
<td>6</td>
<td>1–4 (mostly 1–2)</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Shape of the fusion cell</td>
<td>narrow, thick and discontinuous</td>
<td>ND</td>
<td>wide, thin</td>
<td>NA</td>
<td>ND</td>
<td>NA</td>
<td>narrow, thick and continuous</td>
</tr>
<tr>
<td>Columella (present/absent)</td>
<td>absent</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td></td>
</tr>
<tr>
<td>Distribution of tetra/bisporangia</td>
<td>peripheral</td>
<td>across the conceptacle floor</td>
<td>peripheral and across* the</td>
<td>peripheral</td>
<td>peripheral</td>
<td>peripheral across the conceptacle floor</td>
<td></td>
</tr>
</tbody>
</table>

1 NA, not applicable; ND, no data.
2 Womersley (1996: 274, Fig. 125C) shows peripherally arranged tetrasporangia. However, in the description Womersley (1996: 275) reports tetrasporangia to be distributed across the conceptacle floor.
of only about 10 km, despite extensive collections either side of the recorded distribution.

*Spongites tumidum* (Foslie) K.A. Miller, P.W. Gabrielson, Miklasz, E. van der Merwe & Maneveldt comb. nov.

**BASIONYM:** *Lithophyllum tumidum* Foslie 1900 (9) [1901b]: 18

**LECTOTYPE:** TRH (A3-138), unnumbered, May 1885, W. G. Farlow

**ISOLECTOTYPE:** UC 341301

**TYPE LOCALITY:** Monterey, Monterey County, California

**ETYMOLOGY:** *tumidum* Latin meaning swollen.

**DNA SEQUENCES:** The *rbcL* sequences from seven specimens were obtained: one (1387 bp) from Tatoosh Island, Washington; one (702 bp) from San Juan Island, Washington; one (702 bp) from Lone Ranch Beach, Curry County, Oregon and four (296, 702 and 1387 bp) from Monterey County, California, including the lectotype (TRH A3-138) and isolectotype (UC 341301). Specimens from Del Norte...
County, California, and northward had two or three (Tatoosh Island, Washington specimen) SNP compared with Monterey County, California, material (all identical), representing an intraspecific species sequence divergence of 0.14–0.22%.

The psbA sequences were obtained from the same four field-collected specimens from which rbcL sequences were obtained, as well as from one specimen from Three Entrance Bay (near Sitka), Alaska, and nine provided by Dr Gary Saunders from northern and southern British Columbia, Canada (Table S1). All were identical.

HABIT: Thalli were encrusting to warty (Figs 25, 26), typically adherent to the substratum (but high intertidal specimens were friable and easily removed) and 1–2 mm thick with complex, irregular and variable protuberances to 1–2 mm tall and 1–4 mm diameter. Living thalli were blue–purple to pink in damp habitats, becoming chalky-white when desiccated, and this varied seasonally, with white, desiccated thalli becoming pigmented. Individual thalli were indistinguishable from one another and fused together with abutting margins not clearly visible even under a dissecting microscope. Mostly epilithic, rarely epizoic on live chitons; common in upper intertidal shaded habitats, uncommon in tidepools and in mid- to low-intertidal habitats. This species was intensively grazed by herbivores such as limpets and snails, and radular teeth marks were often observed on thallus surfaces.

VEGETATIVE ANATOMY: Thalli were dorsiventrally organized and dimerous, and haustoria were absent (Figs 27, 28). The single basal layer comprised cells that varied greatly in shape and size in radial view (along the filament) from oval to squarish (Fig. 27); whereas, in tangential view (across the filament) cells of the basal layer were

Figs 15–18. Vegetative anatomy of S. agulhensis.
Fig. 15. Dimerous thallus construction evident in side by side radial view, with large, irregularly square, non-palisade cells (arrow), and tangential view, with palisade-like cells (arrowhead), due to change in direction of growing margin (UWC 11/24). Scale bar = 140 μm.
Fig. 16. Vertical section of leading edge in radial view showing terminal marginal initial (m) and single basal cell (b) layer. Large, irregularly square, non-palisade basal (b) cells linked by primary pit connections (white arrowheads) and giving rise to erect filaments dorsally (black arrowheads). Cells (asterisk) of erect filaments distal to basal cells each divide dichotomously to produce two rows of filaments. Note a cell fusion (f) between cells of two adjoining erect filaments (UWC 11/23). Scale bar = 20 μm.
Fig. 17. Vertical section of inner thallus in tangential view showing basal cell (b) layer. Seen in ‘spine view’ cells of basal layer appear palisade-like. Note primary pit connections (black arrowheads) between adjoining basal and erect cells of same corresponding filaments and cell fusions (f) between cells of adjoining erect filaments (UWC 11/23). Scale bar = 20 μm.
Fig. 18. Vertical section of outer thallus showing several layers of epithallial cells (arrowheads) subtended by a layer of subepithalial initials (arrow) whose cell lumens stain differently from cell lumens of more proximal cells (UWC 11/24). Scale bar = 20 μm.
rectangular to palisade-like (Fig. 28). Fusions between cells of contiguous basal filaments were abundant in tangential view and frequently occupied much of the adjoining cell wall (Fig. 28). The first one or two cells of erect filaments arising from basal cells were comparatively large (Fig. 27), and either one of these but not both, divided dichotomously to produce two rows of filaments that combined occupied more or less the same volume as the basal cells from which they are derived. This dichotomous branching did not occur when cells arising from the basal layer were comparatively small. Dichotomously dividing erect cells were irregularly squarish to rectangular with rounded corners, as were cells of erect filaments that often formed bead-like filaments (Figs 27–30). Fusions between cells of contiguous erect filaments were abundant and frequently also occupied most of the adjoining cell wall. Secondary pit connections were not observed between cells of basal and erect filaments. Subepithelial initials were oval to square to rectangular with rounded corners and had cell lumens that stained no differently to cells of erect filaments (Figs 29, 30). Epithelial cells occurred in mostly 1–2 layers and varied in shape from oval to domed to flattened to triangular (Figs 29, 30). When undergoing shedding or when subepithelial initials were actively dividing, up to 4 layers of epithelial cells were present (Fig. 30) or they were absent, presumably due to shedding or grazing by herbivores.

REPRODUCTIVE ANATOMY: Gametangial thalli presumably were dioecious, although female conceptacles were not found. Spermatangial (male) conceptacles were flush with the surrounding thallus surface (Figs 31, 33). Their chambers were transversely elliptical to flattened, with the roof nearly twice as thick along the pore canal (Fig. 35). The roof was formed from filaments that arose peripheral to the fertile area, the terminal initials of which are more elongated than their inward derivatives (Figs 33, 35). In fully developed conceptacles, these cells projected into the pore canal as papillae and were orientated more or less parallel or at a sharp angle to the conceptacle roof surface (Fig. 38). Throughout early development a protective layer of epithelial cells surrounded the conceptacle primordium (Figs 32, 34, 36); this protective layer was shed once the pore canal and tetrads were fully developed. Throughout development of the immature tetrads, a prominent columella of sterile filaments formed at the centre of the conceptacle chamber (Figs 34, 36). This central columella appeared to be weakly calcified, as with maturity it disintegrated to form a low mound with zonately divided tetrads arranged around its periphery (Figs 37, 38). Mature conceptacles have floors that were sunken 13–21 cells (including the epithelial cell) below the surrounding thallus surface (Fig. 38). Senescent tetrads appeared to be shed from the thallus surface, as no buried conceptacles were observed. Confluent thalli bearing tetrads and spermatangial (male) conceptacles were occasionally observed (Fig. 37). See Tables 2, 3 and S2 for a summary of the morphological and anatomical features.

REPRESENTATIVE SPECIMENS EXAMINED: NCU 588179, NCU 591459, NCU 601317, NCU 600394, NCU 591648, TRH, UC (see Table S1 for specimen data).

DISTRIBUTION: Confirmed by DNA sequences from near Sitka (southeast), Alaska to Monterey County, California. Records from farther south in the northeast Pacific (Mason 1953; Dawson 1960) and from Japan (Yoshida et al. 1985; Baba 2000) have not been confirmed by DNA sequences.

DISCUSSION

Placement in Spongites

It is the generitype species that defines a genus, and to that species all others placed in the genus need to be related. In the absence of some diagnostic anatomical characters and lacking any molecular data about Spongites fruticulosa (type species) based on type or topotype material, it is uncertain but likely that Spongites decipiens, Spongites agulhensis, Spongites timidum and South African Spongites yendoi belong in this genus. We kindly were sent field-collected material identified as S. fruticulosa by Dr Daniella Basso but were unable to obtain any useful DNA sequences that potentially could be
compared with sequences from type material. Kato et al. (2011), using a combination of small subunit and psbA sequences, split from the Mastophoroideae the following clades: Neogoniolithoideae, Porolithoideae, Hydro lithoideae, Spongites and Pneophyllum. The last two taxa, however, were not represented by their generitype species, and therefore, Kato et al. (2011) did not recognise these clades as subfamilies. Kato et al. (2011) characterized Spongites by the following combination of characters, some of which first had been proposed by Penrose & Woelkerling (1992): (1) absence of genicula; (2) presence of cell fusions and absence of secondary pit connections between cells of adjacent (contiguous) filaments; (3) absence of a ventral (basal) layer of palisade cells; (4) absence of trichocytes in tightly packed horizontal fields without vegetative cells between individual trichocytes; (5) uniporate, Type 1 (in which the roof development occurs only from filaments peripheral to the fertile area) tetrasporangial conceptacles; and (6) spermata ngia found only on the floor of male conceptacles. All of these features are confirmed in either type (Woelkerling 1985) or toptype (Basso & Rodondi 2006) material of S. fruticulosa except whether tetr asporangial conceptacles have Type 1 or Type 2 (in which the roof development occurs from filaments peripheral to, and interspersed amongst the developing sporangia) development, the one feature that according to Kato et al. (2011) segregates Pneophyllum from Spongites. We await both additional anatomical/morphological and molecular characterization of the generitypes of these genera based on type or toptype material to confirm placement of the species treated herein in Spongites.

Assignment of species names

The most unequivocal way to link a name of historical or recently collected specimens to type material is to compare informative DNA sequences obtained from both (Hughey et al. 2001). The first application of this methodology to coralline algae was by Gabrielson et al. (2011) for species of the geniculate coralline genus Calliarthron and more recently for species of the non-geniculate coralline genera Clathromorphum, Callilithophyllum, Neopolyplithon (Aday et al. 2015), Mesophyllum (Sissini et al. 2014) and Lithophyllum (Hernandez-Kantun et al. 2015). Using this method, we are confident that the names Spongites agulhensis, Spongites decipiens and Spongites tumidum are correctly applied to field-collected material, as partial rbcL sequences from type specimens are identical over comparable lengths to field-collected specimens and differ from all other sequenced species. Moreover, field-collected specimens that we have sequenced are from localities not far removed from the type locality for each species, except for Spongites yen doi.

Spongites decipiens

Compared with other Spongites species, interspecific sequence divergence values for Spongites decipiens of both rbcL and psbA (Table 1) indicate a clearly distinct species. The partial rbcL sequence from the isotype collected in 1896, which is part of the same stone that bears the holotype (Chamberlain 1993), as well as sequenced field-collected material, shows that S. decipiens is not restricted to the type locality as suggested by Chamberlain (1993), nor is it a warm water species only found south of Point Conception, California, as proposed by Steneck & Paine (1986). It is widely distributed in California, from the northernmost county (Del Norte) to Los Angeles County, covering some 1200 km of coastline, and has a disjunct population in Haida Gwaii, British Columbia, Canada (Table S1), about 1350 km to the north. In its morphological and anatomical features, S. decipiens closely resembles S. agulhensis from the southern coast of South Africa, differing by only a single feature, the absence of a central columella in tetr asporangial conceptacles in the former (Table 3). All other measurable anatomical features overlap between the two species (Table S2).

Recently, Saunders (2014) proposed the kelp conveyor hypothesis to explain the distribution of species widespread in California (mostly north of Point Conception) but known only as disjunct populations in Haida Gwaii, British Columbia, Canada, minimally some 1350 km to the north and not reported from any intervening localities despite intensive, recent collecting, particularly in southern British Columbia. Spongites decipiens fits this distribution pattern, reported from Los Angeles County to the northernmost county, Del Norte, California, and then only from two localities in Haida Gwaii (Table S1). Moreover, owing to its presence on small cobble and particularly on gastropod shells (Table S1), this non-geniculate coralline species could readily be transported in kelp rafts. Genetic population markers are needed to test this hypothesis for many of the taxa in Saunders (2014) list, and S. decipiens should be included.

Owing to the morphological and anatomical similarity among genetically distinct and biogeographically isolated Spongites species, all occurrences of Spongites decipiens and its reported synonyms, e.g. Lithothamnion mangini Me. Lemoine

Fig. 25. Lectotype (TRH A3-138) comprising four individual fragments. Scale bar = 20 mm.
Fig. 26. Magnified view showing confluent warty thalli of S. tumidum that are indistinguishable from one another. Scale bar = 2 mm.
Fig. 27. Vertical section of inner thallus in radial view showing oval to squarish to rectangular, non-palisade basal cells (b) giving rise to erect filaments (e) dorsally. Larger cells (asterisk) of erect filaments adjacent to cells of basal layer often divide dichotomously to produce two rows of filaments. Cell fusions (f) are common between cells of adjoining basal and erect filaments (NCU587541). Scale bar = 20 μm.
Fig. 28. Vertical section of inner thallus in tangential view showing rectangular to palisade-like cells (b) of basal layer. Note cell fusions (f) between cells of adjoining basal and erect filaments (NCU587541). Scale bar = 20 μm.
Fig. 29. Vertical section of outer thallus showing two layers of epithallial cells (e) subtended by layer of subepithallial initials (i) (NCU587541). Scale bar = 20 μm.
Fig. 30. Vertical section of outer thallus showing four layers of epithallial cells (e) subtended by layer of subepithallial initials (i) (NCU587541). Scale bar = 20 μm.
& Rosenvinge (type locality: Petermann Island, Antarctica) outside of the range confirmed by DNA sequencing need to be confirmed also by DNA sequencing. This includes material reported from the northeast Pacific south of California to Panama and the Gulf of California by Dawson (1944, 1960); southern South America by Mendoza & Cabioch (1986); Juan Fernandez Island by Levring (1943); India by Krishnamurthy & Jayagopal (1985) and eastern Russia by Perestenko (1996). It is doubtful that any report outside the northeast Pacific will be confirmed.

Spongites yendoi

DNA sequences confirm the hypothesis of Chamberlain (1993) that S. decipiens and South African Spongites yendoi are distinct species. However, we have DNA sequences only from South African specimens called S. yendoi and not from type or topotype material from Japan. Moreover, psbA sequences deposited in GenBank from 28 specimens called S. yendoi from New Zealand are not the same species as South African material called S. yendoi. We did not include the New Zealand sequences in our phylogenetic analyses, as they clearly represent a mix of species. Consequently, we find that we must question whether any of the sequenced material from either South Africa or New Zealand called S. yendoi is conspecific with type material. We refrain from changing the name of South African specimens called S. yendoi until sequence data are available from type material of S. yendoi. Specimens called S. yendoi in South Africa are one of the most commonly reported non-geniculate coralline algae in the mid-to low-intertidal zones (Maneveldt & Keats 2008; Maneveldt et al. 2008). From other currently recognized Spongites species whose type localities are in South Africa, they can be distinguished by their monomorous thallus construction (Table 3) and rbcL and psbA gene sequences.

Spongites agulhensis

The rbcL and psbA gene sequences (Fig. 1; Table 1), along with a dimerous thallus construction in which cells of the basal filament are book-shaped and a central columella is present in tetrasporangial conceptacles, clearly distinguish S. agulhensis from all other Spongites species worldwide. This is despite its morphological similarity to both South African Spongites yendoi and northeast Pacific Spongites decipiens (Tables 3 and S2) and despite its very narrow distribution range. In the field, S. agulhensis previously was confused with South African S. yendoi but can be distinguished by its characteristically brownish-pink colour compared with the more grey colouration of S. yendoi (Fig. 14), by distinct individual thalli (Figs 13, 14); whereas, those of S. yendoi typically fuse with adjacent conspecifics and by growing in the high intertidal zone (Table 3). Anatomically it is distinguished from S. yendoi by only two characters. The first and most distinctive character is the dimerous thallus construction of S. agulhensis in which basal cells are book-shaped. Second, in S. agulhensis conceptacles are never buried. From northeast Pacific S. decipiens, S. agulhensis anatomically is distinguished by only a single character, the presence of a central columella in its tetrasporangial conceptacles (Table 3).

Spongites tumidum

Foslie (1901a) described Lithophyllum farlowii based on material sent to him by W. G. Farlow from Monterey, California, noting that the species differed morphologically from L. yendoi but was anatomically very similar. The cell and conceptacle measurements of Foslie (1901a) are in Table 2. Setchell and Mason (1943) pointed out that L. farlowii Foslie was a later homonym (by a month) of L. farlowii Heydrich, and they proposed the substitute name L. neofarlowii for the former, not realizing that Foslie (1901b) already had proposed the substitute name L. tumidum. Smith (1944: 228) added the first habitat information and expanded the distribution of L. tumidum (as L. neofarlowii) north to Fort Bragg and south to Carmel Bay, California. Mason (1953) elaborated on the description of Foslie (1901a) (Table 2), further expanded the distribution of the species south to Cambria, California, and north to Puget Sound, Washington. She noted that the species grew higher in the intertidal zone than all other encrusting corallines, where it occurs in large patches, is dull purple to lavender, and varies from somewhat irregular to very bumpy, appearing to be composed of numerous small spheres cemented together. Mason (1953) designated the material in TRH (as Herb. Mus. Nidaros) as the lectotype (TRH A3-138)
and UC 341301 as an isotype (isolectotype). Dawson (1960) repeated the description of Mason (1953) and expanded the distribution south to Bahia Asunciön, Baja California, Norte, Mexico, based on a single collection in a tidepool. Adey (1970) later transferred _L. neofoearlaviit_ to _Pseudolithophyllum_. Steneck & Paine (1986) mostly confirmed the observations of previous authors; these are summarized in Table 2. The only report of this species from outside the northeast Pacific was by Yoshida _et al._ (1985) from Japan, and only much later was its habit and conceptacles illustrated based on Japanese material (Baba 2000).

*Lithophyllum tumidum* clearly belongs in _Spongites_ based on _rbcL_ and _psbA_ gene sequences (Fig. 1) as well as a suite of morpho-anatomical features. Thalli are non-geniculate, lack a ventral (i.e. basal) layer of palisade cells (in radial view), and cells of contiguous filaments are joined only by cell fusions. Tetrasporangial conceptacle pore canals are lined by cells that arise from peripheral roof filaments, and these cells protrude into the canal as papillae orientated more or less parallel or at a sharp angle to the conceptacle roof surface. Spermatangial conceptacles bear unbranched spermatangial systems restricted to the conceptacle floor (see Kato _et al._ 2011). This species has long been recognized as distinct in the northeast Pacific based on its habit and habitat. The findings from earlier reports are confirmed by the species’ unique _rbcL_ and _psbA_ gene sequences. New observations include its dimerous thallus construction and its occurrence in tidepools and on the plates of live chitons (Table 3). Its presence in Japan (Baba 2000) needs to be confirmed by DNA sequences.

Coralline species determinations, distributions and convergent evolution

As shown here, two widely geographically separated _Spongites_ species, _S. aguldensis_ from South Africa and _S. decipiens_ from the northeast Pacific, required detailed anatomical and morphological observations to find even a single character to segregate them (presence vs absence of a central columella in tetrasporangial conceptacles, respectively; Tables 3 and S2). However, _rbcL_ and _psbA_ sequence divergence values (Table 1) clearly indicate that they are distinct species. Moreover, in South Africa, _S. aguldensis_ historically was confused with specimens called _S. yendoi_, as these species appear similar morphologically and their habitats somewhat overlap. Only two anatomical characters segregate these species, dimerous vs monomorous thallus construction and the absence of old, buried conceptacles in _S. aguldensis_ (Tables 3 and S2). As these examples show, it requires detailed morpho-anatomical observations, frequently of material from a particular life history stage, to find even one or two characters that distinguish these species, and these characters may not be present in any given specimen.

This is the first report for non-geniculate coralline algae where names have been unequivocally assigned that demonstrates geographically overlapping species are genetically more similar than morpho-anatomical nearly indistinguishable species whose distributions are widely disjunct. Even the novice collector would not confuse the morphologically and habitat distinct northeast Pacific species _S. decipiens_ and _S. tumidum_, and yet they are most similar genetically in both plastid markers (Table 1). In contrast, the morpho-anatomical nearly indistinguishable but geographically widely separated _S. aguldensis_ and _S. decipiens_ also are among the most distinct species genetically based on these same markers (Table 1). That _S. aguldensis_ from South Africa and _S. decipiens_ from the northeast Pacific are anatomically nearly identical, yet genetically very distinct, argues for convergent evolution of many anatomical features in non-geniculate coralline algae. Moreover, many of these same features have been used both historically and recently to place into synonymy coralline species from different biogeographic provinces. Based on these observations, we find ourselves having to question all reports, based only on morpho-anatomy of the widespread and disjunct distributions of _Spongites_ species, particularly of _S. decipiens, S. tumidum_ and _S. yendoi_ but also of _S. fruticulosus_ [Mediterranean Sea and southern Australia (Penrose 1996)] and _Spongites discoides_ [Tierra del Fuego, Argentina and South Africa (Chamberlain 1994)]. If this observation holds true more generally, then all reports of geographically widespread and disjunct non-geniculate coralline species distributions will need to be re-investigated.

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SUPPLEMENTARY DATA

Supplementary data associated with this article can be found online at http://dx.doi.org/10.2216/15-38.1.s1.

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