

A first account of the semi-endophytic coralline algae *Lithophyllum cuneatum* from the Caribbean Sea and its evolutionary and biogeographic significance

JURAJ HRABOVSKÝ^{1,✉}, ANDRZEJ PISERA² and EBERHARD GISCHLER³

¹Earth Science Institute of the Slovak Academy of Sciences, Dúbravská cesta 9, 840 05 Bratislava, Slovakia; ✉geoljuhr@savba.sk

²Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warszawa, Poland

³Goethe-Universität Frankfurt, Institut für Geowissenschaften, Altenhöferallee 1, 60438 Frankfurt am Main, Germany

(Manuscript received July 20, 2021; accepted in revised form February 7, 2022; Associate Editor: Adam Tomašových)

Abstract: The semi-endophytic coralline alga *Lithophyllum cuneatum*, which grows partially embedded in its host on its surface and lacks haustoria penetration to this host, was formerly known only from reef environments of the Pacific and Indian Ocean. Here, we report it for the first time from coral reefs of the Caribbean Sea (Belize). The morpho-anatomical characteristics of the Caribbean specimens from Holocene sediment cores, which were collected in offshore reef environments, match those of the type material and other specimens reported from the Pacific and Indian Oceans, including the preservation of diagnostic characteristics (cuneate thallus morphology, morphology of the conceptacles and their pore canals, and dimensions of the cells). Similar to *L. cuneatum* from the Holocene of the Indian and Pacific oceans, Holocene specimens from Belize share two unique hosts represented by the coralline algae *Porolithon onkodes* and *Neogoniolithon* sp. The unique occurrence of this species in the Caribbean Sea can be explained either (1) by pre-Pliocene dispersal toward the west from the present-day Indian Ocean area along the Tethyan seaway and/or (2) by dispersal toward the east via the Pacific (Fiji) Ocean when the Panama Isthmus was still open. Although morphologically-equivalent coralline algae can belong to either cryptic or pseudocryptic species, both scenarios imply a broader, more continuous geographic distribution of lineage leading to semi-endophytic *Lithophyllum cuneatum* prior to the Pliocene, which is in contrast to the more fragmented distribution during the Holocene. Although the lack of information about the geographic range of *L. cuneatum* prior to the Holocene can be coupled with sampling biases and cannot discriminate among these scenarios, other cases of such disjunct distributions, which were formerly documented among marine invertebrates, indicate that the geographic distribution of this species was less fragmented in the past, and thus supports the Tethyan dispersal hypothesis, including the relict character of its present-day geographic distribution.

Keywords: Caribbean Sea, distribution, taxonomy, Holocene, Lithophylloideae, *Lithophyllum cuneatum*, *Neogoniolithon* sp., *Porolithon onkodes*, semi-endophytes, Tethyan legacy.

Introduction

At present, few non-geniculate coralline algae from the Corallinales order are known to be parasitic or semi-endophytic. Semi-endophytic coralline algae either (1) penetrate the thallus of the host algae by haustoria in order to obtain nutrients or (2) grow partially embedded in its host on the host's surface, thereby lacking haustoria penetration to this host and thus capable of photosynthesis (Adey et al. 1971, 1974, 2015). The first report of a parasitic to semi-endophytic lithophylloid coralline alga was made by Adey et al. (1974), who established the new genus and species *Ezo epiyessoense* from Hokkaido, Japan. *Lithophyllum cuneatum* was described by Keats (1995) from Fiji (SW Pacific). Keats separated the two taxa, of which both belong to the subfamily Lithophylloideae, based on morpho-anatomical characteristics, such as the number of epithallial cells, presence/absence of trichocytes, presence/absence of haustoria and plastids, thallus organization, and the position within or on the host. *Lithophyllum cuneatum* was later reported from Recent of Australia (Harvey et al. 2009), Pleistocene limestones from

Tahiti (Woelkerling et al. 2013) and in the Pleistocene limestones of the Maldives, Indian Ocean (Gischler et al. 2018). Two other species of semi-endophytic algae, *Hydrolithon bragganum* (Woelkerling et al. 2012) and *Lithophyllum kenjikonishii* (Woelkerling et al. 2013), were also established on the basis of the Pleistocene Tahitian material. The species *Hydrolithon bragganum* bears lateral fusion between the cells of adjacent filaments, while cells in the *L. kenjikonishii* as well as other lithophylloid algae are laterally joined with secondary pit connections (Woelkerling et al. 2012). Biogeographic data suggest that semi-endophytic coralline algae *L. cuneatum* and *L. kenjikonishii* were restricted to the tropics and subtropics of the Pacific and Indian Oceans during the Holocene and Pleistocene (Keats 1995; Woelkerling et al. 2013; Harvey et al. 2009). However, we report here for the first time the occurrences of *L. cuneatum* in sediment cores collected in the Holocene reefs of Belize. These occurrences thus extend the geographic range of this species to the Caribbean Sea. Later in this article, we will discuss the implications of this finding to the biogeographic history of semi-endophytic coralline algae.

Material and methods

Material

The material originated from rotary drill cores collected from the Belize Barrier Reef (BBR), as well as from the offshore atolls of the Turneffe Atol (TR) and Lighthouse Reefs (LR) (Table 1, Fig. 1) (Gischler & Hudson 1998, 2004). The above-mentioned abbreviations, i.e., BBR, TR, and LR are core labels as well. About 80 thin sections that contained coralline algae from 25 cores were examined. The species investigated in this study was found in 13 thin sections in seven cores. We detected fertile specimens in these thin sections only at the BBR. Rotary drill cores were taken from a 20–30 m wide reef crest at the BBR and dated using ^{14}C measured in 32 Holocene corals (Gischler & Hudson 2004). These data suggest that the BBR was established from 8.26 to 6.68 ky BP on Pleistocene reef limestones (Gischler & Hudson 2004). Similar ages of the Holocene limestones were obtained from the TR and LR (Gischler & Hudson 1998). All thin sections analyzed in our study thus belong to the Holocene. Facies successions of the TR and LR begin with soils and are followed by mangrove peats and marine carbonate sediments deposited in lagoons. Initial flooding was dated to 6 ky BP (TI) and 7 ky BP (LR) (Gischler 2003). The Holocene sedimentation rates were estimated as 3.25 m/ky (BBR), 0.82 m/ky (TR), and 0.53 m/ky (LR) (Gischler 2003; Gischler & Hudson 2004). The thin sections are housed in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa, under the collection number ZPAL Al.11. Thin sections were analyzed using Olympus and Nikon optical microscopes, the latter equipped with a Nikon digital camera. Images were captured using Helicon Remote software (Helicon Soft).

Species identification

Morphological data indicate that the specimens belong to *Lithophyllum cuneatum*. This species is semi-endophytic (i.e., growing partially embedded on the surface of the host and lacking haustoria) and in Recent, it is associated with two host coralline algae: (1) *Porolithon onkodes* (earlier reported from the Atlantic as *P. pachydermum*) and (2) *Neogoniolithon* sp. Identification of semi-endophytic coralline algae was based on the comparison of morphological characters observed in our material with those described by Keats (1995), Harvey et al. (2009), and Woelkerling et al. (2013). The genus *Porolithon* was identified predominantly on the basis of monomerous thallus construction, ventral core filaments that are non-coaxially arranged, cells laterally-joined by fusions with secondary pit connections being absent, one or more epithallial cells that are not flared, trichocytes arranged in large, tightly-packed horizontal fields, and bi/tetrasporangial conceptacles developed from cells peripheral to and interspersed among sporangial initials (Type 2 according to Johansen 1981) (Rösler et al. 2016). This morphology fits within the morpho-anatomical description of the *Porolithon onkodes* according to Maneveldt

and Keats (2014). However, it is possible that our specimens also belong to other, genetically-distinct species that still match the morphology of *P. onkodes* (Gabrielson et al. 2018). A second host includes layered encrusting specimens with monomerous thallus construction and coaxial ventral core filament. Cells are laterally joined by fusions, however, secondary pit connections are absent. Epithallial cells are not flared, trichocytes are arranged in vertical rows and bi/tetrasporangial conceptacles are developed from cells located peripherally to sporangial initials (Type 1 according to Johansen 1981). These characteristics match those of the genus *Neogoniolithon* (Kato et al. 2013).

Taxonomy

Order Corallinales Silva et Johansen, 1986
Family Lithophyllaceae Athanasiadis, 2016
Subfamily Lithophylloideae Setchell, 1943

Genus *Lithophyllum* Philippi, 1837

Type species: *Lithophyllum incrustans* Philippi, 1837.
Type locality: Sicily, Mediterranean.

Lithophyllum cuneatum Keats, 1995
Figs. 2–3, Tables 1–2

Holotype: L(UWC 94/1135) (Keats 1995, figs. 1, 3–19, 23).

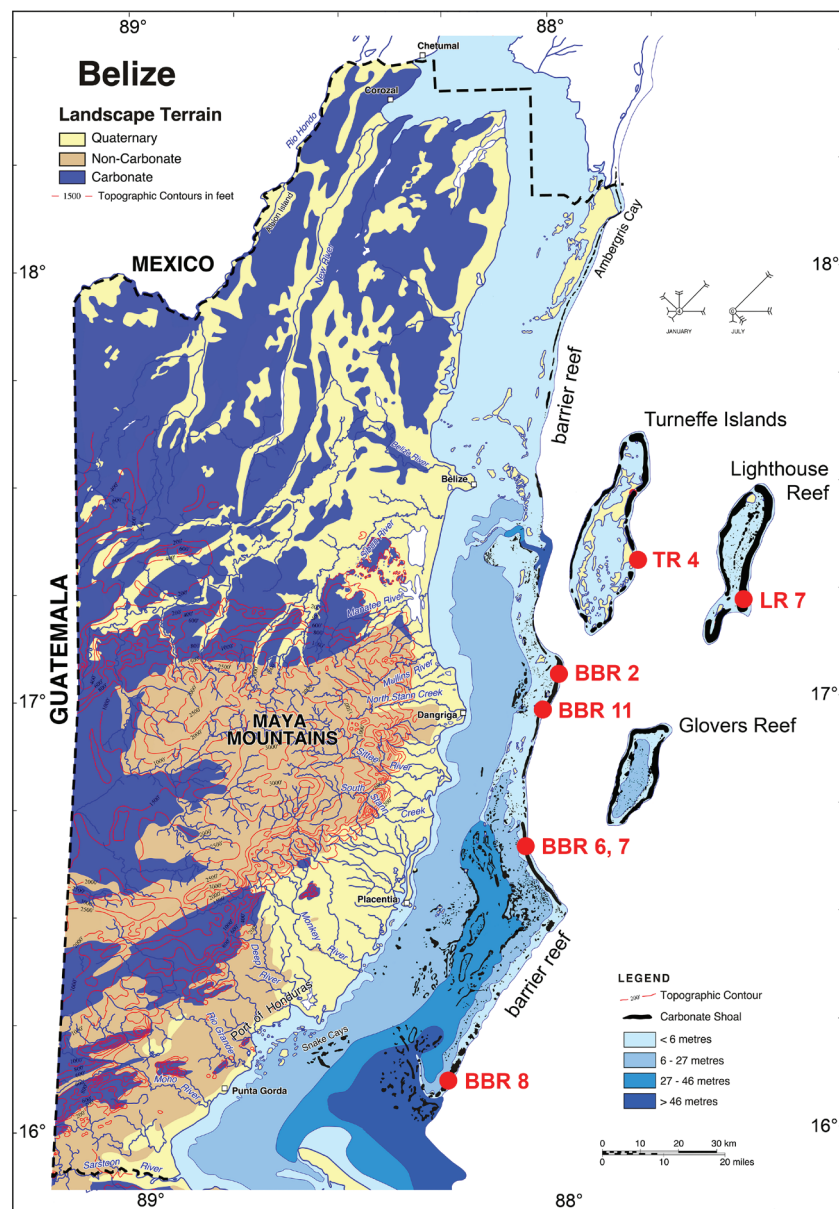
Type locality: Makaluva Island fringing reef, Fiji, on *Porolithon onkodes* (*Hydrolithon onkodes*, Keats, 1995).

Material: Fertile *L. cuneatum* plants were observed in the thin sections of BBR2-1 (at –1.5 m below core top) and BBR 11, core depth levels –1.75 m and –5.25 m, respectively. The other specimens were sterile (Table 1). Only Holocene – recent and sub-fossil specimens are known in Belize cores (Gischler & Hudson 1998, 2004; Gischler 2003). *L. cuneatum* and its hosts were not observed in the older Pleistocene and Pliocene strata. Cuneate thalli are embedded within the hosts. Some plants of *L. cuneatum* are smaller when occurring alone, or they are large when laterally fused. Growth of the new thallus from the surface of the old one was also observed. In general, overgrowing thallus of the host alga protects *Lithophyllum cuneatum* from physical destruction e.g., surficial abrasion. However, we have also observed some features of *L. cuneatum* that can be affected by small-scale taphonomic effects or early-diagenetic by-products of bioerosion that formed after the semi-endophyte became embedded within its host. These features include spots or patches of tissue where the cell walls have been damaged. We assume that the circular openings represent sections of the burrows/tunnels most likely produced by endoliths (Fig. 2a,b).

Description: Plants are semi-endophytic. Cuneate thalli are embedded within the host tissue of *Porolithon onkodes* and *Neogoniolithon* sp. Fertile plants were observed in *Neogoniolithon* sp. Plants are non-geniculate and pseudo-

Table 1: Distribution of all sterile and fertile *Lithophyllum cuneatum* thalli in thin sections from Belize.

Thin section	Approximate depth level in the cores	(n) specimens	Fertile	Host
BBR2-1	-1.75m from the core top	5	2	<i>Neogoniolithon</i> sp.
BBR2-1	-1.75m from the core top	3	0	<i>Neogoniolithon</i> sp.
BBR2-1	-4.25m from the core top	1	0	<i>P. onkodes</i>
BBR6	-0.25m from the core top	2	0	<i>Neogoniolithon</i> sp.
BBR6	-0.25m from the core top	2	0	<i>Neogoniolithon</i> sp.
BBR7	-0.25m from the core top	1	0	<i>P. onkodes</i>
BBR7	-3.75m from the core top	2	0	<i>P. onkodes</i>
BBR8	-0.25m from the core top	1	0	<i>Neogoniolithon</i> sp.
BBR11	-5.25m from the core top	9	3	<i>Neogoniolithon</i> sp.
TR4	-0.25m from the core top	6	0	<i>P. onkodes</i>
TR4	-0.25m from the core top	3	0	uncertain
TR4	-0.25m from the core top	4	0	<i>P. onkodes</i>
LR7	-1.25m from the core top	7	0	<i>P. onkodes</i>
		SUM: 46	SUM: 5	

**Fig. 1.** Map of the Belize barrier reef and offshore atolls, including locations of core holes mentioned in this study.

parchymatous. Individual thalli measure 232–920 µm from the base to the top and 291–1815 µm in diameter, measured at the top. Morphology of these specimens in sections is cuneate, and the thallus is slightly convex at its top (Fig. 2a). The basal wedge-like cell was not observed in this specimen. However, the thallus morphology suggests that its development starts from a single cell (Fig. 2a,b). Filaments are composed of palisade and non-palisade (according to the description of Harvey et al. 2009; columnar according to Keats 1995) cells 3–34 µm long (16 µm mean, sd. 5.8) and 5–13 µm (9 µm mean, 1.7 sd.), joined with primary and secondary pit connections, while lateral fusion of the cells was not observed (Fig. 2c,d). Lengths of the cells within single filaments change, and alternation of long and short cells occurs. However, outlines of the cells in some spots are not clearly delineated because of the taphonomic or diagenetic processes that altered the thallus (Fig. 2d). Trichocytes were not observed in the studied specimens. Epithallial and meristematic cells are poorly preserved (Fig. 2b).

Bi/tetrasporangial conceptacles are uniporate and flush with the surface (Fig. 2e). Chambers are 168–172 µm in diameter (170 µm mean, 2.8 sd.) and are 95–101 µm high (98 µm mean, 4 sd.). Chambers do not have a central columella. Roof filaments are 7–9 celled and composed of cells which are not distinctly elongated. Roof cells are 8–21 µm long (13 µm mean, 3 sd.) and 8–10 µm in diameter (9 µm average, 0.6 sd.). Pore canals are cylindrical, 64–71 µm high and 28–33 µm in diameter, measured in the central portion of the pore canals. Pore canal filaments are perpendicularly-oriented to the chamber. Renewed meristematic activity of the roof cells of one of the conceptacles led to the development of the openings above the pore canal, which enlarge its appearance. In this case, the length of the pore canal is visibly enlarged, and the cells above the pore canal are similar to papillae which project into the pore canal (Fig. 2f), as documented also in the type specimen. However, the presence of papillae was not confirmed in other conceptacles in known fertile specimens from Belize. Gametophytes were not observed.

Remarks: The studied species from Belize possess morpho-anatomical characteristics that overlap with the type material. However, cells and the pore canal dimensions are larger than those of the type material, and a basal wedge-shaped cell was not observed in the studied specimen. Nevertheless, the specimens from Belize are consistent with the known *L. cuneatum* from the Pacific Ocean (Table 2). In contrast, we observed a basal cell in the sterile plant (Fig. 3). Filaments of this specimen are terminated by up to three epithallial cells; meristematic cells occur below them; cells of adjacent filaments are laterally joined with secondary pits while cell fusion is absent, and the specimen possesses a cuneate growth form as well (Fig. 3a,b). Therefore, characteristics of the sterile specimen overlap with the already known specimens from Belize. A non-palisade basal cell was detected at the base of this thallus (Fig. 3b). Its morphology supports species attribution to the genus *Lithophyllum*.

Discussion

Taxonomic position

The specimens of *L. cuneatum* from Belize share common characteristics with the type material and other specimens of *L. cuneatum* from elsewhere (Table 2). There are only minor differences concerning the dimensions of the vegetative filament cells and pore canal of bi/tetrasporangial conceptacles. However, these characteristics broadly overlap with those in other known specimens of *L. cuneatum* (Table 2). Moreover, many characteristics, such as the number of the cells in the roof filaments of bi/tetrasporangial conceptacles also show a certain degree of variability (Keats et al. 1995; Woelkerling et al. 2013). Since minor differences in the cells and pore canal dimensions alone are not considered significant for species delimitation (Woelkerling & Cambell 1992; Harvey et al. 2009), we attribute our specimen to *L. cuneatum* rather than to propose a new species for our material on the basis of morphological characteristics. In addition, similarly as in *L. cuneatum* from the Holocene of the Indian and Pacific oceans, Holocene specimens from Belize share a common host and habitat, i.e., coralline algae *P. onkodes* and *Neogoniolithon* sp. in shallow-water reef environments.

Bleached or damaged cell walls, which appear as secondary cell fusion/lateral anastomosis of cells in adjacent filaments and are a morphological characteristic that is rare or absent in lithophylloid coralline algae (e.g., Braga et al. 1993; Harvey et al. 2009), may complicate species identification. However, a detailed study of the Belize specimens reveals that this feature affects not only the lateral cell walls, but also the roof and bottom walls, and the extension of these cells is rather patchy (Fig. 2a,c). Therefore, we believe that these features represent traces of diagenetic recrystallization and/or taphonomic alteration. Although we did not study the Tahitian and Fijian material, *L. cuneatum* and *L. kenjikonishii* specimens show that they may have undergone a similar post-mortem process, which left similar structures (Keats et al. 1995; Woelkerling et al. 2013). Another type of cell connections observed in specimens of *L. cuneatum* may be confused with lateral cell fusion as well. These connections are represented by up to 3 µm thin and narrow connections between the adjacent and continuous cells and may be separated by remains of thin walls. These connections are in magnitudes smaller than cell fusions and match with known secondary (between adjacent cells) and primary (between continuous cells) pit connections, which are diagnostic in specimen classification within the genus *Lithophyllum* (e.g., Woelkerling 1988; Braga et al. 1993; Harvey et al. 2009).

One could also question the validity of the bi/tetrasporic life cycle phase of the Belizean specimen. Two types of uniporate conceptacles in coralline algae can be discriminated on the basis of the roof and the pore canal formation according to Johansen (1981). Type 1 includes conceptacles formed by filaments peripheral to the fertile area, running more or less parallel to the chamber and bending upwards to form the pore

canal. Type 2 includes conceptacles formed by filaments peripheral to and interspersed among the sporangial initials. Their destruction generates conceptacle chambers, and the filaments in the roof are thus oriented perpendicularly to

the chamber. In the Lithophylloideae, type 1 is characteristic for gametophytes while type 2 is characteristic for sporophytes. However, according to Caragnano et al. (2018), the type of the roof formation cannot be recognized properly

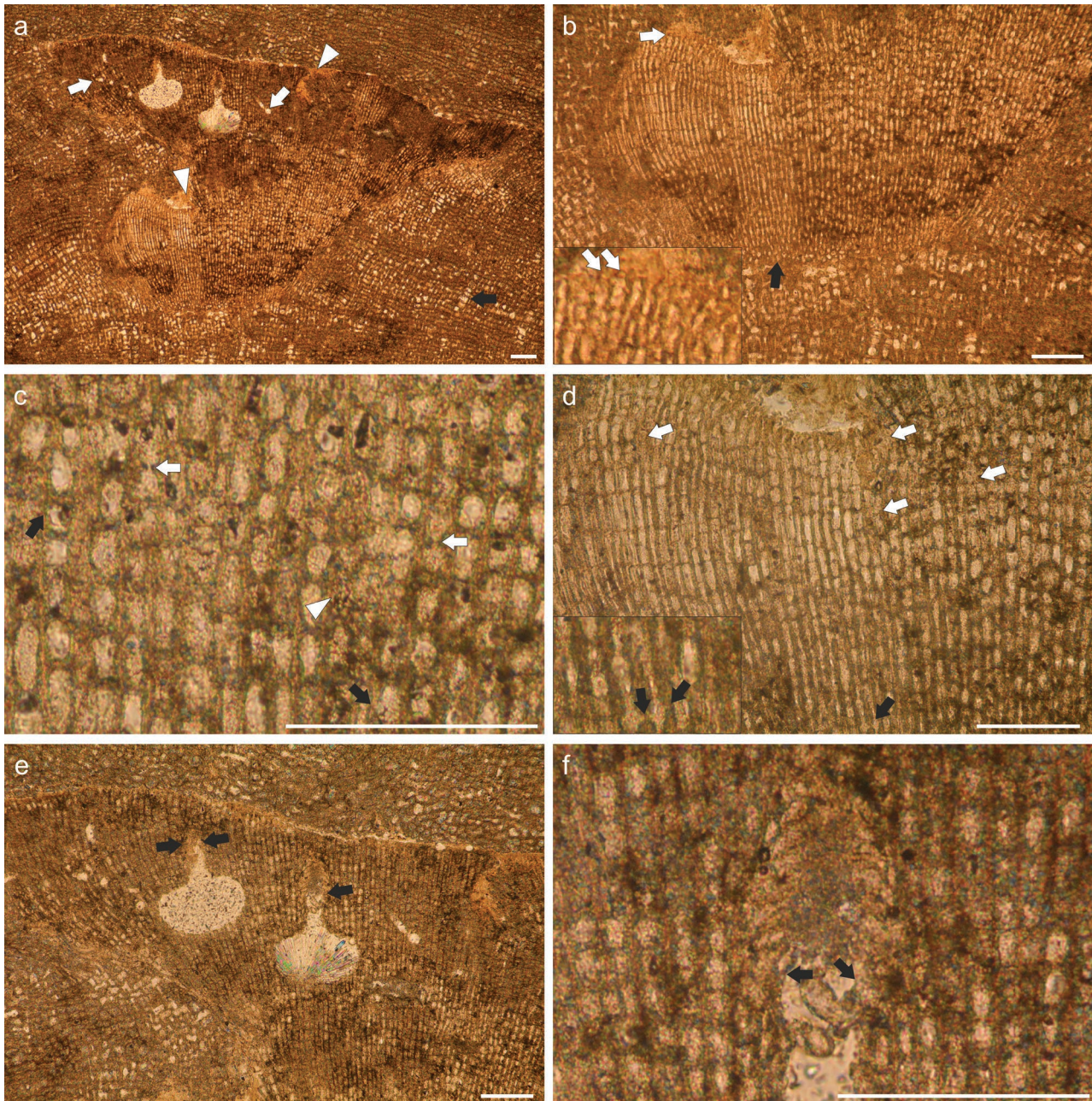


Fig. 2. *Lithophyllum cuneatum*, from the Belize Barrier Reef, core BBR2-1 (–1.75 m from the core top). **a** — Cuneate growth form of the specimen. Note the slightly convex top of the thallus. The specimen is completely embedded within the host tissue. The black arrow points to the vertically arranged trichocytes of the host. Note the circular traces of micro endoliths (white arrows) and fine matter (arrowhead) filling the cavities within and around the thallus of *L. cuneatum*. **b** — Black arrow points to the supposed base of the thallus. Note the badly-preserved epithelial and meristematic cells (white arrows). **c** — Primary (white arrows) and secondary (black arrows) pit connections. The arrowhead indicates the spots in the thallus where the cell outline is not clear. Lateral fusion in cells of the adjacent filaments is absent. **d** — Portion of the thallus showing alternation of long and short cells. Spots in the thallus where the cell walls are destroyed in both directions are indicated by white arrows. Black arrows point to the secondary pit connections. **e** — Two bi/tetrasporangial conceptacles flushed with the thallus surface. The black arrows indicate the top of the pore canals. **f** — Detail of the pore canal. Note the perpendicularly-oriented pore canal filaments at the base of the figure. The black arrows point to the proposed top of the pore canal where renewed meristematic activity of the roof cells produced an opening above the pore canal. Scale bars are 100 μ m.

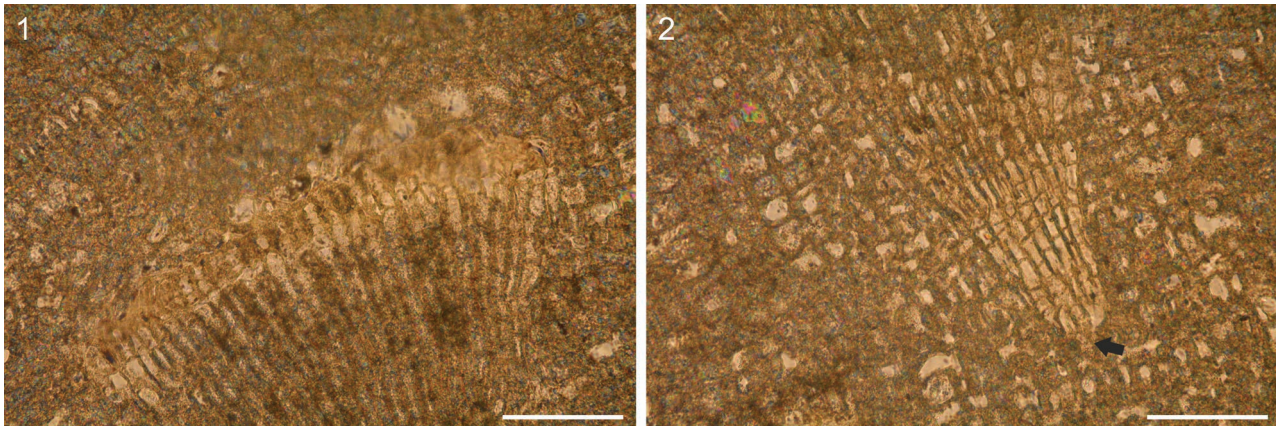


Fig. 3. *Lithophyllum cuneatum*, from the Belize Barrier Reef, core BBR2-1 (at –1.75 m from the core top). **a** — Upper portion of the thallus with epithelial and meristematic cells. **b** — Basal portion of the thallus with indicated basal cell (arrow). Scale bars are 100 µm.

when conceptacle primordia are not detected. Therefore, gametangial and sporangial conceptacles can be confused. Nevertheless, the drawings of Keats et al. (1995) show that the roof filaments of the gametangial conceptacles are obviously parallel with the conceptacle chamber within the whole roof thickness and are thus not perpendicular as those observed in the Belizean material. Therefore, the confusion between carp-sporangial and bi/tetrasporangial conceptacles is unlikely in the specimens of *L. cuneatum* from Belize. The apparent length of the pore canal of one of the conceptacles is distorted by the plane of the section as it is demonstrated by its skewed shape near the pore opening, which is not present in the second adjacent conceptacle. Since the dimensions of the conceptacles and the pore canal match with the type, and the roof filaments orientation is characteristic of bi/tetrasporangial conceptacles, we consider these specimens to be bi/tetrasporophytes.

DNA sequences of extant coralline algae, however, may question our species-level determination. In recent decades, numerous cryptic or pseudo-cryptic (molecularly-defined) coralline algal species have been identified (Richards et al. 2014; Merwe et al. 2015). These species are either (1) morphologically indistinguishable from each other – cryptic, or (2) they are separated by few morphological characteristics – pseudocryptic (Merwe et al. 2015; Caragnano et al. 2018; Puckree-Padua et al. 2020). Some molecular results indicate that morphologically-similar species inhabiting disparate biogeographic provinces should be assigned to distinct species (Merwe et al. 2015). However, although the results from DNA sequences are important, there are still numerous questions that need be clarified. First, the lack of DNA evidence in the extant *L. cuneatum* does not allow us to consider cryptic within the known *L. cuneatum* population. At the present state of knowledge, such consideration would be based solely on the research of other coralline algal taxa. Nevertheless, if morphologically-equal specimens from Belize and the Indo-Pacific Ocean could be separated on the basis of molecular data, the mode and pattern of the ancestor dispersal should still

be disentangled. Second, the biogeographic argument does not need to be applied to all coralline algal species. Although some species ranges have been shortened on the basis of DNA sequences (Merwe et al. 2015), others were confirmed to inhabit remote bioprovinces e.g., *Lithophyllum incrustans* (Hernandez-Kantun et al. 2015), *Phymatolithon ferox* (Maneveldt et al. 2020), or their distribution is cosmopolitan e.g., *Dawsonolithon conicum* (Caragnano et al. 2018). In fact, geographic ranges of some tropical encrusting coralline algal species can be broader than ranges of the temperate species (e.g., Hernandez-Kantun et al. 2016; Rösler et al. 2016; Maneveldt et al. 2017, 2019). Therefore, it remains to be determined whether the two geographically-separated populations of *L. cuneatum* represent the same species, even on the basis of molecular data, or whether they represent genetically-distinct, cryptic, or pseudocryptic species belonging to the same lineage. The morphological criteria suggest rather that this species is characterized by cosmopolitan distribution. Despite the numerous evidences of cryptic species, it also remains to be determined whether these molecularly-defined species are reproductively-compatible, and thus whether they can be considered segments of distinct evolving lineages (ancestor-descendant series) of metapopulations that match the recent species concept (de Queiroz 2007). Therefore, when taking this into consideration, morphology and (paleo)-ecology are the only reliable secondary criteria (according to de Queiroz 2007) available for the time being for Belizean species determination.

Ecology

The ecology of *L. cuneatum* is poorly understood. All occurrences are from the tropics to subtropics (Keats 1995; Harriott 1999; Harvey et al. 2009; Woelkerling et al. 2013) and extant species occur at 0–25 m water depths on coral reefs (Keats 1995) or at 13–17 m water depths in New South Wales (Harvey et al. 2009; Woelkerling et al. 2013), indicating a distinct preference to tropical conditions. As noted by Woelkerling et al.

Table 2: The morphoanatomical characteristics of Belizean specimens and several other specimens described from the Pacific Ocean, including the type species from Fiji (Keats 1995), and two specimens from New South Wales (Harvey et al. 2009) and Tahiti (Woelkerling et al. 2013).

	<i>L. cuneatum</i> Belize BBR2-1 reef semi-endophyte host <i>Neogoniolithon</i> sp.	<i>L. cuneatum</i> Belize BBR11 reef semi-endophyte host <i>Neogoniolithon</i> sp.	<i>L. cuneatum</i> Belize BBR11 reef semi-endophyte host <i>Neogoniolithon</i> sp.	<i>L. cuneatum</i> Fiji reef semi-endophyte host <i>Porolithon onkodes</i> <i>Neogoniolithon</i> sp.	<i>L. cuneatum</i> New South Wales 13-17m depth, semi-endophyte host <i>Lithophyllum corallinae</i>	<i>L. cuneatum</i> Tahiti ND semi-endophyte host <i>Porolithon onkodes</i>
Morphology						
plant height	389–920	898	661	ND	600	665–1125
plant diameter	869–1815	1096	990	6000	1700	1190–2630
raised	up to 100	103–119				
Basal cell	ND	ND	ND	ND	ND	ND
Postigenous filaments						
cells height	3–34	7–23	9–15	15–25	7–23	7–50
cells diameter	5–13	7–13	5–12	7–13	7–12	5–12
fusion of cells	–	–	–	–	–	–
Meristematic cells		ND			ND	ND
height	14–28		20–29	9–20		
diameter	8–13		6–9	6–13		
Epithallial cells		ND				
height	5–7		6–7	4–9	4–6	7–12
diameter	9–11		5–10	7–10	6–9	5–10
number	1		1–2	2–3	ND	ND
shape	square flattened not flared		square flattened not flared	elliptical rounded not flared	rounded flattened not flared	
Gametophyte	ND	ND	ND	monoecious	monoecious/dioecious	ND
Spermatangial conceptacles	ND	ND	ND			ND
height				35–50	27–30	
diameter				115–135	110–125	
Carpogonial conceptacles	ND	ND	ND			ND
height				30–62	23–27	
diameter				74–130	30–40	
Carposporangial conceptacles	ND	ND	ND		ND	ND
height				50–200		
diameter				130–165		
Bi/tetrasporangial conceptacles					ND	
height	95–101	83	95–102	75–137		62–77
diameter	168–172	138–141	126–133	105–200		115–163
pore length	64–71	74	87–100	65–105		ND
pore diameter	39–42	36	32	22		ND
pore cells protrude inside the canal	+	–	+	+		ND
mature roof filaments (n cells)	7–9	7	8	ND		5–6

(2013), *L. cuneatum* is host-dependent based on the high growth rate of the host thallus, i.e., it requires hosts that grow at similar rates as *L. cuneatum*. The host enhances its preservation potential because embedded thalli are better protected from taphonomic processes (Woelkerling et al. 2013). This assumption implies a co-occurrence of *L. cuneatum* and the host. In contrast, the distribution area of *L. cuneatum* is smaller than that of the host and does not completely match the distribution of *L. corallinae* and *P. onkodes*, suggesting either a low level of exploration or the existence of other ecological factors controlling the species distribution (Harvey et al. 2009, Maneveldt & Keats 2014).

Spatio-temporal distribution

L. cuneatum was described first from the Pacific Ocean: Fiji (Keats 1995), New South Wales in Australia (Harvey et al. 2009) and Tahiti (Woelkerling et al. 2013). The first two occurrences are extant and the latter occurrences are from the Pleistocene (Keats 1995; Harvey et al. 2009; Woelkerling et al. 2013). More recently, the presence of *L. cuneatum* was reported from the Holocene of the Great Barrier Reef, Northeastern Australia (Dechnik et al. 2015, 2017; Humblet et al. 2019), the Holocene of Bora Bora (Gischler et al. 2016), and from the Pleistocene (with ages ranging from 114.3–151.2 kyr BP) of the Maldives in the Indian Ocean (Gischler et al. 2018). Radiometric age data of the cores collected off Belize, which are investigated here, show ages younger than 8.26 kyr BP (Gischler & Hudson 1998, 2004) – and Tahitian specimens exhibit an age range of 20–30 kyr BP (Woelkerling et al. 2013). The ages of these particular occurrences may suggest that the Indian Ocean is the center of origin of this species, which later dispersed into the Pacific and Atlantic.

However, this hypothesis would predict a relatively fast dispersal across broad spatial scales if it were assumed that the oldest occurrences in the Indian Ocean, i.e., Pleistocene (114.3–151.2 kyr BP) approximate the time of species origination. On one hand, for example, the oldest record of *Titanoderma pustulatum* (another coralline species with worldwide distribution today) stems from the late Oligocene (~26–27 Ma, Bassi et al. 2009) on the Kōkō seamount (Pacific Ocean), with the early Miocene (~16–23 Ma) occurrence in the Caribbean Sea, and with the middle Miocene (~16–12 Ma) occurrences in the Mediterranean (Bassi et al. 2009). The oldest record of *T. pustulatum* was recently extended by a new occurrence of *T. pustulatum* to the lower Oligocene Uromieh section (Rupelian, NW Iran, Basso et al. 2019). On the other hand, the extant species with the cosmopolitan distribution, such as *T. pustulatum*, also possess very long stratigraphic records. Many well-known and morphologically-defined extant coralline algal species that have cosmopolitan distribution, such as *Lithothamnion crispatum*, *Phymatolithon calcareum*, *Spongites fruticosus*, *Lithoporella melobesioides*, *Lithophyllum dentatum* or *Lithophyllum incrustans* have their counterparts in the Paleogene- or Neogene rocks (Braga et al. 1993; Braga & Aguirre 1995; Basso et al. 1997; Bassi et al. 2009;

Coletti et al. 2016; Hrabovský et al. 2016; Basso et al. 2019). Finally, other cosmopolitan species such as *Mesophyllum macroblastum*, *Hydrolithon farinosum*, *Sporolithon ptychoides* or *Porolithon onkodes* are characterized by very narrow stratigraphic distribution limited only to the Holocene. This lack of fossil records may reflect the limitations with the application of diagnostic characteristics to fossil algae, poor sampling of available outcrops, as well as the simple fact that these algae evolved only recently. As it has been shown from the coralline algae of the Mediterranean Sea, cosmopolitan species may have used routes of dispersal which are not available today due to paleogeographic changes in the development of barriers and oceanic gateways (Athanasiadis 1999; Braga & Bassi 2007; Bassi et al. 2009; Athanasiadis & Ballantine 2014). It is possible that our knowledge of the stratigraphic distribution of *L. cuneatum* is affected by under-sampling, since this plant is very small, can be easily overlooked, and its fossil records may also be incomplete.

Mechanisms of range expansion

One of the most common mechanisms of dispersal of coralline algae, which ultimately leads to the expansion of geographic range, is represented by transport by ocean currents or the rafting of released spores (John 1974; Norton 1992; Macaya et al. in Hu & Fraser 2016). However, these mechanisms are inhibited by biogeographic barriers that developed during the middle and late Miocene between the tropical Atlantic and Indo-Pacific, as well as during the Pliocene between the Eastern Pacific Ocean and the Caribbean Sea. Both options of dispersal are important today among seaweeds. Small seaweed releases spores near the substratum, and spores settle rapidly in the surrounding turf (Norton 1991, 1992). This is the presumably the situation for the majority of non-geniculate coralline algae. Exceptions occur in plants that encrust elevated substrates – other seaweeds or seagrasses – from where the released spores can be dispersed on greater distances by currents (Norton 1992). In our cases, the dispersal mechanism is complicated by the fact that *L. cuneatum* occurs in a thick coralline crust developing in the algal ridges where the wave action is very strong. Thus, despite being small and situated low above the substratum, its spores can be easily carried away and transported for long distances by currents, thereby generating rapid dispersal. According to Norton (1992), however, dispersal range of the propagules released far away from the parent plant may highly increase the mortality of most of them, since they can either be eaten or they do not find a suitable substrate and die. Even when the spore settles on a suitable substrate, factors such as light, temperature, grazers, and the future thallus morphology thus become agents that control its growth rate and therefore have the ability to compete with other algae (Adey 1970, 1975; Adey & McKibbin 1970; Adey & Vassar 1975; Steneck 1982, 1986). The successful colonization is more difficult for semi-endophytes because they require more specific substrate, i.e., its host plant. All of these factors and limitations may reduce the rate

of colonization of new habitats by *L. cuneatum*. Although this pattern can explain the continuous extension of species range along the shores or nearby islands, it cannot properly explain the crossing of long distances between and within the major oceanic basins over short time scales. Therefore, the hypothesis of dispersal by released spores may not thoroughly explain the Holocene occurrences of *L. cuneatum* – *P. onkodes* association on remote islands and reefs of the Maldives, Fiji, or Belize.

Rafting of algae on the biogenic or abiotic objects, i.e., mainly seaweeds, corals, or pumices, usually concerns young plants rather than spores. As was shown by Gregory (1983), Winston (1997), and Saunders (2014), tens of geniculate and non-geniculate coralline algal species are found rafting on seaweeds or plastic debris. Giant kelp is also used as a raft by many organisms dispersing along the northern Californian coasts to British Columbia (Saunders 2014). Winston (1997) also found rafting coralline algae off Bermuda. These algae can face harsh conditions, such as desiccation and high irradiance during rafting, which thus increases their mortality (Macaya et al. 2016). *Porolithon onkodes* may provide suitable substrate for *L. cuneatum* during long distance rafts (Johnson et al. 2014). Therefore, the so-called kelp conveyor hypothesis by Saunders (2014) can be a suitable mechanism for dispersal, as well as for the maintenance of the disjunct distribution of *L. cuneatum* prior to the Late Miocene or Pliocene, i.e., when tropical segments of the Eastern Pacific and Atlantic oceans were still connected.

The transport of spores of coralline algae in the guts of sea birds, also known as endozoochory (Brochet et al. 2010a,b; Lewis et al. 2014; Lovas-Kiss et al. 2015, 2018), can affect geographic distributions; however, this mechanism has been poorly studied (and birds are not known to feed directly on coralline algae). The spores are released into the water column and can be easily swallowed by birds along with other food (Leeuwen et al. 2017). Spores can also be attached to the feathers or legs of sea birds, even to other animals (epizoochory) – a situation well-known in terrestrial and wetland migratory animals (Burgin & Renshaw 2008; Costa et al. 2013; Green et al. 2013; Viana et al. 2016). However, a specific spore morphology found in terrestrial plant propagules subjected to epizoochory does not characterize coralline algal spores (Johansen 1981; Thorsen et al. 2009), and we assume that the key mechanism of range expansion in coralline algae is the dispersal by oceanic currents.

Routes of dispersal

The dispersal barrier between the Indo-Pacific Ocean (the earliest occurrences of this species) on one hand, and the Caribbean on the other, developed after the closure of the Panama Isthmus. Therefore, we suggest that the lineage of this species was characterized by a much broader distribution in the past, and present-day distribution is a relict of previously more continuous distribution. Similar range fragmentation is invoked for the origin of present-day disjunct

distribution of several organisms, i.e., brachiopods (Bitner & Motchurova-Dekova 2016 and references) and sponges (Łukowiak et al. 2014; Łukowiak 2016; Pisera et al. 2018; Schuster et al. 2018) known as “Tethyan legacy” (Reid 1967; Por 1989; Hou & Li 2018). For example, the disjunct distribution of the Recent brachiopods of the genus *Minutella* covers the Caribbean region and the Indo-West Pacific Province, whereas fossil specimens of this genus were documented from the Eocene of Southern France or the Miocene of Bulgaria (Bitner & Motchurova-Dekova 2016). Similarly, the sponge *Vetulina* was restricted to the Caribbean region and Eastern Indian Ocean during the Holocene, while their ancestors are found in fossil records of the ancient Tethys Sea (Pisera et al. 2018). Although both *Minutella* and *Vetulina* do not live in the present-day Mediterranean Sea, it is evident that this region was inhabited by their ancestors in the past. The Tethyan legacy hypothesis suggests that present-day disjunct distribution of some taxa is in fact only the relict of a once larger Tethyan geographic distribution. In this scenario, dispersal can occur along the open Tethyan seaway, e.g., during the early Miocene (Fig. 4) and prior to its closure during the middle Miocene (Popov et al. 2004; Harzhauser et al. 2007; Hou & Li 2019). Available paleo-biogeographical data show that this route was also used by other coralline algae, e.g., some species of *Sporolithon* genus or *Titanoderma pustulatum* that may have settled in the Mediterranean Sea and Paratethys from the Indo-Pacific until the Langhian (Braga et al. 2007; Harzhauser & Piller 2007; Bassi et al. 2009). Another scenario is that the Caribbean region was colonized by *L. cuneatum* from the Pacific side (Fig. 5) (Indian Ocean to Belize via Fiji) by transport via currents from Fiji to Belize earlier than 2.8 to 3 million years ago during the Pliocene (O’Dea et al. 2016; Hou & Li 2018). However, the Pliocene rocks in the Belize are free of *L. cuneatum*, as well as its host *Porolithon onkodes*.



Fig. 4. Paleogeographic configuration during the early Miocene (Popov et al. 2004) with active connections between the major ocean basins via the Mediterranean Sea and Paratethys (arrows).

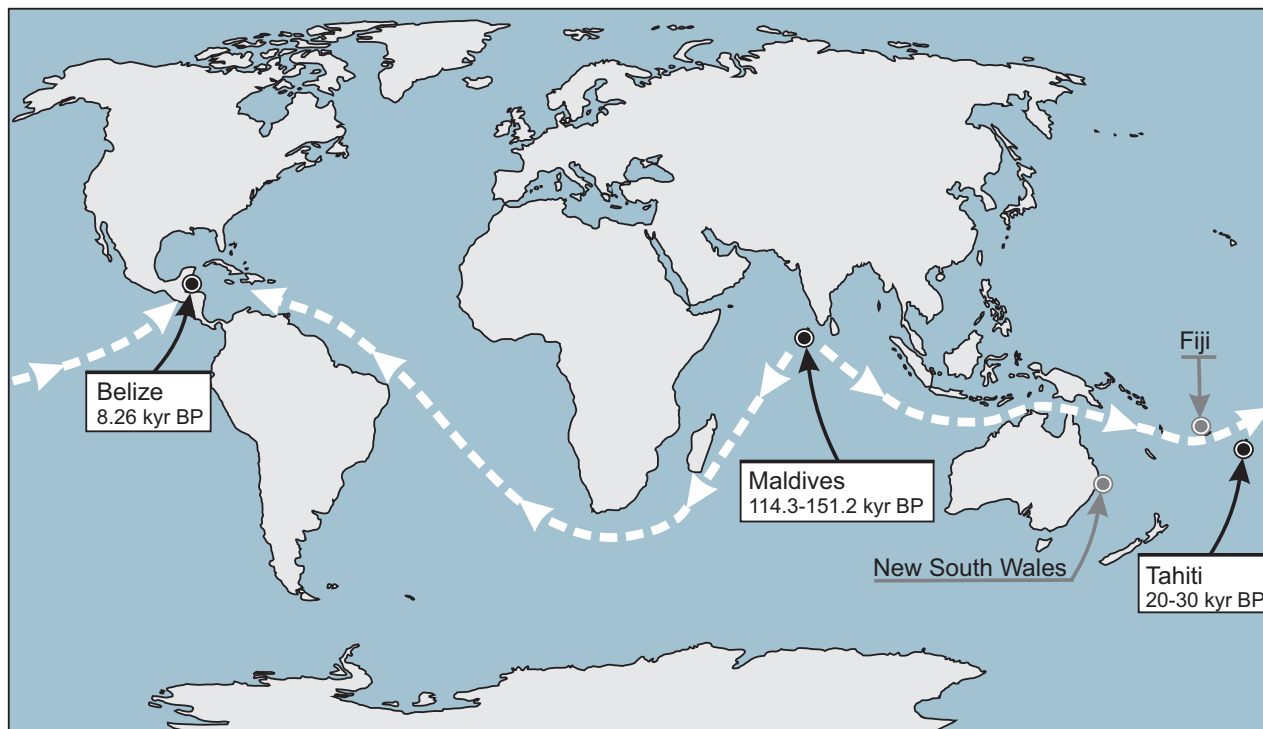


Fig. 5. Occurrences of *L. cuneatum* in Pleistocene and Holocene records in the present-day configuration of the continents. Note that the dispersal of *L. cuneatum* from Pacific to Atlantic Ocean was probably disabled after the closure of the Isthmus of Panama (this occurred 2.8–3 million years ago). The second scenario considers the dispersal from the Indian to the Atlantic Ocean across the temperate climatic zone.

Due to the poor fossil record of semi-endophyte coralline algae, these hypotheses cannot be tested at this stage, although the Tethyan one seems to us more plausible and may suggest that *L. cuneatum* could be another example of the so-called “Tethyan legacy” (Reid 1967; Por 1989; Hou & Li 2018) especially considering another similar case of coralline algae (Athanasiadis 1999; Athanasiadis & Ballantine 2014).

Conclusions

The species *Lithophyllum cuneatum*, which is documented in our study from the Holocene reef sediments of Belize, is the first Caribbean (Atlantic) occurrence of the semi-endophyte lithophylloid coralline alga. These algae were previously known only from the Pleistocene and Holocene of the Pacific and Indian Oceans. It appears that the only reliable mechanism for such long-distance dispersal is the transport by oceanic currents. Two possible scenarios may explain the observed pattern: transport from what is today’s Indian Ocean toward the west along the Tethyan seaway, or transport toward the east through the Pacific (Fiji) and the still-open Panama Isthmus. Both scenarios require earlier origination of the species, which would allow them to cross the large distance, as well as a different paleogeographic situation that would allow for such transport. Although the present state of knowledge does not allow for deciding which scenario is the correct one, judging from the cases of other organisms

(such as sponges or brachiopods) with such disjunct distribution, it seems likely that the Tethyan seaway transportation was in operation, and that *L. cuneatum* has a much older, unrecorded geological history; therefore, it may represent another example of inherited Tethyan distribution.

Acknowledgements: JH contribution was supported by VEGA 2/0122/18 and GACR 18-05935S projects. AP was supported partly by the Hertie Foundation (Frankfurt) and partly by statutory funds of the Institute of Paleobiology. We also gratefully thank G.W. Maneveldt and the anonymous reviewer for their helpful comments that significantly improved the manuscript.

References

- Adey W.H. 1970: The effects of light and temperature on growth rates in boreal-subarctic crustose corallines. *Journal of Phycology* 6, 269–276. <https://doi.org/10.1111/j.1529-8817.1970.tb02392.x>
- Adey W.H. 1975: Temperature control of reproduction and productivity in a subarctic coralline alga. *Phycologia* 12, 111–118. <https://doi.org/10.2216/i0031-8884-12-3-111.1>
- Adey W.H. & McKibbin D.L. 1970: Studies on the Maerl Species *Phymatolithon calcareum* (Pallas) nov. comb. and *Lithothamnion corallioides* Crouan in the Ria de Vigo. *Botanica Marina* 13, 100–106. <https://doi.org/10.1515/botm.1970.13.2.100>
- Adey W.H. & Sperapani C.P. 1971: The biology of *Kvaleya epilaeva*, a new parasitic genus and species of Corallinaceae. *Phycologia* 10, 29–42. <https://doi.org/10.2216/i0031-8884-10-1-29.1>

- Adey W.H. & Vassar J.M. 1975: Colonization, succession and growth rates of tropical crustose coralline algae (Rhodophyta, Cryptonemiales). *Phycologia* 14, 55–69. <https://doi.org/10.2216/i0031-8884-14-2-55.1>
- Adey W.H., Masaki T. & Akioka H. 1974: *Ezo epiyessoense*, a new parasitic genus and species of Corallinaceae (Rhodophyta, Cryptonemiales). *Phycologia* 13, 329–344. <https://doi.org/10.2216/i0031-8884-13-4-329.1>
- Athanasiadis A. 1999: *Mesophyllum macedonis*, nov. sp. (Rhodophyta, Corallinales), a putative Tethyan relic in the North Aegean Sea. *European Journal of Phycology* 34, 239–252. <https://doi.org/10.1017/S0967026299002103>
- Athanasiadis A. & Ballantine D.L. 2014: The genera *Melyvonnea* gen. nov. and *Mesophyllum* s.s. (Melobesioideae, Corallinales, Rhodophyta) particularly from the central Atlantic Ocean. *Nordic Journal of Botany* 32, 385–436. <https://doi.org/10.1111/njb.00265>
- Bailey J.C. 1999: Phylogenetic positions of *Lithothamnium incrustans* and *Titanoderma pustulatum* (Corallinaceae, Rhodophyta) based on 18S rRNA gene sequence analyses, with a revised classification of the Lithophylloideae. *Phycologia* 38, 208–216. <https://doi.org/10.2216/i0031-8884-38-3-208.1>
- Bassi D., Braga J.C. & Iryu Y. 2009: Palaeobiogeographic patterns of a persistent monophyletic lineage: *Lithophyllum pustulatum* species group (Corallinaceae, Corallinales, Rhodophyta). *Palaeogeography, Palaeoclimatology, Palaeoecology* 284, 237–245. <https://doi.org/10.1016/j.palaeo.2009.10.003>
- Basso D., Fravega P. & Vannucci G. 1997: The Taxonomy of *Lithothamnium ramosissimum* (Gümbel non Reuss) Conti and *Lithothamnium operculatum* (Conti) Conti (Rhodophyta, Corallinaceae). *Facies* 37, 167–182. <https://doi.org/10.1007/BF02537377>
- Basso D., Coletti G., Bracchi V.A. & Yazdi-Moghadam M. 2019: Lower Oligocene coralline algae of the Uromieh section (Qom Formation, NW Iran) and the oldest record of *Titanoderma pustulatum* (Corallinophycidae, Rhodophyta). *Rivista Italiana di Paleontologia e Stratigrafia* 125, 197–218.
- Bitner M.A. & Motchurova-Dekova N. 2016: Middle Miocene (Badenian) brachiopods from Yasen, northwestern Bulgaria: taxonomic composition and biogeographical significance. *Neues Jahrbuch für Geologie und Paläontologie* 279, 7–22. <https://doi.org/10.1127/njgpa/2016/0536>
- Bitner M.A., Logan A. & Gischler E. 2008: Recent brachiopods from the Persian Gulf and their biogeographical significance. *Scientia Marina* 72, 279–285. <https://doi.org/10.3989/scimar.2008.72n2279>
- Bittner L., Payri C.E., Maneveldt G.W., Couloux A., Cruaud C., de Reviers B. & Le Gall L. 2011: Evolutionary history of the Corallinales (Corallinophycidae, Rhodophyta) inferred from nuclear, plastid and mitochondrial genomes. *Molecular Phylogenetics and Evolution* 61, 697–713. <https://doi.org/10.1016/j.ympev.2011.07.019>
- Braga J.C. & Aguirre J. 1995: Taxonomy of fossil coralline algal species: Neogene Lithophylloideae (Rhodophyta, Corallinaceae) from southern Spain. *Review of Palaeobotany and Palynology* 86, 265–285. [https://doi.org/10.1016/0034-6667\(94\)00135-7](https://doi.org/10.1016/0034-6667(94)00135-7)
- Braga J.C. & Bassi, D. 2007: Neogene history of *Sporolithon* Heydrich (Corallinales, Rhodophyta) in the Mediterranean region. *Palaeogeography, Palaeoclimatology, Palaeoecology* 243, 189–203. <https://doi.org/10.1016/j.palaeo.2006.07.014>
- Braga J.C., Bosence D.W.J. & Steneck R.S. 1993: New anatomical characters in fossil coralline algae and their taxonomic implications. *Palaeontology* 36, 535–547.
- Brochet A.L., Guillemain M., Fritz H., Gauthier-Clerc M. & Green A.J. 2010a: Plant dispersal by teal (*Anas crecca*) in the Camargue: duck guts are more important than their feet. *Freshwater Biology* 55, 1262–1273. <https://doi.org/10.1111/j.1365-2427.2009.02350.x>
- Brochet A.L., Guillemain M., Gauthier-Clerc M., Fritz H. & Green A.J. 2010b: Endozoochory of Mediterranean aquatic plant seeds by teal after a period of desiccation: Determinants of seed survival and influence of retention time on germinability and viability. *Aquatic Botany* 93, 99–106. <https://doi.org/10.1016/j.aquabot.2010.04.001>
- Burgin S. & Renshaw A. 2008: Epizoochory, algae and the Australian Eastern Long-Necked Turtle *Chelodina longicollis* (Shaw). *The American Midland Naturalist* 160, 61–68. [https://doi.org/10.1674/0003-0031\(2008\)160\[61:EAATAE\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2008)160[61:EAATAE]2.0.CO;2)
- Caragnano A., Foetisch A., Maneveldt G.W., Millet L., Liu L-Ch., Lin S-M., Rodondi G. & Payri C.E. 2018: Revision of Corallinaceae (Corallinales, Rhodophyta): Recognizing *Dawsoniolithon* gen. nov., *Parvicellularium* gen. nov. and Chamberlainoideae subfam. nov. containing *Chamberlainium* gen. nov. and *Pneophyllum*. *Journal of Phycology* 54, 391–409. <https://doi.org/10.1111/jpy.12644>
- Coletti G., Hrabovský J. & Basso D. 2016: *Lithothamnium crispatum*: long-lasting species of non-geniculate coralline algae (Rhodophyta, Hapalidiales). *Carnets de Géologie* 16, 27–41. <https://doi.org/10.4267/2042/58720>
- Costa J.M., Ramos J.A., Silva L.P. Timoteo, S. Araújo P.M., Felgueiras M.S., Rosa A., Matos C., Encarnação P., Tenreiro P.Q. & Heleno R.H. 2013: Endozoochory largely outweighs epizoochory in migrating passerines. *Journal of Avian Biology* 44, 001–006. <https://doi.org/10.1111/j.1600-048X.2013.00271.x>
- de Queiroz K. 2007: Species Concepts and Species Delimitation. *Systematic Biology* 56, 879–886. <https://doi.org/10.1080/10635150701701083>
- Dechnik B., Webster J.M., Davies P.J., Braga J.C. & Reimer P.J. 2015: Holocene “turn-on” and evolution of the Southern Great Barrier Reef: Revisiting reef cores from the Capricorn Bunker Group. *Marine Geology* 363, 174–190. <https://doi.org/10.1016/j.margeo.2015.02.014>
- Dechnik B.J.M., Webb G.E., Nothdurft L., Dutton A., Braga J.C., Zhao J-X., Duce S. & Sadler J. 2017: The evolution of the Great Barrier Reef during the Last Interglacial Period. *Global and Planetary Change* 149, 53–71. <https://doi.org/10.1016/j.gloplacha.2016.11.018>
- Foslie M. 1909: Algologiske notiser VI. *Det Kongelige Norske Videnskabers Selskabs Skrifter* 1909 2, 1–59.
- Gabrielson P.W., Hughey J.R. & Diaz-Pulido G. 2018: Genomics reveals abundant speciation in the coral reef building alga *Porolithon onkodes* (Corallinales, Rhodophyta). *Journal of Phycology* 54, 429–434. <https://doi.org/10.1111/jpy.12761>
- Gischler E. 2003: Holocene lagoonal development in the isolated carbonate platforms off Belize. *Sedimentary Geology* 159, 113–123. [https://doi.org/10.1016/S0037-0738\(03\)00098-8](https://doi.org/10.1016/S0037-0738(03)00098-8)
- Gischler E. & Hudson J.H. 1998: Holocene development of three isolated carbonate platforms, Belize, Central America. *Marine Geology* 144, 333–347. [https://doi.org/10.1016/S0025-3227\(97\)00102-3](https://doi.org/10.1016/S0025-3227(97)00102-3)
- Gischler E. & Hudson J.H. 2004: Holocene development of the Belize Barrier Reef. *Sedimentary Geology* 164, 223–236. <https://doi.org/10.1016/j.sedgeo.2003.10.006>
- Gischler E., Hudson J.H., Humblet M., Braga J.C., Eisenhauer A., Isaack A., Anselmetti F.S. & Camoin G.F. 2016: Late Quaternary barrier and fringing reef development of Bora Bora (Society Islands, south Pacific): first subsurface data from the Darwin type barrier-reef system. *Sedimentology* 63, 1522–1549. <https://doi.org/10.1111/sed.12272>
- Gischler E. Humblet M., Braga J.-C. & Eisenhauer A. 2018: Last interglacial reef facies and late Quaternary subsidence in the

- Maldives, Indian Ocean. *Marine Geology* 406, 34–41. <https://doi.org/10.1016/j.margeo.2018.09.001>
- Green A.J., Frisch D., Michot T.C., Allain L.K. & Barrow W.C. 2013: Endozoochory of seeds and invertebrates by migratory waterbirds in Oklahoma. *Limnetica* 3, 39–46. <https://doi.org/10.23818/limn.32.05>
- Gregory M.R. 1983: Virgin Plastic Granules on Some Beaches of Eastern Canada and Bermuda. *Marine Environmental Research* 10, 73–92. [https://doi.org/10.1016/0141-1136\(83\)90011-9](https://doi.org/10.1016/0141-1136(83)90011-9)
- Harriott V.J. 1999: Coral growth in subtropical eastern Australia. *Coral Reefs* 18, 281–291. <https://doi.org/10.1007/s003380050195>
- Harvey A.S., Woelkerling W.J. & Millar A.J.K. 2009: The genus *Lithophyllum* (Lithophylloideae, Corallinaceae, Rhodophyta) in south-eastern Australia, with the description of *L. riosmenae*, sp. nov. *Australian Systematic Botany* 22, 296–317. <https://doi.org/10.1071/SB08051>
- Harzhauser M., Kroh A., Mandic O., Piller W.E., Göhlich U., Reuter M. & Berning B. 2007: Biogeographic responses to geodynamics: A key study all around the Oligo–Miocene Tethyan Seaway. *Zoologischer Anzeiger* 246, 241–256. <https://doi.org/10.1016/j.jcz.2007.05.001>
- Harzhauser M. & Piller W.E. 2007: Benchmark data of a changing sea – Palaeogeography, Palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253, 8–31. <https://doi.org/10.1016/j.palaeo.2007.03.031>
- Hernandez-Kantun J.J., Gabrielson P., Hughey J.R., Pezzolesi L., Rindi F., Robinson N.M., Peña V. Riosmena-Rodriguez R., Le Gall L. & Adey W. (2016) Reassessment of the branched *Lithophyllum* spp. (Corallinales, Rhodophyta) in the Caribbean Sea with global implications. *Phycologia* 55, 619–639. <https://doi.org/10.2216/16-7.1>
- Hou Z. & Li S. 2018: Tethyan changes shaped aquatic diversification. *Biological reviews* 93, 874–896. <https://doi.org/10.1111/brv.12376>
- Hrabovský J., Basso D. & Doláková N. 2016: Diagnostic characters in fossil coralline algae (Corallinophycidae, Rhodophyta) from the Miocene of Southern Moravia (Carpathian Foredeep, Czech Republic). *Journal of Systematic Palaeontology* 14, 499–525.
- Humblet M., Potts D.C., Webster J.M., Braga J.C., Iryu Y., Yokoyama Y., Bourillot R., Searc C., Droxler A., Fujita K., Gischler E. & Kan H. 2019: Late glacial to deglacial variation of coralgal assemblages in the Great Barrier Reef, Australia. *Global and Planetary Change* 174, 70–91. <https://doi.org/10.1016/j.gloplacha.2018.12.014>
- Johansen H.W. 1981: Coralline Algae: A First Synthesis. *CRC Press*, Boca Raton, 1–239.
- John D.N. 1974: New records of *Ascophyllum nodosum* (L.) Le Jol. from the warmer parts of the Atlantic Ocean. *Journal of Phycology* 10, 243–244. <https://doi.org/10.1111/j.1529-8817.1974.tb02708.x>
- Johnson M.D., Moriarty V.W. & Carpenter R.C. 2014: Acclimatization of the Crustose Coralline Alga *Porolithon onkodes* to Variable pCO₂. *PLoS ONE* 9, e87678. <https://doi.org/10.1371/journal.pone.0087678>
- Kato A., Baba M. & Suda S. 2011: Revision of the Mastophoroideae (Corallinales, Rhodophyta) and Polyphyly in nongeniculate species widely distributed on Pacific coral reefs. *Journal of Phycology* 47, 662–672. <https://doi.org/10.1111/j.1529-8817.2011.00996.x>
- Kato A., Baba M. & Suda S. 2013: Taxonomic circumscription of heterogenous species *Neogoniolithon brassica-florida* (Corallinales, Rhodophyta) in Japan. *Phycological Research* 61, 15–26. <https://doi.org/10.1111/j.1440-1835.2012.00665.x>
- Keats D. 1995: *Lithophyllum cuneatum* sp. nov. (Corallinaceae, Rhodophyta), a new species of non-geniculate coralline alga semi-endophytic in *Hydrolithon onkodes* and *Neogoniolithon* sp. from Fiji, South Pacific. *Phycological Research* 43, 151–160. <https://doi.org/10.1111/j.1440-1835.1995.tb00019.x>
- Leeuwen van C.H.A., Lovas-Kiss Á., Ovegård M. & Green A. 2017: Great cormorants reveal overlooked secondary dispersal of plants and invertebrates by piscivorous waterbirds. *Biology Letters* 13, 20170406. <https://doi.org/10.1098/rsbl.2017.0406>
- Lewis L.R., Behling E., Gousse H., Qian E., Elphick Ch.S., Lamarre J-F., Bêty J., Liebezeit J., Rozzi R. & Goffinet B. 2014: First evidence of bryophyte diaspores in the plumage of transequatorial migrant birds. *PeerJ* 2, e424. <https://doi.org/10.7717/peerj.424>
- Lovas-Kiss Á., Sonkoly J., Vincze O., Green A.J., Takács A. & Molnár A. 2015: Strong potential for endozoochory by waterfowl in a rare, ephemeral wetland plant species, *Astragalus contortuplicatus* (Fabaceae). *Acta Societatis Botanicorum Poloniae* 84, 321–326. <https://doi.org/10.5586/asbp.2015.030>
- Lovas-Kiss Á., Sánchez M.I., Wilkinson D.M., Coughlan N.E., Alves A. & Green A.J. 2018: Shorebirds as important vectors for plant dispersal in Europe. *Ecography* 42, 1–12. <https://doi.org/10.1111/ecog.04065>
- Lukowiak M. 2016: Fossil and modern sponge fauna of southern Australia and adjacent regions compared: interpretation, evolutionary and biogeographic significance of the late Eocene ‘soft’ sponges. *Contributions to Zoology* 85, 13–35. <https://doi.org/10.1163/18759866-08501002>
- Lukowiak M., Piser A. & Schlögl J. 2014: Bathyal sponges from the late early Miocene of the Vienna basin (central Paratethys, Slovakia). *Paläontologische Zeitschrift* 88, 263–277. <https://doi.org/10.1007/s12542-013-0197-x>
- Macaya E.C., López B., Tala F., Tellier F. & Thiel M. 2016: Float and Raft: Role of Buoyant Seaweeds in the Phylogeography and Genetic Structure of Non-buoyant Associated Flora. In: Hu Z-M. & Fraser C. (Eds.): *Seaweed Phylogeography*. Springer Science+ Business Media B.V., Dordrecht, 1–395. https://doi.org/10.1007/978-94-017-7534-2_4
- Maneveltd G.W. & Keats D.W. 2014: Taxonomic review based on new data of the reef-building alga *Porolithon onkodes* (Corallinaceae, Corallinales, Rhodophyta) along with other taxa found to be conspecific. *Phytotaxa* 190, 216–249. <https://doi.org/10.11646/phytotaxa.190.1.14>
- Maneveltd G.W., Gabrielson P.W. & Kangwe J. 2017: *Sporolithon indopacificum* sp. nov. (Sporolithales, Rhodophyta) from tropical western Indian and western Pacific oceans: First report, confirmed by DNA sequence data, of a widely distributed species of *Sporolithon*. *Phytotaxa* 326, 115–128. <https://doi.org/10.11646/phytotaxa.326.2.3>
- Maneveltd G.W., Gabrielson P.W., Townsend R.A. & Kangwe J. 2019: *Lithophyllum longense* (Corallinales, Rhodophyta): a species with a widespread Indian Ocean distribution. *Phytotaxa* 419, 149–168. <https://doi.org/10.11646/phytotaxa.419.2.2>
- Maneveltd G.W., Jeong S.Y., Cho T.O., Hughey J.R. & Gabrielson P.W. 2020: Reassessment of misapplied names, *Phymatolithon ferox* and *P. repandum* (Hapalidiales, Corallinophycidae, Rhodophyta) in South Africa, based on DNA sequencing of type and recently collected material. *Phycologia* 59, 449–455. <https://doi.org/10.1080/00318884.2020.1800298>
- Merwe Van der E., Miklasz K., Channing A., Maneveltd G.W. & Gabrielson P.W. 2015: DNA sequencing resolves species of *Spongiites* (Corallinales, Rhodophyta) in the Northeast Pacific and South Africa, including *S. agulhensis* sp. nov. *Phycologia* 54, 471–490. <https://doi.org/10.2216/15-38.1>
- Norton T.A. 1991: Conflicting Constraints on the Form of Intertidal Algae. *British Phycological Journal* 26, 203–218. <https://doi.org/10.1080/00071619100650191>
- Norton T.A. 1992: Dispersal by Macroalgae. *British Phycological Journal* 27, 293–301. <https://doi.org/10.1080/00071619200650271>

- O'Dea A., Lessios H.A., Coates A.G., Eytan R.I., Restrepo-Moreno S.A., Cione A.L., Collins L.S., de Queiroz A., Farris D.W., Norris R.D., Stallard R.F., Woodburne M.O., Aguilera O., Aubry M-P., Berggren W.A., Budd A.F., Cozzuol M.A., Coppard S.E., Duque-Caro H., Finnegan S., Gasparini G.M., Grossman E.L., Johnson K.G., Keigwin L.D., Knowlton N., Leigh E.G., Leonard-Pingel J.S., Marko P.B., Pyenson N.D., Rachello-Dolmen P.G., Soibelzon E., Soibelzon L., Todd J.A., Vermeij G.J. & Jackson J.B.C. 2016: Formation of the Isthmus of Panama. *Science Advances* 2, e1600883. <https://doi.org/10.1126/sciadv.1600883>
- Penrose D. & Woelkerling W.J. 1992: A reappraisal of *Hydrolithon* and its relationship to *Spongites* (Corallinaceae, Rhodophyta). *Phycologia* 31, 81–88. <https://doi.org/10.2216/i0031-8884-31-1-81.1>
- Pisera A., Lukowiak M., Fromont J. & Schuster A. 2018: First record of the genus *Vetulina* Schmidt, 1879 (Porifera: Demospongiae: Sphaerocladina) from the Indian Ocean with the description of two new species: biogeographic and evolutionary significance. *Marine Biodiversity* 48, 1529–1539. <https://doi.org/10.1007/s12526-017-0658-7>
- Popov S.V., Rögl F., Rozanov A.Y., Steininger F.F., Shcherba I.G. & Kováč M. 2004: Lithological–paleogeographic maps of Paratethys. 10 maps Late Eocene to Pliocene. 46 p., maps 1–10. CFS, Stuttgart.
- Por F.D. 1989: The legacy of Tethys: an aquatic biogeography of the Levant. *Kluwer Academic Publishers, Springer Netherlands, Heidelberg*, 1–216.
- Puckree-Padua C.A., Gabrielson P.W., Guhey J.R. & Maneveldt G.W. 2020: DNA sequencing of type material reveals *Pneophyllum marlothii* comb. nov. from South Africa and *P. discoideum* comb. nov. (Chamberlainoideae, Corallinales, Rhodophyta) from Argentina. *Journal of Phycology* 56, 1625–1641. <https://doi.org/10.1111/jpy.13047>
- Reid R.E.H. 1967: Tethys and the zoogeography of some modern and Mesozoic Perifera. In: Adams C.G. & Ager D.V. (Eds.): Aspects of Tethyan biogeography. *Systematic Association*, London, 171–181.
- Richards J.L., Gabrielson P.W. & Fredericq S. 2014: New Insights into the Genus *Lithophyllum* (Lithophylloideae, Corallinaceae, Corallinales) from Deepwater Rhodolith Beds Offshore the NW Gulf of Mexico. *Phytotaxa* 190, 162–175. <https://doi.org/10.11646/phytotaxa.190.1.11>
- Rösler A., Perfectti F., Peña V. & Braga J.C. 2016: Phylogenetic relationships of Corallinaceae (Corallinales, Rhodophyta): taxonomic implications for reef-building corallines. *Journal of Phycology* 52, 412–431. <https://doi.org/10.1111/jpy.12404>
- Rothäusler E., Gutow L. & Thiel M. 2012: Floating Seaweeds and Their Communities. In: Wiencke C. & Bischof K. (Eds.): Seaweed Biology, Novel Insights Into Ecophysiology, Ecology and Utilization. *Springer-Verlag, Berlin Heidelberg*, 1–514. https://doi.org/10.1007/978-3-642-28451-9_17
- Saunders G.W. 2014: Long distance kelp rafting impacts seaweed biogeography in the Northeast Pacific: the kelp conveyor hypothesis. *Journal of Phycology* 50, 968–974. <https://doi.org/10.1111/jpy.12237>
- Schuster A., Pisera A., Kelly M., Bell L.J., Pomponi S.A., Woerheide G.E. & Erpenbeck D. 2018: New species and a molecular dating analysis of *Vetulina* Schmidt, 1879 (Porifera: Demospongiae: Sphaerocladina) reveal an ancient relict fauna with Tethys origin. *Zoological Journal of the Linnean Society* 184, 585–604. <https://doi.org/10.1093/zoolinnean/zlx114>
- Setchell W.A. & Mason L.R. 1943: *Goniolithon* and *Neogoniolithon*: two genera of crustose coralline algae. *Proceedings of the National Academy of Science of United States of America* 29, 87–92. <https://doi.org/10.1073/pnas.29.3-4.87>
- Steneck R.S. 1982: A Limpet-Coralline Algal Association: Adaptations and Defenses Between a Selective Herbivore and its Prey. *Ecology* 63, 507–522. <https://doi.org/10.2307/1938967>
- Steneck R.S. 1986: The ecology of coralline algal crusts: Covergent patterns and adaptative strategies. *Annual Review of Ecology, Evolution, and Systematic* 17, 273–303. <https://doi.org/10.1146/annurev.es.17.110186.001421>
- Thiel M. & Gutow L. 2005: The ecology of rafting in the marine environment. I. The floating substrata. In: Gibson R.N., Atkinson R.J.A. & Gordon J.D.M. (Eds.): *Oceanography and Marine Biology: An Annual Review* 42. *CRC Press, Boca Raton*, 1–600.
- Thorsen M.J., Dickinson K.J.M. & Seddon P.J. 2009: Seed dispersal system in the New Zealand flora. *Perspective in Plant Ecology, Evolution and Systematics* 11, 285–309. <https://doi.org/10.1016/j.ppees.2009.06.001>
- Viana D.S., Santamaria L. & Figuerola J. 2016: Migratory Birds as Global Dispersal Vectors. *Trends in Ecology & Evolution* 31, 763–775. <https://doi.org/10.1016/j.tree.2016.07.005>
- Winston J.E., Gregory M.R. & Stevens L.M. 1997: Encrusters, Epibionts, and Other Biota Associated with Pelagic Plastics: A Review of Biogeographical, Environmental, and Conservation Issues. In: Coe J.M. et. al. (Eds.): *Marine Debris. Springer-Verlag, New York*, 1–432. https://doi.org/10.1007/978-1-4613-8486-1_9
- Woelkerling W.J. & Campbell S.J. 1992: An account of southern Australian species of *Lithophyllum* (Corallinaceae, Rhodophyta). *Bulletin of the British Museum of Natural History (Botany)* 22, 1–107.
- Woelkerling W.J., Bassi D. & Iryu Y. 2012: *Hydrolithon braganum* sp. nov. (Corallinaceae, Rhodophyta), the first known exclusively fossil semi-endophytic coralline red alga. *Phycologia* 51, 604–611. <https://doi.org/10.2216/11-119.1>
- Woelkerling W.J., Iryu Y. & Bassi D. 2013: Fossil semi-endophytic species of *Lithophyllum* (Corallinaceae, Rhodophyta) from Tahiti, including *L. kenjikonishii* sp. nov., and their taphonomic signatures. *Phycologia* 52, 387–397. <https://doi.org/10.2216/13-129.1>