



A taxonomic and distributional study of the rhodolith-forming species *Lithothamnion muelleri* (Corallinales, Rhodophyta) in the Eastern Pacific Ocean

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Lithothamnion muelleri is reported for the first time as one of the main components of rhodolith beds along the Eastern Pacific Ocean based on samples from Washington State (USA), Pacific Baja California (México), southern Nicaragua, and Costa Rica. Individual rhodoliths ranged from fruticose to lumpy in morphology, and bi-sporangial, tetrasporangial, and gametangial plants were similar to those described from Australia and Brazil. Our study revealed a surprisingly wide latitudinal distribution of this species along the American continent. Its documentation in the Eastern Pacific will facilitate a more accurate interpretation of the ecology, biology, and biogeography of rhodolith beds worldwide.

Key Words: coralline algae; Costa Rica; *Lithothamnion muelleri*; Mexico; Nicaragua; taxonomy; Washington

INTRODUCTION

Rhodoliths beds are widely distributed around the world (reviewed by Foster 2001). Recently, the species composition of these beds has been studied in the Gulf of California (Steller et al. 2009, Riosmena-Rodríguez et al. 2010), the northeastern Atlantic in Spain (Peña and Bárbara 2010), the southwestern Atlantic in Brazil (Amado-Filho et al. 2007, 2010, Figueiredo et al. 2007, Villas-Boas et al. 2009, Henriques et al. 2012), and southern Australia (Harvey and Bird 2008). These accounts are part of an increasing interest in the taxonomy, distribution, and ecology of this poorly known habitat.

In the Eastern Pacific Ocean, rhodolith beds are known from the Galapagos Islands, Costa Rica, and Panama

and from the Gulf of California to Alaska (Lemoine 1929, Dawson 1960, Konar et al. 2006, Fernández 2008, Littler and Littler 2008, Riosmena-Rodríguez et al. 2010). However, characterization of the species forming these beds is still incomplete. Recently, a number of rhodolith collections from these sites became available for taxonomic study. Amazingly, most of them appeared to be a single widespread species (Fig. 1) with wide ecological tolerances. This species, occurred in both intertidal and subtidal zones, at depths of up to 85 m, and was found growing on small stones, large rocks, and reef tops as well as on other algae (Wilks and Woelkerling 1995, p. 556, Womersley 1996, p. 183). In order to confirm that these collec-

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tions were truly a single species, we carried out a detailed morphological and anatomical study of the material from throughout its geographic range in the Eastern Pacific Ocean.

MATERIALS AND METHODS

Collections used for the study came from seven sites in the Eastern Pacific Ocean (Table 1). Specimens were collected by snorkeling at depths of 1-4 m and by SCUBA diving at depths of 5-16 m. Anatomical measurements and reproductive features were determined for specimens from each collection, including a total of 71 rhodolith individuals and all possible morphological variants. Terminology for the growth forms of coralline algal thalli follows Woelkerling et al. (1993), and anatomical terminology follows Woelkerling (1988). Permanent slides for optical microscopy were prepared using the methodology described by Riosmena-Rodríguez et al. (1999). Specimens for scanning electron microscopy (SEM) were air-dried, fractured under the stereoscope, placed on aluminum stubs and then gold-coated for observation under the SEM (S-2600N; Hitachi, Tokyo, Japan), at 20 kV at the Ryan Institute, National University of Galway, Ireland.

The following collections were examined: GIH 5800, One Mile Reef, San Juan Island, San Juan County, Washington, USA, 11 m depth, April 20, 1983, collector (col.) S. Norton and G. Hansen, determiner (det.) R. Riosmena; CFNI-582 and CFNI-643, La Peña Rota and Guacalito, Nicaragua, 11 and 5.5 m depth respectively, July 3, 2009, col. C. Fernández-García, det. N. M. Robinson; GGMX-1023c, GGMX-1023d, GGMX-1024e, Maria Magdalena Island, Mexico, 3-4 m depth, November 16, 2010, col. G. Gallard and R. Riosmena, det. N. M. Robinson; INMX-1066, Santa Rosalia, Gulf of California, Mexico, 1 m depth, March 28, 2009, col. R. Riosmena, det. N. M. Robinson; CFCR-876, Bahía Virador, Costa Rica, 5-6 m depth, August 1, 2009, col. C. Fernández-García, det. N. M. Robinson; CFCR-798, Marino Ballena National Park, Ballena Island, Costa Rica, 15-16 m depth, July 16, 2009, col. C. Fernández-García, det. N. M. Robinson.

RESULTS

The vegetative and reproductive anatomy of the specimens examined indicated that all thalli did fall within the morphological circumscription of *Lithothamnion muelleri* even with striking differences in their habitats.



Fig. 1. Map showing the new distribution of *Lithothamnion muelleri* along the coast of the Americas. 1, San Juan Island, Washington, USA; 2, Bahía Concepción, Gulf of California, Mexico; 3, Punta Galeras, Mexico; 4, Santa Rosalia, Mexico; 5, Loreto, Mexico (Rivera et al. 2004, Foster et al. 2007, Riosmena-Rodríguez et al. 2012); 6, María Magdalena Island, Mexico; 7, La Peña Rota, Nicaragua; 8, Ballena Island (Marino Ballena National Park), Costa Rica; 9, Bahía Virador, Costa Rica; 10, Archipelago Juan Fernández, Chile (Ramírez and Santelices 1991); 11, Espirito Santo, Brazil (Amado-Filho et al. 2010, Henriques et al. 2012); 12, Fuegia, Argentina (Papenfuss 1964). Records for 1-4 and 6-9 are from the present study.

Lithothamnion muelleri Lenormand ex Rosanoff 1866 (Tables 1 & 2, Figs 2-4)

Lectotype. CN (herb. Lenormand), from Western Port Bay, Victoria, collected by W. H. Harvey 1851, communicated by F. Mueller, lectotype designed by Woelkerling 1983, p. 193, Fig. 1A.

Type locality. Western Port Bay, Victoria, collected by W. H. Harvey 1851, communicated by F. Mueller.

Illustrations of type material. Wilks and Woelkerling 1995, p. 572, Figs 1 & 2.

Heterotypic synonyms. *Archaeolithothamnion mirabile* Foslie 1899, p. 3; *Lithothamnion muelleri* f. *cingens* Foslie 1900, p. 69; *Lithothamnion gabrieli* Foslie 1905, p. 3; *Lithothamnion mirabile* (Foslie) Foslie 1909, p. 4; *Mesophyllum gabrielii* (Foslie) Adey, 1970 p. 24.

Vegetative morphology and anatomy

The vegetative structure of all specimens from the Eastern Pacific showed only slight variations. All thalli formed rhodoliths that were lumpy to fruticose in morphology

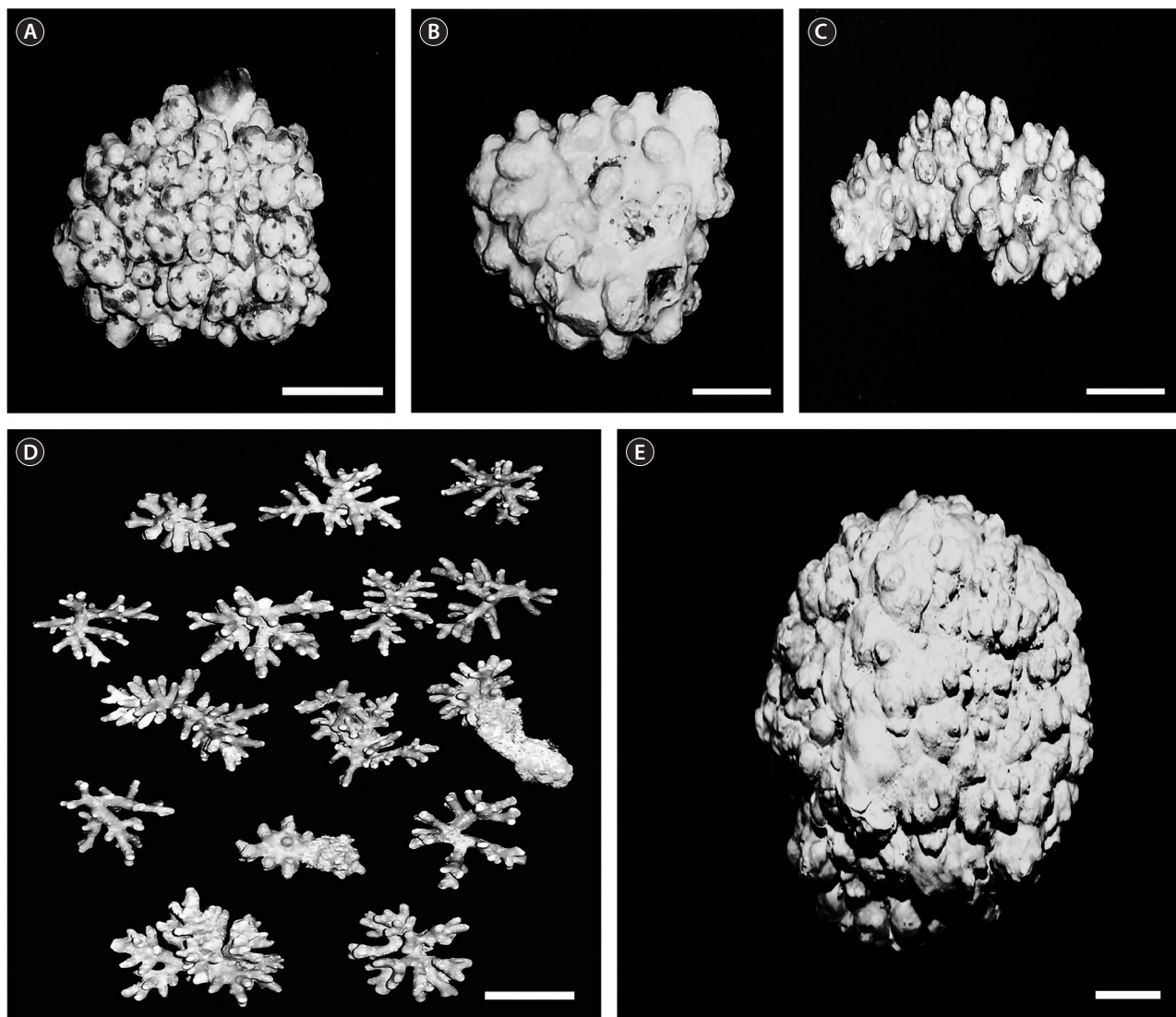


Fig. 2. *Lithothamnion muelleri*. Habit of the rhodolith thalli from different geographic areas. (A) Thallus from Mexico (María Magdalena Island). (B) Thallus from Nicaragua. (C) Thallus from Costa Rica. (D) Fruticose growth-form of *L. muelleri* from Washington. (E) Gametophyte from Costa Rica. Scale bars represent: A-E, 1 cm.

Table 1. Geographical sites where rhodolith samples were collected in Washington, Mexico, Nicaragua, and Costa Rica

Sampling site	Date	Latitude	Longitude	Depth (m)	Rhodoliths collected	Herbarium / Collection No.
Washington: One Mile Reef, San Juan Island	Apr 20, 1983	48°32.1' N	122°59.7' W	11	25	GIH/HMSC 5800
Mexico: Santa Rosalia, Gulf of California	Mar 28, 2009	27°19.9' N	112°14.9' W	1	1	INMX-1066
Mexico: María Magdalena Island	Nov 16, 2010	21°26.9' N	106°21.8' W	3-4	15	GGMX-1023c, GGMX-1023d, GGMX-1024e
Nicaragua: La Peña Rota	Jul 3, 2009	11°14.0' N	85°52.0' W	11	10	CFNI-582
Nicaragua: Guacalito	Jul 3, 2009	11°2.3' N	86°00.1' W	5.5	10	CFNI-643
Costa Rica: Bahía Virador	Aug 1, 2009	10°36.9' N	85°41.4' W	5-6	6	CFCR-876
Costa Rica: Marino Ballena National Park, Ballena Island	Jul 16, 2009	9°06.3' N	83°43.6' W	15-16	4	CFCR-798

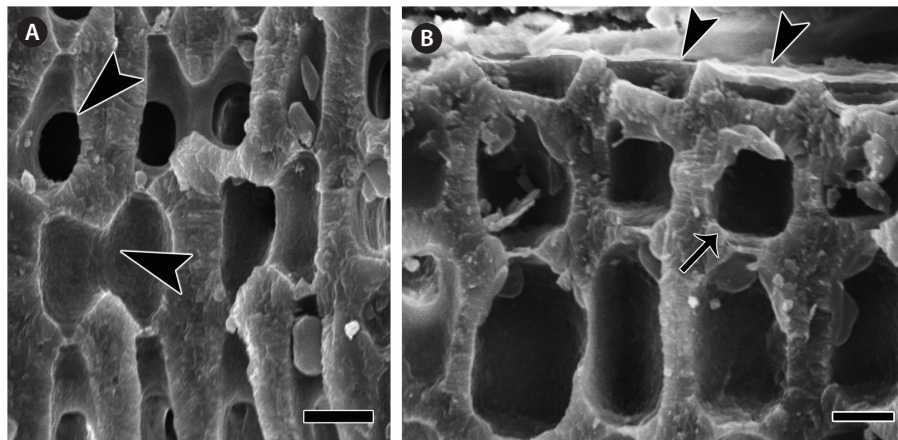


Fig. 3. *Lithothamnion muelleri*. Vegetative features. Scanning electron microscopy (SEM) photograph. (A) Longitudinal section showing fusion cells (arrowheads). (B) Longitudinal section showing flared epithallial cells (arrowheads) and subepithallial cells (arrow) that are similar in length to their immediate inward derivatives. Scale bars represent: A & B, 25 µm.

(Fig. 2). The protuberances were cylindrical and typically 5-7 mm in diameter and 2-8 mm long. All branches were pseudoparenchymatous with monomerous construction. Cells of the filaments were 10-30 µm long and 7-15 µm in diameter, and they were joined by cell fusions (arrowheads in Fig. 3A). In the epithallus filaments terminated in flared cells (arrowheads in Fig. 3B), 2-5 µm long and 7-10 µm in diameter. The subepithallial cells (arrow in Fig. 3B) were similar in length or shorter than their immediate inward derivatives. Trichocytes were absent. Clear growth bands were visible in many specimens. The monomerous internal structure of the rhodoliths consisted of a single system of branched filaments that formed a core and peripheral region. Portions of the core filaments and their derivatives curved outwards to the thallus surface forming a regular banding in the peripheral region.

Reproductive anatomy

The reproductive thalli, when present, also shared critical features (see Table 2). The bi and tetrasporangial thalli all had multiporate conceptacles with 20-60 pores per chamber, and in surface view each had a protruding roof that sometimes sank centrally leaving the margin elevated like a ring (Fig. 4A & B). In tetrasporangial conceptacles, the roof filaments bordering the pore canals (arrowhead in Fig. 4C) were composed of 3-5 cell layers of similar size and shape to other roof filament cells, and there was no depression around the pore. In surface view each pore was surrounded by 7-9 rosette cells which normally appeared collapsed and equal in size and shape to the other epithallial cells (Fig. 4D). Bisporos, found only

in Washington and Costa Rica, had dimensions similar to or larger than those known from Australian populations of this species. Carposporangial conceptacles were uniporate (Fig. 4E & F), and the roofs protruded above the thallus surface. Commonly, the conceptacle pores lacked senescent cells lining the pore (arrowhead in Fig. 4F). Spermatangial conceptacles were uniporate, and the roofs protruded above or were flush with the surrounding thallus surface. Branched spermatangial filaments arose from the floor and wall of the conceptacle chamber. In the type material, sterile cells were present within the conceptacle chamber. However, in our collections, these cells were either not evident or appeared degenerated due to tetrasporangial development or to poor preservation of the older collections.

Habitats and ecology

There were some similarities and some surprising differences in the habitats of the collections. At One Mile Reef in Washington (located one nautical mile SE of the Friday Harbor Laboratories), the bed contained only one rhodolith-forming species, *L. muelleri*. Swept by strong tidal currents, the rhodoliths occurred at 11 m depth and were located near a gravel bottom at the base of a rocky reef composed of outcroppings and boulders honeycombed with caves and crevices. The water temperature ranged from 7 to 10°C. In the Gulf of California, the beds always contained more than one rhodolith-forming species (Riosmena-Rodríguez et al. 2010). The habitats had flat to gently sloping bottoms, and they were in semi-protected sites around islands and in bays with depth ranges

of 3-40 m. In Nicaragua and Costa Rica, the rhodolith beds occurred at depths of 5.5-16 m, and they were on sandy and rocky bottoms associated with coral communities. Most of the material for this study was collected during the dry season when upwelling occurs, and the sites were located in Papagayo, an upwelling region where the water is rich in phosphates and nitrates. In this area the water temperature typically ranges from 23 to 27°C, but a single upwelling episode can cause the temperature to drop 12°C (Fernández-García et al. 2012).

Geographic distribution

L. muelleri is a species with previous records for South and Western Australia (Wilks and Woelkerling 1995, Womersley 1996), New Zealand (Nelson 2012), and the tropical and subtropical Western Atlantic (Wynne 2011). It is known from South America (Espírito Santo) (Amado-Filho et al. 2010), the Gulf of California (Rivera et al. 2004, Foster et al. 2007, Riosmena-Rodríguez et al. 2012), and Korea (Lee and Kang 2001). These records and the localities provided in our work indicate a wide distribution of this species in the Western Pacific (Australia and New Zealand), the Eastern Pacific (Washington to Costa Rica), and the Southwestern Atlantic (Brazil).

DISCUSSION

The exceedingly wide range of this species makes us wonder if the taxonomy is correct and if there might be cryptic species involved such as those described in recent molecular studies (Broom et al. 2008, Walker et al. 2009, Bittner et al. 2011). Unfortunately, our material was not well enough preserved to use molecular methods to detect these species. So instead, we carefully examined the diagnostic morphological and life history features that were available in an attempt to shed light on variations that might offer clues to any hidden species. Most characteristics were quite uniform, but a few were variable.

Tetrasporangial roof anatomy

Wilks and Woelkerling (1995) considered characteristics of tetrasporangial roof anatomy as diagnostic for Australian species of *Lithothamnion* Heydrich. In order to differentiate genera and species in the subfamily Melobesioideae, recent descriptions have included the following features: 1) the position and shape of the conceptacle chambers, 2) the number and shape of cells forming the roofs of conceptacles, 3) the presence or absence of palisade cells within the chamber, and 4) the number of

Table 2. Morphometric reproductive characteristics of *Lithothamnion muelleri* from populations in Washington, Mexico (María Magdalena Island), Costa Rica, Nicaragua, Southern Australia, and Brazil

	Washington	Mexico	Costa Rica	Nicaragua	Southern Australia	Brazil	Brazil
No. of cells in conceptacle chamber roof	3-5	3-5	3-5	3-5	5-9	5-6	7-9
Bisporangial conceptacle chamber diameter (µm)	400-450	ND	300-480	ND	ND	ND	ND
Bisporangial conceptacle chamber length (µm)	250-350	ND	200-350	ND	ND	ND	ND
Tetrasporangial conceptacle chamber diameter (µm)	400-700	210-350	350-700	250-700	280-780	350-500	375-755
Tetrasporangial conceptacle length (µm)	200-250	100-210	170-250	150-200	150-200	150-190	200-320
Mature tetra / bisporangia length (µm)	120-200	50-120	80-120	ND	100-175	ND	145-147
Mature tetra / bisporangia diameter (µm)	30-150	25-60	50-80	ND	30-140	ND	57-59
No. of rosette cells around the pore	ND	7-8	7-9	7-8	ND	6-7	8-10
Source	Present study	Present study	Present study	Present study	Wilks and Woelkerling 1995, Womersley 1996	Amado-Filho et al. 2010	Henriques et al. 2012

ND, not detected.

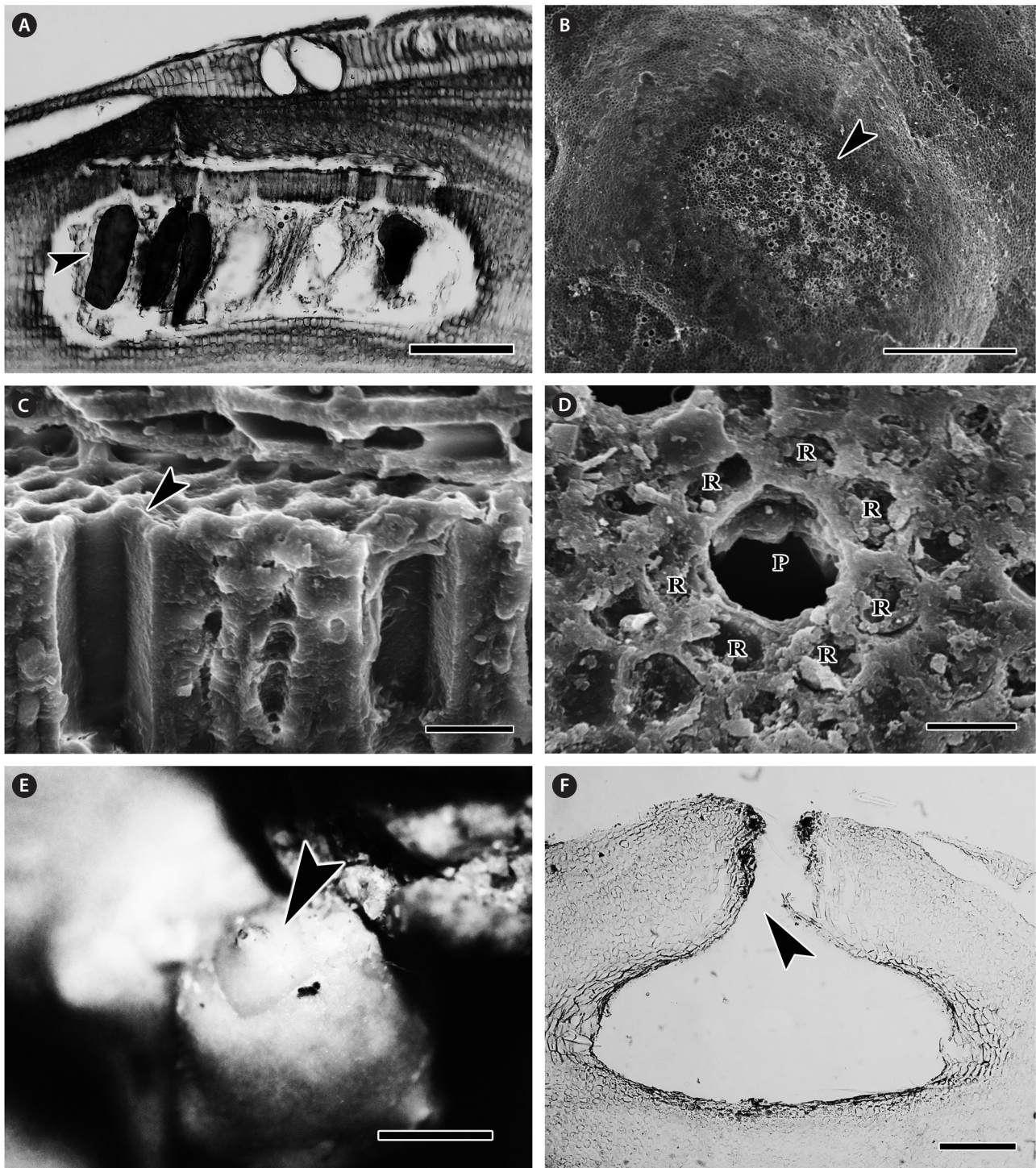


Fig. 4. *Lithothamnion muelleri*. Reproductive features. (A) Longitudinal section of a tetrasporangial conceptacle bearing tetraspores (arrowhead). (B) Surface view of the multiporate conceptacle chamber (arrowhead). (C) Longitudinal section of the pore area (arrowhead) of a multiporate conceptacle showing cells lining the pore that are of equal length and shape to other cells that compose the roof. (D) Surface view of one pore (P) belonging to a multiporate chamber surrounded by 7 rosette cells (R). (B-D) Scanning electron microscopy (SEM) photograph. (E) Uniporate carposporangial conceptacle (arrowhead). (F) Carposporangial conceptacle, empty after release of carposporangia, that is lacking senescent cells lining the pore (arrowhead). Scale bars represent: A & F, 100 µm; B, 500 µm; C & D, 25 µm; E, 2 mm.

rosette cells around the pore area. We looked closely at the last feature. Athanasiadis et al. (2004) and Athanasiadis and Adey (2006) considered the characteristics of the rosette cells surrounding the pore area in multiporate roofs as a reliable and easily accessible feature for separating species in the genera *Phymatolithon* Foslie and *Mesophyllum* Me. Lemoine in the North Pacific. We investigated this feature for North Pacific *Lithothamnion* species and have found that it is only reliable when used in combination with other characteristics such as the shape and position of the rosette cells in relation to pore area. In *L. muelleri* the rosette cells in surface view normally appear collapsed and similar in size and shape to the other epithallial cells. Moreover, the number of rosette cells around the pores is variable in different regions. In our material from the Eastern Pacific, there were 7-9 rosette cells present. Specimens from Brazil are reported to have 6-7 cells (Amado-Filho et al. 2010), 8-10 cells (Henriques et al. 2012) and most specimens from Australia have 8-9 cells (Womersley 1996, Fig. 76C), and 9-11 (Wilks and Woelkerling 1995, p. 575, Fig. 4D, LTB 15364). However, these differences did not seem to be significant enough to indicate separate species within *L. muelleri*.

Growth-form differences in populations

In Australia, the crustose stage of *L. muelleri* does not form rhodoliths (Wilks and Woelkerling 1995), but in North America, it generally does (Foster et al. 2007). In the literature growth-form variations have been attributed to differences in environmental factors such as hydrodynamic conditions, depth, coastal morphology or bioturbation (Bosellini and Ginsburg 1971, Riosmena-Rodríguez et al. 1999, Goldberg 2006, Gagnon et al. 2012). However, recent studies have shown that the ability to form rhodoliths may be caused by a genetic feature, a plesiomorphic trait inherited from a common ancestor (Hernández-Kantún unpublished data). Further genetic and environmental studies on rhodolith-forming species are obviously necessary if we are to accurately understand the factors generating their development.

Life history differences in populations

The major life history difference we see in our collections of *L. muelleri* is the occurrence of only bisporic populations at the end points of its range in Washington and Costa Rica. We assume this is due to environment stress. Indeed, this has been proposed by Adey et al. (2005) for another species, *L. tophiforme* (Esper) Unger,

from arctic / subarctic regions. These authors discovered bisporic populations of this species at depths of >10 m and temperatures of <10°C that they felt were apomictic, reproducing asexually. The low light and low temperature conditions could easily stress these populations. The end-point populations of *L. muelleri* endure high current and upwelling conditions, the latter often associated with rapid temperature changes. In the San Juan Islands, strong tidal currents and upwelling are common. In Costa Rica, periodic changes in currents and temperature have been well-studied in the Papagayo upwelling region where most of our collections were made. Upwelling occurs between December and April each year when the NE Trade Winds cross the lowlands from the Caribbean to the Pacific (Legeckis 1988, McCreary et al. 1989), and water temperatures fluctuate dramatically. Although temperature and current conditions appear to be the obvious environmental stressors generating bisporic populations, the exact mechanism of how this occurs has yet to be investigated in rhodolith populations.

Our collections and detailed morphological studies have documented the surprisingly wide latitudinal distribution of *L. muelleri* along the American continent. We have been unable to find stable morphological features that might differentiate cryptic subspecies. However, our study has underscored for us the critical need for additional studies on the taxonomy, distribution, and biology of coralline algae. These taxonomically difficult species dominate much of the subtidal zone, and their presence or absence may herald detrimental environmental changes. It is particularly urgent that basic taxonomic and distributional studies are completed on this important group so that the information can be used to recognize and possibly prevent future long-term damages to the marine environment.

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