Systematic survey of *Lithothamnion*, *Melobesia* and *Mesophyllum* species (Hapalidiaceae, Corallinales, Rhodophyta) recorded along the Atlantic coast of Mexico

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**Abstract**

Family Hapalidiaceae is represented in the Atlantic coast of Mexico by three genera and five species. *Lithothamnion sejunctum* is a new record for Mexico and represents the third record since it was first described and *L. crispatum* is recorded for the first time for North America Continent. *L. crispatum* and *L. occidentale* are developing as maerl in the subtidal zone to 50 m depth. *Melobesia membranacea* has the widest distribution interval in the study area. *Mesophyllum mesomorphum* is a species which it has few records in the study area. Detailed accounts are provided for each species along with information on synonymy, collections examined, distribution, and habitat. Qualitative characters associated with tetrasporangial / bisporangial conceptacle roof morphology and anatomy have provided a reliable basis for delimiting the Atlantic Mexican species of Hapalidiaceae.

**Key words:** description, morphology, *Lithothamnion, Melobesia, Mesophyllum*, new, records

**Introduction**

The biodiversity of Coralline red algae (Corallinales, Rhodophyta) along the Atlantic coast of Mexico is insufficiently known. These algae are characterized by cells walls impregnated with calcium carbonate, mainly calcite and aragonite which gives the thallus a hard, rigid texture (Chamberlain, 1983). *Lithothamnion* Heydrich, 1897: 412; *Melobesia* Lamouroux, 1812: 186 and *Mesophyllum* Lemoine, 1928: 251 are members of the subfamily Melobesioidae, Bizzozero, 1865: 109; Family Hapalidiaceae, Gray, 1864: 22. Although at least 46 species have been so far known as currently accepted taxonomically, no world monograph of this family exists and few detailed accounts of species have been produced (Woelkerling & Harvey 1992, Keats & Chamberlain 1994, Athanasiadis 1999, 2010, Harvey et al. 2003). Few records of these genera are reported from the Mexican coasts, they are uncommon species and habits mainly in subtidal settings. This paper presents the first detailed systematic account of corallines species belonging to the genera *Lithothamnion, Melobesia* and *Mesophyllum* (Hapalidiaceae, Rhodophyta) recorded from 2000 to 2013 along the Atlantic coast of Mexico.

**Material and methods**

Specimens of Hapalidiaceae were collected by reef-walking, snorkeling, SCUBA diving or dredged at Cabezo Sur (Veracruz); Isla Cozumel, Punta Pelicanos (Quintana Roo) and Sonda de Campeche (Campeche). Samples were preserved in 5% formalin/seawater. Preserved specimens were decalcified with 0.6M HNO₃ and dehydrated with ethyl alcohol. Small segments were embedded in paraffin and sectioned 9–12 µm thick with a manual microtome, fixed on slides with Riuter’s adhesive (Martoja & Martoja-Pierson 1970), and stained with aniline blue and hematoxilin-eosine for anatomical observations and measurements.
The morphological terms follow Woelkerling (1988) and Woelkerling et al. (1993). The classification system of Harvey et al. (2003) and Peña et al. (2011) are used throughout this paper. The diameters and lengths of epithallial cells (epithallus), dorsal region (cortex) and basal layers (medulla) were measured. Conceptacle measurements are given for height, inside diameter (the distance from one side to the other of a conceptacle chamber), and conceptacle canal diameter and height. Pertinent remarks about the morphology/anatomy, detailed descriptive accounts, specimens examined and distribution are provided for each species. In this study we made observations on a total of 50 specimens, of which only 21 belong to the genera of Hapalidiaceae. Specimens are housed at herbarium of the National School of Biological Sciences (ENCB), México City, Mexico.

**Results**

Three genera and five species of Hapalidiaceae were distinguished.

**Subfamily Melobesioideae Bizzozero, 1865:109**

*Lithothamnion* Heydrich 1897: 412
*Lithothamnion crispatum* Hauck (1878: 289) Figs. 1–6
Basionym: *Lithophyllum crispatum* (Hauck) Hauck 1885: 270
Heterotypic synonyms: see Basso et al. (2011)
Type Locality: Rovigno, Adriatic Sea

Description: Thalli belongs rhodolith with fruticose to foliose growth form. The protuberances are cylindrical to compressed, up to 15 mm long and up to 3 mm wide at their flared, distal end. Thallus is pseudoparenchymatous, monomerous and dorsiventrally organized; haustoria are unknown. The crustose portion of the thallus is 200–500 µm thick, with a medulla (ventral region) 50–100 µm thick, composed of filaments running more or less parallel to the thallus surface. The mean size of medullar cells is 19 µm in length and 10 µm in diameter. The ventral filaments curve toward the thallus surface to form a zoned dorsal region (cortex). Cortex cells measure 14.5–23.5 µm in length and 7–18 µm in diameter. Epithallial cells occur singly: they are flattened and flared and measure 3–5.5 µm in length and 7–14.5 µm in wide. Subepithallial initials longer than or as long as their inward derivatives. Cells of adjacent medulla and cortex are connected by cell fusions. Secondary pit connections and trichocytes have not been observed. The conceptacle roof is slightly protruding above the surrounding thallus surface, 20–50 µm thick, and composed of four to six layers of cells filaments lining the pore canals differ from other roof cell filaments in usually consisting of only two to three cells. In the Mexican material, the size of multiporate conceptacle chambers is 270–720 µm in diameter and 100–315 µm in height. Gametangial plants dioecious; 500–600 µm thickness, with the same vegetative structure as the vegetative plants; spermatangia produced in conceptacles in different thalli, spermatangial conceptacles uniporate, buried in the pseudoparenchymatous tissue or protruding, apiculate, scattered, elliptical chambers 450–500 µm diameter and 50–150 µm high, male conceptacle showing dendroid (branched) spermatangial systems on the floor, and simple (unbranched) spermatangial systems on the walls and roof of the conceptacle. Spermatangia are 2–3µm in diameter.

Remarks: The vegetative and reproductive features of our specimens correspond to those reported by Basso et al. (2011) from Mediterranean Sea material. These authors indicated that *L. crispatum* not only occurs in the Mediterranean, also is known to occur throughout the Atlantic and Indian Ocean and eastward to the Pacific coast of Australia. Geographical distribution: Adriatic, Croatia, France, Greece, Italy, Spain, Algeria, Libya, Turkey, Mauritania, Sudan, New Zealand, Australia, South Africa, Tanzania, Revillagigedo Islands, Maldives, Panama, Brazil (Basso et al. 2011, Guiry & Guiry 2014).

FIGURES 1–6. Lithothamnion crispatum, Campeche Banks (ENCB 19635). 1) Habit of a plant encrusting pebbles. 2) Habit of three rhodoliths. 3) Section through the thallus showing a strongly coaxially medulla (brace). 4) Section throughout dorsal region note cellular fusion (arrow). 5) Section through mature tetrasporangial conceptacle. 6) Mature male conceptacle with spermatangial filaments on the floor and roof of the chamber.
FIGURES 7–9. *Lithothamnion occidentale*, Campeche Banks (ENCB 19646). 7) Habit of two rhodoliths. 8) Transversal Section of branches, note the medulla (arrow) and cortex. 9) Section through mature tetrasporangial conceptacle, note the tetrasporangium (arrow) and in the box at the top right note two pore canal (arrows). FIGURES 10–12: *Lithothamnion sejunctum*, Banco Chinchorro (ENCB 18682). 10) Habit of a plant encrusting rocks. Brace indicated a species of *Lithophyllum*. 11) Section through the thallus showing monomorous construction, note the medulla (brace). 12) Section through dorsal region note the cortex (arrow).
**Lithothamnion occidentale** (Foslie) Foslie (1908: 3–4) Figs. 7–9

Basionym: *Lithothamnion fruticulosum var. occidentale* Foslie 1904: 12
Homotypic synonyms: *Lithothamnion fruticulosum var. occidentale* Foslie 1904: 12
Type Locality: Cruz Bay, St. John Island, US Virgin Islands.

Description: Thalli constitute rhodoliths, unattached, smooth and glossy and irregularly branched, others highly branched. Branches terete and 1–2 mm in diameter. Thallus is pseudoparenchymatous, haustoria are unknown. Branches with a medulla composed of plumose filaments running more or less parallel to the thallus surface. The mean size of medullar cells is 14–16 µm in length and 17–18 µm wide. The ventral filaments curve toward the thallus surface to form a zoned dorsal region (cortex). Cortex cells measure 35–37 µm in length and 15–19 µm in diameter. Epithallial cells occur singly: they are flattened and flared and measure 6–8 µm in length and 7–10 µm wide. Subepithallial cells are rounded-shape. Cells of adjacent medulla and cortex are connected by cell fusions. Secondary pit connections and trichocytes have not been observed. The multiporate conceptacle chamber is 240–330 µm in diameter and 170–180 µm high. The conceptacle roof is protruding above the surrounding thallus surface, 40–50 µm thick, and composed of two or three layers of cells filaments lining the pore canals differ from other roof cell filaments in usually consisting of only two to three cells. Tetrasporangia 70–80 µm high and 30–35 µm wide.

Remarks: Fragmented thallus was observed, representing the likely form of propagation of this species.

Geographical distribution: Florida, North Carolina, South Carolina, Cuba, Hispaniola, Puerto Rico, Brazil, Colombia, Venezuela, Indonesia (Taylor 1960, Guiry & Guiry 2014).


**Lithothamnion sejunctum** Foslie (1906: 3) Figs. 10–14

Type Locality: St. Croix, US Virgin Islands.

Description: Thalli are encrusting grown on intertidal rocks, following the contour of the substrate, without protuberances, attached to the substratum ventrally by cell adhesion, 180–250 µm thick. Thallus with monomorous construction; in transversal section medullar cells 30–38 µm long and 7–9 µm wide. Cortical cells 10–12 µm high and 6–7.5 µm wide. Subepithallial cells compressed, epithallial cells 2.5–3.5 µm high and 7–8 µm wide. Adjacent filaments linked by cell fusions, secondary pit-connections and trichocytes absent. The multiporate conceptacle chamber is 150–170 µm in diameter and 70–80 µm high. The conceptacle roof is protruding above the surrounding thallus surface, 50–70 µm thick, and composed of three or four layers of cells filaments lining the pore canals differ from other roof cell filaments in usually consisting of only two to three cells. Tetrasporangia 45–50 µm high and 20–25 µm wide.

Remarks: Taylor (1960) mentions that the thalli of *L. sejunctum* are epilithic and encrusting. Also, dimensions of tetrasporangial conceptacles are similar to those cited of Taylor. This is a new record for Mexico and represents the third record since it was first described.

Geographical distribution: Virgin Islands, Brazil (Taylor 1960, Guiry & Guiry 2014).

FIGURES 13–14. *L. sejunctum*. 13) Section through mature tetrasporangial conceptacle with tetrasporangium (arrow). 14) Pore canal lined by elongated-shape cells (arrow). FIGURES 15–18: *Melobesia membranacea*, Vigia Chico, Ascension Bay (ENCB 19327). 15) Superficial view of a multiporate conceptacle. The elevated conceptacles belong to *Pneophyllum* sp. 16) Section through the thallus showing a monostromatic crust. 17) Section through tetrasporangial conceptacle showing sporangia with zonately arranged spores (arrow). 18) Section through the thallus showing 4-5 layers of cells near the conceptacle.
**Melobesia** Heydrich 1897: 408

*Melobesia membranacea* (Esper) J.V. Lamouroux (1812: 186) Figs. 15–18

**Basionym:** *Corallina membranacea* Esper 1796: pl. Corallina XII

**Homotypic Synonyms**

- *Corallina membranacea* Esper 1796
- *Epilithon membranaceum* (Esper) Heydrich 1897
- *Lithothamnion membranaceum* (Esper) Foslie 1898

**Heterotypic Synonyms**

- *Hapalidium roseolum* Kützing 1843
- *Melobesia corticiformis* Kützing 1849
- *Hapalidium roseum* Kützing ex Areschoug 1852
- *Melobesia rosea* Rosanoff 1866
- *Lithothamnion corticiforme* (Kützing) Foslie 1898
- *Melobesia hildenbrantioides* (P.L.Crouan & H.M.Crouan) Foslie 1898
- *Melobesia coccinea* (P.L.Crouan & H.M.Crouan) Foslie 1898
- *Epilithon corticiforme* (Kützing) Heydrich 1908

**Type Locality:** West coast of France (Dawson 1960:8).

**Description:** Thallus pseudoparenchymatous, encrusting without protuberances, rounded, contiguous thalli ever overlapped. Continuous margin without orbital ridges which is confused with the substratum, lobed, crenate edge. Intertidal habitat epiphytic on leaves of *Thalassia testudinum*. Internal organization dorsiventral, thallus dimerous: composed of two distinct groups of filaments: a single ventral layer of laterally cohering filaments composed of rectangular cells: 10–12 µm length and 5–7 µm wide; and a second layer composed by epithallial cells: triangular or elliptical (partially covering the mother cell lying beneath), erect filaments: absent or reduced to few cells. Tetrasporangial conceptacles: multiporate (7–18 pores), hemispherical with flat roof, numerous, raised, spread on surface or grouped and confluent. Old conceptacles break leaving small oval cavities with raised edge, tetrasporangial chamber: 90–100 µm diameter and 50–60 µm high. Tetrasporangia 26–50 µm high and 15–26 µm wide.

**Remarks:** *Melobesia membranacea* was the commonest species in this study, observed at several localities. It was also the most frequently recorded species in earlier studies, probably because *M. membranacea* is readily recognized by multiporate conceptacle. *Melobesia* appears to be widespread, but many records require confirmation.

**Geographical distribution:** Florida, México, Virgin Islands, Panamá, Venezuela, Brazil, Ireland, Great Britain, New Zealand, Australia, Angola (Guiry & Guiry 2014).

**Examined material:** Mexico: Veracruz: Monte Pío (Sánchez-Rodríguez 1965: 12); Enmedio Island, Verde Island, Sacrificios Island (Ortega et al. 2001: 155); Campeche, Campeche (Ortega et al. 2001: 155); Yucatán: Dzilam de Bravo, 15-April-2007, Mendoza González & Mateo Cid (ENCB 20094); Alacranes Reef, 27-June-1961, Azis & Humm (ENCB 20093); Quintana Roo: Laguna Nichupté, 01-August-1984, Mendoza González & Mateo Cid (ENCB 20076); Playa del Carmen, 03-November-1984, Mendoza González & Mateo Cid (ENCB 20075); Punta Valencia, Ascensión Bay, 14-March-2009, Acosta Calderón (ENCB 20090); Punta Sacrificios, 16-April-2012, Mendoza González, García López & Mateo Cid (ENCB 20097); Vígia Chico, 18-May-1998, Mendoza González & Mateo Cid (ENCB 19327); Mujeres Island, 13-October-1983, Huerta Múzquiz, Mendoza González & Mateo Cid (ENCB 20095); Cozumel Island, San Juan Beach, 03-November-1984, Mendoza González & Mateo Cid (ENCB 20078); Chen Río, 21-June-2010, Mendoza González, Mateo Cid & Trinidad Calderón (ENCB 20092).

**Mesophyllum** Lemoine 1928:251

One species representing the genus *Mesophyllum* was identified during the present study.


**Basionym:** *Lithothamnion mesomorphum* Foslie 1901:5–6

**Homotypic Synonym:** *Lithothamnion mesomorphum* Foslie 1901

**Type locality:** Bermuda; [no other locality data]
FIGURES 19–24. *Mesophyllum mesomorphum*, Cozumel Island (ENCB 18725). 19) Habit of foliose thalli attached to red algae. 20) Section through the thallus showing a strongly coaxially medulla (brace). 21) Section through dorsal region noted the cortex (arrow). 22) Section through bisporangial conceptacle shows mature bisporangium (arrow). 23) Enlarged section through bisporangial conceptacle showing pore canal lined by elongated cells (arrow). 24) Detail of a pore canal of a multiporate roof shows from above, is surrounded by 6 rosette cells (arrows).
**Description**: Thalli are foliose, up to least 2 cm in extent, weakly attached and grow with major parts of their thallus unattached. The surface of the thallus is smooth, protuberances are lacking. The margins are always free and have a whitish border (cuticle). Growing on *Flahaultia* sp., collected by SCUBA at 11 m deep. The thallus is organized dorsiventrally and reaches 120–300 µm in thickness and composed of a predominantly coaxial medulla 80–200 µm thick, where cells form arching decumbent tiers in length series, medullar cells are 15–20 µm length and 10–12 µm wide; cortical cells are 6–9 µm length and 7–9 µm wide. The epithallium develop one or two layers of cells, epithallial cells are roundish to slightly flattened, 7–9 µm in diameter and 7–9 µm length. Fusions between medullar and cortex cells are common. Trichocytes and secondary pit connections are absent. Multiporate conceptacles are perforated by 60–90 pores develop bisporangia, within chambers that are 400–750 µm in diameter and 300–350 µm high and bisporangia are 110–120 µm high 50–60 µm wide. Pores are 45–50 µm length and 8–10 µm in apical diameter, in superficial view the pores of the conceptacle are surrounded by 6–7 rosette cells, in section roof the cells lining the pore canal are rounded and different in size and shape to contiguous epithallial cells. Gametangial thalli not observed.

**Remarks**: *M. mesomorphum* is easily distinguishable by its habit almost free, thallus lamellate, epithallium d gistomatic and the diameter of chambers’ bisporangial of 400–750 µm in diameter. However, the diameters of the sporangial chambers recorded by Taylor (1960) of 100–140 µm in diameter do not match with our specimens. Geographical distribution: Mexico: *Veracruz* Enmedio Island (Lehman & Tunnell 1992); *Quintana Roo* Puerto Morelos (Dreckmann *et al.* 1996); Cozumel Island (Mateo-Cid *et al.* 2006); Caribbean Islands, Colombia (Wynne 2011), Comoros, Seychelles, Korea, Australia, New Zealand, Hawaii and Federate States of Micronesia (Guiry & Guiry 2014).

Examined material: Mexico; *Campeche*: Campeche Banks, 15-June-2005, Mendoza González & Mateo Cid (ENCB 19201); *Quintana Roo*, Cozumel Island, Colombia Reef, 20°13’53”N, 87°01’09”W; 21-March-1994, Searles (ENCB 18725).

**Discussion**

*Morphological and reproductive features*

Eight *Lithothamnion* species are involved in Wynne’s (2011) checklist for the tropical and subtropical western Atlantic. Of these, *Lithothamnion glaciale* Kjellman and *L. muelleri* Rosanoff are well-studied species, both producing a thick thallus, to 4 mm, and lacking conceptacle protuberances. *Lithothamnion brasiliense* Foslie (1900) and *L. occidentale* (Foslie) Foslie (1908) have not been studied in a modern context, but the illustrations of putative type specimens in Printz (1929, pl. 14 fig. 6 and pl. 13 figs 15, 17) show the presence of extensive cortical branches, several millimeters in length. *Lithothamnion occidentale* has been described in shallow and maximum depth of 15–45 m in Florida, Colombia, Puerto Rico and Bermuda, this species grows unattached or entangled with other algae. Mexican plants of *L. occidentale* correspond to those described by Ballantine *et al.* (2004) for Puerto Rico. Mexican plants of *Lithothamnion sejunctum* Foslie (1906) possess sunken multiporate conceptacles (160–260 µm in diameter according to the protologue), while *L. ruptile* (Foslie) Foslie (1907) is a rhodolith-forming species lacking conceptacle protuberances. Recently, Athanasiadis & Ballantine (2011) described the nine species of *Lithothamnion* for the Atlantic Ocean: *L. carpoklonium* whom grows in shallow-sheltered waters attached to mangrove prop roots, in addition to developing dorsal protuberances formed by superimposition of uniporate (carpogonial) or multiporate conceptacles. On the other hand, Harvey *et al.* (2003) considered to *Lithothamnion indicum* Foslie and *Lithothamnion heteromorphum* (Foslie) Foslie as heterotypic synonyms of *L. superpositum*; whereas da Nóbrega *et al.* (2010) analyzed the morphology and anatomy of the specimens collected in Brazil and the type of *L. heteromorphum*, both the *L. heteromorphum* type and their collection, were identical to other species reported as *L. superpositum* around the world. On basis of their results they concluded that among the species described from the Brazilian coast, *L. heteromorphum* (Foslie) Foslie presented anatomical and reproductive characteristics similar to the referred species described from southern Africa and Australia. Consequently, these authors proposed to consider *L. heteromorphum* as a heterotypic synonym of *L. superpositum* and extending its distribution to the Western Atlantic. Finally, Basso *et al.* (2011) suggested that *Lithothamnion indicum* Foslie, 1907, *Lithothamnion heteromorphum* Foslie 1908 and *Lithothamnion superpositum* Foslie, 1900 are therefore conspecific with, and thus heterotypic synonyms of *Lithothamnion crispatum* Hauck, 1878, because of the latter having nomenclatural priority.
In our study, *Lithothamnion crispatum* occurs in two forms: a hard crust with small protuberances and others as unattached branched nodules with branches generally irregularly dichotomous or branches thought to be fused, but obvious branching; these differences observed with respect to morphology can be attributed to phenotypical plasticity, which is common in *Corallinales* (Woelkerling et al. 1993). Besides, the growth-form variations have been attributed to differences in environmental factors such as hydrodynamic conditions, depth, coastal morphology or environmental disruption (Robinson et al. 2013). In addition, the vegetative and reproductive features of our *L. crispatum* fully correspond to those described by Basso et al. (2011) for Mediterranean material. The presence of *L. crispatum* in the Atlantic coast of Mexico supports the deduction of Basso et al. (2011) that this species is cosmopolitan and that its forms is very variable.

Mexican plants of *Melobesia membranacea* always were found epiphytically on *Thalassia testudinum* together other epiphytic nongeniculate corallines. The vegetative and reproductive features of our *M. membranacea* fully correspond to those described by Wilks & Woelkerling (1991) from Western Australia. Finally, Mexican plants of *Mesophyllum mesomorphum* are in good agreement with the original material from the Bermuda (Ballantine et al. 2011), particularly in the development of unattached-superimposed branches with lobate margins, and having a predominantly coaxial medulla and a thicker thallus (up to 850 µm) resulting from a well-developed cortex.

**Diversity and distribution**

There are 200 species names in the Family Hapalidiaceae at present, of which 84 corresponds to *Lithothamnion*, 17 to *Melobesia* and 59 to *Mesophyllum*, all of them are currently accepted taxonomically (Guiry & Guiry 2014). *Lithothamnion* is widely distributed around the world from the poles to the tropics and from intertidal areas to deep in the oceans (Basso et al. 2011). If we compare the number of species of Hapalidiaceae in Mexican Atlantic with other places, we find that in southern Australia 15 species have been recorded (Harvey et al. 2003); while, Guiry & Guiry (2014) report ten species for New Zealand and 14 for South Africa. These data shows that Atlantic coast of Mexico has a very low number of species of Hapalidiaceae compared to Australia, New Zealand and South Africa. However, this fact may be due to the deficiency of studies on non-geniculate coralline algae in Mexico. For example, *Lithothamnion sejunctum* is a new record for Mexico and represents the third record since it was first described from St. Croix in 1906 and its distribution is restricted in the reefs of the Mexican Atlantic (Fig. 25). In the case of *Lithothamnion crispatum* this species is the first occurrence for North America Continent. Basso et al. (2011) indicate that *L. crispatum* occurs in the Mediterranean and throughout Atlantic and Indian Ocean and eastward to the Pacific coast of Australia; therefore it is necessary to perform more research for improving our knowledge on this cosmopolitan species.

The distribution of *Lithothamnion, Melobesia* and *Mesophyllum* is observed in Figures 25 and 26; this indicates that these genera are poorly represented in the study region, for example *Mesophyllum mesomorphum* is restricted to Campeche banks and Cozumel Island. Furthermore, *M. mesomorphum, Lithothamnion crispatum* and *L. occidentale* were located in Mexico habits mainly in the subtidal zone, an area little studied in Mexico.

**FIGURE 25.** Distribution of *Melobesia and Mesophyllum* in the Atlantic coast of Mexico.
Conclusions

The family Hapalidiaceae is underrepresented in the study area; we reported five species, three of them habits subtidal zone, an area unwel studied in Mexico. *Lithothamnion crispatum* and *L. sejunctum* are new records for Mexico. Furthermore, there are taxonomically difficult species, because of morphological and anatomical features. Consequently, further genetic and environmental studies on rhodolith-forming species are needed. Finally, our results indicate that it is particularly crucial carry out taxonomic and distributional studies on this family so little studied in the Atlantic coast of Mexico.

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