



Diversity of Halimedaceae (Bryopsidales, Chlorophyta) in Mexico

Diversidad de Halimedaceae (Bryopsidales, Chlorophyta) en México

Anahi Carranza Ramirez^{1,3} , María Luisa Núñez Resendiz² , Kurt M. Dreckmann² , Abel Sentíes^{2,3} 

Abstract:

Background and Aims: Halimedaceae are a group of tropical and subtropical coenocytic green marine macroalgae, notable for their role in carbon fixation and production of calcareous sediments. In Mexico, knowledge of their diversity has been based mainly on non-specialised floristic records, highlighting the need for an updated inventory. Therefore, our objective was to produce a comprehensive review of the Halimedaceae along the Mexican coasts. In addition, we include a preliminary phylogenetic analysis that highlights the need for molecular studies to clarify the diversity of the group Mexico.

Methods: A review of specialized literature and herbarium specimens was conducted to compile an updated taxonomic checklist, from which species richness was obtained for each coastal state. Additionally, GenBank was consulted to obtain available molecular sequences, and a preliminary phylogenetic analysis based on the *rbcL* marker was carried out. Finally, a species accumulation curve by decade, since the first record to the present, was generated.

Key results: A total of 46 species, 11 forms and two varieties were recorded, representing approximately 19% of global diversity in the family. In the Atlantic, 41 species, 11 forms and two varieties were documented across five states, and in the Pacific, 10 species were found across nine states, while five species were shared in between both regions. The phylogenetic analysis revealed that Halimedaceae is monophyletic and resolved into several polyphyletic clades within different genera. Records of Halimedaceae in Mexico started in the early 20th century, with few studies in the Pacific and a progressive increase in the Atlantic.

Conclusions: Knowledge of Halimedaceae diversity in Mexico is limited and based primarily on floristic lists, with few studies integrating morphological and molecular analyses. This study underscores the need for comprehensive and updated research to better understand the taxonomy and phylogeny of this group in Mexico.

Key words: distribution, macroalgae, phylopecies, species richness, taxonomy.

Resumen:

Antecedentes y Objetivos: Halimedaceae es un grupo de macroalgas marinas verdes cenocíticas tropicales y subtropicales, relevantes por su papel como fijadoras de carbono y generadoras de sedimentos calcáreos. En México, el conocimiento de su diversidad se ha basado principalmente en listados florísticos no especializados, resaltando la necesidad de contar con un inventario actualizado. Por lo tanto, nuestro objetivo fue elaborar una revisión exhaustiva de la familia Halimedaceae en los litorales mexicanos. Además, se incorpora un análisis filogenético preliminar que resalta la necesidad de estudios moleculares para esclarecer la diversidad del grupo en México.

Métodos: Se realizó una revisión de literatura especializada y ejemplares de herbario para elaborar un listado taxonómico actualizado, del cual se obtuvo la riqueza específica por cada estado litoral. Además, se consultó GenBank para obtener secuencias moleculares y se realizó un análisis filogenético preliminar, a partir del marcador *rbcL*. Finalmente, se generó una curva de acumulación de especies por década, desde el primer registro hasta la actualidad.

Resultados clave: Se registraron 46 especies, 11 formas y dos variedades, representando aproximadamente 19% de la diversidad mundial de la familia. En el Atlántico se registraron 41 especies, 11 formas y dos variedades distribuidas en cinco estados y en el Pacífico 10 especies en nueve estados; cinco especies fueron compartidas entre ambas regiones. El análisis filogenético reveló que Halimedaceae es monofilético, resuelto en diversos clados polifiléticos al interior de varios géneros. El conocimiento de Halimedaceae en México comenzó a inicios del siglo XX, con pocos estudios en el Pacífico y un aumento progresivo en el Atlántico.

Conclusiones: El conocimiento sobre la diversidad de Halimedaceae es limitado y se basa principalmente en listados florísticos con escasos estudios que integren la morfología con análisis moleculares. Este trabajo destaca la necesidad de estudios integrales y actualizados para comprender la taxonomía y filogenia sobre este grupo en México.

Palabras clave: distribución, filoespecies, macroalgas, riqueza específica, taxonomía.

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Introduction

Halimedaceae is a family of green, strictly marine macroalgae that hosts the largest number of genera of any family in the order Bryopsidales. Currently, it is composed of 68 genera, of which 250 taxonomically valid species are distributed in 53 of them. They inhabit predominantly tropical and subtropical environments in the oceans through the world (Kooistra and Verbruggen, 2005; Verbruggen et al., 2009a; Dijoux et al., 2012; Acosta-Calderón et al., 2018). In these regions, most members of the family are major producers of calcareous sediments (Rees et al., 2007; van Tussenbroek and van Dijk, 2007; Ries 2009; van Tussenbroek and Barba Santos, 2011), with the exception of some genera (e.g., *Chlorodesmis* Harvey and Bailey and *Boodleopsis* A.Gepp & E.S.Gepp) (not calcified) (Littler and Littler, 2000; Cassano et al., 2004), as they are able to precipitate calcium carbonate in the form of aragonite within their tissues (Nelson, 2009; Bedinger et al., 2013). These macroalgae continuously release calcareous segments into the sediment, either during their growth or after their death, when their highly calcified thalli disintegrate and contribute to the formation of carbonate sediments (Kooistra et al., 2002; Verbruggen et al., 2009a; Ford and Kench, 2012). Ecologically, Halimedaceae species play a fundamental role in primary production, functioning as early colonisers for the establishment of seagrass meadows (van Tussenbroek and Barba Santos, 2011; Bedinger et al., 2013), serving as food for various herbivorous species (Mantyka and Bellwood, 2007; Ferrari et al., 2012; Castro-Sanguino et al., 2016), and providing habitat and refuge for a diverse fauna (Llobet et al., 1986; Beach et al., 2003; Zayas et al., 2006; García-Ríos et al., 2008). In addition, other species are considered a valuable biotechnological source for the pharmaceutical industry (de Oliveira Silva et al., 2017; Salehi et al., 2019; Ojitos Ramos and Espinosa-Antón, 2023).

Halimedaceae species display a wide morphological diversity, ranging from simple siphonal filaments to complex multiaxial structures. They include tufts of long, free, sparsely branched, uncalcified filaments (e.g., *Chlorodesmis* (Fig. 1A), calcified, brush-like thalli (e.g., *Penicillus* Lamarck (Fig. 1B, C) and *Rhipocephalus* Kützling (Fig. 1D, E)), calcified funnel- or fan-shaped laminae (e.g., *Udotea* J.V.Lamouroux (Fig. 1F, G)), or highly calcified flattened segments (e.g.,

Halimeda J.V.Lamouroux (Fig. 1H, I)) (Barton, 1901; Hillis-Colinvaux, 1980; Littler and Littler, 1990, 2000). However, despite the complexity of the most elaborate and branched siphon systems, anatomically they are all formed by a single multinucleated tubular cell (Kooistra et al., 2002). This cell, in which nuclei, cytoplasm, and organelles are freely transported, branches to form an organized network of siphons (Barton, 1901; Hillis-Colinvaux, 1980). In the medulla the siphons are arranged axially with few branches, while in the cortex the siphonal branching is denser; there, the short cortical branches of the siphon have an inflated structure and are called utricles (Littler and Littler, 2000). It is worth mentioning that the anatomy of the siphon varies depending on its location in the thallus and the stage of the life cycle in which it is found (Littler and Littler, 2000; Verbruggen et al., 2009b).

In other parts of the world, very complete monographic works describing the species of several genera of Halimedaceae exist (Barton, 1901; Littler and Littler, 1990; El-Manawy and Shafik, 2008; Cabrera and Alfonso, 2009), with molecular support (Hillis-Colinvaux, 1959; Kooistra et al., 2002; Bandeira-Pedrosa et al., 2003; Verbruggen and Kooistra, 2004; Kooistra and Verbruggen, 2005; Verbruggen et al., 2005a, b, 2009a; Curtis et al., 2008; Coppejans et al., 2011; Dijoux et al., 2012; Pongparadon et al., 2015; Sauvage et al., 2020; Lagourgue et al., 2022), including studies that integrate morphological and molecular characterisation (Coppejans et al., 2011; Lagourgue et al., 2018, 2020; Lagourgue and Payri, 2021, 2022; Huisman and Verbruggen, 2023). In Mexico, the only specialised studies describing species, in particular of the genus *Udotea*, are those of Collado-Vides et al. (2009) and Acosta-Calderón et al. (2018), since in other studies they are only mentioned in floristic lists and catalogs with species records, without additional information to the name (Dreckmann, 1998; Ortega et al., 2001; Pedroche et al., 2005; Mendoza-González et al., 2007; Senties and Dreckmann, 2013; Ortégón-Aznar et al., 2024). However, these works have allowed us to know, in a general way, the specific richness of the Halimedaceae species on the Mexican coasts. For the Mexican Pacific coast, the works of Serviere-Zaragoza et al. (2007), Rosas-Alquicira et al. (2011), Mateo-Cid and Mendoza-González (2012), Bastida-Zavala et al. (2013) and López et al. (2022) stand

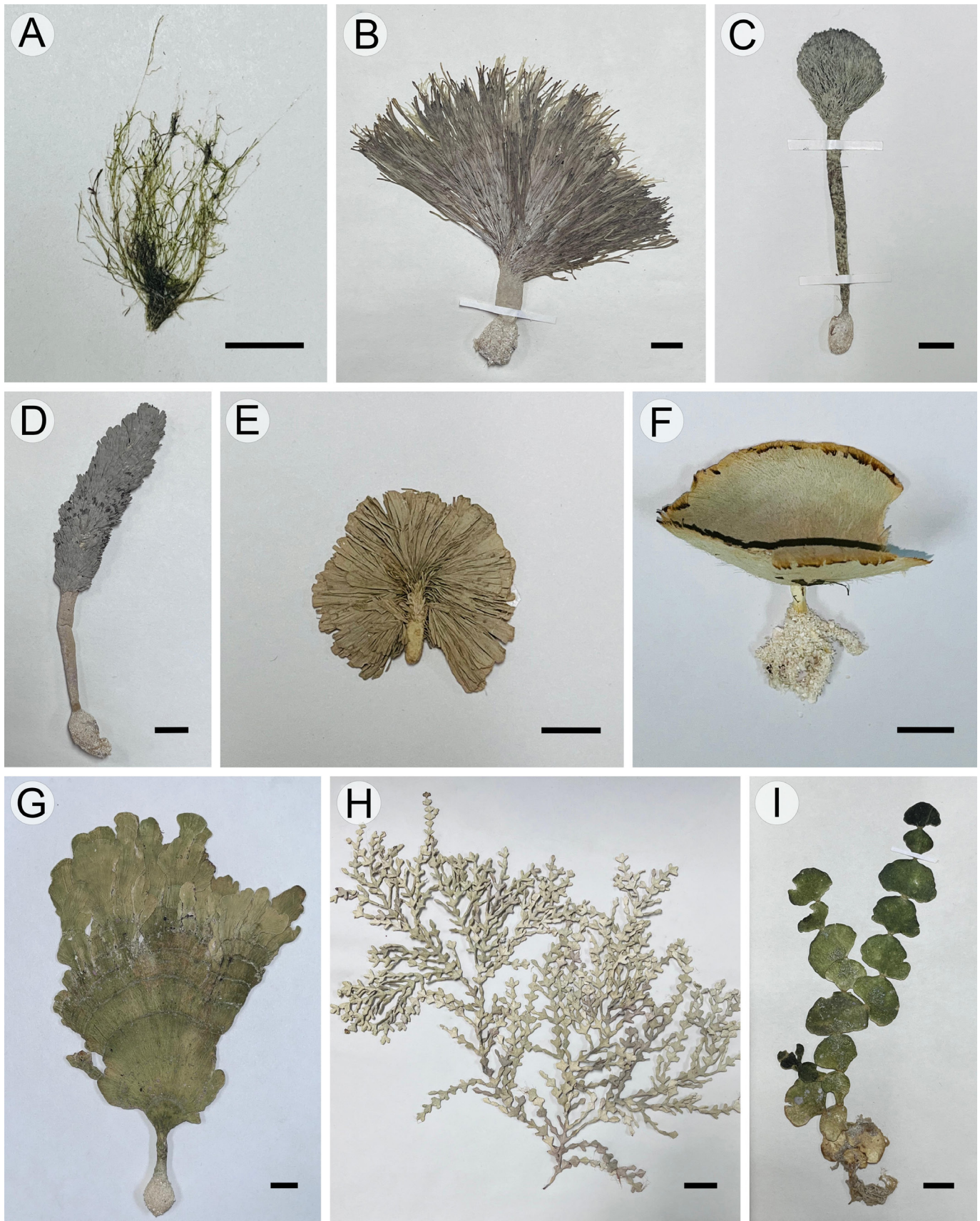


Figure 1: General appearance of the thallus of A. *Chlorodesmis* Harvey & Bailey (UAMIZ-25); B-C. *Penicillus* Lamarck (UAMIZ-915, UAMIZ-653); D-E. *Rhypocephalus* Kützing (UAMIZ-530, UAMIZ-1271); F-G. *Udotea* J.V.Lamouroux (UAMIZ-1461, UAMIZ-583); H-I. *Halimeda* J.V.Lamouroux (UAMIZ-1115, UAMIZ-916). Scale bar: A, I = 1 cm; H = 2 cm.

out. For the Atlantic coast of Mexico, the works of Collado-Vides et al. (1998), Quan-Young et al. (2004), Mateo-Cid and Mendoza-González (2007), Valadez et al. (2014) and Acosta-Calderón et al. (2016) stand out. In this context, the aim of this study was to compile a floristic checklist based on an exhaustive review of the Halimedaceae in Mexico, as well as to present a preliminary phylogenetic analysis that highlights the need to promote specialized studies on this family in the country.

Material and Methods

To determine the morphospecific diversity of the family Halimedaceae in Mexico, a comprehensive review of the published literature was conducted, including scientific articles, book chapters, and floristic catalogs (Collado-Vides and González-González, 1993; Dreckmann et al., 1996; Ortega et al., 2001; Pedroche et al., 2005; Mendoza-González et al., 2011, 2018; Sentíes and Dreckmann, 2013; Valadez et al., 2014; Pedroche and Sentíes, 2020; Mateo-Cid et al., 2024). Based on these records, the total species number was counted to obtain the specific richness from each one of the 17 coastal states, encompassing both Atlantic and Pacific regions. Based on this review, an updated taxonomic list of the family was compiled, detailing the distribution of each species by state.

Additionally, and with the goal of supplementing and updating existing floristic records, specimens deposited in the Metropolitan Herbarium UAMIZ (Thiers, 2025) of the Universidad Autónoma Metropolitana were examined. This review allowed the identification of species that had been collected but not previously reported in the literature. The floristic list was organised according to the classification and nomenclature proposed by Wynne (2022), and the taxonomic status of each species was verified using the Algae-Base database (Guiry and Guiry, 2025).

To analyse the phyllospecific diversity of Halimedaceae, the GenBank (2025) database was queried to obtain available molecular sequences from both Mexican oceans and other parts of the world. Using sequences of *rbcl*, a preliminary phylogenetic analysis was conducted through Bayesian inference (BI) with MrBayes v. 3.2.2 (Ronquist et al., 2012), employing the GTR+I+G evolutionary model (General Time Reversible + Invariable Sites + Gamma

Distribution). *Bryopsis africana* Areschoug, *B. corymbosa* J. Agardh, *B. corticulans* Setchell, *B. pennatula* J. Agardh, *B. plumosa* (Hudson) C. Agardh, *Codium fragile* (Suringar) Hariot, *C. lucasii* Setchell, *C. torulosum* A.R. Sherwood, *Derbesia marina* (Lyngbye) Solier and *D. tenuissima* (Moris & De Notaris) P. Crouan & H. Crouan were selected as out-group based on previous phylogenetic studies that identified them as closely related species to Halimedaceae (Lam and Zechman, 2006; Verbruggen et al., 2009c; Cremen et al., 2019).

Finally, a species accumulation curve was generated by decades using spreadsheet software (Excel v. 2505), covering the period from the first documented records (1935 for the Atlantic and 1911 for the Pacific) to the present year (2026).

Results

Morphospecific diversity

Since the circumscription of the family Halimedaceae by Link in 1832, about 250 species names have been recorded in 68 genera, of which 13 are currently considered nomenclatural synonyms, and the taxonomic status of two of them is still unresolved, leaving 17 genera in disuse (*Ancestria* Farghaly, *Baratangia* Badve and Kundal, *Botryella* Shuysky, *Botryodesmis* Kraft, *Coralliodendron* Kützing, *Corallocephalus* Kützing, *Decaisnella* Farghaly, *Espera* Decaisne, *Flabellaria* J.V. Lamouroux, *Flabellaria* Lamarck, *Geppina* Farghaly, *Nesaea* J.V. Lamouroux, *Poropsis* Nizamuddin, El-Menifi et Godeh, *Rhipidodesmis* A. Gepp & E.S. Gepp, *Rhipozonium* Kützing, *Rudicularia* Heydrich, and *Siphonoclatrus* S.A. Earle & Jer R. Young). Of the 53 taxonomically valid genera for the family, 32 correspond to fossil records, or even genera whose type species are also fossil records. From the remaining 21, 11 are distributed along Mexican coasts (Appendices 1, 2), representing 21% of the generic diversity of the family worldwide. Of the 250 currently taxonomically accepted taxa for the family, 46 species, 11 forms and two varieties have been reported for Mexico, representing 24% of the species diversity worldwide. Of this diversity, 41 species (16%), 11 forms and two varieties have been reported from the Atlantic states (Appendix 1), while 10 species (4%) have been recorded from the Pacific states (Appendix 2); of these, five species



are shared between both regions. According to **Pedroche and Sentfies (2020)**, the diversity of Chlorophyta in Mexico comprises 213 species in the Atlantic and 181 in the Pacific. In this context, the 41 species recorded for the Atlantic represent 19% of the national diversity, while the 10 species reported for the Pacific constitute 6%. Of the genera recorded in Mexico, only *Halimeda* and *Penicillus* are amphioceanic, that is, they have been reported in both oceans. On the other hand, *Rhipocephalus*, *Udotea*, *Rhipilia* Kützinger, *Pseudocodium* Weber Bosse, *Rhipidosiphon* Montagne, *Boodleopsis* A. Gepp & E.S. Gepp, *Johnson-sea-linkia* N.J. Eisman & S.A. Earle, and *Rhipiliopsis* A. Gepp & E.S. Gepp are exclusive to Atlantic, while *Chlorodesmis* has only been identified in the Pacific. Besides, *Halimeda discoidea* De-

caisne, *H. tuna* (J. Ellis & Solander) J.V. Lamouroux, *H. copiosa* Goreau & E.A. Graham, *H. opuntia* (Linnaeus) J.V. Lamouroux, and *H. scabra* M. Howe are present in both oceans, highlighting that *H. discoidea* was recorded for all states.

Distribution

On the Mexican coasts, the records of Halimedaceae show a greater diversity in the Atlantic, standing out Quintana Roo with the highest number of genera and species (9/40, 11 forms, two varieties), followed by Campeche (8/33, six forms, one variety) and Yucatán (5/27, five forms), Veracruz (5/17, three forms) and, finally, Tamaulipas (2/2) which presents the lowest diversity. It is worth noting that Tabasco does not have any records (**Fig. 2**). Regarding the Pacific-

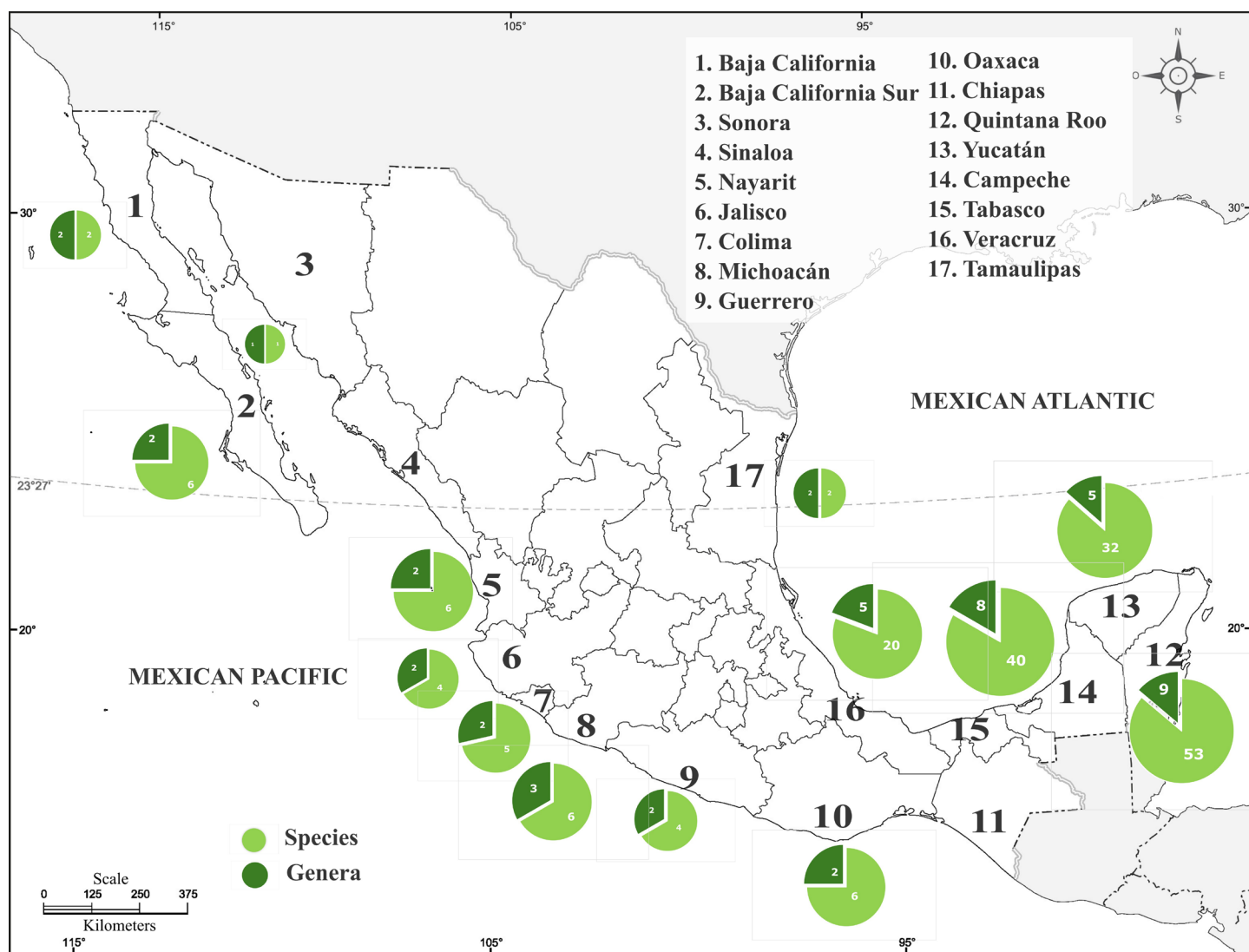


Figure 2: Map of Mexico showing the distribution of the number of species and genera of Halimedaceae in the coastal states.



ic coasts, the states with the highest number of records are Michoacán (3/6), Baja California Sur (2/6), Nayarit (2/6) and Oaxaca (2/6), to a lesser extent Colima (2/5), Jalisco (2/4) and Guerrero (2/4). The states with the fewest records are Baja California (2/2) and Sonora (1/1). In addition, in Sinaloa and Chiapas there are no records (Fig. 2).

Phylosppecific diversity

Of the 53 valid genera for the family, the GenBank (2025) database has molecular records for 20 of them. *Halimeda* is the genus with the largest number of available molecular sequences (1658), followed in descending order by *Udotea* (445), *Rhipilia* (345), *Kraftalia* Lagourgue & Payri (225), *Rhipiliopsis* (220), *Chlorodesmis* (213), *Flabellia* Reichenbach (175), *Rhipidosiphon* (138), *Penicillus* (122), *Rhipiliospina* Lagourgu & Payri (89), *Pseudochlorodesmis* Børgesen (71), *Tydemania* Weber Bosse (68), *Poropsis* Nizamuddin, El-Meni-fi et Godeh (34), *Pseudocodium* (32), *Rhipocephalus* (26), *Rhipiliella* Kraft (25), *Callipsygma* J. Agardh (8), *Boodleopsis* (7), *Siphonogramen* I.A.Abbott & Huisman (7) and *Johnsonsea-linkia* (6). A preliminary phylogenetic analysis based on *rbcl* gene sequences (Fig. 3) reveals that the Halimedaceae family forms a monophyletic group, with maximum phylogenetic support (BI=1.0%), resolved into two clades (A and B). Clade A, with maximum phylogenetic support (BI=1%), presents the genus *Tydemania*. Clade B shows high phylogenetic support (BI=94%) and is subdivided into two subclades; subclade I, with low support (BI=70%), includes the clade formed by *Rhipiliospina* and *Callipsygma* in the most basal position, resolved in turn as the sister group of the clade formed by *Pseudocodium* and *Halimeda* as the sister genera of the group of *Pseudochlorodesmis*, *Rhipiliopsis*, *Kraftalia*, *Rhipiliella* and *Rhipilia*. Subclade II, also with low support (BI=76%), comprises *Flabellia* occupying the most basal position and is resolved as the sister group of the clade formed by *Chlorodesmis*, *Rhipidosiphon*, *Penicillus*, *Rhipocephalus* and *Udotea*. It should be noted that, in this preliminary analysis, the genera *Rhipiliopsis*, *Rhipidosiphon*, *Penicillus* and *Udotea* are distributed in more than one clade.

Species accumulation curve

Knowledge of the Halimedaceae in Mexico started at the beginning of the 20th century. On the Atlantic coast, the first

record was *Halimeda tuna* (J.Ellis & Solander) J.V.Lamouroux in 1935. Figure 4 shows the accumulated knowledge of the species, genera and even synonyms that have been described from 1930 to date for the Atlantic. In the first three decades (30's, 40's, 50's) records were scarce. However, from 1960 to 1980, half of the total records were already known. From this decade onwards there is a considerable increase in the number of registered genera and species, which has continued to increase to the present day. Nevertheless, it can be seen that there have been records that are synonyms of other species, so there was an overestimation in the number of records of approximately 10 species. On the other hand, the first record for the Pacific coast was in 1911 with the identification of *Halimeda discoidea*. Figure 5 presents the number of species and genera accumulated for the Pacific coast by decade. It can be observed that, although the first record dates back to 1911, species richness remained low until 1990, when, to date, there has been no significant increase in the number of recorded species (10). In both the Pacific and the Atlantic, the proportion of the increase in species and genera is observed to be constant.

Discussion

Morphosppecific diversity

Morphospecies are understood as groups of organisms that share similar morphological traits and that are generally distributed within the same geographic region (De Queiroz, 2007). Under this approach, the identification of marine algae has traditionally been based on morphological and anatomical characters of the thalli. However, relying exclusively on these traits may lead to either an overestimation or an underestimation of species diversity (Núñez Resendiz et al., 2025). This situation is particularly evident in the family Halimedaceae, where a high degree of morphological variability has been documented in several taxa (Verbruggen et al., 2005c; Verbruggen, 2009b; Zainee et al., 2018). In Mexico, most of the available records come from floristic studies that mainly provide species lists, in which identification is largely based on morphological criteria.

In this context, a considerable morphosppecific diversity of Halimedaceae has been reported in Mexican waters, encompassing genera with structurally simple thalli, such as *Chlorodesmis* in the Pacific, where rocky sub-



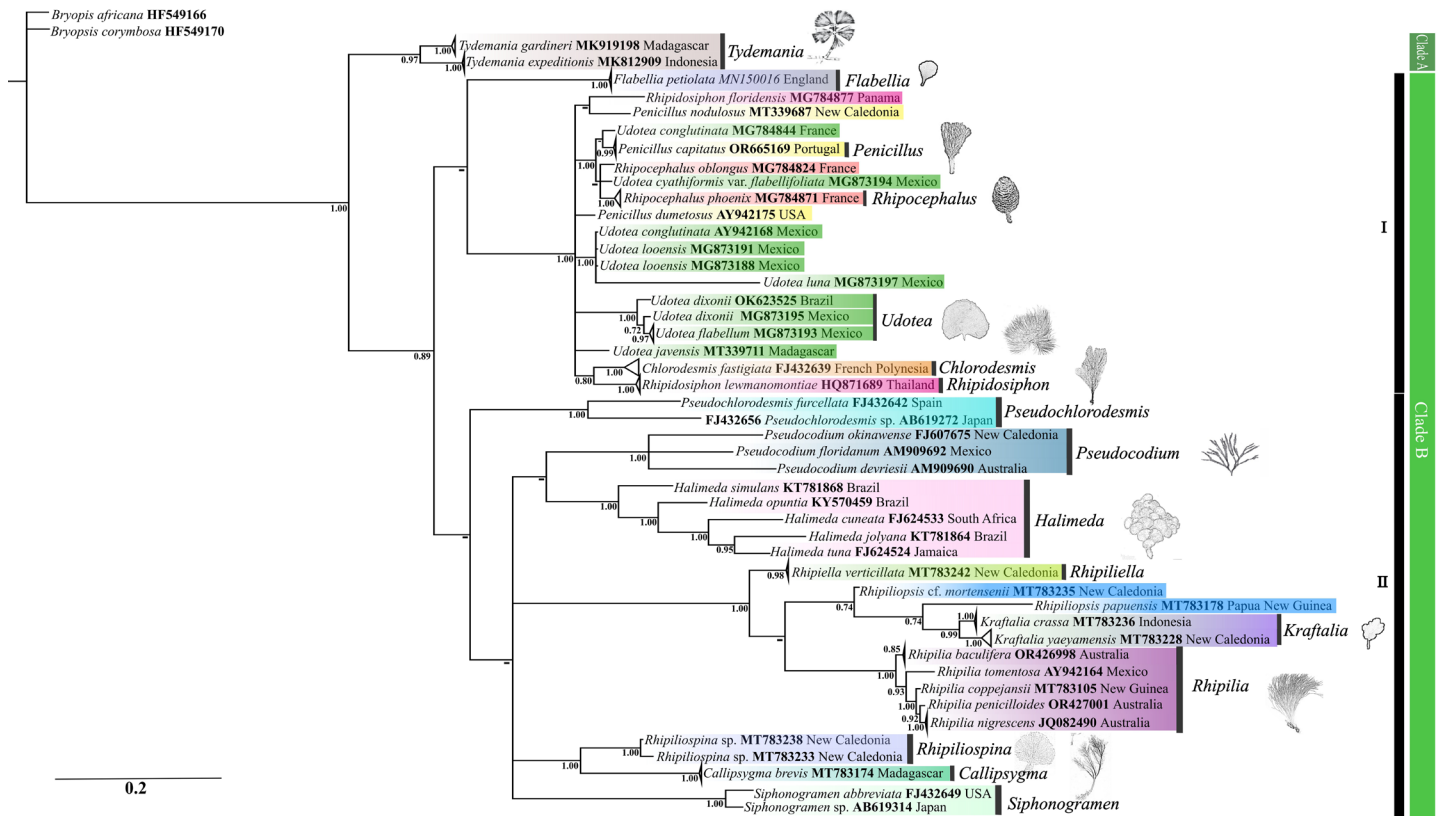


Figure 3: Bayesian inference (BI) topology based on *rbcL* sequence data. BI (Bayesian Inference) values. Dashes indicate values below 70%. The color indicates the specimens corresponding to each genus. Illustrations of Halimedaceae modified from Coppejans et al., 2011; Cremen et al., 2019; Lagourgue et al., 2020; Huisman and Verbruggen, 2023.

strates predominate, to more complex multiaxial forms, including *Rhipocephalus*, *Udoatea*, and *Halimeda*, which are more abundant in the Atlantic region, characterised by calcareous sandy substrates. The higher concentration of morphospecies in this region suggests that environmental conditions and substrate heterogeneity promote greater structural diversification within the group. Nevertheless, some species exhibit broad ecological tolerance, colonizing a wide range of marine habitats due to their ability to adapt to varying environmental conditions. This is particularly evident in *Halimeda*, which is widely distributed and capable of attaching to both hard and sandy substrates.

Several species, including *Halimeda discoidea*, *H. copiosa*, *H. opuntia*, and *H. scabra* have been recorded in both Pacific and Atlantic oceans, and can thus be considered amphioceanic species also documented in other algal groups (Dawson, 1963; Dreckmann and Sentfies, 1994;

Camacho et al., 2019; Hernández et al., 2021). However, records of Halimedaceae in Mexico have been based primarily on morphological characters, and therefore the presence of cryptic diversity among these species cannot be ruled out. In this regard, phylogenetic studies have shown that *H. discoidea*, traditionally considered amphioceanic, represents a complex of cryptic or pseudocryptic species (Verbruggen et al., 2005c). This highlights the need for integrative studies incorporating molecular analyses to clarify their taxonomic boundaries and biogeographic patterns.

Distribution

Halimedaceae are mainly distributed in tropical and subtropical regions of the world (Kooistra and Verbruggen, 2005; Verbruggen et al., 2009a; Dijoux et al., 2012; Acosta-Calderón et al., 2018), which explains their presence along the Mexican coasts (León-Tejera and González-

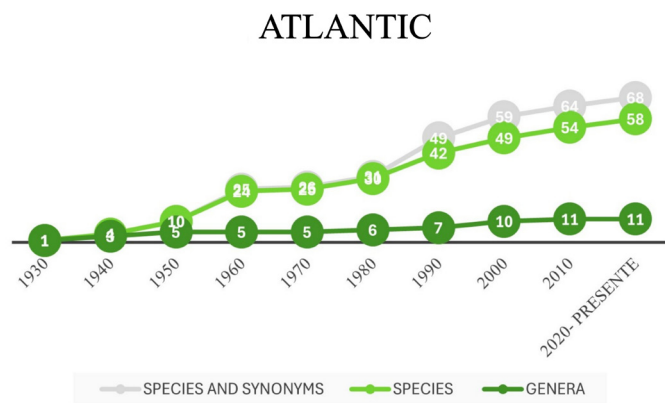


Figure 4: Cumulative curve of records of Halimedaceae species and genera in the Mexican Atlantic, including both valid species and synonyms. Records are grouped into 10-year intervals from 1930 to the present.

González, 1993; Mendoza-González et al., 2000; Acosta-Calderón et al., 2018; Piñón-Gimate et al., 2022; Mateo-Cid et al., 2024). However, their distribution is not homogeneous, as the establishment and persistence of these algae depend on several environmental and ecological factors (Ries, 2009; Patiño-Espinosa et al., 2022). In general, the states with the greatest specific richness are Quintana Roo, Campeche, and Yucatán on the Atlantic coast, and Michoacán, Baja California Sur, and Nayarit on the Pacific coast. However, species richness in the Atlantic was significantly higher than in the Pacific. This richness could be due to multiple factors related to physiographic conditions. In this regard, Patiño-Espinosa et al. (2022) mentioned that the growth and propagation of macroalgae depends on specific substrates. In this sense, Halimedaceae shows affinity for sandy substrates, which predominate on the coasts of Quintana Roo, Campeche and Yucatán, sites in the Atlantic where the highest species richness is recorded compared to the Pacific, where unstable substrates, pebble beaches and other types of sediments less conducive to their development are recorded (Pedroche and Senties, 2003). Furthermore, currents and tides play a key role in the distribution of macroalgae (Huerta, 1961). In particular oceanic dynamics in the Pacific are influenced by intense and variable current systems (Pantoja et al., 2012), which hinders the establishment of Halimedaceae. In contrast, the more stable

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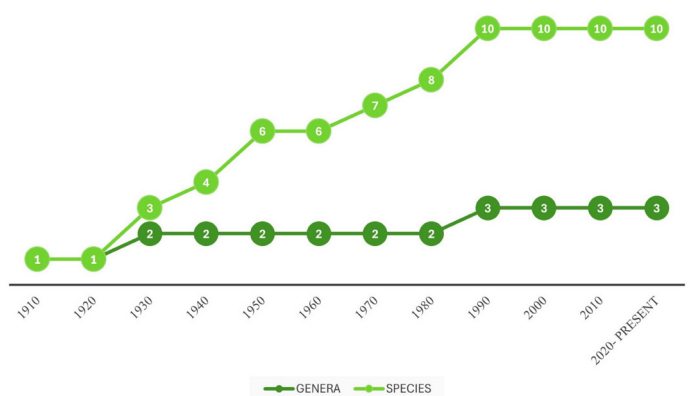


Figure 5: Cumulative curve of records of Halimedaceae species and genera in the Mexican Pacific, including only valid species. Records are grouped into 10-year intervals from 1910 to the present.

conditions of the Atlantic (Uribe-Martínez et al., 2019) favour the growth of algae from this family. It should be noted that there are other factors that can influence the records of Halimedaceae in Mexico, such as the climatic season, the sampling effort, the objectives of researchers, among others (Patiño-Espinosa et al., 2022).

Phylospecific diversity

Despite the fact that morphological characterization has been the first criterion for discrimination between species, its use in taxonomic identification has several limitations. Firstly, the restricted number of characters for its description and delimitation (Pedroche and Senties, 2003). Additionally, the morphological monotony and phenotypic plasticity have led to the existence of cryptic and pseudocryptic species (Verbruggen et al., 2005c), giving rise to various names that correspond to varieties, forms or even species without taxonomic identity yet (Valadez et al., 2014; Carranza Ramirez et al., 2023). This highlights the need to use complementary approaches to achieve a more robust and accurate taxonomic classification. In this context, the use of molecular tools has allowed the generation of more precise and robust classification systems that help to give identity and taxonomic independence to the “phylopecies”, contributing to a better understanding of biological diversity and its evolutionary relationships

(Núñez Resendiz et al., 2025). In this study the preliminary phylogenetic analysis based on *rbcl* gene sequences (Fig. 3) reveals that the family Halimedaceae forms a monophyletic group, consistent with previous phylogenetic studies (Lam and Zechman, 2006; Verbruggen et al., 2009c; Cremen et al., 2019). It is worth noting that the genera *Rhipidosiphon*, *Rhipiliopsis*, *Penicillus* and *Udotea* are distributed in more than one clade, which could evidence a polyphyletic nature or species erroneously identified in GenBank (2025). Therefore, it is essential to carry out a formal analysis of the phylogenetic relationships of the family, in which its evolutionary history is reflected, involving a higher number of genetic markers.

Although there are sequences from specimens collected in Mexico, including 15 records of *Halimeda*, 10 of *Udotea*, three of *Chlorodesmis*, three of *Pseudocodium*, and one of *Rhipocephalus*, these have mainly contributed to studies on the phylogenetic, phylogeographic, and ecological relationships, as well as those on the evolutionary niche dynamics of the genus *Halimeda* (Kooistra et al., 2002; Verbruggen et al., 2009a), the biogeography of *Pseudocodium* (De Clerck et al., 2008), and the morphological and genetic diversity of *Udotea* (Lagourgue et al., 2018). However, it is important to note that these studies are not specifically focused on Mexico, as the Mexican sequences were incorporated solely to increase the robustness and resolution of global phylogenetic analyses.

Although several studies and taxonomic reclassifications within the family have been proposed (Lam and Zechman, 2006; Cremen et al., 2019), the preliminary analysis conducted in this study aimed to highlight the lack of studies among several genera, with emphasis in the Mexican flora. For the genus *Udotea*, Mexican sequences have previously been analysed by Acosta-Calderón et al. (2018). However, the absence of a formal comparison with other available sequences of the genus in GenBank (2025) and the lack of a comprehensive phylogenetic inference has limited the recognition of these entities as phylospecies (Núñez Resendiz et al., 2025). Consequently, it can be inferred that the analysed species do not correspond to the genus *Udotea* but may represent a previously unrecognised specific diversity, underscoring the need for a more exhaustive taxonomic revision within the group.

Species accumulation curve

The patterns observed in the accumulation of Halimedaceae records in Mexico largely reflect the history of phylogenetic exploration and the development of taxonomic studies along the country's coasts. The notable increase in the number of records since the second half of the twentieth century coincides with a period of greater activity in floristic and systematic studies of macroalgae, suggesting that the rise in documented richness is not only the result of biological processes, but also of intensified sampling and the consolidation of marine phycology in Mexico. In this context, the presence of numerous synonyms in historical records highlights the limitations of identifications based exclusively on morphological characters and emphasizes the need for continuous taxonomic revisions to refine and update the knowledge of the group's real diversity.

These historical trends also help explain the differences observed between the Pacific and Atlantic coasts. Although the Pacific coast has earlier records, the documented species richness remained relatively low throughout much of the twentieth century. This pattern may be related to a lower intensity of specialized studies in the region, as well as differences in sampling effort, the focus of floristic research, and the availability of specialists working on particular taxonomic groups. In contrast, the Atlantic coast shows a more marked increase in the number of records beginning in the 1960s, suggesting a greater concentration of floristic and taxonomic studies in this area during that period. Nevertheless, these differences may not be explained solely by sampling effort, as they could also reflect real variations in the floristic composition between both coasts. As mentioned previously, environmental conditions, ecological factors, and substrate characteristics influence the establishment and distribution of macroalgae and therefore may also contribute to the differences observed in species records between the Pacific and Atlantic coasts of Mexico.

Conclusions and perspectives

From the above, it is evident that the Halimedaceae family is a poorly explored group in Mexico. Although there are records that document its presence, most of them correspond to phycofloristic lists that do not delve into specific studies of the species that make up this family. To date,

there is little work that comprehensively addresses key aspects, including detailed morphological characterization, molecular tools, and phylogenetic analyses that allow us to understand their diversity, distribution, and evolutionary relationships. This lack of integrative studies has led to limited knowledge about the true diversity of the group, since identification based exclusively on morphological characteristics (as occurs in the aforementioned lists) can lead not only to an underestimation or overestimation of the true diversity of the family, but also to the presence of amphioceanic diversity. This has important implications for the advancement of other areas of the biology, with the group's basic knowledge being essential in ecological, biogeographic, and even applied studies, given its enormous potential in industry and its role in coastal ecosystems. Therefore, there is a need to conduct detailed studies that integrate traditional approaches, such as morphological characterization, with molecular methodologies, to correctly identify and characterise the Halimedaceae phylospecies present in Mexico.

Author contributions

Formal analysis: ACR, MLNR; Conceptualization: ACR, MLNR, KMD, AS; Data curation: ACR, MLNR; Investigation: ACR, MLNR, KMD, AS; Methodology: ACR, MLNR, KMD, AS; Writing - original draft: ACR, MLNR, KMD, AS; Writing - review and editing: ACR, MLNR, KMD, AS.

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Data Availability Statement

The dataset supporting the results of this study was submitted to SciELO Data and can be accessed at: <https://doi.org/10.48331/SCIELODATA.ZWIKW9>

Declaration of use of Artificial Intelligence

The authors declare that no artificial intelligence tools were used in the writing of this new and original text. All written content was produced directly by the authors.

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Appendix 1: Floristic list and distribution by state of the genera and species of Halimedaceae in the Mexican Atlantic. TAMPS = Tamaulipas; VER = Veracruz; CAMP = Campeche; YUC = Yucatán; QROO = Quintana Roo; * = UAMIZ Herbarium records. 1 = Acosta-Calderón et al. (2016), 2 = Acosta-Calderón et al. (2018), 3 = Aguilar Rosas et al. (1998), 4 = Aguilar-Rosas et al. (2001), 5 = Callejas-Jiménez et al. (2005), 6 = Carranza Ramirez et al. (2023), 7 = Cetz-Navarro et al. (2007), 8 = Collado-Vides et al. (2009), 9 = Collado-Vides and González-González (1993), 10 = Collado-Vides et al. (1998), 11 = Cuevas Sánchez et al. (2022), 12 = Taylor (1935), 13 = Huerta-Múzquiz (1960), 14 = De la Campa (1965), 15 = Sánchez Rodríguez (1980), 16 = Mateo Cid and Mendoza-González (1991b), 17 = Mateo-Cid and Mendoza-González (1992b), 18 = de la Cruz-Francisco et al. (2020), 19 = Dreckmann et al. (1996), 20 = Díaz-Martín et al. (1998), 21 = Díaz-Martín and Quan-Young (2001), 22 = Dreckmann (1998), 23 = Galicia and Morales (2007), 24 = Garduño-Solórzano et al. (2005), 25 = Godínez-Ortega et al. (2019), 26 = González-Gándara et al. (2007), 27 = González-Solis et al. (2018), 28 = Kooistra et al. (2002), 29 = Landa-Cansigno et al. (2019), 30 = Mateo-Cid and Mendoza-González (2007), 31 = Mateo-Cid et al. (2013), 32 = Mateo-Cid et al. (2024), 33 = Mendoza-González et al. (2000), 34 = Mendoza-González et al. (2007), 35 = Mendoza-González et al. (2013), 36 = Mendoza-González et al. (2016), 37 = Núñez Resendiz et al. (2025), 38 = Ortega et al. (2001), 39 = Ortegón-Aznar et al. (2001), 40 = Ortegón-Aznar and Aguilar-Perea (2014), 41 = Ortegón-Aznar et al. (2024), 42 = Patiño-Espinosa et al. (2022), 43 = Quan-Young et al. (2004), 44 = Quan-Young et al. (2006), 45 = Robinson et al. (2012), 46 = Robledo et al. (2003), 47 = Sánchez-Molina et al. (2007), 48 = Valadez et al. (2014), 49 = Vázquez-Machorro et al. (2016).

Species	State					Herbarium UAMIZ Collection year/collector + voucher	Reference
	TAMPS	VER	CAMP	YUC	QROO		
<i>Boodleopsis</i> A.Gepp & E.S.Gepp							
<i>B. pusilla</i> (Collins) W.R.Taylor, A.B.Joly & Bernatowicz		x	x	x	x		9, 14, 19, 31, 34, 36
<i>Halimeda</i> J.V.Lamouroux							
<i>H. copiosa</i> Goreau & E.A.Graham		x	x	x	x		6, 7, 19, 22, 31, 34, 36, 40
<i>H. discoidea</i> Decaisne	x	x	x*	x	x*	1994/ K. Dreckman 565; 1995/ M. Callejas 864; 2001/ M. Callejas 903, 910, 916	1, 4, 5, 13, 16, 17, 18, 19, 22, 23, 27, 28, 29, 30, 31, 32, 34, 36, 39, 40, 41
<i>H. favulosa</i> M.Howe					x		1, 7, 34
<i>H. goreau</i> W.R.Taylor		x	x	x	x		1, 3, 4, 13, 16, 17, 19, 22, 28, 31, 34, 35, 38
<i>H. gracilis</i> Harvey ex J.Agardh			x	x	x		1, 4, 19, 28, 29, 31, 32, 34, 36, 48
<i>H. gracilis</i> var. <i>opuntioides</i> Børgesen					x		17, 27
<i>H. incrassata</i> (J. Ellis) J.V.Lamouroux			x*	x	x*	1993/ A. Senties and L. Morquecho 532; 1994/ A. Senties and K. Dreckmann 577; 1995/ K. Dreckmann 860; 2001/ M. Callejas 937	1, 3, 4, 5, 9, 14, 16, 17, 19, 22, 26, 27, 28, 29, 31, 32, 33, 34, 36, 37, 38, 39, 40, 41, 42, 45, 48
<i>H. lacrimosa</i> M.Howe				x	x		1, 3, 4, 15, 16, 17, 19, 32, 34, 36, 41
<i>H. monile</i> (J.Ellis & Solander) J.V.Lamouroux			x	x	x*	1994/ A. Senties 646; 1988/ A. Senties 1186	1, 3, 4, 14, 16, 17, 19, 22, 24, 26, 27, 28, 31, 34, 36, 40, 48



Appendix 1: Continuation.

Species	State					Herbarium UAMIZ Collection year/collector + voucher	Reference
	TAMPS	VER	CAMP	YUC	QROO		
<i>H. opuntia</i> (Linnaeus) J.V.Lamouroux		x	x	x	x*	1993/ A. Sentías and L. Morquecho 554; 1994/ A. Sentías 657; 1995/ K. Dreckmann 865; 2001/ A. Sentías 1115	1, 3, 4, 6, 13, 14, 16, 17, 18, 19, 20, 22, 23, 26, 27, 28, 30, 31, 33, 34, 36, 38, 39, 40, 41, 42, 43, 46, 48, 49
<i>H. opuntia</i> f. <i>triloba</i> (Decaisne) J.Agardh		x		x	x		12, 23, 26, 27, 28, 38
<i>H. scabra</i> M.Howe		x	x	x	x		1, 3, 4, 6, 14, 16, 17, 18, 19, 25, 26, 27, 28, 29, 30, 34, 35, 36, 40, 41, 43, 48
<i>H. simulans</i> M.Howe			x	x	x		1, 9, 15, 16, 17, 19, 26, 28, 29, 31, 34, 35, 36, 41, 48
<i>H. tuna</i> (J.Ellis & Solander) J.V.Lamouroux		x*	x*	x	x	1990/ A. Sentías 370; 2001/ M. Callejas 947, 949; 1990/ C. Suárez 1100/ 1990 R. Muciño 1174	1, 3, 4, 5, 6, 9, 11, 12, 14, 16, 17, 18, 19, 22, 23, 24, 26, 27, 28, 29, 30, 31, 32, 34, 35, 36, 38, 39, 40, 41, 42, 46, 48
<i>Johnson-sea-linkia</i> N.J.Eisman & S.A.Earle							
<i>J. profunda</i> Eiseman & S.A.Earle					x		7, 31
<i>Penicillus</i> Lamarck							
<i>P. capitatus</i> Lamarck		x	x	x	x*	1993/ A. Sentías and Morquecho 537; 1993/ A. Sentías and Morquecho 541; 1993/ Sentías and Morquecho 559; 1994/ A. Sentías and K. Dreckman 582; 1994/ A. Sentías 653; 1988/ M. Gallegos 1103	1, 3, 4, 9, 12, 13, 14, 16, 17, 18, 19, 22, 26, 27, 28, 29, 30, 31, 32, 33, 34, 36, 37, 39, 40, 41, 42, 48
<i>P. capitatus</i> f. <i>elongatus</i> (Decaisne) A.Gepp & E.S.Gepp					x		17, 27, 36
<i>P. capitatus</i> f. <i>laxus</i> Børgesen			x	x	x		17, 26, 27, 28, 34, 36
<i>P. dumetosus</i> (J.V.Lamouroux) Blainville			x*	x	x*	1994/ A. Sentías and K. Dreckmann 580; 2001/ M. Callejas 908; 2001/ M. Callejas 915; 2001/ F. Aguilar 1087	1, 3, 5, 6, 14, 16, 17, 19, 22, 26, 27, 28, 31, 34, 36, 38, 39, 41, 42, 44, 48
<i>P. dumetosus</i> f. <i>expansus</i> Børgesen			x	x	x		28, 31, 34
<i>P. lamourouxii</i> Decaisne	x	x	x	x	x		1, 3, 4, 6, 9, 13, 14, 16, 17, 19, 21, 26, 27, 28, 31, 32, 34, 36, 41, 42, 48



Appendix 1: Continuation.

Species	State					Herbarium UAMIZ Collection year/collector + voucher	Reference
	TAMPS	VER	CAMP	YUC	QROO		
<i>P. pyriformis</i> A.Gepp & E.S.Gepp			x	x	x*	1995/ K. Dreckmann 866	1, 3, 4, 6, 14, 16, 17, 19, 22, 26, 27, 28, 31, 32, 33, 34, 36, 38, 41, 42, 48
<i>Pseudocodium</i> Weber Bosse							
<i>P. floridanum</i> Dawes & A.C.Mathieson			x				29
<i>Rhipidosiphon</i> Montagne							
<i>R. floridensis</i> D.S.Littler & Littler			x		x		7, 29, 32, 34
<i>R. javensis</i> Montagne					x		17
<i>Rhipocephalus</i> Kützing							
<i>R. oblongus</i> (Decaisne) Kützing		x		x	x*	1993/ A. Sentías and L. Morquecho 543	1, 3, 4, 6, 16, 17, 19, 26, 28, 30, 31, 34, 36, 41, 48
<i>R. phoenix</i> (J.Ellis & Solander) Kützing		x	x	x	x*	1993/ A. Sentías and L. Morquecho 528; 1993/ A. Sentías and L. Morquecho 530; 1994/ Stout and A. Sentías 576; 1994/ A. Sentías 639; 1995/ K. Dreckmann 870	1, 3, 6, 9, 12, 14, 16, 17, 18, 19, 21, 22, 23, 26, 27, 28, 30, 34, 35, 36, 40, 41, 42, 46, 48
<i>R. phoenix</i> f. <i>brevifolius</i> A.Gepp & E.S.Gepp		x	x	x	x		1, 3, 4, 12, 13, 14, 16, 17, 18, 23, 26, 27, 28, 33, 34, 36, 41, 43, 48
<i>R. phoenix</i> f. <i>longifolius</i> A.Gepp & E.Gepp		x	x	x	x		1, 3, 4, 12, 14, 17, 18, 26, 27, 28, 29, 30, 31, 34, 36, 38, 39, 41, 48, 49
<i>Rhipilia</i> Kützing							
<i>R. tomentosa</i> Kützing			x		x		1, 3, 16, 17, 19, 22, 26, 27, 28, 34, 36, 48
<i>R. tomentosa</i> f. <i>zonata</i> A.Gepp & E.S.Gepp					x		36
<i>Rhipiliopsis</i> A.Gepp & E.S.Gepp							
<i>R. stri</i> (Earle & Jer.R.Young) Farghaly & Denizot					x		7
<i>Udotea</i> J.V.Lamouroux							
<i>U. abbottiorum</i> D.S.Littler & Littler			x		x		2, 8, 17
<i>U. caribaea</i> D.S.Littler & Littler		x	x	x	x		1, 2, 8, 17, 20, 29, 34, 38, 39, 48
<i>U. cf. unistratea</i> D.S.Littler & Littler					x		6
<i>U. conglutinata</i> (J.Ellis & Solander) J.V.Lamouroux			x	x	x		1, 2, 3, 4, 8, 14, 16, 17, 19, 26, 27, 28, 29, 34, 36, 44, 48



Appendix 1: Continuation.

Species	State					Herbarium UAMIZ Collection year/collector + voucher	Reference
	TAMPS	VER	CAMP	YUC	QROO		
<i>U. cyathiformis</i> Decaisne		x	x	x	x		2, 3, 4, 6, 8, 14, 16, 17, 18, 19, 22, 26, 27, 28, 29, 31, 34, 35, 36, 39, 41, 42, 48
<i>U. cyathiformis</i> f. <i>infundibulum</i> (J.Agardh) D.S.Littler & Littler					x		6
<i>U. cyathiformis</i> f. <i>sublitorallis</i> (W.R.Taylor) D.S.Littler & M.M.Littler			x		x*	1993/ A. Sentías and L. Morquecho 542; 1995/ K. Dreckmann 854	1, 2, 6, 16, 17, 26, 28, 31, 34, 36, 41, 48
<i>U. cyathiformis</i> var. <i>flabellifolia</i> D.S.Littler & M.M. Littler			x		x		1, 2
<i>U. dixonii</i> D.S.Littler & Littler		x	x	x	x		1, 2, 6, 8, 17, 19, 20, 28, 29, 31, 34, 35, 39, 40, 48,
<i>U. dotyi</i> D.S.Littler & Littler			x		x		2, 8
<i>U. fibrosa</i> D.S.Littler & Littler					x		1, 2, 8
<i>U. flabellum</i> (J.Ellis & Solander) M.Howe		x	x*	x	x*	1993/ G. Castillo 463; 1993/ A. Sentías and L. Morquecho 533; 1993/ A. Sentías and Morquecho 558; 1994/ A. Sentías and K. Dreckmann 583, 642; 1995/ K. Dreckmann 851; 2001/ M. Callejas 914, 924	1, 2, 3, 4, 5, 8, 9, 13, 14, 16, 17, 19, 22, 26, 27, 28, 31, 32, 34, 35, 36, 37, 38, 40, 41, 42, 44, 45, 48
<i>U. looensis</i> D.S.Littler & Littler			x	x	x		2, 8, 17, 19, 28, 29, 31, 34, 35, 48
<i>U. luna</i> D.S.Littler & Littler			x	x	x		1, 2, 6, 8, 17, 29, 34, 35, 48
<i>U. norrisii</i> D.S.Littler & Littler			x		x		2
<i>U. occidentalis</i> A.Gepp & E.S.Gepp			x	x	x*	1994/ A. Sentías 658	1, 3, 16, 19, 22, 27, 28, 29, 31, 32, 34, 36, 41, 48
<i>U. spinulosa</i> M.Howe		x	x	x	x*	1995/ K. Dreckmann 843, 849	2, 14, 16, 17, 18, 19, 22, 26, 27, 28, 29, 31, 34, 36, 41, 44, 45,
<i>U. spinulosa</i> f. <i>palmettoidea</i> A.Gepp & E.S.Gepp			x		x		3, 29
<i>U. unistrata</i> D.S.Littler & Littler		x	x*		x	2001/ M. Callejas 938	1, 5, 6, 8, 17, 19, 20, 28, 29, 31, 33, 34
<i>U. verticillosa</i> A.Gepp & E.S.Gepp					x		17, 19, 27, 36
<i>U. wilsonii</i> A.Gepp, E.S.Gepp & M.Howe			x		x		1, 2, 3, 8, 14, 16, 17, 19, 22, 27, 28, 29, 31, 32, 34, 36, 41, 48



Appendix 2: Floristic list and distribution by state of the genera and species of Halimedaceae in the Mexican Pacific. BC = Baja California; BCS = Baja California Sur; SON = Sonora; NAY = Nayarit; JAL = Jalisco; COL = Colima; MICH = Michoacán; GRO = Guerrero; OAX = Oaxaca; * = UAMIZ Herbarium records. 1 = Acosta Calderón et al. (2023), 2 = Bastida-Zavala et al. (2013), 3 = Enciso-Padilla et al. (2019), 4 = Howe (1911), 5 = León-Tejera et al. (1993), 6 = León-Tejera and González-González (1993), 7 = León-Tejera et al. (1996), 8 = López et al. (2022), 9 = Mateo-Cid and Mendoza-González (1991a), 10 = Mateo-Cid and Medoza-González (1992a), 11 = Mateo-Cid and Mendoza-González (1994), 12 = Mateo-Cid and Mendoza-González (2012), 13 = Mateo-Cid et al. (2022), 14 = Mendoza-González et al. (2011), 15 = Mendoza-González et al. (2018), 16 = Norris et al. (2017), 17 = Núñez Resendiz et al. (2025), 18 = Pacheco and Dreckmann (1997), 19 = Paul-Chávez and Riosmena-Rodríguez (2000), 20 = Pedroche et al. (2005), 21 = Piñón-Gimate et al. (2020), 22 = Piñón-Gimate et al. (2022), 23 = Rosas-Alquicira et al. (2011), 24 = Serviere-Zaragoza et al. (1993), 25 = Serviere-Zaragoza et al. (2007).

Species	State										Herbarium UAMIZ Collection year/ collector + voucher	Reference
	BC	BCS	SON	NAY	JAL	COL	MICH	GRO	OAX			
<i>Chlorodesmis</i> Harvey & Bailey												
<i>C. hildebrandtii</i> A.Gepp & E.S.Gepp		x		x	x	x	x	x	x			1, 2, 5, 8, 9, 10, 14, 16, 20, 24
<i>C. mexicana</i> W.R.Taylor		x		x*						x	1988/ A. Senties 25	2, 6, 7, 10, 16, 24
<i>C. caespitosa</i> J.Agardh	x			x		x	x	x	x			1, 8, 15, 16, 18, 20, 25
<i>Halimeda</i> J.V.Lamouroux												
<i>H. copiosa</i> Goreau & E.A.Graham							x					20
<i>H. cuneata</i> Hering		x		x	x					x		10, 13, 16, 20, 24
<i>H. discoidea</i> Decaisne	x	x	x	x	x*	x	x*	x	x		1986/ J. Quintana 374; 1988/ A. Senties 683	1, 2, 3, 5, 6, 7, 8, 10, 11, 12, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25,
<i>H. opuntia</i> (Linnaeus) J.V.Lamouroux		x				x						16, 20, 25
<i>H. scabra</i> M.Howe		x										20
<i>H. tuna</i> (J.Ellis & Solander) J.V.Lamouroux				x	x	x	x	x*	x		1988/ J. Quintana 1178; 1988/ K. Dreckmann 1194	1, 2, 15, 16, 20, 23, 25
<i>Penicillus</i> Lamarck												
<i>P. sibogae</i> A.Gepp & E.S.Gepp							x					18, 15, 20

