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Bryophytes of mangroves of Bocas del Toro, Panama

NORIS SALAZAR ALLEN[1], GREGORIO DAUPHIN[2], JUAN CARLOS VILLARREAL[3], CALEB CASWELL-LEVY[4], ERIN R. COX[5], BRYAN A. ESPINOZA P.[6], JOSÉ GUDIÑO L.[7], ENRIQUE HERNÁNDEZ-RODRÍGUEZ[8,9], KARLA Y. MAGAÑA-MARCIAL[10], ANNA MEZĂKA[11], JUAN DIEGO RAMÍREZ-ROMÁN[12], LILISBETH RODRÍGUEZ[13], ARIANTI ROJAS CARVAJAL[14], CAMILA ROMERO-MORENO[15], AKIKO TOMITANI[16] & KATHERINE ZEBALLOS-GRIJALVA[17]

[1]*Smithsonian Tropical Research. Institute. Panama City, Panama. salazarn@si.edu; https://orcid.org/0000-0002-5546-2195*
[2]*Research Associate, Museo Nacional de Costa Rica, Apartado 749-1000, San José, Costa Rica; Apartado 114-1250, Escazú, San José, Costa Rica, Código postal 10201. adriaendauphin@gmail.com; https://orcid.org/0000-0003-3430-6000*
[3]*Department of Biologie, Institut de Biologie Intégrative et des Systèmes (IBIS), Université Laval, Québec, Canada. juan-carlos-villarreal-aguilar@bio.ulaval.ca; https://orcid.org/0000-0002-0770-1446*
[4]*University of California, Berkeley, California, USA. calebcaswelllevy@berkeley.edu*
[5]*Department of Botany, University of Alberta, Alberta, Canada. ercox@ualberta.ca*
[6]*Universidad Mayor Nacional de San Marcos, Perú. bryane.1890@gmail.com; https://orcid.org/0000-0001-7696-1279*
[7]*Smithsonian Tropical Research Institute, Panama, Panama. gudinoj@si.edu; https://orcid.org/0000-0001-6675-943X*
[8]*Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, México.*
[9]*Institut de Recherche sur les Forêts, Université du Québec en Abitibi Témiscamingue, Canada. enrique.hernándezrodriguez@uqat.ca; https://orcid.org/0000-0001-8339-5826*
[10]*Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, México. yunuenmagana@gmail.com*
[11]*Daugavpils University, Daugavpils, Latvia. anna.mezaka@biology.lv; https://orcid.org/0000-0002-1900-8614*
[12]*Universidad Industrial de Santander, Venezuela. juan.diego-rmr@outlook.com*
[13]*Departamento de Botánica, Universidad de Panamá. lili_0990@outlook.es*
[14]*Universidad de Costa Rica, Costa Rica. arianti.rojas@gmail.com; https://orcid.org/0000-0002-1560-8436*
[15]*Universidad de Los Llanos, Colombia. camiromero128@gmail.com*
[16]*Centro Agronómico Tropical de Investigación y Enseñanza. a.tomitani@gmail.com*
[17]*Universidad Nacional Agraria La Molina, Perú. katherine.zevallosg@gmail.com*

Abstract

This is the first survey of bryophyte diversity in the mangroves of Panama. The study was done in the mangroves of Bocas del Toro Province, Panama, in September 2016 and, July, May and August 2017. Bryophytes were collected from prop or stilt roots of mangroves, the mid-lower part of the trunks and the lower branches. In areas inundated at high tide, additional samples were collected on the cortex of palms, its rootlets, other angiosperm trees and from decomposing logs. Twenty-six species of liverworts and seven of mosses were identified. The most diverse and predominant liverwort family was the Lejeuneaceae with twenty-two species and two varieties and, among the mosses, the Calymperaceae with three species. Species affinities with other tropical mangroves were analyzed and liverworts were found to be the dominant element. Among the liverworts collected, two are new reports for Panama: *Ceratolejeunea confusa* and *Frullanoides mexicana*. Additional surveys of the cryptogamic vegetation of Panamanian mangroves are urgently needed due to the accelerated deforestation caused by anthropic activities and the potential loss of important biodiversity.

Resumen

Este es el primer estudio de la diversidad de briofitas en los manglares de Panamá. El estudio se realizó en los manglares de la provincia Bocas del Toro, Panamá, durante los meses de septiembre de 2016 y, julio, mayo y agosto de 2017. Se colectaron briofitas de las raíces fúlcreas, la parte media-inferior de los troncos y ramas inferiores de los mangles. En áreas inundables durante la marea alta, se hicieron colectas adicionales en la corteza de las palmas, su manto de raíces, en otras angiospermas y troncos en descomposición. Se identificaron veintiséis especies de hepáticas y siete de musgos. La familia de hepáticas más diversa y predominante fue la Lejeuneaceae con veintidós especies y dos variedades y, entre los musgos, la Calymperaceae con tres especies. Se analizaron las afinidades de las especies con aquellas de otros manglares tropicales y se encontró que las hepáticas eran el elemento dominante. De las hepáticas colectadas dos son nuevos registros para Panamá: *Ceratolejeunea confusa* y *Frullanoides mexicana*. Se necesitan con urgencia estudios adicionales sobre la vegetación de criptógamas de los

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manglares de Panamá debido a la acelerada deforestación causada por actividades antrópicas y la pérdida potencial de una importante biodiversidad.

Keywords: Marchantiophyta, Bryophyta, species diversity, Atlantic coast

Introduction

Mangroves are distinctive tropical plant communities that occupy the intertidal zone between sea and land (Tomlinson 1986). They are very important ecosystems in the tropics with crucial roles in carbon sequestration and storage, as timber and plant products, retention of nutrients, habitat for many species of arthropods, mollusks, fishes, and crustaceans, as coastal protection from the effects of hurricanes and storms, and for fisheries, among their many functions (Tomlinson 1986, Spalding *et al*. 2010, van Lavieren *et al*. 2012, to mention few). Mangroves are more abundant in the Paleotropics than in the New World tropics (Tomlinson 1986). There are two main centers of mangrove diversity, the Eastern center (including mangroves from East Africa, India, Southeast Asia, Australia, and Western Pacific) and the Western center (including mangroves from West Africa, Florida, the Caribbean, Central America, Atlantic South America and Pacific North and South America) (Tomlinson 1986).

Panama has an estimated area of 174,400 ha of mangroves on both the Atlantic and the Pacific coasts (Recio *et al.* 2016, ANAM-ARAP 2013), corresponding to 2.3% of the Panamanian surface area (ANAM-ARAP 2013). Of these, ca. 5.4% are on the Caribbean coast. The Pacific coast of Panama has the most extended surface of mangroves on the Pacific coast of Central America, with ca. 165,000 ha (Jiménez 1994, Vega *et al.* 2007). Of the 11 tree species of mangroves that grow in Latin America and the Caribbean, the species of *Rhizophora* (*R. mangle* L., *R. racemosa* G. Mey., *R. x harrisonii* Leechm.) and *Avicennia* (*A. bicolor* Stand., *A. germinans* (L.) L.) are the dominant taxa in Panama (Lacerda 1993). Approximately 70,000 ha of mangroves are included in the National System of Protected Areas (SINAP for the Spanish acronym) of Panama. Botanical studies of the epiphytic flora of the Panamanian mangroves have centered on the vascular vegetation (D'Croz 1993, Lovelock *et al*. 2005, CONADES/ARAP 2008, ANAM-ARAP 2013). These studies have ignored the cryptogams (bryophytes, algae, fungi and lichens).

Bryophytes can be found in the most extreme environments (even in Antarctica) however most species are known to be intolerant of salinity and there is not a single purely marine species (Richards 1932, Schuster 1969, Richardson 1981). The only bryophytes known to grow in salt dominated habitats belong to the family Riellaceae (Engel & Schuster 1973, Frahm 2001). The ephemeral genus *Riella* Mont. includes aquatic species that grow erect and submerged in fresh or usually brackish, alkaline standing water and on saline muds, at margins of ponds and lakes at low elevations (Banwell 1951, Bischler-Causse *et al.* 2005). Similar saline habitats in drier conditions have also been described for the genus *Austroriella* Cargill & J. Milne. Distributed in subtropical and Mediterranean regions, Riellaceae has been reported in the Americas from the United States, northern Mexico, and South America (Proctor 1972).

However, a few liverworts and mosses do grow in coastal areas. Engel & Schuster (1973) reported 36 liverworts in some tidal zones in South Chile that were "either washed by waves from the sea or on rocks directly exposed to ocean sprays." They indicated that the constant rainfall and drainage of fresh water from nearby forests or forest scrubs, during low tide might serve to wash the salts from the thalli. These authors signaled that reports of leafy liverworts at intertidal zones are almost nonexistent, citing only *Scapania undulata* (L.) Dumort. from Latouche Island, Alaska (Shacklette 1961). According to Engel & Schuster (1973), very few leafy liverworts occur in the mangrove ecosystem; they mentioned *Neolepidozia mamillosa* (Schiffn.) E.D. Cooper (as *Lepidozia mamillosa* Schiffn.) growing on soil in "*Rhizophora* swamps'' in Malaysia. Grolle (1967) reported the same species as a characteristic plant species of Malaysian mangroves. Furthermore, some seashore mosses (*e.g.*, *Schistidium maritimum* (Turner ex Robt. Scott) Bruch. & Schimp.) can withstand 24 hours immersion in sea water without damage to their physiological functions (Bates & Brown 1974, 1975). Boerner & Forman (1975) suggested that salt tolerance must be a species level trait.

Studies on bryophytes in tropical and subtropical tidal, salt marshes and mangrove zones are not as extensive as those for vascular plants. Nonetheless, several species of liverworts and mosses have been reported for some mangrove forests. Interesting to note is the absence of hornworts in mangroves around the world.

In Japan, on a mangrove branch, Nakanishi (1964) found a community composed of the liverworts *Myriocoleopsis minutissima* (Sm.) R.L. Zhu, Y. Yu & Póc (as *Cololejeunea minutissima* (Sm.) Steph.), *Frullania muscicola* Steph. and *Acrolejeunea pusilla* (Steph.) Grolle & Gradst. (as *Ptychocoleus nipponicus* S. Hatt.), and an equal number of lichens (one crustose and two cyanolichens). Yamaguchi *et al.* (1987), studying terrestrial bryophytes in mangroves, recorded a moss, *Fissidens microcladus* Thwaites & Mitt. and a liverwort, *Neolepidozia mamillosa* (as *Lepidozia* *mamillosa*). The moss grew on soil mounds made by crabs and was not subjected to sea water even at high tides, while *Neolepidozia* was found on sandy soil around mangrove swamps. Later, Yamaguchi *et al.* (1990) reported 53 bryophytes in mangrove forests in southern Japan. Of these, 43 were growing on trunks of mangrove trees. Thirty-seven were liverworts in three families: Lejeuneaceae, Frullaniaceae and Radulaceae. The Lejeuneaceae was the most important family in number of species with 25, followed by the Frullaniaceae with 11 and the Radulaceae with one. Six species of mosses in four families (Calymperaceae, Orthotrichaceae, Plagiotheciaceae and Sematophyllaceae) were growing on bark of mangrove trees. Except for the Calymperaceae and Orthotrichaceae with two species each, the other families included one species each.

Thaithong (1984) collected bryophytes in the National Reserve Mangrove Forests of the eastern and western coasts of Thailand. Of the 40 species of trees studied in those Thai mangrove forests, only ten have bryophytes on them. Of the bryophytes collected, 22 were mosses pertaining to five species and 89 were liverworts representing 21 species.

Two liverworts were reported from the mangroves of Singapore: *Neolepidozia mamillosa* and *Myriocoleopsis minutissima* subsp. *myriocarpa* (Nees & Mont.) R.L. Zhu, Y. Yu & Pócs. Ng & Sivasothi (1999) reported *N. mamillosa* (as *Lepidozia mamillosa*) growing on mud-lobster mounds in the mangroves. This species has been reported from other substrates from Borneo and New Guinea (Grolle 1967, Cooper *et al.* 2013). The pantropical *M. minutissima* subsp. *myriocarpa* was collected on a tree branch of a mangrove in Sengei Buloh Nature Park (Yu *et al*. 2014). It has also been reported for the Black Spring swamp forest of Florida (Yu *et al*. 2014). Like *Neolepidozia*, this subspecies occurs also on other substrates (Yu *et al.* 2014).

Windolf (1985), collecting liverworts and hornworts along the Sunshine coastal region of Queensland, reported 12 leafy liverworts in mangrove swamps. In 1989, he reported 13 species of liverworts and three species of mosses from the sub-tropical mangroves of Australia in the Queensland area. The dominant bryophyte in the mangroves was *Frullania subtropica* Steph., an endemic species to the central-east coast of Australia. Windolf (1989) found many similarities between the liverwort flora of the mangroves of Thailand (Thaithong 1984) and those of Queensland, seven genera were common to both sites. Reese & Stone (1995) reported one species of *Syrrhopodon* and six species of *Calymperes* on mangrove trees in Australia. Later, in a revision of the Australian *Calymperes*, Reese & Stone (2012) reported 14 species, six of which also grew on bark of mangroves.

In North America, Testrake *et al.* (1986), working in mangroves and with adjacent shoreline plants of Tampa Bay, Florida (USA), indicated that the bryoflora showed a patchy distribution. Of the 30 species collected by him (18 liverworts and 12 mosses) only five liverworts, namely *Acrolejeunea heterophylla* (A. Evans) Grolle & Gradst., *Myriocoleopsis minutissima* subsp. *myriocarpa*, *Microlejeunea globosa* (Spruce) Steph. (as *Lejeunea globosa* Spruce), *Lejeunea laetevirens* Nees & Mont. and *Frullania kunzei* (Lehm. & Lindenb.) Lehm. & Lindenb., and one moss, *Octoblepharum albidum* Hedw., were growing on mangrove bark. These mangrove inventories in Florida, depict a dryer environment with greater diversity of smaller xerotolerant species in the genera *Frullania*, *Lejeunea* and *Cololejeunea*. Unlike Testrake *et al*. (1986), Whittier & Miller (1976) did not find any bryophytes on mangroves associations in previous work on the bryophytes of Merritt Island, Florida. For Mexico, Delgadillo (pers. comm., 2019) registered only *O. albidum* in mangroves.

Knowledge of the bryophytes growing on mangroves of the Caribbean, Central and South America is scarce except for Brazil (Mello & Yano 1991, Yano & Carvalho 1994, Yano & Mello 1999, Yano 2002, Visnadi 2008) and a single report from Cocos Island, Costa Rica (Dauphin 1999). The latter reported five bryophytes from a coastal mangrove-like *Annona glabra* L. swamp, including the liverworts *Symbiezidium transversale* (Sw.) Trevis., *Radula macrostachya* Lindenb. & Gottsche (=*Radula javanica* Gottsche), and *Plagiochila rutilans* Lindenb., and the mosses *Calymperes afzelii* Sw. and *Fissidens neglectus* H.A. Crum. The species found in the mangrove-like *Annona glabra* association were present in most vegetation types sampled in the lower elevation areas.

Studies of the bryophytes in mangroves of Brazil are the most extensive and detailed in the Neotropics. Visnadi (2008) reviewed published studies on the bryophytes in mangroves of São Paulo state, Brazil. She listed 19 families, 56 genera and 115 species of liverworts (particularly Lejeuneaceae) and mosses collected in the mangroves of Ubatuba, São Vicente, Praia Grande, Itanhaém, Peruíbe, Iguape and Cananéia. Species diversity of liverworts was higher than in the Cerrado, but lower than in the Restingas and the Atlantic Forest biomes in São Paulo state. She added that the species composition was very similar to that registered for the Atlantic Forest of that state and that all species also occurred in other ecosystems.

In 2016, Dr. Rachel Collin, Director of the Bocas del Toro Research Station (Smithsonian Tropical Research Institute), proposed to the first author the organization of an international workshop on bryophytes (*Taxonomy and Biology of Tropical Bryophytes*) to increase knowledge on the diversity of these plants in the Province of Bocas del

Toro. Forty-three bryophytes are registered for this province in the data base of the University of Panama Herbarium (PMA). Most of these are from mainland forests. In contrast, about 1260 species of bryophytes are reported for Panama. Of these, ca. 491 are liverworts and 17 hornworts (Stotler *et al.* 1998, Dauphin *et al*. 2006, Dauphin 2007, Reiner-Drehwald *et al.* 2013, Schäfer-Verwimp 2014, Dauphin *et al.* 2015, Arrocha *et al*. 2020) and ca. 752 are mosses (Salazar Allen & Gudiño 2014). Bryophytes of the mangroves of Bocas del Toro and other Panamanian mangroves have not been studied and their diversity is unknown. Thus, one of the aims of this workshop was to do an inventory of the Bocas del Toro mangrove bryophyte flora in selected areas. Additionally, and to contribute to the knowledge of the bryophyte flora of Bocas del Toro, other sites were inventoried including an inland lowland forest in Isla Bastimentos (Salt Creek Forest), two cacao plantations and a mainland cloud forest. Findings regarding the bryophytes of these additional sites will be treated in other publications. Thirteen students from ten countries attended the workshop.

Bocas del Toro Province is situated in the northwestern part of Panama on the Caribbean coast. It is among the areas of the country with the highest rainfall. Average annual rainfall varies from over 3000 mm to more than 4000 mm with little seasonality (Lovelock *et al.* 2005, CONADES/ARAP 2008). The meteorological year in Bocas del Toro is divided into four periods: two periods of wetness (June–July and November–December) and two periods of low rainfall (approximately from mid-December to the end of May, and the months of August to October).

The province has ca. 500 km of coastline, about half the Caribbean coastline of all Panama (CONADES/ARAP 2008). An extensive mangrove forest fringed most of the coastline along with wetlands, coral reefs, and sea grasses (Lovelock *et al.* 2005), particularly in the Almirante Bay and the Chiriquí Lagoon (Fig. 1) which represents about 32% of the Panamanian Caribbean mangroves (CONADES/ARAP 2008).

In Bocas del Toro, the red mangroves *Rhizophora mangle* and few individuals of the white mangrove *Avicennia germinans* and *Laguncularia racemosa* (L.) C.F. Gaertn. dominate the mangrove forests (Lovelock *et al.* 2005). All mangroves in this area are surrounded by inland lowland forests. According to Köppen´s climate classification (ETESA in POTF 2008), The climate in these coastal areas is very humid tropical. The coastal environment of Bocas del Toro and its archipelago is defined by various relevant and important factors: the freshwater intake provided by the flowing rivers, the semi-diurnal tidal regime with relatively low changes and tidal amplitude (+0.43 m of the base line and the low ones –0.06 m, with a tidal amplitude of ~0.5 m, according to the National Oceanic and Atmospheric Administration, NOAA) and the semi-closed nature of their bays. Even during lunar phases, the coastal area does not experience great changes in tidal amplitude and, important fluctuations by climatological seasons and the impact of the multiannual phenomena are limited. Due to all these factors, there is little variation in the salinity of the system (POTF 2008).

Material and methods

Study area

Two mangroves were surveyed during the workshop in August 2017, one in Dolphin Bay (9° 13’ 14.7” N, 82° 13’ 02.9” W) on the NW site of a mainland Peninsula and the other in Salt Creek (9º 17’ 39.7” N, 82º 06’ 11.2” W) on Isla Bastimento (Figs. 1, 2). Previously, in September 2016 and May 2017, N. Salazar Allen, J. Gudiño L. & D. González collected in the mangroves of Tranquilo Bay Eco Adventure Lodge (9º 15’ 23.1’’ N, 82º 08’ 41.4” W) in Isla Bastimento and Punta Donato (9º 22’ 45.5’’ N, 82º 22’ 07.8’’ W) (Figs. 1, 2). All these collections are included in this report.

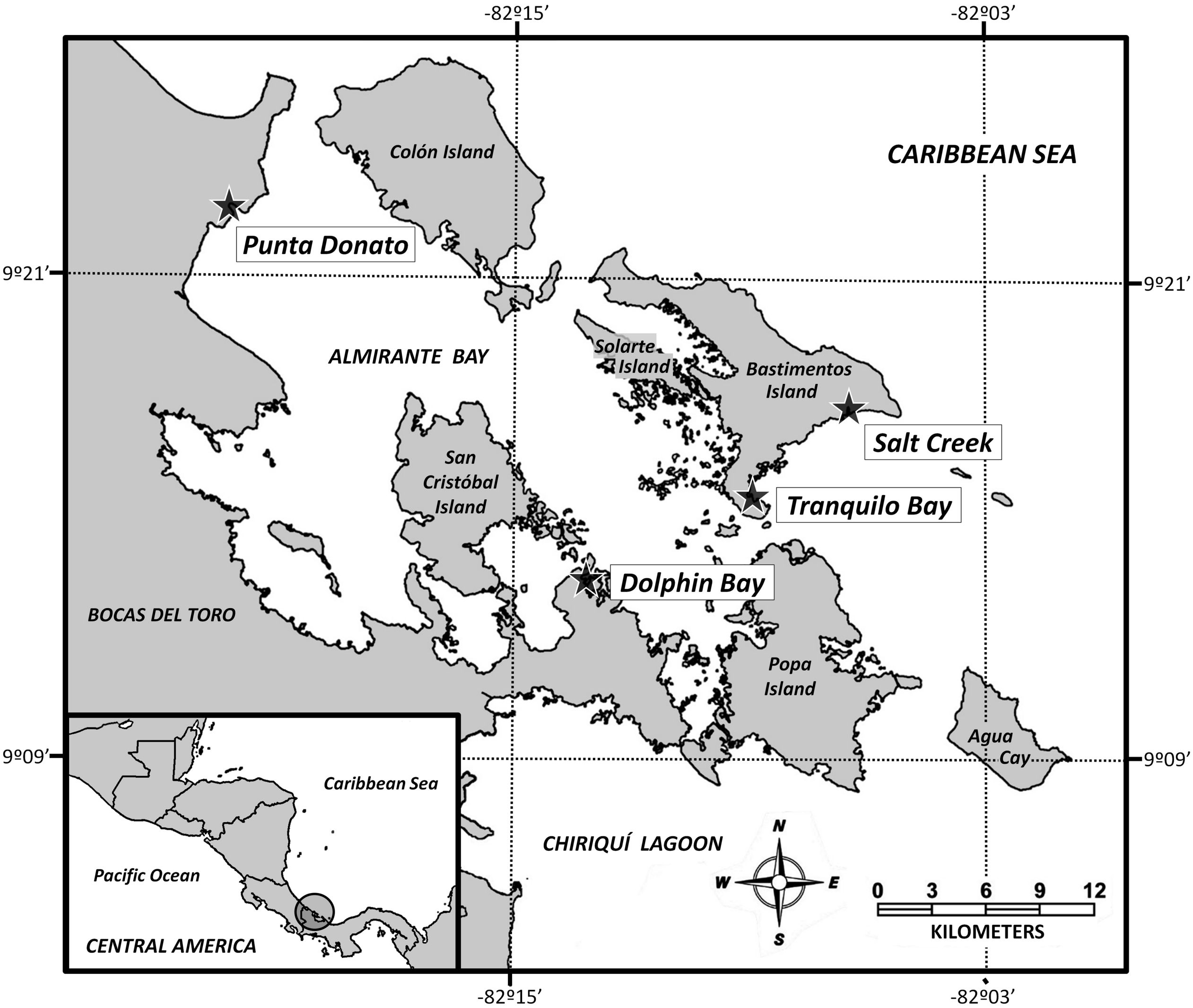

FIGURE 1. Northwest coastal area of Bocas del Toro Province with mangroves study sites (Dolphin Bay, Punta Donato, Salt Creek and Tranquilo Bay) indicated by stars.

Bryophyte sampling

Bryophytes were collected from all substrates, including soil, rocks, decomposing logs, prop roots, lower trunk, and branches of the phorophytes (>2-3 m above the soil). The lower canopy of the mangrove trees (*i.e.*, upper parts of trunks, branches, and twigs) were only eventually sampled (Fig. 2).

Various keys, monographs and the protologues of some species were used for identification of samples. Accepted names for liverworts follow Gradstein (2021), Söderström *et al.* (2016) and, family arrangements Crandall-Stotler *et al.* (2009). Systematics of the moss families follows Goffinet *et al.* (2009). Duplicates of the collections are deposited at PMA.

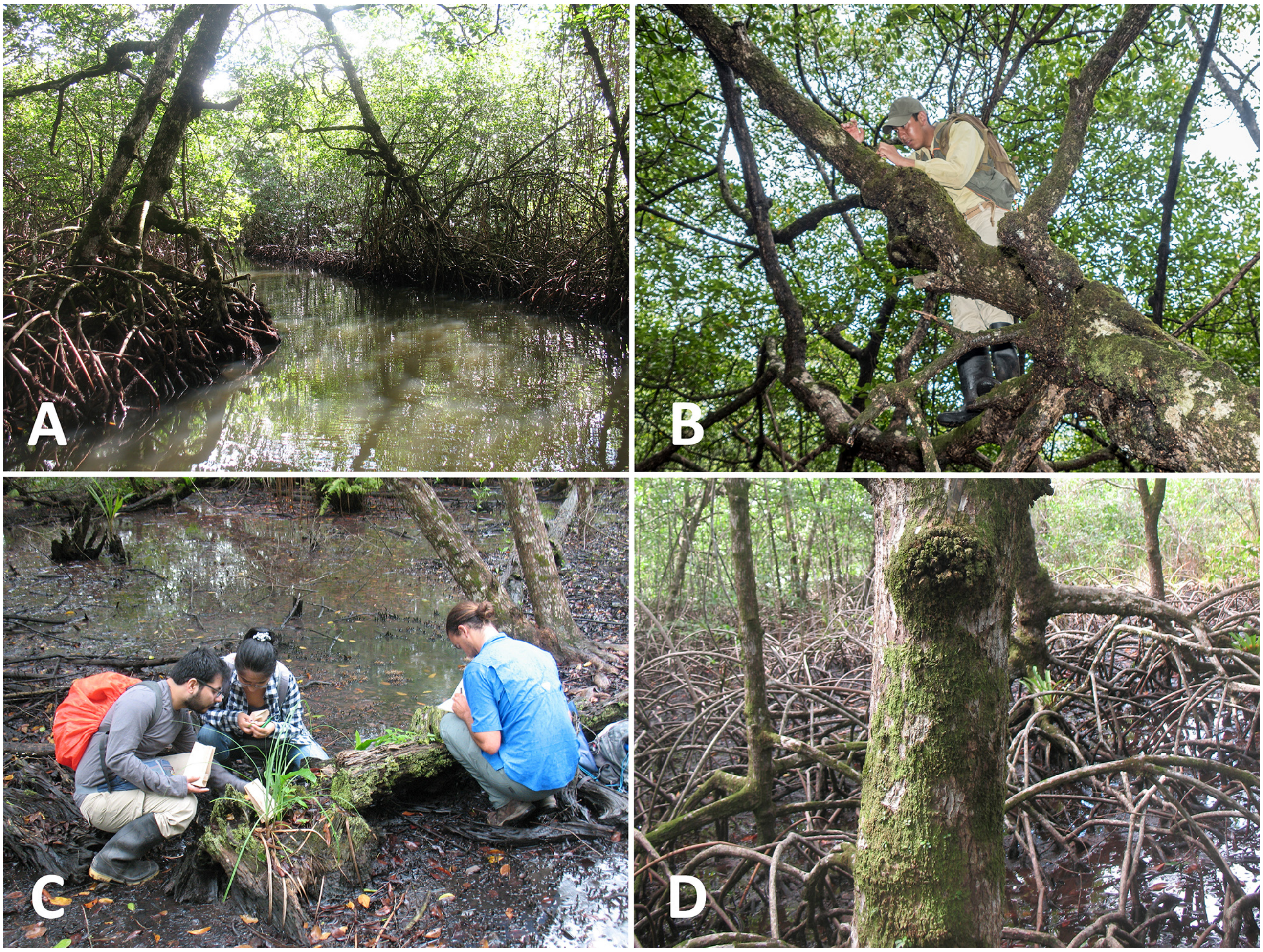

FIGURE 2. View of the mangroves. A−B. Salt Creek. C. Dolphin Bay. Students collecting at the border of mangrove during low tide. D. Tranquilo Bay. (Photos A–C by M. Madrid; D by J. Gudiño L.)

Diversity analysis

To evaluate the richness and species turnover in Bocas del Toro mangroves statistically, we used the sampling data from Dolphin Bay and Salt Creek because they were sampled similarly by the workshop participants. We used the approach proposed by Chao *et al.* (2014) using rarefaction/extrapolation curves with Hill number = q0 to evaluate species richness. The diversity curve was extrapolated to double sampling (four sites) with 95% confidence intervals for presence/absence data (Chao *et al.* 2014). The curve was generated with the R software version 4.1.3 (R Core Team 2022) using the package iNEXT (Hsieh *et al.* 2016). The species turnover was assessed with the method proposed by Carvalho *et al.* (2012), which considers the species replacement (βrepl) and richness differences between sites (βriq) to explain the species turnover (βtotal) in the whole community. We performed the species turnover analysis with the Jaccard index through the BAT package (Cardoso *et al.* 2021). In both analyses, we included mosses and liverworts species and their varieties.

Results

A total of 220 collections were made by the students and instructors in the mangroves. Thirty-three species and two varieties of bryophytes were identified. Of the bryophytes identified, 26 species and two varieties were liverworts in four families and seven species were mosses in four families (Table 1). Two Lejeuneaceae were also collected on angiosperm trees at the border of the mangroves. These were *Colura tortifolia* (Nees & Mont.) Trevis. and *Otigoniolejeunea huctumalcensis* (Lindenb. & Gottsche) Y.M. Wei, R.L. Zhu & R. Gradst. (Table 1). Two liverworts, *Ceratolejeunea confusa* R.M. Schuster (Dauphin 4612, 4614, PMA) and *Frullanoides mexicana* van Slageren (Magaña-Marcial 246, PMA) are new reports for Panama.

Species of bryophytes collected in Salt Creek (19), Tranquilo Bay (eight) and Punta Donato (five) were all from prop roots, trunks, and branches of *Rhizophora mangle*. In Dolphin Bay the number of species collected was higher (26) than in the other mangroves. They included some species that also grow in the adjacent lowland forest like the mosses *Isopterygium tenerum* (Sw.) Mitt. growing on soil accumulated on leaf litter at mangrove margins. Inside the mangrove *Octoblepharum pulvinatum* (Dozy & Molk.) Mitt. was collected on a decomposing log. The collection of *O. albidum* from Tranquilo Bay is the first record for that species at the base of a mangrove tree where it can be inundated periodically by sea water during storms or high tides and regularly covered with spray.

Bryophytes collected in adjacent coastal vegetation, above Dolphin Bay mangrove included among the mosses, *Acroporium longirostre* (Brid.) W.R. Buck, *Sematophyllum subsimplex* (Hedw.) Mitt., *Taxithelium planum* (Brid.) Mitt., *Meteorium nigrescens* (Hedw.) Dozy & Molkenb., *Meteoridium remotifolium* (Müll. Hal.) Manuel, *Syrrhopodon incompletus* Schwägr. var. *berteroanus* (Brid.) Reese and, among the liverworts, *Lejeunea laetevirens*, *Frullanoides mexicana*, *Plagiochila montagnei* Nees and *Zoopsidella integrifolia* (Spruce) R.M. Schuster. *Zoopsidella* was growing epiphytically on other liverworts.

In all mangroves studied, the liverworts outnumbered the mosses representing about 80% of the total diversity of bryophytes (Table 1). Among the liverworts collected, 22 species and two varieties are Lejeuneaceae while Frullaniaceae have two species and, Aneuraceae and Cephaloziellaceae have one species each (Table 1).

TABLE 1. Families and species of the mangrove bryophyte flora of Bocas del Toro, the sites studied, affinities (overlap) with those reported from mangroves of United States (USA), Brazil, Thailand and Australia, and total geographic distribution of the species. Sources: Gradstein *et al.* (1983), Gradstein (1994), Reese (1993), Salazar Allen (1994), Reiner-Drehwald (1998), Dauphin (2003, 2005), Schäfer-Verwimp *et al.* (2013), Gradstein (2013), Macedo & Ilkiu-Borges (2014), Schäfer-Verwimp (2014), Bastos (2017), Stotler & Crandall-Stotler (2017), Gradstein & Reeb (2018), Bastos & Gradstein (2020), Gradstein (2021), and Hagbord (unpublished data base) for *D. pellucida* in Africa. (x = Present; - = Absent; * = New record for Panama; x[1] = *C. palisotii* subsp. *moluccensis*; ? = doubtful distribution). Neo = Neotropical; Neo-SUSA = Neotropical into southern USA; Neo-Afr = Amphiatlantic; Pan = Pantropical. Species with their authorities are those not discussed in the text.

Family and species	**Sites studied**				**Mangroves affinities**				**Geographic distribution**
	Dolphin Bay	Salt Creek	Tranquilo Bay	Punta Donato	USA (Florida)	Brazil	Thailand	Australia	
				Marchantiophyta (Liverworts)					
Aneuraceae									
Riccardia regnellii	x	x	-	-	-	-	-	-	Neo-Afr?
Cephaloziaceae									
Odontoschisma variabile	x	x	-	-	-	-	-	-	Neo-Afr
Frullaniaceae									
Frullania kunzei	-	x	-	-	x	x	-	-	Neo-SUSA
F. subtilissima (Nees ex Mont.) Lindenb.	-	x	-	x	-	x	-	-	Neo-Afr?
Lejeuneaceae									
Acrolejeunea emergens (Mitt.) Steph.	x	x	-	-	-	x	-	-	Pan
A. torulosa (Lehm. & Lindenb.) Schiffn.	x	-	-	-	-	-	-	-	Neo
Archilejeunea juliformis (Nees) Gradst.	x	-	-	-	-	-	-	-	Neo
Ceratolejeunea coarina (Gottsche) Schiffn.	x	-	-	-	-	x	-	-	Neo-Afr
**C. confusa*	x	-	x	-	-	x	-	-	Neo
C. cornuta	x	x	-	-	-	x	-	-	Pan
C. cubensis (Mont.) Schiffn.	x	x	x	-	-	x	-	-	Neo

...*Continued on the next page*

TABLE 1. (Continued)

Family and species	Sites studied				Mangroves affinities				Geographic distribution
	Dolphin Bay	Salt Creek	Tranquilo Bay	Punta Donato	USA (Florida)	Brazil	Thailand	Australia	
C. guianensis (Nees & Mont.) Steph.	x	-	-	-	-	-	-	-	Neo-SUSA
C. laetefusca (Austin) R.M. Schuster	x	-	-	-	-	x	-	-	Neo-SUSA
Cheilolejeunea adnata (Kunze ex Lehm.) Grolle	x	-	-	-	-	-	-	-	Neo-SUSA
C. rigidula	x	-	x	x	-	x	-	-	Pan
C. trifaria (Reinw., Blume & Nees) Mizut.	x	x	x	x	-	x	-	-	Pan
C. trifaria var. *clausa* (Nees & Mont.) Bastos & Gradst.	-	x	-	-	-	x	-	-	Neo
Colura tortifolia	x	-	-	-	-	-	-	-	Neo
Diplasiolejeunea pellucida	-	x	-	-	-	-	-	-	Neo-Afr
Frullanoides corticalis	x	x	-	x	-	x	-	-	Neo
F. liebmaniana	x	x	-	-	-	-	-	-	Neo
Leptolejeunea elliptica (Lehm. & Lindenb.) Besch.	-	x	-	--	-	x	-	-	Pan
Lopholejeunea subfusca	-	x	-	-	-	x	x	-	Pan
Otigoniolejeunea huctumalcensis	x	-	-	-	-	-	-	-	Neo
Rectolejeunea flagelliformis	x	x	-	-	-	-	-	-	Neo
Symbiezidium barbiflorum (Lindenb. & Gottsche) A. Evans	-	x	-	-	-	x	-	-	Neo
S. transversale	x	x	x	-	-	-	-	-	Neo
S. transversale var. *hookerianum* (Gottsche, Lindenb. & Nees) Gradst. & J. Beek	x	-	-	-	-	-	-	-	Neo
Total species no. by site	**20 +1 var.**	**16 +1 var.**	**5**	**4**	**1**	**14 +1 var.**	**1**	**0**	
					Bryophyta (Mosses)				
Calymperaceae									
Calymperes afzelii	x	x	-	-	-	-	-	-	Pan
C. erosum	x	-	-	-	-	-	x	x	Pan
C. palisotii	x	x	x	x	-	x	-	x[1]	Pan
Pylaisiadelphaceae									
Isopterygium tenerum	x	-	-	-	-	-	-	-	Neo
Octoblepharaceae									
Octoblepharum albidum	x	-	x	-	x	x	x	-	Pan
O. pulvinatum	x	-	x	-	-	-	-	-	Neo
Orthotrichaceae									
Groutiella sp.	-	x	-	-	-	-	-	-	Neo
Total species no. by site	**6**	**3**	**3**	**1**	**1**	**2**	**2**	**2**	

Considering the rarefaction/extrapolation analysis estimation, the bryophyte richness in Bocas del Toro mangroves may include between 39 and 51 species. Also, we found a high species turnover (βtotal = 82%) between mangroves influenced mainly by the replacement (βrepl = 53%) and, to a lesser extent, by the richness differences between sites (βriq = 29%). These results indicate that the mangroves have a high bryophyte diversity, mainly driven by their variation in species composition (Fig. 3).

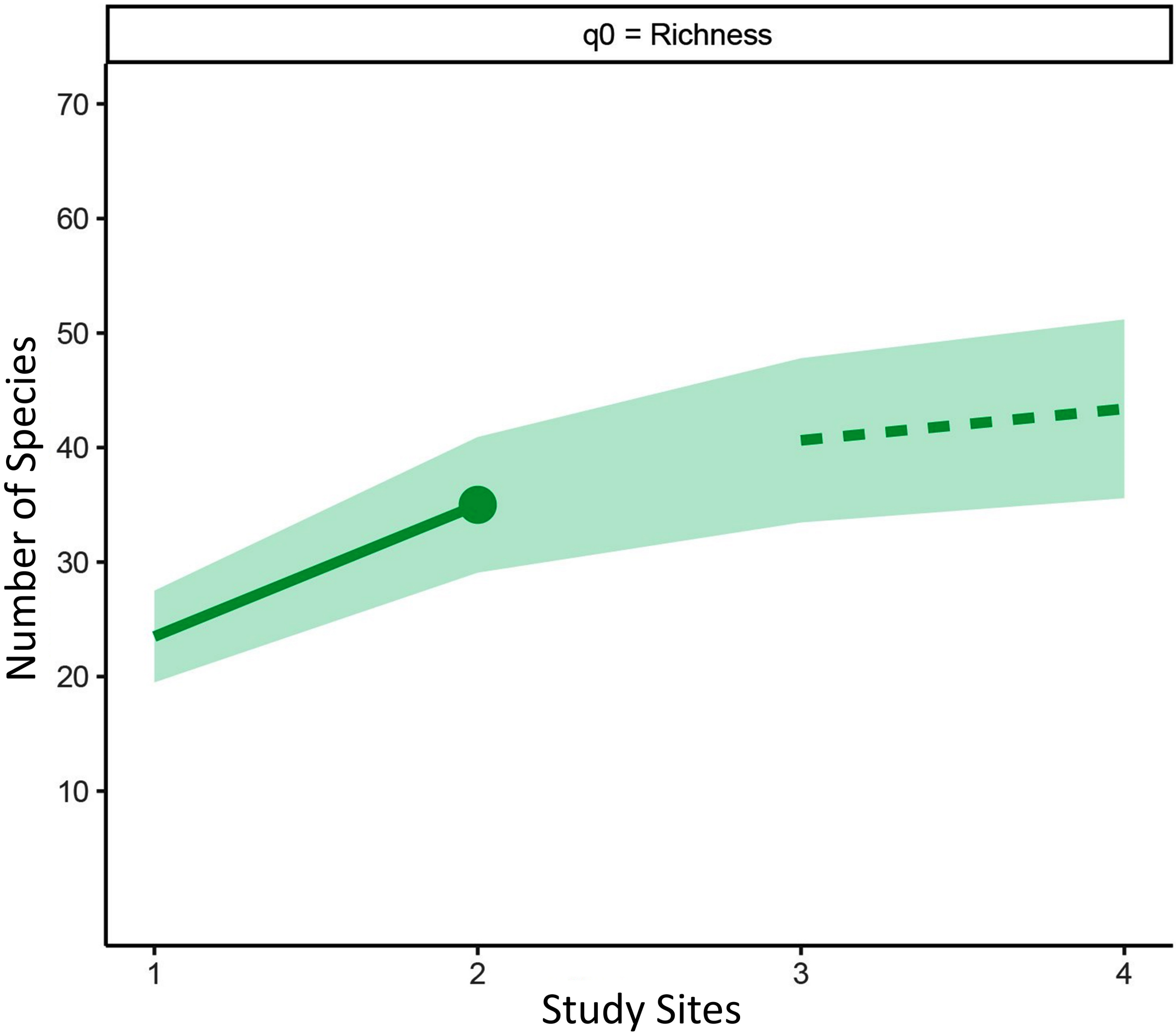

FIGURE 3. The rarefaction/extrapolation curve shows 33 species and two varieties observed (●) in the Dolphin Bay and Salt Creek mangroves, as well as the interpolation (continuous line) and extrapolation (dotted line) of its richness (q0). The shaded area corresponds to the 95% confidence intervals.

Discussion

We recorded a significant bryophyte richness representing between 65 and 92 % (~36 and 51 species) of the bryoflora on Bocas del Toro mangroves (Fig. 3). These findings, supported by the beta diversity results, are the first ecological approximation assessing and estimating the bryoflora of these mangroves.

The high number of species found in the mangroves of Dolphin Bay and Salt Creek could be an artifact of the number of collectors, thirteen versus three in Tranquilo Bay and Punta Donato and the time spent in each site. The last two mangroves were visited when selecting the sites for the workshop, thus collections were gathered only at the border of the mangroves, on the stilt roots where the boat could approach. The mangroves of Dolphin Bay, unlike those of Salt Creek, are very close to the adjacent vegetation with palms, herbs and some other angiosperms fringing the outer border of the mangrove. Several species were collected on bark of *Laguncularia racemosa* in Dolphin Bay. According to Tomlinson (1986), this tree is typically restricted to the landward fringe of the mangrove community, but also can be a pioneer in disturbed sites. In Salt Creek, *Rhizophora mangle* was the only phorophyte available. The proximity of inland forest and of some islands to the west of the mangrove (Fig. 1) may have served as a pool for spores and vegetative diaspores of bryophytes.

Marchantiophyta (Liverworts)

With over 60% of the species found, the Lejeuneaceae was the dominant family of bryophytes in the mangroves of Bocas del Toro (Fig. 4). This is a common pattern throughout neotropical primary and secondary forests, especially in wet lowland areas (*e.g.,* Lücking 1995, Dauphin 1999, Gehrig-Downie *et al.* 2013), where this family is most diverse. In general, the liverwort flora found in the mangroves of Bocas del Toro comprise foliose species and typical sun epiphytes, including widespread species from the genera *Acrolejeunea, Frullanoides*, and *Lopholejeunea* (Table 1). These genera are very common elements of the surrounding wet lowland forests and are among the most xerotolerant Lejeuneaceae. Except for *Acrolejeunea*, they do not produce vegetative propagules. Another xerotolerant Lejeuneaceae associated with coastal areas and restricted to lowlands below 200 m above sea level, *Ceratolejeunea confusa* and the widespread *Cheilolejeunea rigidula* (Nees ex Mont.) R.M. Schuster were found on stems of the mangrove *Laguncularia racemosa* (Fig. 4).

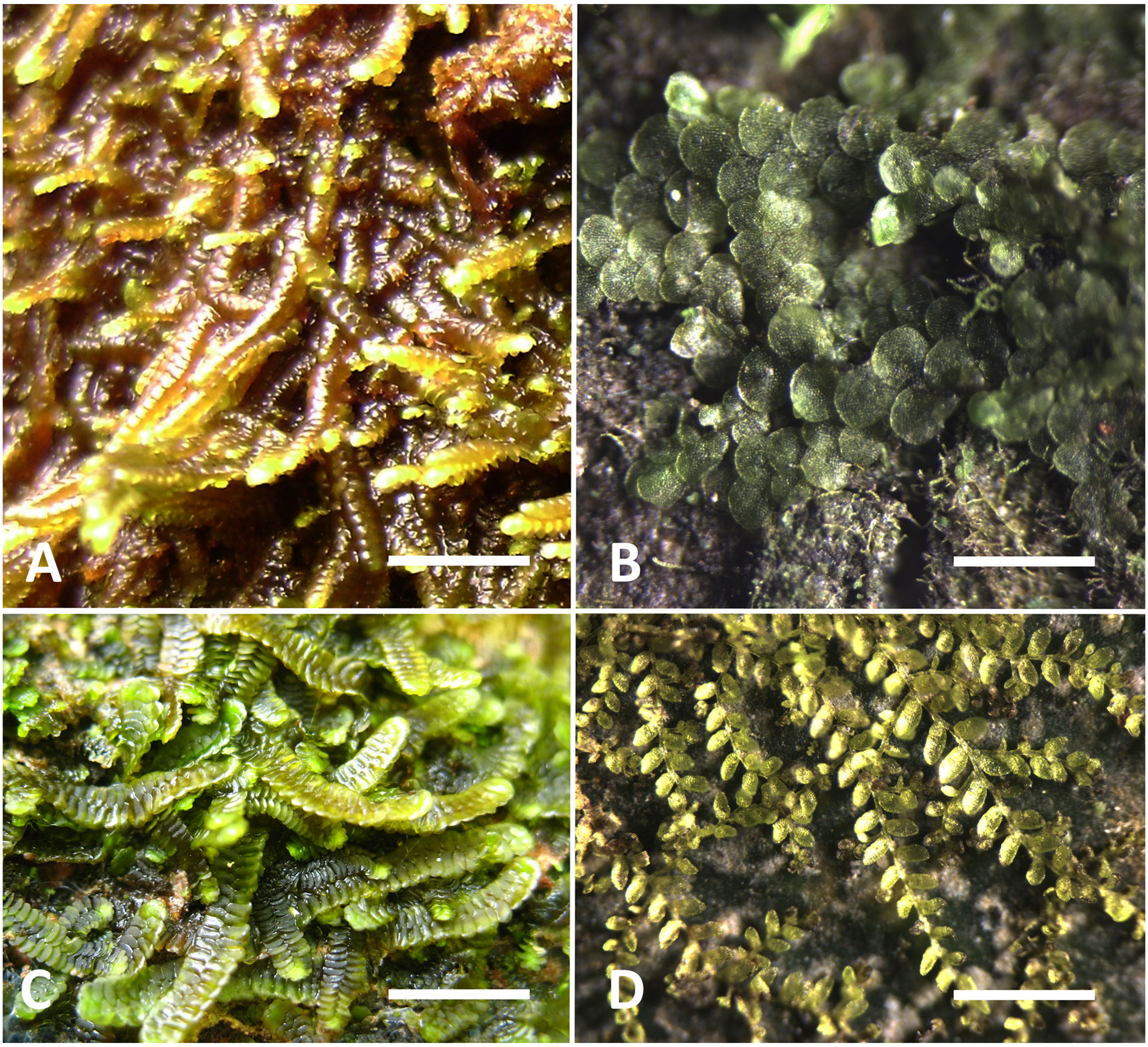

FIGURE 4. Marchantiophyta, Lejeuneaceae. A. *Ceratolejeunea cornuta.* B. *Cheilolejeunea rigidula*. C. *Symbiezidium transversale*. D. *Leptolejeunea elliptica.* Scales: A= 3.99 mm, B= 0.80 mm, C= 6.29 mm, D= 1.18 mm. (Photos by J. Gudiño L.).

Common species growing on *Rhizophora mangle* bark were *Ceratolejeunea cornuta* (Lindenb.) Steph., *Diplasiolejeunea pellucida* (C.F.W. Meissn. ex Spreng.) Schiffn., *Frullanoides liebmaniana* (Lindenb. & Gottsche) van Slageren, *F. corticalis* (Lehm. & Lindenb.) van Slageren, *Otigoniolejeunea huctumalcensis* and *Rectolejeunea flagelliformis* A. Evans. *Odontoschisma variabile* (Lindenb. & Gottsche) Trevis. was frequent growing on mangrove trunk bases and fallen logs. It is the most common *Odontoschisma* species in Tropical America, ranging from Cuba and Honduras to Bolivia and SE Brazil (Table 1) and grows on rotten wood, humus, soil or rock in rainforests, scrub, and open vegetation, from almost sea level up to 4000 m elevation (Gradstein 2021).

In the mangroves of Dolphin Bay and Salt Creek, *Riccardia regnellii* (Ångstr.) K.G. Hell grows on decomposing logs or mangrove roots in mangrove areas exposed at low tides. This species was not found in the adjacent lowland secondary forest. Due to its compact thallus several cell layers in thickness (perhaps, aiding in preventing dehydration), and its growth form tightly appressed to the substrate, *R. regnellii* could be adapted to the variable tidal and saline environment (see in Introduction, POTF 2008) of the mangrove at Dolphin Bay and Salt Creek ameliorated by the constant rainfall and runoff from adjacent forests. *Riccardia regnellii,* formerly known as *R. amazonica* (Spruce) Schiffn. ex Gradst. & Hekking (Gradstein & Reeb 2018) is rather widespread in Tropical South America, West Indies and perhaps Africa (Gradstein 2021) (Table 1). It grows in soil, shaded rocks and rotten wood in lowland and montane rainforests, from sea level up to 3700 m elevation (Gradstein & Reeb 2018).

There is no report of halophilous species of *Riccardia* growing submerged in coastal marine ecosystems or mangroves. Engel & Schuster (1973) listed four species of *Riccardia* growing in tidal zones in Southern Chile: *R. alcicornis* (Hook.f. & Taylor) Trevis., *R. fuegiensis* C. Massal., *R. georgiensis* (Steph.) Hässel and *R. spectabilis* (Steph.) A. Evans. Only in *R. georgiensis* (*cit. per*. Engel & Schuster 1973) did Hässel de Menéndez observe "slight structural differences, with the outer wall of the ventral thallus cells more thickened than the usual condition." *Riccardia regnellii* and *Symphyogyna brasiliensis* Nees & Mont. reported from Brazil without substrate data (Visnadi 2008), are the only thalloid liverworts known from mangrove areas.

Most liverwort species found in the mangroves of Bocas del Toro are very common elements of the surrounding wet lowland secondary rain forest and orchards, but none can be considered a specialist. Similar results were found by Vannucci (2003, *cit. per* Visnadi 2008), who viewed the liverwort flora of mangroves as a set of a reduced number of species that could occur in other coastal ecosystems. No adaptations to saline environments can be signaled in the species found. Due to the high rainfall in the Bocas del Toro area, its mangrove forests do not represent an extremely saline habitat as would be expected in mangroves on the Pacific coast, where there is a more marked seasonality in rainfall and mangrove tidal ranges (Jiménez 1994).

Roughly half of the liverwort species and their varieties are neotropical in distribution, 21% are pantropical, 18% amphiatlantic, 14% extend north into Southern United States (Table 1). Bryophytes reported from mangroves of Japan were not found in mangroves of Bocas del Toro. In terms of species composition, the mangroves of Bocas del Toro are more likely related to the tropical Atlantic Brazilian mangroves. Only the pantropical *Lopholejeunea subfusca* (Nees) Schiffn. has been detected in neotropical and paleotropical mangroves but cannot be considered a specialist.

Bryophyta (Mosses)

Four species of mosses, *Calymperes afzelii, C. erosum* Müll. Hal., *C. palisotii* Schwägr. and *Octoblepharum albidum* are pantropical in distribution, sometimes extending their range into subtropical areas (Sharp *et al.* 1994, Reese 1993, Salazar Allen 1994) (Table 1). *Calymperes erosum* and *C. palisotii* have been reported from Australian mangroves (Reese & Stone 1995) and *C. erosum* also from Thailand (Thaithong 1984) (Table 1).

Species of *Calymperes* are dioicous, mostly epiphytic and occur in lowland forests of tropical and subtropical regions around the world (Reese 1987). The leaves are composed of an upper layer of green cells subtended by a basal layer of porose hyaline cells, the cancellina (Fig. 5). These cells absorb water readily.

Species of *Calymperes* also occur epiphytically on trees along the Northeast Caribbean coast of Panama, in the Province of Colón where they are subject to saline spray during high tides. Most probably the high rainfall throughout the year in Bocas del Toro and Colón, may serve to wash any salt accumulated on the plants. Additionally, the water retained in the porose hyaline cells of the cancellina may ameliorate the effects of the salt sprays on the upper chlorophyllous cells of the leaves.

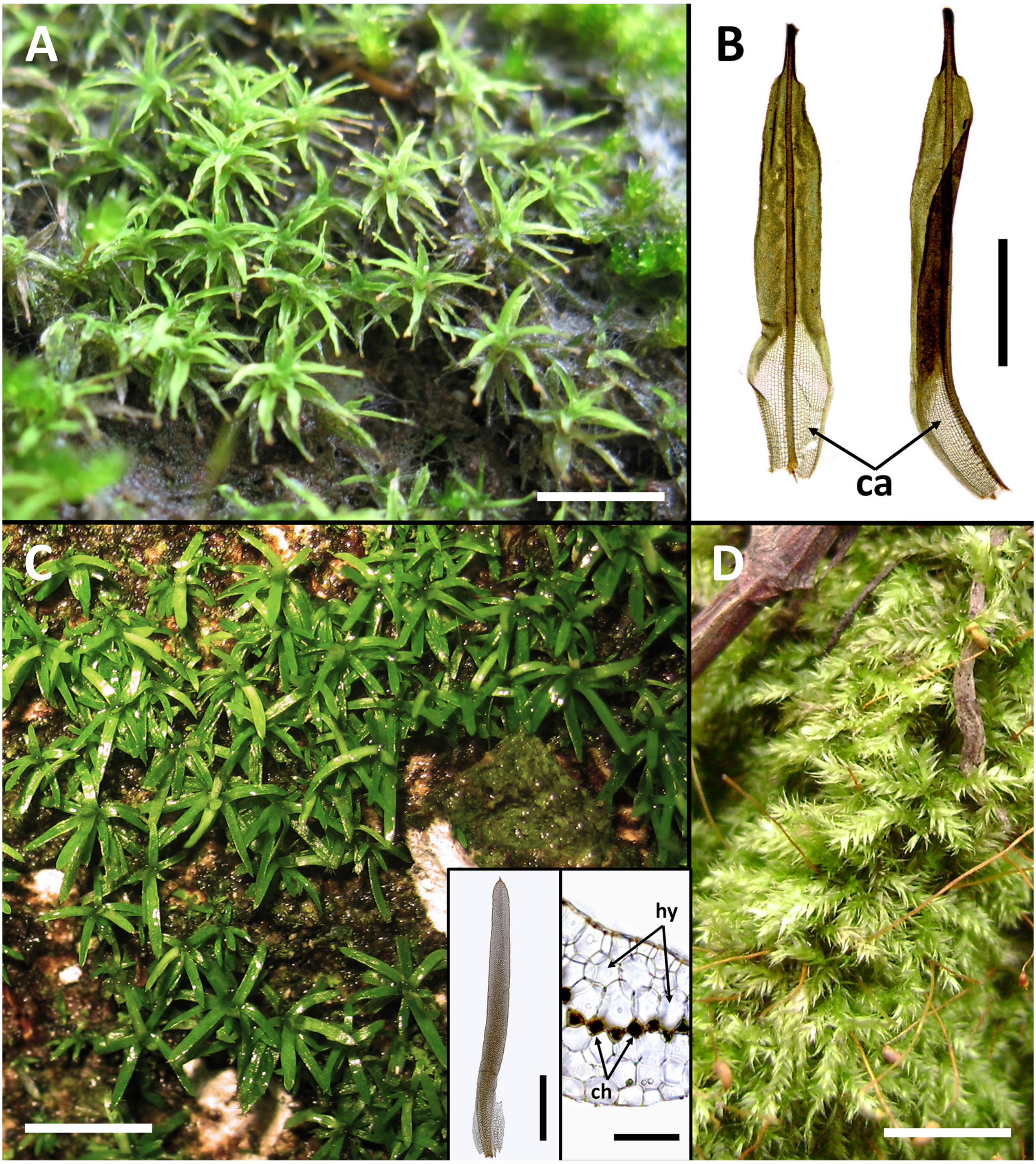

FIGURE 5. Bryophyta. A-B. Calymperaceae, *Calymperes afzelii*; A. Habit. B. Leaf with cancellina at base (ca). C. Octoblepharaceae, *Octoblepharum albidum*. Insets: leaf (scale = 1.65 mm) and cross-section at midleaf (scale= 63.53 µm), ch= chlorocysts, hy= hyalocysts. D. Pylaisiadelphaceae, *Isoptegygium tenerum*. Scales: A= 7.48 mm, B= 1.16 mm, C= 6.71 mm, D.= 6.63 mm. (Photos by J. Gudiño L.)

In the species of *Calymperes* found in the mangroves of Bocas del Toro, sporophytes are infrequent, suggesting a low rate of fertility. However, leaf gemmae are very common and often are produced abundantly (Reese 2001). In addition, morphological foliar specialization for gemmae production and dispersal are quite remarkable (Reese 1997, 1998, 2000, 2001). Gemmae production in some species of *Calymperes* is episodic and appears to be under endogenous control and possibly subject to environmental modification (Odu & Owotomo 1982). In Panama, gemmae are produced mainly during the rainy season (Salazar Allen, pers. obs.). Windborne dispersal of gemmae from mainland coastal areas to the islands could account for the presence of the three species of *Calymperes* found in the mangroves and in island forests as it is accounted by Reese (1987) for the distribution of *Calymperes* in Oceania and the Indo-Malaya region. Also, dispersal by sea birds may be possible as suggested by Fife & Lange (2009) for the dispersal of *Calymperes tenerum* Müll. Hal. in the New Zealand islands of Chatham and the Kermadecs. The three species of *Calymperes* that occur in the mangroves of Bocas del Toro grow in mainland forests throughout the Isthmus.

Unlike *Calymperes*, the leaves of *Octoblepharum albidum* are composed of a zigzagging layer of chlorophyllous cells surrounded by one or more layers of porose hyalocysts (Fig. 5). Leaf cells are difficult to hydrate due to the air trapped in the hyalocysts (Robinson 1985, Salazar Allen pers. obs.). Also, the high rainfall in Bocas del Toro can help to wash the excess salt accumulated in the plants allowing the only *Octoblepharum* sample collected in the mangroves of Tranquilo Bay to grow epiphytically close to sea levels. *Octoblepharum albidum* is monoicous and produces abundant sporophytes; in addition, leaf breakage and three modes of asexual reproduction by specialized propagules are known. These are the production of foliar gemmae along the upper half of leaf margins, the production of protonemal gemmae on protonema originating from foliar gemmae and the production of buds and new shoots at leaf tip (Zhang *et al.* 2003, Maciel-Silva *et al.* 2013). Both the production of abundant spores and asexual propagules aid in its dispersal by wind and perhaps by birds (when leaf fragments stick to their feathers) contributing to its successful establishment and broad geographical distribution (Robinson 1990).

All the species of mosses discussed above can be found in exposed and moist habitats, Nevertheless, gemmae and protonema in *O. albidum* are produced in shaded and moist habitats or during the rainy season (Zhang *et al*. 2003, Maciel-Silva *et al.* 2013, Salazar Allen, pers. obs.). This strategy will favor dispersal by wind during the dry season when northern winds are strong on the Atlantic coasts of Panama. Maciel-Silva *et al.* (2009) have found that spores and early protonemata in *O. albidum* tolerate very low water potentials that allow the establishment of new plants during the dry season.

The Neotropical *Octoblepharum pulvinatum* was not expected to occur in the mangroves. The decomposing log where it grew was probably from the logged lowland forest adjacent to and above the mangroves and was washed down by the copious rain and strong winds characteristic of the storms that occur frequently there during the rainy season. This moss grows from lowland to cloud forests above 1000 m, but it is more frequent in mid-elevation forests.

Isopterygium tenerum is a small plant, the stems seldom 2 cm long, sometimes with filamentous, multicellular, and papillose asexual reproductive bodies on the stem (Ireland 1991). *Isopterygium* has been reported previously growing in the salty swamps of the Society Islands (Whittier 1976). It is unknown whether it can withstand long periods of high salinity. The species found is widely distributed in Panama from lowlands to cloud forests to ca. 1260 m, although in other areas of the Neotropics it can grow above 3000 m (Sharp *et al*. 1994).

The only *Groutiella* collected could not be determined to species due to lack of sporophytes. Characters of the gametophyte are like *G. apiculata* (Hook.) Crum & Steere and *G. mucronifolia* (Hook. & Grev.) Crum & Steere. Allen (2002) separated both species based on sporophytic characters.

Conclusions

Leafy liverworts of the Lejeuneaceae are the most distinctive bryophyte component of the mangroves in Bocas del Toro, Panama. The species are mostly widespread sun epiphytes characteristic of primary and secondary lowland forests. A single thalloid liverwort, *Riccardia regnellii,* was found in the mangroves of Dolphin Bay. This is the second report of a thalloid liverwort in neotropical mangroves. The predominance of liverworts, particularly of the family Lejeuneaceae, in the mangroves of Bocas del Toro is similar to reports published for other tropical mangroves studied. The moss component is dominated by three members of the Calymperaceae, specifically *Calymperes* and one species of the Octoblepharaceae, *Octoblepharum albidum*, which also grow in lowland inland forests. Their remarkable production of asexual reproductive propagules (*e.g.,* leaf-tip gemmae, rhizoidal gemmae, broken leaves, production of new shoots at leaf tips) and spores could account for their potential for wind and animal dispersal favoring their establishment and wide distribution on mangroves. The high annual rainfall in Bocas del Toro may play a role in washing any salt deposit on the plants.

Additional surveys of the bryophytes in other areas of mangroves in Bocas del Toro (*e.g*., Punta Donato, Tranquilo Bay and, San Cristobal, Colón and Popa islands) are needed, including the tree canopy. Furthermore, a survey of the mangroves on the Pacific coasts of the Isthmus is urgently needed. Unlike those on the Atlantic coasts, these mangroves have been highly degraded due to the anthropogenic impact (wood for fuel, fishery, urban and commercial development, and new roads). They are also subject to a marked seasonality in rainfall and tide ranges. Reforestation projects in restricted areas of these mangroves are currently in process. They offer a unique opportunity for studies of bryophyte reforestation and resilience.

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