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A new *Pisonia* (Nyctaginaceae) from Jamaica, with an updated list of species in the genus and a key to the West Indian taxa

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Abstract. Here we describe a new species of *Pisonia* (Caryophyllales: Nyctaginaceae) from Jamaica, named *P. jamaicensis* Proctor ex Caraballo, K.Campbell, & S.Cross, restricted to limestone hills in the central and western part of the island. The species description is complemented with an illustration, pictures, a distribution map, and notes on its biology and conservation, including an IUCN evaluation. We also present a list of the 27 currently accepted species of *Pisonia* with their general distributions, and a key to separate the 16 taxa reported for the West Indies.

Keywords: Caribbean islands, Caryophyllales, Dioecious trees, Island endemic trees, Karst endemics, West Indies.

INTRODUCTION

The genus *Pisonia* L. (Caryophyllales: Nyctaginaceae) is widely distributed in tropical regions around the globe, although its diversity certainly lies within the American continent (Stevens 2001 onwards). Recent studies have reexamined the circumscription of the genus and transferred a number of species to other genera within tribe Pisonieae (Rossetto et al. 2019; Chagas and Costa-Lima 2020; Rossetto and Caraballo-Ortiz 2020). As a result, the number of currently accepted species in *Pisonia* has been estimated to be around 25 (The Plant List 2013 onwards; Ulloa Ulloa et al. 2018 onwards).

In the West Indies, the genus is represented by approximately 15 species, most of them endemic to the region (Acevedo-Rodríguez and Strong 2012). During current studies on the diversity of *Pisonia*, Caraballo-Ortiz found collections from Jamaica that did not match any of the previously published congeners. After morphological comparisons with all known species for the West Indies, we concluded that this taxon represents an undescribed species.

This finding concords with the view of George R. Proctor, who labeled a series of specimens from the Institute of Jamaica Herbarium as “*Pisonia jamaicensis* Proctor” during the early 2000’s, although he did not provide a description and effectuate its publication. In this work, we decided to adopt Proctor’s proposed name and formally describe the species as *P. jamaicensis* Proctor ex Caraballo, K.Campbell, & S.Cross.

Pisonia jamaicensis is a tree restricted to wooded summits and upper cliffs of limestone hills in central and western Jamaica. We complement the species’ description with an illustration, pictures, a distribution map, and notes on its biology. We also discuss how to separate this species from the other congener in Jamaica, and present a preliminary conservation assessment following the IUCN criteria. A table summarizing the currently accepted *Pisonia* worldwide with their general distributions is also included, along with a dichotomous key to separate the taxa reported for the West Indies.

MATERIALS AND METHODS

We studied all the collections identified as *Guapira* Aubl., *Pisonia*, and *Neea* Ruiz & Pav. from Jamaica deposited in 18 herbaria (CAYM, F, FLAS, FTG, HACC, IJ, JBSD, K, MAPR, MO, NY, P, SJ, UC, UPR, UPRRP, US, and UCWI). Measurements presented in the description were taken from dried plants using physical or virtual specimens (including types, accessible through the JSTOR Global Plants website [<https://plants.jstor.org/>]), while notes on colors of fresh structures for the new species were taken from plants in the field.

The estimated area of occupancy (AOO) and extent of occurrence (EOO) were calculated using GeoCat (Bachman et al. 2011) by plotting estimated points of all known localities based on herbarium specimens and field explorations. The AOO and EOO were complemented with information on number of known populations, demographic profile and trends, and known threats to conduct an IUCN evaluation based on criteria B and D. The categories and criteria obtained were verified with the Species Information Services (SIS) tool from IUCN (2020) using the same input information as in GeoCat. The SIS tool generated a draft assessment for *P. jamaicensis* which will be submitted to IUCN and updated as more information on the species became available in the future.

To prepare the updated list of *Pisonia*, first we retrieved all currently accepted species from the Vascular Plants of the Americas website (Ulloa Ulloa et al. 2018 onwards). Then, we compiled all *Pisonia* species included

in recent regional floras across the American continent and evaluated any discrepancies. For *Pisonia* species from the West Indies, we conducted a deeper study by examining types and protologues of all published taxa reported for the region. We found that most species presented in Ulloa Ulloa et al. (2018 onwards) matched with the ones we found as accepted in regional studies.

One of the species listed in Ulloa Ulloa et al. (2018 onwards) and Acevedo-Rodríguez and Strong (2012) for the West Indies, *P. suborbiculata* Hemsl., was excluded from the final list because it was transferred to *Guapira* by Lundell (1968) as *G. suborbiculata* (Hemsley) Lundell (Graveson 2012; The Plant List 2013 onwards). Conversely, we added the species *P. clarensis* (Borhidi) M.A.Díaz because it was transferred to *Pisonia* by Díaz Dumas (1991), and *P. proctorii* Lundell, which was accepted in a regional study (Balick et al. 2000). Following Acevedo-Rodríguez and Strong (2012) and Ulloa Ulloa et al. (2018 onwards), we recognized *P. macranthocarpa* (Donn. Sm.) Donn. Sm., although some floristic treatments have merged this taxon under the widespread *P. aculeata* L. (Jørgensen and León-Yáñez 1999).

Recently, many species of *Pisonia* from the Indian and Pacific Oceans were transferred to *Ceodes* J.R.Forst. & G.Forst. and *Rockia* Heimerl (Rossetto and Caraballo-Ortiz 2020), and species from Brazil were transferred to *Guapira* (Chagas and Costa-Lima 2020), and therefore, were excluded from this assessment. Our final list contained 27 species of *Pisonia* (including the one described in this study), of which 16 taxa – representing 15 species and one subspecies – are present in the West Indies (Table 1).

TAXONOMIC TREATMENT

***Pisonia jamaicensis* Proctor ex Caraballo, K.Campbell, & S.Cross sp. nov.** (Figures 1 & 2)

Pisonia subcordata sensu Adams, Fl. Pl. Jamaica 262. 1972, not Swartz, Prodr. 60. 1788. Pro parte (specimen Proctor 28854).

Type: Jamaica, St. Catherine Parish, along road between Ewarton and Worthy Park, woodland over limestone, 1500–1700 ft [457–518 m], 5 July 1968 [♀, fr], Proctor 28854 (holotype, FTG! (barcode № 00038146).

Diagnosis

Pisonia jamaicensis is distinguished from its only other known congener in Jamaica, *P. aculeata*, by a combination of the following characteristics: tree with unarmed branches (vs. scandent shrubs or treelets with

Table 1. List of all currently accepted species of *Pisonia* (Nyctaginaceae), with their major and minor distributions and selected reference studies where each taxon has been recognized.

| No. | Scientific name | Major distribution | Minor distribution | References |
|-----|--|--|---|--|
| 1 | <i>Pisonia aculeata</i> L. | Pantropical | Africa, America, Asia, Australia, India, Malagasy, Mauritius, Myanmar, Seychelles, Sri Lanka | Acevedo-Rodríguez and Strong (2012); Pramanick et al. (2016) |
| 2 | <i>Pisonia albida</i> (Heimerl) Britton ex Standl. | West Indies | Hispaniola, Puerto Rico | Acevedo-Rodríguez and Strong (2012) |
| 3 | <i>Pisonia ambigua</i> Heimerl | South America | Argentina, Bolivia, Brasil, Paraguay, Perú | Furlan and Giulietti (2014); Nee (2014) |
| 4 | <i>Pisonia byrsonimifolia</i> Heimerl & Ekman | West Indies | Cuba | Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012) |
| 5 | <i>Pisonia calafia</i> León de la Luz & R.A.Levin | Central America | Mexico | León de la Luz and Levin (2012); Villaseñor (2016) |
| 6 | <i>Pisonia capitata</i> (S.Watson) Standl. | North America | Mexico, United States of America (AZ) | Clement and Spellenberg (2003); Villaseñor (2016) |
| 7 | <i>Pisonia clarensis</i> (Borhidi) M.A. Díaz | West Indies | Cuba | Díaz Dumas (1991) |
| 8 | <i>Pisonia donnellsmithii</i> Heimerl ex Standl. | Central America | El Salvador, Guatemala, Mexico | González-Martínez and Cruz Durán (2016); Villaseñor (2016) |
| 9 | <i>Pisonia costata</i> (Bojer ex Bouton) Choisy | Indian Ocean | Mascarenes | Philcox and Coode (1994) |
| 10 | <i>Pisonia ekmanii</i> Heimerl | West Indies | Cuba | Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012) |
| 11 | <i>Pisonia flavescens</i> Standl. | North America | Mexico | González-Martínez and Cruz Durán (2016); Villaseñor (2016) |
| 12 | <i>Pisonia floribunda</i> Hook. f. | Pacific Ocean | Galapagos | Jørgensen and León-Yáñez (1999) |
| 13 | <i>Pisonia grandis</i> R.Br. | Asia, scattered islands from western Indian Ocean to eastern Pacific Ocean | Australia, China, India, Laccadive, Malagasy, Maldives Islands, Malaysia, New Caledonia, Pakistan, Polynesia, Sri Lanka | Airy-Shaw (1952); Pramanick et al. (2016) |
| 14 | <i>Pisonia horneae</i> Caraballo & Trejo | West Indies | Puerto Rico | Caraballo-Ortiz and Trejo-Torres (2017) |
| 15 | <i>Pisonia indecora</i> Heimerl | South America | Bolivia | Nee (2014) |
| 16 | <i>Pisonia jamaicensis</i> Proctor ex Caraballo, K.Campbell, & S.Cross | West Indies | Jamaica | This study |
| 17 | <i>Pisonia macranthocarpa</i> (Donn. Sm.) Donn. Sm. | West Indies, Central America, South America | Cuba, Mexico, Central America, South America | González (2007); Acevedo-Rodríguez and Strong (2012) |
| 18 | <i>Pisonia margaretae</i> Proctor | West Indies | Grand Cayman Island | Acevedo-Rodríguez and Strong (2012); Proctor (2012) |
| 19 | <i>Pisonia ochracea</i> Heimerl | West Indies | Hispaniola | Acevedo-Rodríguez and Strong (2012) |
| 20 | <i>Pisonia petiolaris</i> Heimerl & Ekman | West Indies | Cuba | Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012) |
| 21 | <i>Pisonia proctorii</i> Lundell | Central America | Belize | Balick et al. (2000) |
| 22 | <i>Pisonia roqueae</i> Trejo & Caraballo | West Indies | Puerto Rico | Caraballo-Ortiz and Trejo-Torres (2017) |
| 23a | <i>Pisonia rotundata</i> Griseb. subsp. <i>acutiuscula</i> (Heimerl) M.A.Díaz & Esquivel | West Indies | Cuba | Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012) |
| 23b | <i>Pisonia rotundata</i> Griseb. subsp. <i>rotundata</i> | West Indies, North America | Bahamas, Cuba, Hispaniola, and United States of America (FL) | Díaz Dumas (1991); Acevedo-Rodríguez and Strong (2012) |
| 24 | <i>Pisonia silvatica</i> Standl. | Central America | Costa Rica, Panama | González (2007) |
| 25 | <i>Pisonia subcordata</i> Sw. | West Indies | Puerto Rico, Lesser Antilles, Virgin Islands | Acevedo-Rodríguez and Strong (2012) |
| 26 | <i>Pisonia taina</i> Trejo | West Indies | Puerto Rico | Trejo-Torres (2005) |
| 27 | <i>Pisonia zapallo</i> Griseb. | South America | Argentina, Bolivia, Brazil, Paraguay | Furlan and Giulietti (2014); Nee (2014) |

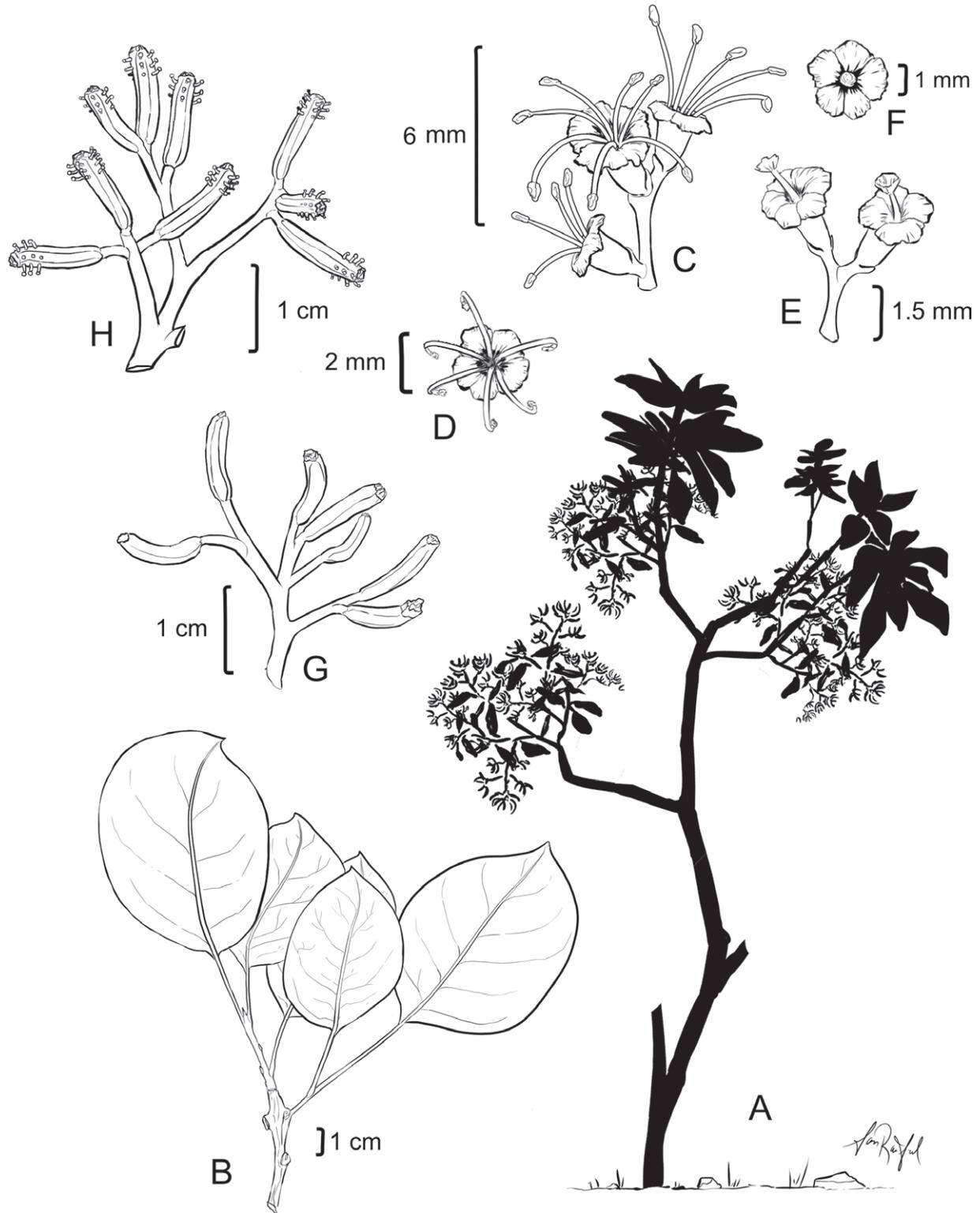


Figure 1. *Pisonia jamaicensis*. A. Silhouette of a tree showing its habit and branches with leaves and infructescences. B. Branch with leaves. C. Partial inflorescence with staminate flowers. D. Top view of a staminate flower. E. Partial inflorescence with pistillate flowers. F. Top view of a pistillate flower. G. Partial infructescence with unripe anthocarps (fruits). H. Partial infructescence with ripe anthocarps. Note the sticky glands present at the distal portion of the anthocarp. Reference specimens: *Cross & Campbell 151* (panels A, E–H); *Proctor 28854* (panel B); *Cross & Campbell 150* (panels C–D). Illustration credit: Ramos Sepúlveda.

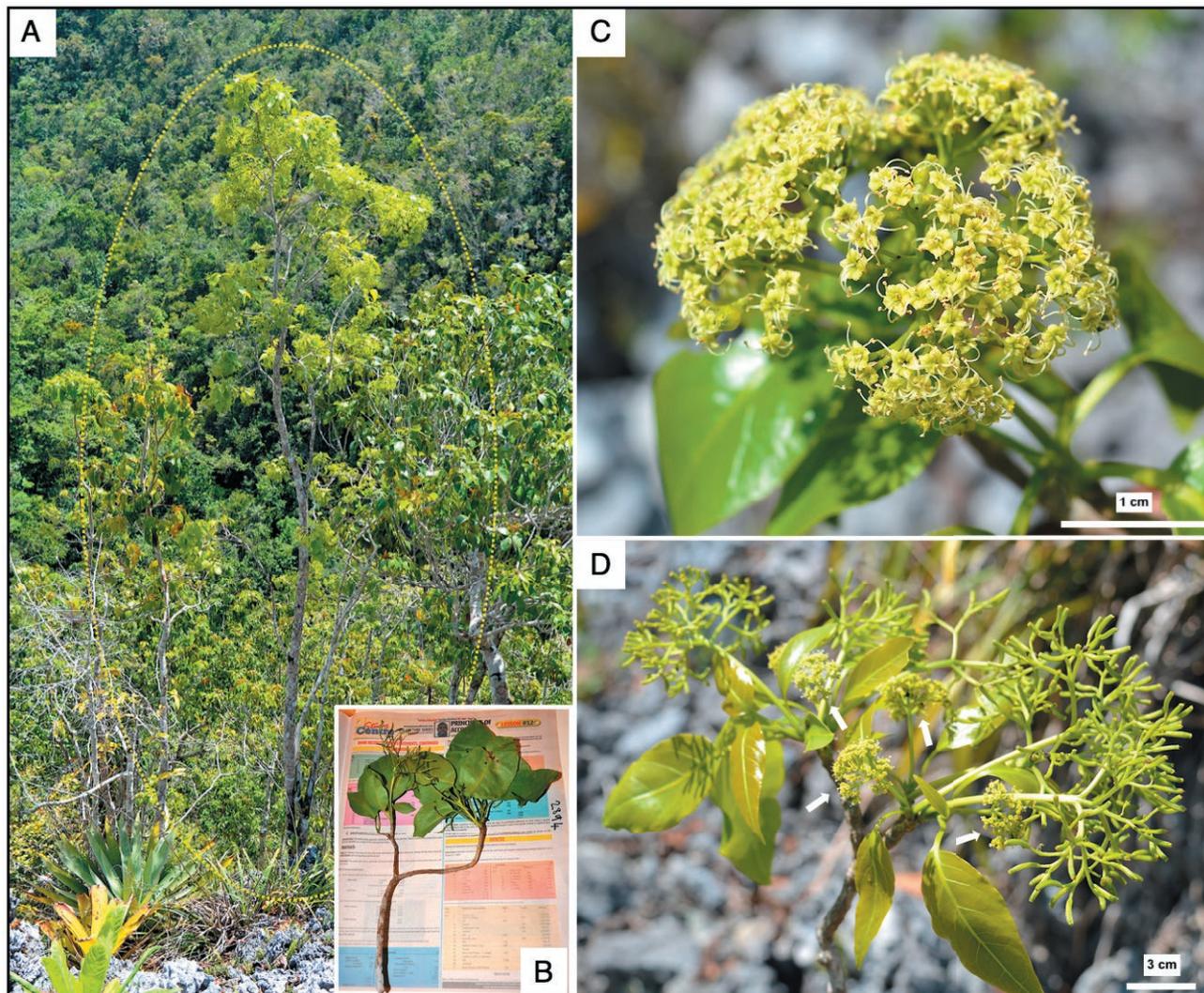


Figure 2. *Pisonia jamaicensis*. A. Mature tree in a rocky limestone slope. B. Branch with developed leaves and ripe fruits. C. Inflorescence with staminate flowers in anthesis. D. Inflorescences with pistillate flowers in anthesis (white arrows) and infructescences with unripe fruits. Note the young leaves (panels A, C–D), which were produced after the first massive flowering in late March when the tree was completely leafless. Reference specimens: *Cross & Campbell 151* (panels A, D); *Abdo et al. 2894* (panel B); *Cross & Campbell 150* (panel C). Photo credits: K.C.S.E.C (A, C & D) and Courtney Lyn (B).

branches armed with spines), leaves ovate and shiny when fresh (vs. leaves elliptic and dull when fresh), and anthocarps narrowly elliptic or oblong, slightly curved when unripe, with viscid glands restricted to the distal 1/3 portion (vs. anthocarps clavate or obovate, straight, with viscid glands along their whole length). *Pisonia jamaicensis* is endemic to Jamaica whereas *P. aculeata* has a pantropical distribution.

Description

Trees dioecious 6–8 m high. Bark vertically striated, grayish. Twigs slightly ancipitous, greenish, and puberu-

lent when young, especially at leaf nodes; terete, glabrous, and grayish when old; prominent vertical lenticels 2–4 x 1 mm, brown. Leaves deciduous, clustered towards distal portion of branches; opposite or subopposite, decussate; young leaves at apical tip brown, resiniferous; petioles 2–7 (–11) cm long, green; blade ovate, rarely elliptic, the blade sometimes asymmetric, 7–12 (–22) x 4–8 (–16) cm, apex acute, rarely rounded, slightly plicate and unequal at the tip, base acute to rounded, rarely oblique or truncate, slightly cuneate at connection with petiole; margin entire; adaxial side glabrous or slightly puberulous, glossy; abaxial side puberulent, pubescent along veins

and at the base of the blade, semi-glossy; blade slightly thick when fresh, drying chartaceous or soft coriaceous and brittle; abaxial and adaxial sides light green when fresh, turning greenish or brown when dry; veins pinnate, reticulate, adaxially glabrous, not raised, abaxially puberulent or pubescent; main vein yellowish-greenish on fresh leaves, drying black; secondary veins arcuate, positioned about 45° from the midvein, up to ten pairs, opposite or subopposite, drying blackish or dark brown; tertiary veins not raised, inconspicuous. *Inflorescences* mostly terminal, sometimes axillary, dendroid, 5–9 cm long, pale green when fresh, drying brownish, puberulent; crown expanded, semi-rounded; bracts and bracteoles subulate, subtending each flower, sometimes present at the base of two flowers. *Flowers* sessile or with a short pedicel ca. 1 mm long, puberulent, tube greenish with five dark longitudinal ridges bearing slightly visible glands, lobes cream-whitish; staminate flowers campanulate at anthesis, 3–4 mm long, with five exerted stamens, filaments 1–3 mm long, filiform; pistillate flowers campanulate at anthesis, 2.5–3 mm long, style exerted ca. 1 mm, with two arcuate lobes, penicillate. *Infructescences* dendroid, 5–9 cm long, green when fresh, drying brown; peduncle terete at base, slightly ancipitous distally; crown lax, branches forked or pseudo-dichotomous. *Fruits* anthocarps (achenes), narrowly elliptic to oblong, 12–15 x 1 mm, light green, ripening black, straight or slightly curved, crowned with five calix lobes, stigma persistent, exerted ca. 0.8 mm; husk softly ligneous, pubescent, about 0.2 mm thick, with 5 longitudinal ridges, viscid glands over the ridges restricted to the distal 1/3, glands capitate, about 1 mm long, stalk pubescent, tip resinous. *Seeds* narrowly elliptic, 1 mm long, light brown.

Etymology

We named the species after the island of Jamaica, where the species is endemic.

Phenology

Pisonia jamaicensis has been recorded flowering from March to April and fruiting from April to July. Trees shed leaves before flowering, and produce new leaves during or just after the flowering stage. Apparently, adult trees do not shed their leaves if they are not reproductive on a given year. The vast majority of *Pisonia* species seems to follow the same synchronized phenological pattern to shed leaves between February and March and produce a mast flowering during March and April. This behaviour might help facilitate cross pollination events in this mainly dioecious genus.

Some reproductive individuals of *P. jamaicensis* were observed bearing a few inflorescences of the opposite sex

(i.e., subandroecious or subgynoecious). This situation can be interpreted as an uncommon adaptation in *Pisonia* to ensure fruit set in small populations or when first colonizing an island, and has been previously reported in three other species from the Caribbean (Proctor 2012; Caraballo-Ortiz and Trejo-Torres 2017).

Distribution

Pisonia jamaicensis is restricted to karstic limestone hills in central and western Jamaica (Figure 3) at elevations between 350–700 m. The 22 known collections for the species span the parishes of Hanover, Manchester, St. Catherine, St. James and Trelawny (Figure 3). The estimated AOO and EOO for its current distribution were 48 km² and 1,934 km², respectively. Although not reported yet from the parishes of Clarendon, St. Ann, St. Elizabeth, and Westmoreland, it is probable that *P. jamaicensis* is also present there.

Ecology

Pisonia jamaicensis is apparently restricted to woodlands on exposed or semi-exposed hilltops and hillsides in dog-toothed moist limestone with loose rocks. We currently lack information on many ecological aspects for the species including suitable habitat and substrate, floral visitors, seed dispersers, and germination rates.

Associated species (ranked by family) include: *Comocladia* sp. (Anacardiaceae), *Plumeria* sp. (Apocynaceae), *Syngonium* sp. (Araceae), *Dendropanax* sp. (Araliaceae), *Agave* sp. (Asparagaceae), *Asplenium* sp. (Aspleniaceae), *Tournefortia staminea* Griseb. (Boraginaceae), *Hohenbergia* sp. (Bromeliaceae), *Pitcairnia bromeliifolia* L'Hér. (Bromeliaceae), *Bursera aromatica* Proctor, (Burseraceae), *Clusia* sp. (Clusiaceae), *Euphorbia punicea* Sw. (Euphorbiaceae), *Jatropha* sp. (Euphorbiaceae), *Pithecellobium alexandri* (Urb.) Urb. var. *alexandri* (Fabaceae), *Lisianthus* sp. (Gentianaceae), *Miconia fadyenii* (Hook.) Judd & Skee (Melastomataceae), Myrtaceae spp., *Peperomia* sp. (Piperaceae), *Phyllanthus* sp. (Phyllanthaceae), *Adiantum* sp. (Pteridaceae), *Spathelia* sp. (Rutaceae), *Sapindus* sp. (Sapindaceae), and *Lagetta lagetto* (Sw.) Nash (Thymelaeaceae).

Demography and conservation notes

Detailed demographic profiles for *P. jamaicensis* have not been developed yet. However, preliminary field observations suggest that the estimated total number of individuals is greater than 250, distributed across five to seven subpopulations (Figure 3). At the St. James population (Abdo *et al.* 2894; Cross & Campbell 150; Cross & Campbell 151), over 50 mature and immature plants were observed. Here, the ratio between observed pistil-



Figure 3. Map of Jamaica showing the distribution of *Pisonia jamaicensis*. The localities where the species has been reported are indicated with yellow circles. Map credit: Google Earth.

late (female) and staminate (male) trees was estimated to be approximately 3:2.

Pisonia jamaicensis does not seem to be directly threatened by targeted harvesting or collection, and we are not aware of any commercial or traditional use for the species. Given its restricted distribution to tops and upper slopes of limestone hills, the species can be threatened by local farming and associated activities such as slash and burn, development, mining (especially for bauxite), and the impact of climate change such as intense droughts, fires, and hurricanes.

Most (82%) of the known specimens for the species were collected over 20 years ago and we currently have little knowledge about their current status. This is especially relevant for half of the localities, which were found more than 40 years ago. It is likely that some of the sites where *P. jamaicensis* was reported have been altered, especially the ones outside protected areas. Fortunately, approximately 70% of the known localities are within areas with some level of legal protection such as the Cockpit County and Dolphin Head forest reserves. In addition, the rugged terrain where the species grows might offer certain degree of protection from forest clearing for agricultural purposes.

The relatively widespread distribution of *P. jamaicensis* across the rugged terrain from central and western Jamaica, the low levels of direct threats, and the estimated AOO and EOO estimated indicate that the species should be classified as Vulnerable, under the specific IUCN criteria B2ab(i,iii,iv);D1 (IUCN 2020). However, some subpopulations in unprotected lands might be at high risk of disappearing. We thus recom-

mend conducting surveys to assess the current status of all known populations to refine this first evaluation and focus conservation efforts where most needed.

Additional specimens examined (paratypes)

JAMAICA: Hanover Parish: Dolphin Head Mountain, NE side of mountain, top of Dolphin Head Mountain, on hillside, 544 m, 7 Sep 2001 [sterile], *P. Acevedo-Rdgz. et al.* 11987 (IJ [barcode № 000015910]; US [barcode № 01012906]). Manchester Parish: 1.5 mi due SE of Mandeville, wooded limestone hillside, ca. 2100 ft [640 m], 30 Mar 1974 [sterile], *G.R. Proctor* 33759 (IJ [barcode № 000015899]); Marshalls Pen, about 2.25 mi due NW of Mandeville, wooded rocky limestone hillside, ca. 2100 ft [640 m], 5 Mar 1980 [sterile], *G.R. Proctor* 38632 (IJ [barcode № 000015917]). St. Catherine Parish: Charlton to Worthy Park, in woodland on limestone, 1700 ft [518 m], 3 Mar 1963 [sterile], *C.D. Adams* 12313 (UCWI [accession № 28290, two sheets]); Dodds Valley district, about 2 mi W of Lluidas Vale, wooded limestone hillside, ca. 1500 ft [457 m], 24 Apr 1965 [♀, fl], *G.R. Proctor* 26393 (IJ [barcode № 000015922]); Halfway between Ewarton and Worthy Park, on exposed limestone near quarry and in woodland, 1500 ft [457 m], 17 Aug 1967 [sterile], *C.D. Adams* 13009 (UCWI [accession № 27980]). St. James Parish: Jericho, N ca. 2 km past last settlement on an overgrown track towards Crownlands, NW atop steep hill (surrounded by boulders), Plummer's Mountain, 580–600 m, 15 Jun 2011 [♀, fr], *M. Abdo, K. Campbell, et al.* 2894 (FTG [barcode № 00148023]); Henny Mountains, Jericho, exposed craggy limestone hilltop, 540 m, 18°20'14.58"N, 77°51'47.24"W [WGS84], 3 April

2019 [♂, fl], S. Cross & K. Campbell 150 (IJ [two sheets]); Henny Mountains, Jericho, exposed craggy limestone hilltop, 540 m, 18°20'14.58"N, 77°51'47.24"W [WGS84], 3 April 2019 [♀, fl, fr], S. Cross & K. Campbell 151 (IJ [three sheets]). Trelawny Parish: Wilson Valley district, 1.5 mi N of Warsop, Island View Hill, wooded limestone hilltop, 2000–2200 ft [610–671 m], 10 Apr 1961 [♂, fl], G.R. Proctor 22188 (IJ [barcode № 000015905]); Wilson Valley district, 1.5 mi N of Warsop, Island View Hill, wooded limestone hilltop, 2000–2200 ft [610–671 m], 10 Apr 1961 [sterile], G.R. Proctor 22189 (IJ [barcode № 000015896]); Belmore Castle area, N of Quick Step, wooded rocky limestone hillside, ca. 1500 ft [457 m], 12 Jun 1976 [♀, fr], G.R. Proctor 36294 (MO [barcode № MO-653339]); Belmore Castle district, about 2 mi N of Quick Step, moist forest on limestone, ca. 1500 ft [457 m], 12 Jun 1976 [♀, fr], R. F. Thorne & G. R. Proctor 48233 (MO [barcode № MO-2062567]); Along road N of Burnt Hill, wooded rocky limestone hillside, ca. 1700 ft [518 m], 23 Feb 1980 [sterile], G.R. Proctor 38599 (IJ [barcode № 000015897]); Cockpit Country, vicinity of Ramgoat Cave, wooded rocky limestone hillside, ca. 1500 ft [457 m], 20 Apr 2000 [♂, fl], G.R. Proctor 51686 (IJ [barcode № 000015920]); Cockpit Country, vicinity of Ramgoat Cave, wooded brink of limestone cliff, ca. 1500 ft [457 m], 23 Apr 2000 [♀, fl], G.R. Proctor 51690 (IJ [barcode № 000015886; 000015908]); Cockpit Country, vicinity of Ramgoat Cave, wooded brink of limestone cliff, ca. 1500 ft [457 m], 23 Apr 2000 [♂, fl], G.R. Proctor 51692 (IJ [barcode № 000015918]); Ram Goat Cave, 450 m, 18°20'07"N, 77°33'29"W, 9 Dec 2000 [sterile], T. Parker 3513 (IJ [barcode № 000015921]); Cockpit Country, vicinity of Ramgoat Cave, brink of limestone cliff, ca. 400 m, 28 Jun 2007 [sterile], G.R. Proctor 52602 (IJ [barcode № 000015930]); Cockpit Country, Ramgoat Cave, near brink of limestone cliff, ca. 1200 ft [366 m], 6 May 2000 [♀, fr], G.R. Proctor 51698 (IJ [barcode № 000015909]); Cockpit Country, vicinity of Ramgoat Cave, wooded brink of limestone cliff, ca. 1500 ft [457 m], 10 Jun 2000 [sterile], G.R. Proctor 51720 (IJ [barcode № 000015894]).

Dichotomous key to separate species of Pisonia from the West Indies

The following dichotomous artificial key contain the 16 taxa of *Pisonia* that, based on our assessment, are currently accepted for the West Indies. Most members in this genus have short flowering and fruiting periods, and therefore, many collections in herbaria are sterile. In consequence, the characters used to build this key are mostly vegetative, complemented with geographic

locations and reproductive features. Certain taxa appear more than once to cover variations in their morphology. Some entries have been modified from Trejo-Torres (2005) and Caraballo-Ortiz and Trejo-Torres (2017).

The key to separate the nine genera within Pisonieae presented in Rossetto and Caraballo-Ortiz (2020) should help users verify that their specimens are actually *Pisonia* and not *Guapira* or *Neea*, which are the only other genera from this tribe present in the West Indies.

- 1 a. Twigs armed with spines..... 2
 - b. Twigs unarmed..... 3
- 2 a. Scandent shrubs, or treelets; leaves glabrous or with sparse trichomes; twigs pubescent, drying grayish *P. aculeata*
 - b. Shrubs or trees; leaves with dense trichomes along mid-vein; twigs smooth, drying blackish *P. macranthocarpa*
- 3 a. Leaves mainly > 10 cm long and > 10 cm wide 4
 - b. Leaves mainly ≤ 10 cm long and ≤ 10 cm wide..... 5
- 4 a. Fresh leaves dull green on both sides; leaf apex mostly rounded; flowers > 5 mm long; fruits 5-ribbed; Grand Cayman..... *P. margaretiae*
 - b. Fresh leaves shiny green on both sides; leaf apex mostly acute; flowers ≤ 5 mm long; fruits 10-ribbed; Puerto Rico.. *P. horneae*
- 5 a. Leaves with apex acute 6
 - b. Leaves with apex rounded, obtuse, or emarginate..... 11
- 6 a. Leaves with base acuminate to attenuate; fruits with viscid glands distributed along the whole length *P. macranthocarpa*
 - b. Leaves with base rounded to oblique; fruits with viscid glands restricted to the distal half..... 7
- 7 a. Leaf veins at abaxial side raised to the finer ramifications *P. taina*
 - b. Leaf veins at abaxial side not raised to the finer ramifications..... 8
- 8 a. Leaves > 3 cm wide; Jamaica and Puerto Rico to Lesser Antilles..... 9
 - b. Leaves ≤ 3 cm wide; Cuba 10
- 9 a. Leaves ovate, chartaceous; staminate inflorescence an expanded, non-flabellate crown; Jamaica..... *P. jamaicensis*
 - b. Leaves broadly elliptic or rounded, coriaceous; staminate inflorescence with flabellate crown; Puerto Rico to Lesser Antilles..... *P. subcordata*

- 10 a. Leaves elliptic with revolute margins
.....*P. rotundata* subsp. *acutiuscula*
- b. Leaves ovate with flat margins *P. clarensis*
- 11 a. Leaf veins at abaxial side raised to the finer ramifica-
tions *P. taina*
- b. Leaf veins at abaxial side not raised to the finer ramifi-
cations..... 12
- 12 a. Leaves with base acuminate to attenuate; fruits with viscid
glands distributed along the whole length
.....*P. macranthocarpa*
- b. Leaves with base rounded to oblique; fruits with viscid
glands restricted to the distal half..... 13
- 13 a. Leaves elliptic or oblong..... 14
- b. Leaves rounded or obovate..... 18
- 14 a. Petioles 5 (–7) mm long..... 15
- b. Petioles > 7 mm long.....16
- 15 a. Leaves oblong; twigs densely covered with yellowish
indumenta; Hispaniola*P. ochracea*
- b. Leaves elliptic; twigs densely covered with dark brown
or blackish indumenta; Cuba.....
.....*P. rotundata* subsp. *rotundata*
- 16 a. Leaves > 4 cm wide; twigs and leaves drying grayish;
Hispaniola and Puerto Rico..... *P. albida*
- b. Leaves ≤ 4 cm wide; twigs and leaves drying brownish
or greenish; Cuba 17
- 17 a. Leaves elliptic, drying brownish; apex rounded or obtuse
P. petiolaris
- b. Leaves oblong, drying greenish; apex emarginate or
obcordate.....*P. ekmanii*
- 18 a. Leaf blade ≤ 5 cm long × 3 cm wide *P. petiolaris*
- b. Leaf blade > 5 cm long × 3 cm wide 19
- 19 a. Leaves drying shiny yellow on adaxial side and dull light
brown on abaxial side; blade margins slightly revolute;
petioles 0.9–1.7 cm long; Cuba *P. byrsonimifolia*
- b. Leaves drying dull black on adaxial side and dull dark
brown on abaxial side; blade margins flat; petioles 1.7–4
cm long; Puerto Rico 20
- 20 a. Leaves puberulent, especially on the abaxial side and
along veins; staminate inflorescences with a globose crown
.....*P. roqueae*
- b. Leaves glabrous, sometimes slightly puberulent on the
abaxial side at base of main vein; staminate inflorescences
with a flabellate crown..... *P. subcordata*

DISCUSSION

The addition of *P. jamaicensis* increases to 27 the number accepted species of *Pisonia* and brings in a second species – the first endemic – of this genus to the flora of Jamaica. The rest of the Greater Antilles and Grand Cayman also have endemic *Pisonia*, making the West Indies a hotspot for the genus. In fact, more than half (16 taxa; 59%) of its diversity is found in the Caribbean, of which 88% are restricted to the region and 69% are single-island endemics (Table 1). Cuba is the most diverse island with seven taxa (six species and one subspecies), of which 71% are endemics. The second most diverse island is Puerto Rico holding six species with half of them endemics, followed by Hispaniola with three species and 33% endemism. All other islands or archipelagos (i.e., Bahamas, Cayman Islands, Jamaica and the Lesser Antilles) have two species of *Pisonia*, with the only endemics in Grand Cayman and Jamaica.

The records of *P. subcordata* from Jamaica reported by Adams (1972) and Acevedo-Rodríguez and Strong (2012) are in part based on the misidentification of *Guaipira rotundifolia* (Heimerl) Proctor (e.g., Adams 12610 [UCWI], 13010 [UCWI]; Goodfriend & Tanner 2281 [UCWI]; Harris 10958 [US], 10985 [B, K, NY, UCWI, US], 11183 [US]; Proctor 27530 [US], 32481 [MO, US], 34371 [MO]) or *Neea nigricans* Fawc. & Rendle (Proctor 21346 [NY]), as clarified by Proctor (1982). However, some specimens originally labeled as *P. subcordata* were, in fact, the species here described. When sterile, *G. rotundata* can be separated from *P. jamaicensis* based on mature leaves, which are elliptic or obovate, stiffly leathery, and dry yellowish brown with secondary veins brown, thin and inconspicuous. These characters contrast with the leaves of *P. jamaicensis*, which are ovate (rarely broadly elliptic or rounded), chartaceous or soft leathery, and dry brown with secondary veins black, corky and conspicuous.

After clarifying that *P. subcordata* is not present in Jamaica, this island now contains two species of *Pisonia*: *P. aculeata* and the newly described *P. jamaicensis*. The former can be separated from the latter by having a scandent habit with twigs bearing spines, and broadly elliptic fruits with viscid glands distributed along the whole length (vs. tree habit with unarmed twigs, and narrowly elliptic fruits with viscid glands restricted to the upper third portion in *P. jamaicensis*). Regarding the distribution of *P. subcordata*, this species is now restricted to coastal habitats in northern and eastern Puerto Rico, Virgin Islands and the Lesser Antilles, extending to Martinique (Acevedo-Rodríguez and Strong 2012; Caraballo-Ortiz and Trejo-Torres 2017).

Our estimate of 27 accepted species in *Pisonia* is still in need of more investigation as some taxa are poorly known and it is difficult to assess their validity. For example, *P. proctorii*, a spineless liana from Belize, could be a variation of *P. aculeata*. Moreover, *P. indecora* Heimerl might represent a species of *Guapira*, possibly *G. boliviana* (Britton ex Rusby) Lundell (E.F.S. Rossetto, pers. comm.). Therefore, further work on *Pisonia* is needed to help refine its taxonomy and reach a more precise estimation of accepted species.

Although no comprehensive phylogenetic or biogeographic study of *Pisonia* have been published to date, a recent study of tribe Pisonieae by Rossetto et al. (2019) found an intriguing relationship between *P. grandis* and the taxa from the West Indies. However, *P. grandis* – renowned as the Birdcatcher tree – has a native range covering myriads of islands across the Indian and Pacific Oceans but does not reach the American continent. Further systematic studies on the genus might shed light on this finding and help reconstruct the evolutionary relationship among species to resolve taxonomic uncertainties, especially within the *P. aculeata* complex, whose members have a shrubby-scandent habit and are often armed with stout spines.

AUTHOR CONTRIBUTIONS

MACO prepared a first draft of the manuscript, revised herbaria, prepared the species description, compiled the list of accepted *Pisonia*, and built the dichotomous key. KCSEC and SJC collected the species, revised herbaria, prepared the distribution map, and performed the IUCN evaluation. All authors contributed to the manuscript and approved the final version.

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