



A systematic revision of the vulnerable mangrove genus *Pelliciera* (Tetrameristaceae) in equatorial America

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Key words

Atlantic-East Pacific
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Tetrameristaceae

Abstract *Pelliciera* is a genus of mangrove trees with distinct showy flowers with five petals subtended by two large foliaceous bracts. The genus, thought to be monotypic, only containing *P. rhizophorae*, was classified recently in the small diverse family, the Tetrameristaceae. This distinctive genus occurs in a relatively restricted distribution in Central and northern South America in the Atlantic-East Pacific region. In this recent decade, two varietal forms have been reported across its range, of which one appears to be a colour morph referred to much earlier as *P. rhizophorae* var. *benthamii*. The taxonomic status of the earlier morph was, however, insufficient to warrant individual recognition at the time, so the genus remained monotypic with no varietal forms. The aim of this treatment has been to review the systematic history of the genus, to thoroughly re-assess available observations and to re-evaluate the current taxonomic status. In conclusion, the genus is recognised now as having two closely related species, described here as *P. benthamii* along with a redefined *P. rhizophorae*. Characters such as leafy bract colour, leaf dentition and petal shape used in their discrimination are provided, along with notes on the ecology, phenology, a diagnostic key, and a revised distribution map that displays the oddly overlapping occurrences.

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INTRODUCTION

Pelliciera Planch. & Triana (Triana & Planchon 1862) is an unusual and poorly known tree genus represented until now by one species *P. rhizophorae* Planch. & Triana. This evergreen taxon is restricted to mangrove forests in Central and South America in the Atlantic-East Pacific region. These plants occur on both Pacific and Atlantic coasts of the Central American Isthmus and range south to northern South America. On the Pacific coast, they extend from Costa Rica and Panama, to western Colombia and Ecuador. On the Atlantic coast, they are found in Honduras and Nicaragua, to Panama and north-eastern Colombia. Knowledge of the extant range has been notably expanded in relatively recent times from occurrences only on the Pacific coast of Central America (Kobuski 1951, Wijmstra 1968), to progressively include sites along the Atlantic coast from Honduras to Colombia (Calderón-Sáenz 1982, 1983, 1984, Winograd 1983, Roth & Grijalva 1991, Blanco-Libreros et al. 2015, Nelson & Perez 2018).

The unique morphological and anatomical features of this plant have seen it categorized as its own family, *Pelliciereaceae* (Planch. & Triana) Beauvis., or as a distinct tribe, the *Pelliciereae* Planch. & Triana within the *Theaceae*, and more recently within the *Tetrameristaceae* (Stevenson 2004, Culham 2007). *Pelliciera* has affinities with other groups also, including *Temstroemiaceae* Mirb. ex DC. and the *Marcgraviaceae* Bercht. & J.Presl. The *Tetrameristaceae* are classified in the Order *Ericales*. Members of the family are characterized by flowers with five stamens, a single ovule per locule, and glands on the

inner surfaces of the sepals. The family consists of five species of trees and shrubs in three genera, *Pentamerista* Maguire in the Guyanas, *Tetramerista* Miq. in South-east Asia, and *Pelliciera* in Central and South America. Features which specifically distinguish *Pelliciera* include raphides in the parenchymatous tissue, pronounced decurrent leaf bases, plus an annular structure in the vascular strands of the petioles (e.g., Kobuski 1951). Overall, *Pelliciera* is distinguished by its spirally arranged leaves with asymmetrical bases and short stalks, long pointed terminal buds, regularly pentamerous flowers enclosed by a pair of large foliaceous bracteoles emergent from the axils of leaves. The genus also has a 1-seeded indehiscent fruit with a sharply pointed corky pericarp with a large embryo inside and no seed coat.

While *Pelliciera* was first described by Triana & Planchon (1862) as '*Pelliceria*', the genus name was corrected later by authors like Hemsley (1879) and Kobuski (1951). Triana & Planchon (1862) also recorded two colour morphs of white or red floral parts based on two contemporary collections:

- 1 the type from south-western Pacific Colombia (*Triana & Planchon s.n.* (P & COL) collected in 1852 – having white flower parts and five locules); and
- 2 another collection from Pacific Panama (*Sutton Hayes 76* (K), collected in 1861 – having red flower parts and two locules).

The latter collection was seen to be distinct and named *P. rhizophorae* var. *benthamii* Planch. & Triana (Triana & Planchon 1862). This intraspecific entity, however, was reduced within subsequent treatments after it was found to have two locules instead of five (see Kobuski 1951). The two-colour morphs were combined as variation within a sole taxon based on systematic evidence available at the time.

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In recent decades, similar colour morphs have been raised again as two varieties based on additional characters identified (Castillo-Cárdenas et al. 2015a–c, Garzón-Bautista et al. 2018). The aim of the current treatment has been to review these studies, to re-evaluate prior botanical descriptions and to summarise recent observations in view of further evidence presented with this treatment. Based on all findings, a revision of the taxonomic status is provided for *Pelliciera* with the conclusion that there are two species, *P. rhizophorae* and *P. benthamii* stat. nov. Both are described along with assessments of distinguishing characters identified in various studies of morphology, genetics, pollen, ecology, nectar, along with an updated map of current distribution records.

METHODS

Study sites

Location records of *Pelliciera* were listed for 65 sites where the genus was sampled or confirmed to occur in recent decades (Appendix 1). These records cover the known range along both Pacific and Atlantic coasts bordering the Atlantic-East Pacific region. The 15 additional sites reported with the current study are shown in **bold**. A combination of aerial photographs, detailed maps and GPS position records permitted accurate identification of location coordinates. Specific taxon determinations were affirmed using the diagnostic characters identified in morphometric assessments made with this treatment. These determinations have been compared with detailed descriptions of material collected at both Atlantic and Pacific distributional extremes in Honduras, Costa Rica and Colombia.

Plant sampling

Plant material of *Pelliciera* was collected specifically from forest stands in Bocas del Toro on the Atlantic coast of Panama, and from near Diablo at the Pacific entrance to the Panama Canal (Appendix 1, Map 1). Voucher collections were deposited with the Herbarium of the Smithsonian Tropical Research Institute (STRI) in Panama by J.G. Jones. The collections were used in various aspects of this study, including morphological descriptions, numerical analyses, floral and vegetative phenologies, pollen studies and analyses of nectar from sepal nectaries. Morphological measurements and descriptive features of vegetative and reproductive components were used to assign taxon groupings, and compared with prior published accounts of intra-specific variants (Castillo-Cárdenas et al. 2015a–c).

Morphological attributes

The measurement and scoring of morphological character states was made from fresh, intact leafy shoots, mature flower buds, and attached mature propagules. Based on these reproductive stages, up to 79 numeric and multistate attributes (Appendix 2) were measured and recorded for each specimen. This comprehensive selection of measured attributes was compiled and standardised in view of prior publications concerning the genus (e.g., Kobuski 1951, Duke 2013, 2014, Castillo-Cárdenas et al. 2015b) and other mangrove genera (e.g., Duke & Jackes 1987, Duke 2010, Duke & Ge 2011). Three specimens with white flower parts and three with red flower parts were assessed. All characters were scored and later used in the detailed description of each taxon.

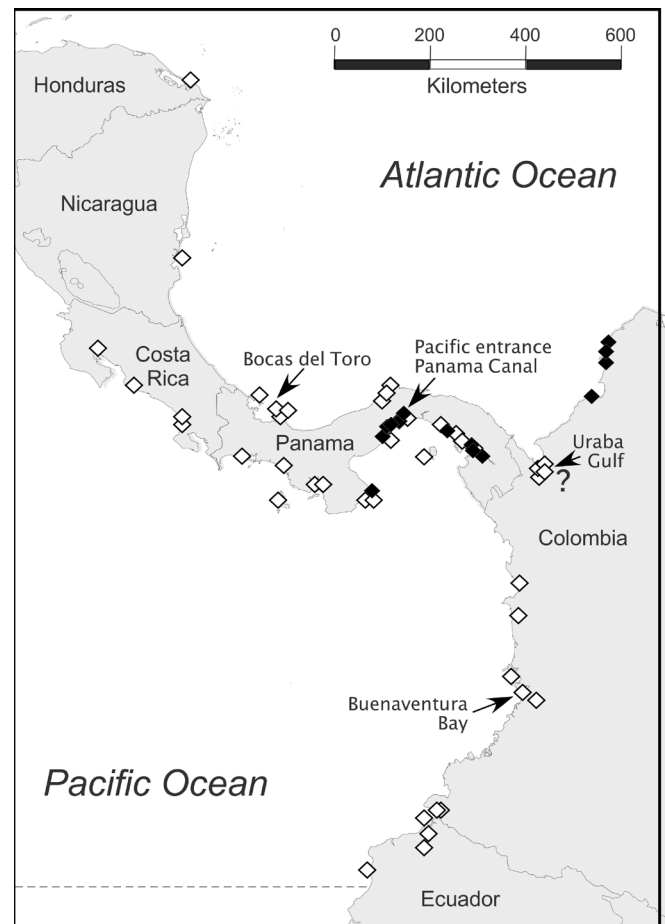
Classificatory analyses

A comparative classificatory evaluation was undertaken to show patterns in morphological relationships of foliage and floral attributes amongst specimens collected for this study. In this assessment, 11 multistate and numerical attributes of leaves and mature open flowers were used since no consistent

patterns were seen using characters of mature fruits alone (Appendix 3). For the 24 specimens analysed, there were no missing data from the matrix. However, data for two additional specimens were included for comparison, namely 'Variant A' and 'Variant B' (Castillo-Cárdenas et al. 2015b) using averaged values for 6 of the 11 attributes given (= leaf width; single bract colour; foliaceous bract width and colour; petal width and colour). These data were analysed using two standard classificatory techniques, namely the non-parametric ordination Multi-Dimensional Scaling (MDS) and a Cluster Analysis. This combination of analytical methods was used because the attributes scored comprised both numeric and multistate data that were not necessarily normally distributed. Tests followed standard methods and applied using PAST 3.x software (<https://folk.uio.no/ohammer/past/>). The MDS ordination was performed using a Gower similarity index with 2-D dimensionality. Cluster analyses were undertaken using a Gower Matrix and the Paired group algorithm using the Unweighted Pair Group Method with Arithmetic mean (UPGMA).

Pollen studies

A brief assessment of pollen grain size, exine surface sculpture and shape (as collapsed or normal) was used to characterize



Map 1 Distribution of two *Pelliciera* species, *P. benthamii* (◆) and *P. rhizophorae* (◇) in Central and northern South America (see Appendix 1). Two study locations are shown for botanical descriptions, assessments of morphology, pollen characters and phenologies – including Bocas del Toro (allopatric *P. rhizophorae*) and the Pacific entrance to the Panama Canal (sympatric occurrence). Sympatric occurrences are likely to include intermediates comparable to collections from the Pacific entrance of the Panama Canal. The latter is also the location of collections made by Sutton Hayes in 1861 and used as the type location for *P. benthamii* in this treatment. The site at Buenaventura Bay in Pacific Colombia marks the location of the type for *P. rhizophorae* collected in 1852. Note: the presence of *P. rhizophorae* in Uraba Gulf was determined from an image of the flower (Blanco-Libreros pers. comm.).

differences amongst 13 individual trees of *Pelliciera* plants also assessed in morphometric assessments. This assessment specifically focused on the sympatric populations at the Pacific entrance to the Panama Canal (Appendix 1, Map 1). Pollen taken from flowers were cleaned using a conservative and standardised processing treatment leaving the exine intact (Erdtman 1969). In all cases, sufficient quantities of pollen were obtained from 5 individuals of each of the two species present and three intermediate taxa. Samples were examined on a JOEL 5300LV Scanning Electron Microscope (SEM) at STRI, and examined at 10kv, at a working distance of 13–18 mm at magnifications ranging from 350 to 5000 diameters. SEM sample stubs were coated with 60 Ångstroms of gold palladium in a Hummer VI sputter coater.

Since normal pollen grains of *Pelliciera* were radially symmetric, oblate-spheroidal and tricolporate (Garzón-Bautista et al. 2018), the size could be indicated by diameter. Furthermore, for this study, the exine surface structure was classified as having three broad categories being ‘smooth’ = punctuate (Fig. 3j), ‘rough’ = perforate to verrucose (Fig. 4i, upper grain) and ‘between’ = finely perforate-verrucose (Fig. 4i, lower grain). Numbers of grains with the respective exine characters were counted and used to determine the relative amounts of each grain type. Their viable state was also classified where grains were either ‘full’ or ‘collapsed’.

Sepal nectary sugar content

The sugary solution from sepal nectaries of open flowers was collected *in situ* from 5 individual trees of *Pelliciera* plants from the same site at the Pacific entrance to the Panama Canal (Appendix 1; Map 1). Nectar was collected using a glass capillary tube and later dissolved in 0.5 mL of de-ionised water before being run on a high-performance liquid chromatography (HPLC) laboratory instrument. Sample weights ranged between 0.2 to 5 mg each. Results for the carbohydrates detected and identified were quantified as grams of solute dissolved in 100 g of solution (w/w units).

RESULTS

Description of taxa

Based on diagnostic characters and morphometric assessments (Appendix 2), two species of *Pelliciera* were recognised in the mangrove forests of the Atlantic-East Pacific region, *P. rhizophorae* and *P. benthamii*. These taxa are described in this treatment. The floral diagrams for these species were the same – having flowers subtended by a single leaf-like bract, two (paired) foliaceous bracteoles, five distinct petals and five distinct sepals. Species were distinguished by characters of the leaves, bracts and petals, including their length, width, colour, shape, and presence or absence of dentition on margins

	<i>Pelliciera rhizophorae</i>	<i>Pelliciera benthamii</i>
Leaf	<p>narrow-side dentition absent wide-side dentition green W > 34 mm</p>	<p>narrow-side dentition partial wide-side dentition green W < 34 mm</p>
Single Bract	<p>narrow-side dentition absent wide-side dentition green L > 100 mm W > 30 mm</p>	<p>narrow-side dentition partial wide-side dentition green L < 100 mm W < 30 mm</p>
Paired Foliaceous Bracts	<p>narrow-side dentition absent wide-side dentition absent pale whitish-green W > 35 mm</p>	<p>narrow-side dentition absent wide-side dentition partial red, pink or whitish-green W < 35 mm</p>
Five Petals	<p>oblong mostly, sometimes lanceolate white, rarely tinged pink W < 14 mm</p>	<p>lanceolate mostly red, pink or white W > 14 mm</p>

Fig. 1 Diagnostic characters for *Pelliciera rhizophorae* and *P. benthamii*. Occasional intermediate individuals, occurring in sympatric populations, have differing attribute combinations. Measures of length (L) and width (W) used are derived from fresh collection data means.

(Fig. 1). Measurements of the 79 numeric and multi-state attributes measured are presented in Appendix 2. These include the diagnostic characters, identified with asterisks (*), while other notable attributes are marked in **bold**, are illustrated in Fig. 1.

Numerical analyses

The numerical analyses displayed relative distances between and amongst taxa based on the range of key morphological characters. This included the separation of two species although between them there were 3 intermediate individuals (Fig. 2). The cluster dendrogram (Fig. 2a) showed species entities grouped according to *a priori* classification, with a close grouping of *P. benthamii* specimens, separate and dissimilar from the *P. rhizophorae* specimens. Of interest, the averaged measure of 'Variant A' (Castillo-Cárdenas et al. 2015b) was grouped with *P. rhizophorae*. However, 'Variant B' was grouped more closely with the intermediate plants. Similar findings were shown in the MDS plot (Fig. 2b). In that figure, *P. rhizophorae* (◇) and *P. benthamii* (■) had clear separation along the first coordinate axis with intermediate individuals (○) positioned between. In this ordination, while the Castillo-Cárdenas et al. (2015b) 'Variant A' (☆) was central within the grouping of *P. rhizophorae* individuals, 'Variant B' (★), was positioned outside the tightly grouped *P. benthamii* individuals, and nearer to the three intermediates. One likely explanation is that intermediates were included along with *P. benthamii* individuals into the 'Variant B' grouping of Castillo-Cárdenas et al. (2015b). This is consistent with these authors having not recognised the occurrence of the two species growing in sympatry in the Pacific Panama Canal site.

Pollen studies

The assessment of pollen grain condition and viability found the intermediate individuals to have 30–90 % collapsed grains compared with the 70 % normal grains in the other individuals that either grouped with *P. rhizophorae* or *P. benthamii* (Table 1). The collapsed condition of pollen grains was considered indicative of intermediate individuals being less viable and infertile and likely to be of hybrid origin. A similar pollen condition was observed in hybrids in other mangrove genera, like *Sonneratia* L.f. (Duke & Jackes 1987), *Rhizophora* L. (Duke 2010) and possibly *Bruguiera* Lam. (Duke & Ge 2011). This was taken as evidence of limited reproductive isolation and reduced genetic

compatibility between parent taxa. However, unlike *Sonneratia*, *Rhizophora* and *Bruguiera* hybrids, *Pelliciera* hybrids did not appear to have a consistent or morphologically distinct intermediate form. This was thought to be indicative of greater genetic closeness between these two species – where sibling species give rise to intermediate individuals – more like the situation for *Rhizophora stylosa* Griff. and *R. mucronata* Lam. in the Indo-West Pacific (Duke 2006), and possibly *R. mangle* L. and *R. samoensis* (Hochr.) Salvoza in the Atlantic-East Pacific (Duke & Allen 2006).

While pollen grains were comparable in overall shape and size (~ 60 micron) amongst taxa, this treatment also confirmed variations in the surface texture of the grains (Garzón-Bautista et al. 2018). These differences extend to different combinations of grain exine structure observed in pollen from individual flowers (Fig. 3j, 4l). Our results (Table 1) showed the three pollen exine conditions for each of the three groups, *P. rhizophorae*, *P. benthamii* and intermediates, thus neither of the three pollen types was exclusive to any taxon. However, 'rough' grains were mostly present in *P. rhizophorae* (~ 23 %), a lesser amount (~ 1 %) in the intermediate taxa, and none in *P. benthamii*. *Pelliciera rhizophorae* individuals had the full range of exine surfaces, but most grains (~ 76 %) were either 'rough' or 'between'. By contrast, 'smooth' grains were found in all taxa although the proportion was far greater (~ 84 %) in *P. benthamii*.

Distribution of species

Pelliciera rhizophorae was the most widespread of the two taxa, extending along both Atlantic and Pacific coasts, and mainly on the Pacific coast from Costa Rica to Ecuador (Appendix 1, Map 1). By contrast, the distribution of *P. benthamii* occurs more or less equally on the Pacific coast of Panama and the Atlantic coast of Colombia. Panamanian occurrences were notably sympatric in at least four estuarine locations, including Rio Caimito, the Pacific entrance to the Panama Canal (Rio Grande), Rio Maje, and the Golfo de San Miguel in the Darien region. In sites of co-occurrence, there was often ecological separation with *P. benthamii* individuals growing as undercanopy to taller *P. rhizophorae* individuals. Furthermore, there was also a tendency for *P. rhizophorae* stands to occur towards the estuary mouth, while *P. benthamii* extended further upstream. While this trait was not entirely consistent in other sites, the overall upriver pattern is exemplified in the Darien

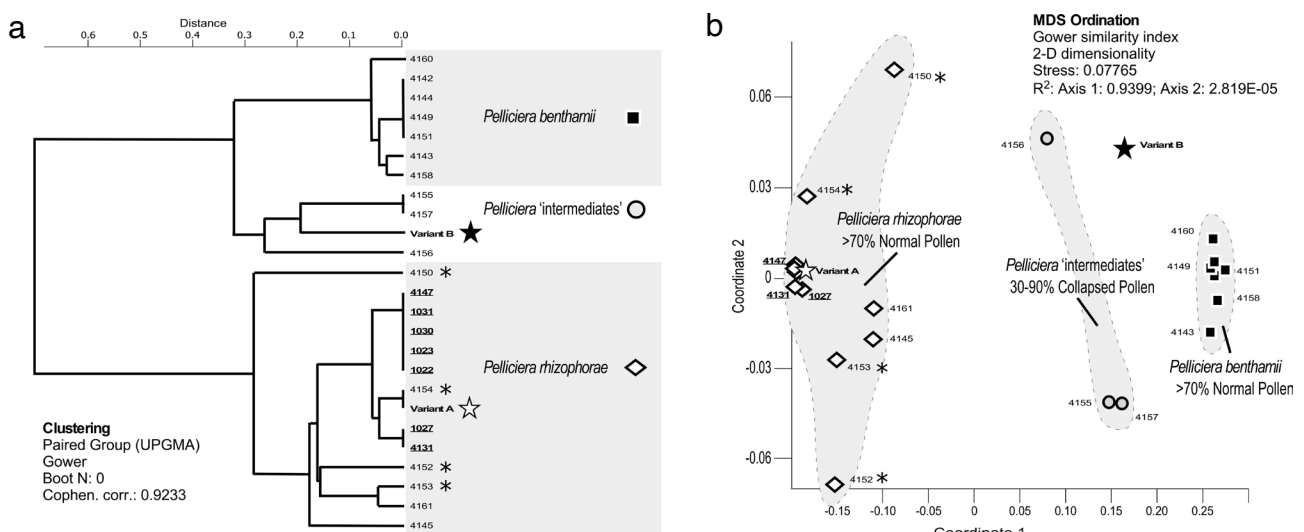


Fig. 2 Graphs: a. UPGMA Gower clustering; b. MDS ordination analyses. Both show distinction between *Pelliciera rhizophorae*, *P. benthamii* and hybrid intermediates. Ordination plots derived from multistate plots of 11 morphological attributes from 25 samples (Appendix 2). The sampled specimens are indicated in Appendix 1. All taxa occurred in sympatry in the Pacific Entrance Panama Canal (Diablo) site (Map 1). Collections marked with asterisks (*) had pollen grains with rough and intermediate exine surfaces; all *P. benthamii* collections analysed had 'smooth' pollen (Table 1). 'Variant A' and 'Variant B' data were taken from averaged morphological measures reported by Castillo-Cárdenas et al. (2015b).

Table 1 Pollen viability and exine character of *Pelliciera* taxa (Appendix 1) for 13 individual trees from the Pacific entrance to the Panama Canal. The three exine states for this study were 'Smooth', 'Rough' and 'Between'; see text. Viability was indicated by pollen grains being full (= 'Normal') compared to partially or fully collapsed (= 'Collapsed'). Averaged relative proportions of ($n = 10-77$) grains in each character for the two taxa and the intermediates determined from the assessment of morphological characters (Appendix 2, Fig. 2).

Pollen Character	State	<i>P. rhizophorae</i>	Intermediates	<i>P. benthamii</i>
		N = 5	N = 3	N = 5
Exine	Rough	22.9 ± 10.8	1.0 ± 1.0	0.0 ± 0.0
	Between	53.2 ± 12.5	76.2 ± 23.8	15.8 ± 9.0
	Smooth	23.9 ± 14.5	22.9 ± 22.9	84.2 ± 9.0
Viability	Normal	84.4 ± 5.3	28.4 ± 19.9	86.6 ± 5.0
	Collapsed	15.6 ± 5.3	71.6 ± 19.9	13.4 ± 5.0

where *P. benthamii* extended up the Rio Sabana and Rio Balsa, while *P. rhizophorae* was apparently restricted to the mouth and the Golfo de San Miguel.

TAXONOMIC TREATMENT

Pelliciera Planch. & Triana — Map 1

Pelliciera Planch. & Triana in Triana & Planch. (June 1862) 380 ('*Pelliciera*'); Benth. & Hook.f. (7 Aug. 1862) 186; Hemsl. (1879) 96; Kobuski (1951) 257. — Type: *P. rhizophorae* Planch. & Triana.

Etymology. The genus name commemorates the French prelate, diplomat and naturalist, Bishop Guillaume Pellicier (1527–1568) of Montpellier, whom King Francis I sent as an ambassador to Venice, after Scèveole de Sainte-Marthe 'the most learned man of his century'.

Trees of mangrove tidal wetlands, columnar, somewhat tiered; crowns often acute; branches distally arcuate, with conspicuous circular leaf scars and stubs of stalks of fallen fruits at intervals. **Bark** dark, roughly fissured, grey; stem slender. **Trunk** buttressed at base, swollen, markedly fluted below, ridges each originating as an acropetally developed series of short aerial roots; roots at stem base, no pneumatophores. **Foliage** comprised of 7–11 leaves arranged spirally in a rosette around the apical shoot, phyllotaxis regular, 2/5. **Stipules** and **bud scales** absent. **Leaves** sessile; blades asymmetric, oblong-lanceolate, broadest at the middle, glabrous, leathery to coriaceous, base abruptly narrowed to the insertion with 2 glands, occasionally one (extrafloral nectary), margins initially with a series of prominent but ephemeral glandular-denticulate glands (presumed salt glands), apex bluntly rounded, surfaces dark glossy green; young leaves involute in bud. **Flowers** hermaphroditic, axillary, up to 14 cm wide at anthesis; lower single bract broadly oblong, green, with or without 2 glands towards base of pedicel; bracteoles 2, opposite, foliaceous, involute, white or reddish, without basal glands; sepals 5, imbricate, unequal, free, caducous, mostly whitish; petals 5, free, entire, ligulate, white or reddish, much longer than sepals, tapered distally to a blunt point; stamens 5, free, up to 6 cm long, alternate with petals, filaments thread-like, closely appressed (but not adnate) within grooves of the ovary, anthers long sagittate, subequal, 2-thecate, dehiscing by elongated slits, connective narrow, projected into an apical mucro; pistil long-conical, almost equally divided into a ridged ovary and a smooth style, the ovary imperfectly 2-celled, occasionally 1-celled by abortion, with a single large, campylotropous ovule in each cell; stigma punctiform. **Fruits** coriaceous capsules, napiform in lateral outline, irregularly longitudinally furrowed, apically tapering to a point with the persistent style remnant as a woody but brittle

beak, at first green but (with maturity) becoming reddish brown with resinous pustules, inner layer spongy. **Seeds** consisting solely of two large cotyledons; endosperm lacking; radicle pointed; plumule hooked, long, slender, reddish; germination semi-epigeal, rapid separation of cotyledons and radicle, and straightening of plumule.

Distribution — Two species in the Atlantic-East Pacific region occurring along both Atlantic and Pacific coasts of southern Central America and Northern South America.

KEY TO SPECIES OF PELLICIERA

1. Foliaceous paired bracteoles less than 35 mm wide, mostly red, rarely whitish pale green, wide-side dentition present. Petals white, pink or red, 14 or more mm wide, lanceolate. Leaf blades less than 34 mm wide, narrow-side dentition often present 1. *P. benthamii*
1. Foliaceous paired bracteoles more than 35 mm wide, whitish pale green, wide-side dentition absent. Petals mostly white, rarely pink tinged, to 14 mm wide, oblong to lanceolate. Leaf blades more than 34 mm wide, narrow-side dentition absent 2. *P. rhizophorae*

1. *Pelliciera benthamii* (Planch. & Triana) N.C. Duke, *comb. nov. & stat. nov.* — Fig. 1, 3; Map 1

Pelliciera rhizophorae Planch. & Triana ('*Pelliciera*') var. (β) *benthamii* Planch. & Triana in Triana & Planch. (1862) 381. — Type: *Sutton Hayes 76* (holo K!), Panama, Pacific entrance to the Canal, Rio Grande.

Pelliciera rhizophorae auct. non Planch. & Triana: Triana & Planch. (1862) 381, p.p.; M. Howe (1911) 61, f. 16–23, p.p.; E. Calderón (1982) 102; (1983) 102; Von Prah (1987) 118, p.p.; Castillo-Cárdenas et al. (2015b) 503, t. 2, as 'Variant B', p.p.

Etymology. The epithet '*benthamii*' honours the 19th century botanist George Bentham.

Trees, to 5 m high. **Foliage** comprised of 9–11 leaves, apical shoots 6.4–9.8 cm long. **Leaves** 9.5–12.2 by 2.8–3.2 cm, 3.4–4 times longer than wide, widest 5.0–6.4 cm from base, wide-side 1.7–1.9 cm wide, margins dentate with glands, 13–15 per 20 mm in central part of blade, often shed with age, distance of furthest gland from leaf base 0.9–1.1 cm (Fig. 1). **Bracts** 8.2–9.2 by 2.9–3 cm, 2.7–3.2 times longer than wide, widest 2.8–3.9 cm from base, narrow-side dentition often present, wide-side dentition present, length of non-dentate portion 1.6–1.7 cm, teeth 12–22 per 2 cm (Fig. 1); bracteoles narrow, 7.3–8.9 by 2.5–3 cm, 2.9–3.1 times longer than wide, widest 4.1–4.4 cm from base, narrow-side dentition absent, wide-side dentition present mostly towards distal end (Fig. 1), mostly red or rarely whitish green. **Flowers**: sepals 1.7–2.2 by 1.3–1.7 cm, 1.3–1.4 times longer than wide, glands 99–280, gland-free margin at apex 5.6–7.7 mm wide, gland-free margin at sides 2.9–3.1 mm long; petals lanceolate, 6.3–7.4 by 1.4–1.6 cm, 3.8–5.2 times longer than wide, widest 0.9–1.3 cm from base, pink or red with a white midvein, rarely white; anthers 2.6–3.3 cm long; pistil 5.9–7.5 cm long, ovary 2.8–4.1 by 5–5.2 mm, style 3.2–3.4 cm by 2.6–2.8 mm, surface percentage ribbed vs smooth 47–54%. **Fruits** c. 9.3 by 5.5 by 4 cm, c. 1.7 times longer than wide, less than 1.5 cm in width; wall to 6 mm thick at base. **Paired cotyledons** c. 5.5 by 4.7 by 3 cm, c. 1.2 times longer than wide, individually c. 1.6 cm wide, plumule base c. 0.7 cm wide, stem base c. 0.6 cm wide.

Distribution — *Pelliciera benthamii* has a restricted distribution (less than 15 sites) in the Atlantic-East Pacific region, partly on the Pacific coast of Panama, but also on the Atlantic coast of northern Colombia.

Habitat & Ecology — *Pelliciera benthamii* often grows in closed canopy stands, or as undercanopy in forests dominated by other species like *Rhizophora racemosa* G.Mey. and

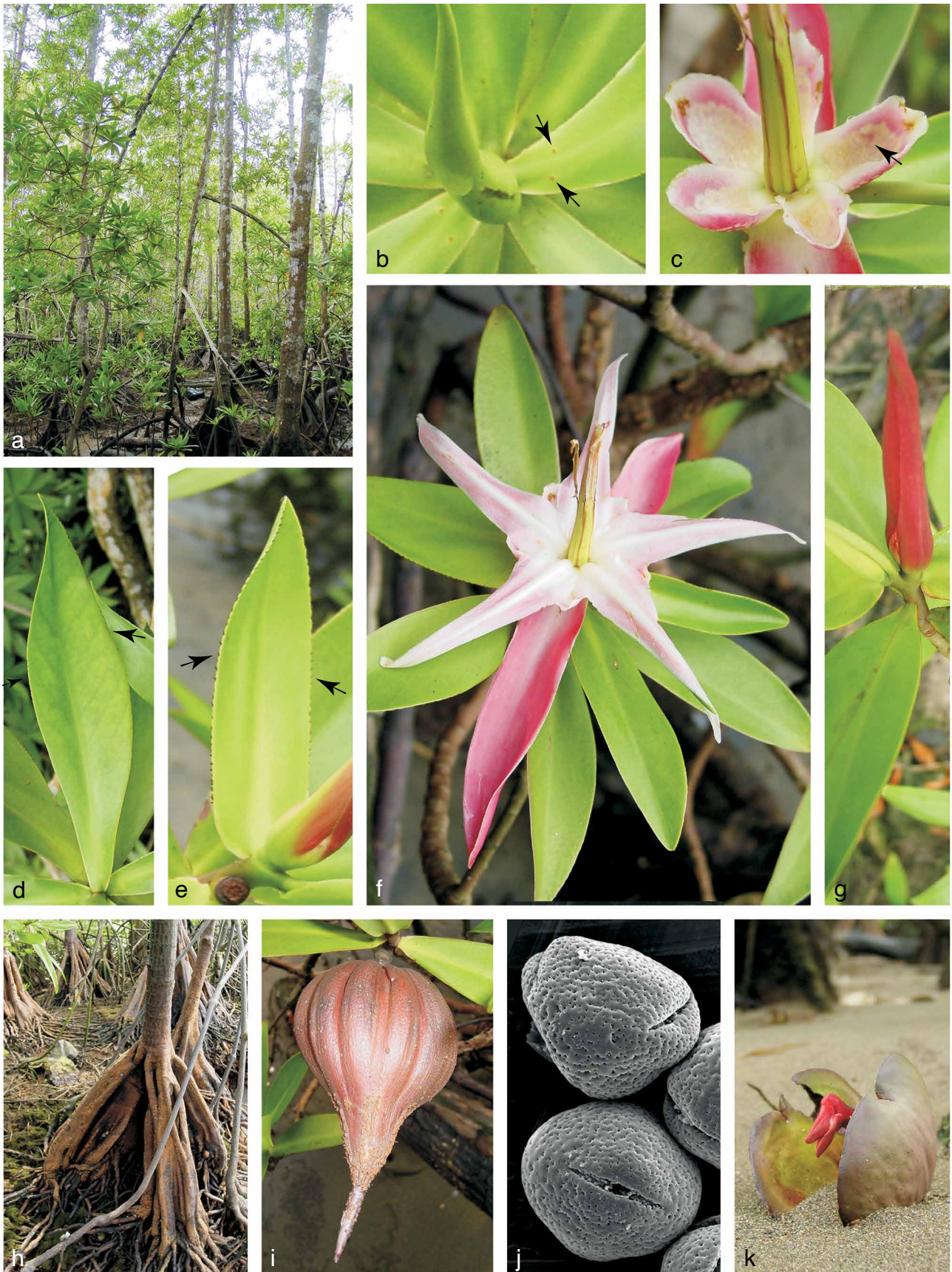


Fig. 3 *Pelliciera benthamii* (Planch. & Triana) N.C.Duke. a. Habit, Diablo at Pacific entrance to the Panama Canal, Panama; b. leaf stems with paired extrafloral nectaries (arrows); c. calyx lobes with multiple nectar glands (arrow); d. leaf margins, narrow edge and wider edge with serrate glands (arrows); e. single foliar bract, narrow edge and wider edge with serrate glands (arrows); f. open flower showing 5 lanceolate, white-pink petals, reddish paired bracteoles, single green foliar bract, and numerous leaves; g. mature floral bud enclosed by a pair of red foliar bracts; h. stem base with sinuous, spreading buttress roots; i. mature fruit capsule; j. pollen grains, mostly 'smooth', c. 60 µm diam; k. emergent seedling plumule. — Photos: a–i, k: N.C. Duke; j: J.G. Jones.

P. rhizophorae. It occurs mostly in estuarine locations within larger freshwater dominated tidal systems. Plants are evergreen with leaf emergence and leaf fall occurring all year round. Flowering: April to June; fruiting: November to December (Duke & Pinzón 1993a–b). Flowers were visited by various nectar eating birds, moths, bats and hummingbirds. Hummingbirds were observed gathering nectar from individual stand patches by way of trapline foraging. The sugar content of flower nectaries was around 11.8 ± 1.6 % w/w fructose, 14.4 ± 1.5 % w/w glucose and 15.7 ± 3.7 % w/w sucrose. In addition, there were extra-floral nectaries at the base of each leaf, the use of which appeared to support ants and other insects, as well as hummingbirds (Von Prah 1987, Gutiérrez et al. 1989).

Conservation status — Populations of *P. benthamii* are often distant from each other, and propagules are buoyant and considered likely to be dispersed by water (Rabinowitz 1978a–b). Genetic evidence indicates that there has been minimal gene flow between populations (Castillo-Cárdenas et al. 2015a–b). The total area of occupancy is less than 100 km². The quality of habitat for this rare mangrove species is seriously threatened where it occurs close to human development. The conservation status of this newly recognised taxon is best listed as Vulnerable and Threatened (see <http://www.iucnredlist.org/>).

Additional specimens examined. COLOMBIA, Atlantic coast, near Cartagena, N10°08' W75°35', 6 Aug. 1985, *Zarucchi JL 3971* (MO, PMA); Atlantic coast, Bolívar, Isla Baru, N10°08' W75°42', 6 Aug. 1985, *Zarucchi & Cuadros 3971* (K, MO). — PANAMA, Pacific coast, Chame, Chame Point, 2014, *Ramirez & Castillo 100446, 99753* (PMA); Canal Zone, Balboa, Dec. 1909, *Howe n.s.* (NY); Canal Zone, Pacific entrance to the Canal, east of Santa Fe east, 16 July 1966, *Tyson, Dwyer, Blum & Duke 4678* (K); Canal Zone, Diablo Heights, 2014, 'Variant B', *Buitrago & Castillo 109428, 99839* (PMA).

2. *Pelliciera rhizophorae* Planch. & Triana — Fig. 1, 4; Map 1

Pelliciera rhizophorae Planch. & Triana ('*Pelliceria*') in Triana & Planch. (1862) 381, p.p.; Hemsl. (1879) 97, t. 8, p.p.; Kobuski (1951) 256, p.p.; Toml. (1974) 293; Von Prah (1987) 118, p.p.; Castillo-Cárdenas et al. (2015b) 503, t. 2, 'Variant A'. — Type: *Triana & Planchon s.n.* (holo P!; iso COL 16552), Columbia, Pacific coast, Dept. del Valle, Port of Buenaventura Bay.

Etymology. The epithet '*rhizophorae*' refers to similarities in root structures with the family *Rhizophoraceae*.

Trees, to 12(–18) m high. *Foliage* comprised of 7–10 leaves, apical shoots 8.5–11.8 cm long. *Leaves* 11.7–12.7 by 3.5–3.7 cm, 3.3–3.5 times longer than wide, widest 6.3–6.7 cm from base, wide-side 2–2.1 cm wide, margins entire on narrow side, dentate with glands on the wider margin, 12–15 per 20 mm in central part of blade, often shed with age, distance of furthest gland from leaf base 0.8–1 cm (Fig. 1). *Bract* 10.4–12.7 by 3.1–3.8 cm, 3–3.4 times longer than wide, widest 1.8–3 cm from base, narrow-side dentition absent, wide-side dentition present, length of non-dentate portion 1.7–1.9 cm, teeth c. 14 per 2 cm (Fig. 1); bracteoles foliaceous, 8.7–8.9 by 3.6–4.5 cm, 2–2.5 times longer than wide, widest 3.6–4.2 cm from base, narrow-side and wide-side dentition absent, whitish green. *Flowers*: sepals 2–2.4 by 1.6–1.9 cm, 1.1–1.4 times longer than wide, glands 196–400, gland-free margin at apex 5.3–7.3 mm wide, gland-free margin at sides 2.8–4.3 mm long (Fig. 1); petals oblong to lanceolate, 6.9–7.3 by 1.2–1.4 cm, 4.9–6.1 times longer than wide, widest 1.2–1.7 cm from base, white mostly, rarely tinged pink with a white midvein; anthers 2.5–3.9 cm long; pistil 6.7–7.3 cm long, ovary 3–4.1 cm by 4.7–6.6 mm; style 2.8–3.8 cm by 2.4–2.8 mm, surface percentage ribbed vs smooth 44–59 %. *Fruits* 10.5–12.3 by 7.2–8.5 by 4.3–4.7 cm, c. 1.5 times longer than wide, thick, less than 2 cm in width; wall 6.9–7 mm thick at base. *Paired cotyledons* 7.7–8.3 by 6.6–7.4 by c. 2.9 cm, 1–1.3 times longer than wide, individually 1.5–1.7 cm thick, plumule base 1–1.1 cm wide, stem base 0.6–0.7 cm wide.

Distribution — *Pelliciera rhizophorae* has a limited distribution (c. 48 populations) in the Atlantic-East Pacific region, mostly on the Pacific coast of the Central American Isthmus and northern South America (Costa Rica, Panama, Colombia to Ecuador), but with notable occurrences also on the Atlantic coast (Honduras, Nicaragua to Panama and possibly to Uraba Gulf in Colombia (Blanco-Libreros pers. comm.; Appendix 1, Map 1). The genus has a broad relict fossil range extending from Mexico and throughout the Caribbean region across northern South America to Brazil, to Nigeria and Europe across the north Atlantic.

Habitat & Ecology — *Pelliciera rhizophorae* occurs often as closed canopy stands at low to mid-intertidal positions of downstream to intermediate estuarine locations within larger freshwater dominated estuaries. Plants are evergreen with leaf emergence and leaf fall occurring all year round. Flowering: April to June; fruiting: November to December (Duke & Pinzón 1993a–b). Flowers were visited by various nectar eating birds, moths, bats and hummingbirds. Hummingbirds gathered nectar by trapline foraging. The sugar content of sepal nectaries was around 14.1 % w/w fructose, 15.8 % w/w glucose and 13.7 % w/w sucrose. In addition, there were extra-floral nectaries at the base of each leaf. All these nectaries were used by ants and other insects (Collins et al. 1971), as well as by hummingbirds (Von Prah 1987, Gutiérrez et al. 1989, Von Prah et al. 1990).

Conservation status — Populations of *P. rhizophorae* are often distant from each other, and propagules are partially buoyant and appear to be dispersed by water (Rabinowitz 1978a–b). Genetic evidence indicates there has been minimal gene flow between populations (Castillo-Cárdenas et al. 2015a–b). The total area of *P. rhizophorae* populations is estimated to be less than 500 km². The quality of habitat for this uncommon species is declining throughout its range (e.g., Blanco-Libreros et al. 2015), primarily due to coastal development. The IUCN Red List status for *P. rhizophorae* needs to be revised from Vulnerable under criterion B (see <http://www.iucnredlist.org/>) to a higher threatened level, in consideration of this revision.

Additional specimens examined. COLOMBIA, Pacific coast, Dept. del Choco, trocha de Ultra al Valle, June 1950, *Fernandez 263* (COL 34074); Pacific coast, Dept. del Valle, Buenaventura Bay, mangrove, May 1922, *Killip 5222* (AA, NY, US); Pacific coast, Dept. de Narino, Tumaco, June 1955, *Romero-Castaneda 5298* (COL 65857, 65858). — COSTA RICA, Pacific coast, Punta Mala, Mar. 1892, *Tonduz 6723* (US). — ECUADOR, Prov. Esmeraldas, Borbon on Rio Santiago, May 1943, *Little 6423* (US). — HONDURAS, Atlantic coast, Gracias a Dios, Barra de Karataska, June 2014, *Helder Perez 129217* (EAP). — PANAMA, Pacific coast, Prov. Bocas del Toro, Mouth of Cricamola river, 2014, 'Variant A', *Ramirez & Buitrago n.s.* (PMA).

DISCUSSION

Based on the evidence presented, two species of *Pelliciera* are recognised including *P. rhizophorae* and *P. benthamii* plus undefined hybrid intermediates in locations where the species occur in sympatry. While the species are considered genetically close (also see Castillo-Cárdenas et al. 2005, 2012, 2015a–c), the intermediates lacked distinctive morphological features and they appeared to have reduced fertility, unlike the newly recognised species.

The two species of *Pelliciera* occur in a significant zone of overlap (Appendix 1, Map 1) where more hybrid intermediates are likely. In the overlap zone, the two species grow in sympatry in at least four estuaries, including Diablo at the mouth of the Pacific entrance to the Panama Canal. The hybrid individuals found at the Diablo site had demonstrable deficiencies in pollen grains (30–90 % collapsed) indicative of their low viability (e.g., Graham 1977) compared to less than 30 % in either parent species (Fig. 2; Table 1). These hybrid intermediates are consistent with hybrids in other mangrove species (Duke 2017).

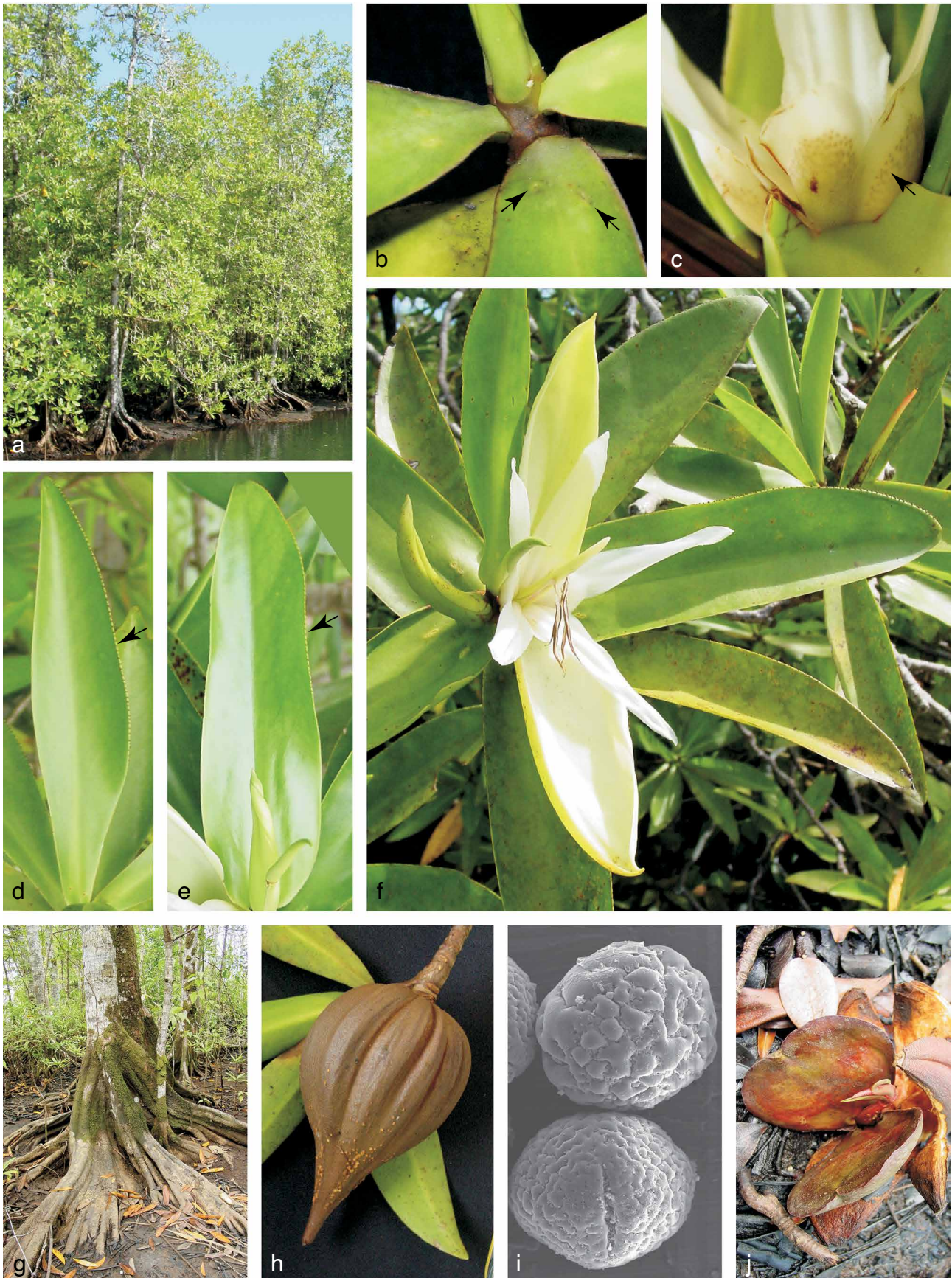


Fig. 4 *Pelliciera rhizophorae* Planch. & Triana. a. Habit, Bocas del Toro, Panama; b. leaf stems with paired glands (arrows); c. calyx lobes with multiple nectar glands (arrow); d. leaf margins, narrow edge entire, and wider edge with serrate glands (arrow); e. single foliar bract, narrow edge entire, and wider edge with serrate glands (arrow); f. open flower showing 5 oblong, white petals, whitish paired bracteoles, single green foliar bract, and numerous leaves; g. stem base with sinuous, spreading buttress roots; h. mature fruit capsule; i. pollen grains, some rugose, c. 60 μm diam; j. emergent seedling plumule. — Photos: a–h, j: N.C. Duke; i: J.G. Jones.

The distribution of each species of *Pelliciera* is notably disjunct on either side of the Central America Isthmus. There is no explanation for these odd distributional patterns, but it is likely they are the consequence of range contraction during the formation of the Central American Isthmus. To assist in explaining these patterns further, however, it is important to emphasize the outcomes from these latest findings. The newly defined distributions overlap on the Pacific coast of Panama, but it is unclear whether this is the only coastline where such an overlap occurs. It seems likely there will be additional occurrences in other locations, especially given past difficulties in the discrimination of taxa within this genus. The possibility of further mixed stands plus additional location records is of great relevance to the broader understanding of the global biogeography and evolution of these mangrove plants.

In this study it was apparent there were differences in pollen grain exine surfaces, where *P. rhizophorae* had many 'rough' grains, while *P. benthamii* had mostly 'smooth' grains. Further study is needed to fully quantify these differences in pollen grains, but these findings provide a basis for a greater knowledge of suspect *Pelliciera* fossil pollen occurrences. Such detailed assessments are highly relevant because of reported inconsistencies in prior palynological studies. According to Fuchs (1970), the identification of some *Pelliciera* fossil records need to be re-checked because, as in one example, fossil pollen grains of *Pelliciera* were very much like those of *Hura* L. (*Euphorbiaceae*) – an upland, non-mangrove species. While these genera have similar shaped pollen, the grains were distinguished more by their size with smaller grains being those of *Hura*, 40–50 µm diam, and slightly larger grains in *Pelliciera*, around 60 µm. This small size difference matters greatly. Consider the study by Graham (1977), where there was an observation about the size of so-named *Pelliciera* pollen records from the Caribbean region. In this case, those from Jamaica and Puerto Rico, were noticeably smaller (like *Hura*) compared to other locations. If so, an alternate conclusion might be that *Pelliciera* was instead absent from these islands at the time. This determination would have significant implications for the reconstruction of ancestral dispersal pathways. And, it would also have negated the authors need to explain why other mangrove inhabitants, like *Rhizophora*, were absent.

In conclusion, while there remain notable knowledge gaps and uncertainties regards both extant and fossil distributions for *Pelliciera*, there are a number of significant outcomes from this treatment. These include the recognition of two species, along with hybrid intermediates with reduced fertility, the occurrence of sympatric populations, the identification of new, distinguishing morphological characters, and the affirmation of distinguishing characters in pollen exine structure. These findings further show the conservation status of the two *Pelliciera* species as considerably more vulnerable than previously recorded by the IUCN Global Red List rankings. In fact, the status of Vulnerable under criterion B (see <http://www.iucnredlist.org/>) was based on the combination of the two species. With these now separated, the status of the two species must be significantly more threatened – especially for the more restricted *P. benthamii*. Meanwhile, both species are considered highly vulnerable and seriously threatened by ever-increasing pressures from development and global climate change (e.g., Blanco-Libreros et al. 2015).

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Appendix 1 Collections of two *Pelliciera* taxa, *P. rhizophorae* (= PR) and *P. benthamii* (= PB) from 65 recorded locations (some in close proximity) in the Atlantic-East Pacific region, listing: ocean realm (Pacific or Atlantic), country, location, species code, latitude, longitude, and information source. The 17 locations in **bold** are reported with the current study. Abbreviations in the column Species code: Species (see above), sample locations of species investigated for morphometric descriptions (-m), numeric analyses (-x), pollen assessments (-p) and phenology studies (-f). Any doubt regards species determination is marked with a question mark (?). See Map 1 for locations.

Ocean realm	Country	Location and estuarine system	Species code	Latitude	Longitude	Source (Year)
Atlantic	Honduras	Barra de Karataska, Gracias a Dios	PR	15.36012	-83.73955	Nelson & Perez (2018)
Atlantic	Nicaragua	Isla del Venado, Bay of Bluefields	PR	11.91667	-83.75000	Roth & Grijalva (1991)
Atlantic	Panama	Bocas del Toro	PR	9.33000	-82.16670	Castillo-Cárdenas et al. (2015a)
Atlantic	Panama	Tobobe Estuary, Valiente	PRmxp	9.11458	-81.84922	Duke & I. Feller, this study, data from 2005
Atlantic	Panama	Río Nuree, Valiente	PRm	8.94055	-81.81183	Duke & I. Feller, this study, data from 2005
Atlantic	Panama	Río Lago, Valiente	PRm	9.00952	-81.79112	Duke & I. Feller, this study, data from 2005
Atlantic	Panama	Bocas del Toro	PRm	9.01067	-81.79102	Castillo-Cárdenas et al. (2015b–c), Garzón-Bautista et al. (2018)
Atlantic	Panama	Río Cania, Valiente	PRm	9.01133	-81.71500	Duke & I. Feller, this study, data from 2005
Atlantic	Panama	Río Chagras, Bahía Limón	PR	9.31241	-79.92681	Duke et al. (1994)
Atlantic	Panama	Colon, Panama Canal mouth	PR	9.33766	-79.90464	Duke et al. (1994)
Atlantic	Panama	Bahía las Minas	PR	9.40000	-79.83330	Duke et al. (1994), Castillo-Cárdenas et al. (2015a)
Atlantic	Panama	Río Las Mercedes, Bahía Las Minas	PRf	9.43444	-79.78473	Duke & Pinzón (1993a–b)
Atlantic	Colombia	Suriquí River, S Uraba Gulf, Antioquia	PR?	7.91778	-76.73970	Blanco-Libreros, pers. comm. (2020)
Atlantic	Colombia	Atrato River delta, SW Uraba Gulf, Antioquia	PR?	8.04899	-76.91191	Blanco-Libreros, pers. comm. (2020)
Atlantic	Colombia	Punta Coquillo, Uraba Gulf, Antioquia	PR?	7.95000	-76.73333	Blanco-Libreros et al. (2015)
Atlantic	Colombia	Punta Las Vacas, Uraba Gulf, Antioquia	PR?	8.08333	-76.73333	Blanco-Libreros et al. (2015)
Atlantic	Colombia	Cispata Bay	PB	9.41667	-75.81667	Castillo-Cárdenas et al. (2015a)
Atlantic	Colombia	Barbacoa Bay	PB	10.01667	-75.56667	Castillo-Cárdenas et al. (2015a)
Atlantic	Colombia	Cienaga Honda, Bahía de Cartagena	PB	10.27601	-75.53779	Calderón-Saenz (1982)

Appendix 1 (cont.)

Ocean realm	Country	Location and estuarine system	Species code	Latitude	Longitude	Source (Year)
Atlantic	Colombia	Canal de Dique, Bahía de Barbaçoas	PB	10.24062	-75.52085	Calderón-Saenz (1983)
Atlantic	Colombia	Cienaga del Picon, Tierra Bomba Island, Cartegena Bay	PB	10.33899	-75.55421	Calderón-Saenz (1984)
Atlantic	Colombia	Ahorcazorra, Cartegena Bay	PB	10.29986	-75.51645	Calderón-Saenz (1984)
Atlantic	Colombia	Cienaga La Plata, Barbaçoas Bay	PB	10.13219	-75.53297	Calderón-Saenz (1984)
Pacific	Costa Rica	Tempisque, Tempisque Gulf	PR	10.25426	-85.25245	Castillo-Cárdenas et al. (2015a)
Pacific	Costa Rica	Punta Mala, Puntarenas	PR	9.529734	-84.54031	Kobuski (1951)
Pacific	Costa Rica	Guaramai estuary, Terraba-Sierpe	PR	8.86059	-83.56611	Duke & H. Polania, this study, data from 1993
Pacific	Costa Rica	Río Sierpe, Terraba-Sierpe	PR	8.79468	-83.56226	Duke & H. Polania, this study, data from 1993
Pacific	Panama	Pedregal, El Pedregal	PR	8.36666	-82.43333	Castillo-Cárdenas et al. (2015a)
Pacific	Panama	Isla Coliba	PR	7.46000	-81.79420	Castillo-Cárdenas et al. (2015a)
Pacific	Panama	Uvas landing, Golfo de Chiriquí	PR	8.13679	-81.71212	Duke & R. Robertson, this study, data from 1989
Pacific	Panama	Río de Jesús, Gulf of Montijo	PR	7.77194	-81.13083	Gross et al. (2014)
Pacific	Panama	Montijo Gulf	PR	7.80933	-81.06267	Castillo-Cárdenas et al. (2015a)
Pacific	Panama	Isla Canas, Canas	PR	7.43175	-80.23529	Duke & R. Robertson, this study, data from 1989
Pacific	Panama	Oña	PR	7.43357	-80.13312	Castillo-Cárdenas et al. (2015a)
Pacific	Panama	Pedasi	PB	7.56433	-80.02705	Castillo-Cárdenas et al. (2015a)
Pacific	Panama	Punta Chame, Chame	PR	8.61670	-79.74383	Duke, this study, data from 1990
Pacific	Panama	Chame	PB	8.64382	-79.87197	Castillo-Cárdenas et al. (2015a-c), López et al. (2015), Gaizón-Bautista et al. (2018)
Pacific	Panama	Río Perreque	PB	8.77976	-79.77752	Duke et al. (1994)
Pacific	Panama	Río Cairito	PR, PB	8.88341	-79.70820	Duke et al. (1994)
Pacific	Panama	Cairito Port	PB	8.87863	-79.70815	Castillo-Cárdenas et al. (2015a)
Pacific	Panama	Veracruz	PB	8.89400	-79.59403	Duke et al. (1994), Castillo-Cárdenas et al. (2015a)
Pacific	Panama	Diablo, Río Curundu, Panama Canal Zone	PRm, PBmf	8.6641	-79.57226	Duke et al., this study, data from 1989-1992
Pacific	Panama	Río Grande, Panama Canal Zone	PRmxp, PXXp, PBmxp	8.94304	-79.57419	Duke et al. (1994), Duke, this study, data from 2005
Pacific	Panama	Panama Canal Zone	PB	8.98848	-79.58183	Kobuski (1951), Castillo-Cárdenas et al. (2015a-c)
Pacific	Panama	Río Juan Díaz, Tocumun	PB	9.02190	-79.43312	Duke et al. (1994)
Pacific	Panama	Río La Maestra, Panama	PR	8.877831	-78.80654	Kobuski (1951)
Pacific	Panama	Río Maje, Panama	PR, PB	8.70420	-78.57408	Duke et al., this study, data from 1992
Pacific	Panama	Darien	PR	8.51736	-78.42463	Castillo-Cárdenas et al. (2015a)
Pacific	Panama	Río Sabana, Darien	PB	8.48328	-78.11368	Duke et al., this study, data from 1993
Pacific	Panama	Golfo de san Miguel, Darien	PR, PB	8.40772	-78.16020	Duke et al., this study, data from 1993
Pacific	Panama	Río Balsa, Darien	PB	8.19512	-77.92568	Duke et al., this study, data from 1993
Pacific	Panama	San Jose Island, Perlas Archipelago	PR	8.259652	-79.120321	Kobuski (1951)
Pacific	Colombia	Utría Inlet	PR	6.00000	-77.35000	Castillo-Cárdenas et al. (2015a)
Pacific	Colombia	Virudo, Choco	PR	5.40000	-77.40000	Castillo-Cárdenas et al. (2005)
Pacific	Colombia	Charambira, Choco	PR	4.28500	-77.45000	Castillo-Cárdenas et al. (2005)
Pacific	Colombia	La Plata Island, Valle del Cauca	PR	4.01833	-77.25000	Castillo-Cárdenas et al. (2005)
Pacific	Colombia	Malaga Bay	PR	4.03306	-77.25000	Von Prah (1987), Castillo-Cárdenas et al. (2015a)
Pacific	Colombia	Buenaventura Bay, El Valle	PR	3.873249	-77.048792	Kobuski (1951)
Pacific	Colombia	Turnaco, Narino	PR	1.81667	-78.76867	Castillo-Cárdenas et al. (2005)
Pacific	Colombia	Tumaco Inlet, Narino	PR	1.81677	-78.83281	Castillo-Cárdenas et al. (2015a)
Pacific	Colombia	Milagros, Narino	PR	1.60000	-79.01667	Castillo-Cárdenas et al. (2005)
Pacific	Colombia	Chontal, Narino	PR	1.51833	-78.86833	Castillo-Cárdenas et al. (2005)
Pacific	Ecuador	La Tola	PR	1.16670	-78.98330	Kobuski (1951), Castillo-Cárdenas et al. (2015a)
Pacific	Ecuador	Río Santiago, Borbon, Esmeraldas, La Tola	PR	1.08179	-78.967966	Kobuski (1951)
Pacific	Ecuador	Muisne	PR	0.61670	-80.01670	Castillo-Cárdenas et al. (2015a)

Appendix 2 Data compilation of 6 specimens scored for 79 measured and multistate morphological attributes of *Pelliciera* specimens to establish the diagnostic characters. Species codes: PR = *P. rhizophorae* and PB = *P. benthamii*. Locations include: 'Bocas' = Bocas del Toro, north west Panama, Atlantic coast; 'Diablo' = central Panama, Pacific coast (see Map 1). Specimen codes are those used in Fig. 2 and Appendix 3. Attributes (16) defining the two species are marked in **bold**. 'Dentition' refers to the series of teeth-like glands along edges of leaves and bracts (Fig. 1, 3–4) – these fall off with age and handling. Multistate attributes and conditions are listed in the notes.

#	Component	Attribute	Sites	Bocas	Bocas	Diablo	Diablo	Diablo	Diablo
			Species code Specimen #	PR #4147	PR #4131	BR #4145	PB #4144	PB #4143	PB #4142
1	Foliage	Leaf blade length (mm)		124	127	117	122	117.8	95
2		Leaf blade width (mm)		35	37	35	32	29.4	28.2
3		Ratio leaf length / width		3.54	3.43	3.34	3.81	4.01	3.37
4		Leaf length from widest width to base (mm)		64	67	63	64	64.2	50.4
5		Ratio – leaf length / widest width to base		1.94	1.90	1.86	1.91	1.83	1.88
6		Leaf wide-side width (mm)		20.2	–	21	19	17.3	16.6
7		Ratio – leaf length / w-side width		6.14	–	5.57	6.42	6.81	5.72
8		Leaves per leafy shoot (count)		7	8	10	9	11	9.5
9		Apical shoot length (mm)		97	118	85	98	80	64
10		Leaf dentition length per 20 mm		15	12.8	14.2	15	13.4	14
11		Leaf narrow-side dentition (multi-state)		2	2	2	1	1	1
12		Leaf wide-side dentition (multi-state)		1	1	1	1	1	1
13		Gland furthest from leaf base (mm)		9.7	–	8.1	8.9	11	9.6
14		Gland number at leaf base		2	–	1.8	2	2	2
15	Single bract	Length (mm)		127	113	104	91	91.5	82
16		Width (mm)		37	38	31	30	28.8	30
17		Ratio - length / width		3.43	2.97	3.35	3.03	3.18	2.73
18		Length from widest width to base (mm)		17.8	–	30	28	39	28
19		Ratio - length / widest width to base		7.13	–	3.47	3.25	2.35	2.93
20		Wide-side width (mm)		18.6	–	17.3	16.4	16.8	16.5
21		Dentition length per 20 mm		–	14	13	12	22	–
22		Narrow-side dentition (multi-state)		0	0	0	1	1	1
23		Wide-side dentition (multi-state)		1	1	1	1	1	1
24		Gland furthest from base (mm)		0	–	–	4.8	8.2	0
25		Gland number at base		0	–	2	2	1	0
26		Colour (multi-state)		1	1	1	1	1	1
27	Foliaceous bracts	Length (mm)		88.4	89	87.6	86	89	72.5
28		Width (mm)		45.2	36	38.3	30	29	25.2
29		Ratio - length / width		1.96	2.47	2.29	2.87	3.07	2.88
30		Length from widest width to base (mm)		35.8	–	42.3	41	44	43.4
31		Ratio - length / widest width to base		2.47	–	2.07	2.10	2.02	1.67
32		Length of absent dentition (mm)		0	0	0	19	–	–
33		Narrow-side dentition (multi-state)		1	1	1	1	1	1
34		Wide-side dentition (multi-state)		1	1	1	2	2	2
35		Dentition length per 20 mm		0	0	0	13	9	0
36		Gland furthest from base (mm)		0	–	0	0	0	0
37		Gland number at base		0	–	0	0	0	0
38		Colour (multi-state)		1	1	1	2	1	2
39	Sepal	Length (mm)		20.3	22.9	23.9	21.8	21.1	17.1
40		Width (mm)		18.9	16.1	16.8	15.3	16.7	12.9
41		Ratio - length / width		1.07	1.42	1.42	1.42	1.26	1.33
42		Area (mm²)		383.67	368.69	401.52	333.54	352.37	220.59
43		Gland numbers		196	285	400	250	280	99
44		Gland density (count/mm ²)		0.51	0.77	1.00	0.75	0.79	0.45
45		Margin of no glands, distal (mm)		5.3	–	7.3	5.7	7.7	5.6
46		Margin of no glands, sides (mm)		3.7	4.3	2.8	3.1	2.9	2.9
47		Colour (multi-state)		1	1	1	1	1	1
48	Petal	Length (mm)		69.7	69	72.5	69	74.4	63
49		Width (mm)		13.4	14	11.9	15.3	14.3	16.4
50		Ratio - length / width		5.20	4.93	6.09	4.51	5.20	3.84
51		Length from widest width to base (mm)		17.1	–	11.9	9.3	13.1	11
52		Ratio - length / widest width to base		4.08	–	6.09	7.42	5.68	5.73
53		Colour (multi-state)		1	1	1	2	2	2
54		Form (multi-state)		1	1.5	2	2	2	2
55	Stigma	Distal length (mm)		28.2	34	37.5	32.8	34	31.5
56		Distal width (mm)		2.4	–	2.8	2.8	2.7	2.6
57		Distal cross-section (multi-state)		1	1	1	1	1	1
58		Distal colour (multi-state)		1	1	1	1	1	2
59		Distal form (multi-state)		1	1	1	1	1	1
60		Basal length (mm)		40.8	39	29.8	32.3	40.5	27.5
61		Basal width (mm)		4.7	6.6	4.9	5.2	5	5.2
62		Basal cross-section (multi-state)		1	1	1	1	1	1
63		Basal colour (multi-state)		1	1	1	1	1	1
64		Basal form (multi-state)		1	1	1	1	1	1
65		Pistol total length (mm)		69	73	67.3	65.1	74.5	59
66	Anther	Total length (mm)		24.5	39	34.2	32.8	30	26.3

Appendix 2 (cont.)

#	Component	Attribute	Sites	Bocas	Bocas	Diablo	Diablo	Diablo	Diablo
			Species code Specimen #	PR #4147	PR #4131	BR #4145	PB #4144	PB #4143	PB #4142
67	Mature fruit	Length (mm)		105	123	–	–	–	92.5
68		Mid width (mm)		72	85	–	–	–	54.5
69		Ratio - length / width		1.46	1.45	–	–	–	1.70
70		Thickness (mm)		42.5	47	–	–	–	39.8
71		Distal width (mm)		20.4	–	–	–	–	14.6
72	Pericarp	Thickness (mm)		6.9	7	–	–	–	6
73	Cotyledon	Length (mm)		83	77	–	–	–	54.9
74		Mid width (mm)		66.3	74	–	–	–	46.5
75		Ratio - length / width		1.25	1.04	–	–	–	1.18
76		Thickness (mm)		29.2	–	–	–	–	30
77		Single lobe thickness (mm)		15	17.2	–	–	–	16.2
78		Plumule width (mm)		10	10.5	–	–	–	7.4
79		Stem width (mm)		6.1	7.1	–	–	–	5.6

Notes — multistate attribute conditions

Code #	Components	Attribute	1	2	3	4
11	Leaves	Narrow-side dentition	Absent	Present	–	–
12		Wide-side dentition	Absent	Present	–	–
22	Single bracts	Narrow-side dentition	Absent	Present	–	–
23		Wide-side dentition	Absent	Present	–	–
26		Colour	Green	Non-green	–	–
33	Foliaceous bracts	Narrow-side dentition	Absent	Present	–	–
34		Wide-side dentition	Absent	Present	–	–
38		Colour	Pale green	Pale green-pink	Pink	Red
47	Sepals	Colour	White	Other	–	–
53	Petals	Colour	White	White-pink	Pink	–
54		Form	Oblong	Oblong-lanceolate	Lanceolate	–
57	Stigma	Distal cross-section	Terete	Other	–	–
58		Distal colour	Pale green	Pink	Other	–
59		Distal form	Smooth	Other	–	–
62		Basal cross-section	Grooves	Other	–	–
63		Basal colour	Pale green	Other	–	–
64		Basal form	Ribbed	Other	–	–

Appendix 3a Data matrix of 25 specimens scored for 11 diagnostic attributes of *Pelliciera* specimens used in the multivariate ordination in Fig. 2. See Appendix 2 for attribute codes and measures. Species codes: PR = *P. rhizophorae*; PB = *P. benthamii*; PX = intermediate individuals. Note PB? represents an unmatched entity of *P. benthamii*, see text. Locations include: 'Bocas' = Bocas del Toro, north west Panama, Atlantic coast; 'Diablo' = central Panama, Pacific coast. 'VAR A' & 'VAR B' are two variants scored here for comparison from averaged data reported by Castillo-Cárdenas et al. (2015b). Attribute condition states are listed in Appendix 3b. Specimens and data in **bold** are those also listed in Appendix 2.

Diagnostic attributes			38	28	34	53	54	49	2	11	26	16	22
Spp/Loc'n	Sample #												
PR/Bocas	1022		1	1	1	1	1	1	1	1	1	1	1
PR/Bocas	102R3		1	1	1	1	1	1	1	1	1	1	1
PR/Bocas	1027		1	1	1	1	2	1	1	1	1	1	1
PR/Bocas	1030		1	1	1	1	1	1	1	1	1	1	1
PR/Bocas	1031		1	1	1	1	1	1	1	1	1	1	1
PR/Bocas	4131		1	1	1	1	2	1	1	1	1	1	1
PB/Diablo	4142		4	3	2	3	3	3	3	2	1	3	2
PB/Diablo	4143		2	3	2	3	3	3	3	2	1	3	2
PB/Diablo	4144		4	3	2	3	3	3	3	2	1	3	2
PR/Diablo	4145		1	1	2	1	2	1	2	1	1	1	1
PR/Diablo	4147		1	1	1	1	1	1	1	1	1	1	1
PB/Diablo	4149		4	3	2	3	3	3	3	2	1	3	2
PR/Diablo	4150		2	1	2	1	3	3	1	1	1	1	1
PB/Diablo	4151		4	3	2	3	3	3	3	2	1	3	2
PR/Diablo	4152		1	1	1	1	2	2	1	1	1	1	2
PR/Diablo	4153		1	1	1	1	2	2	2	1	1	1	1
PR/Diablo	4154		1	1	1	1	2	1	1	2	1	1	1
PX/Diablo	4155		3	3	2	3	2	2	3	1	1	1	2
PX/Diablo	4156		4	3	2	1	2	3	3	1	1	1	1
PX/Diablo	4157		3	3	2	3	2	2	3	1	1	1	2
PB/Diablo	4158		3	3	2	3	3	3	3	2	1	3	2
PB/Diablo	4160		4	3	2	3	3	2	3	2	1	3	2
PR/Diablo	4161		1	2	1	1	2	2	2	1	1	1	1
PR/mean*	VAR A		1	1	–	1	–	1	1	–	1	–	–
PB?/mean*	VAR B		3.5	3	–	2	–	1	3	–	1	–	–

Appendix 3b Attribute multistate conditions for 11 attributes compiled in Appendix 3a, and listed in Appendix 2.

Attribute states			1	2	3	4
Attribute	Attribute					
38	Foliaceous bracts	Colour	Pale green	Pale green-pink	Pink	Red
28		Width	> 35 mm	~ 35 mm	< 35 mm	–
34		Wide-side dentition	Absent	Present	–	–
53	Petals	Colour	White	White-pink	Pink	–
54		Form	Oblong	Oblong-lanceolate	Lanceolate	–
49		Width	< 14 cm	~ 14 cm	> 14 cm	–
2	Leaves	Width	> 34 cm	~ 34 cm	< 34 cm	–
11		Narrow-side dentition	Absent	Present	–	–
26	Single bracts	Colour	Green	Non-green	–	–
16		Width	> 31 cm	~ 31 cm	< 31 cm	–
22		Narrow-side dentition	Absent	Present	–	–