

# A new species and two new records of *Quercus* (Fagaceae) from northern Vietnam

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## Abstract

A new species, *Quercus xuanlienensis* Binh, Ngoc & Bon, is described from Xuan Lien Nature Reserve, Vietnam. The new species is morphologically similar to *Q. edithiae* Skan, in having 8–11 pairs of secondary veins, bowl-shaped cupules and ellipsoid to cylindrical-ellipsoid and basally convex nuts. It differs in having serrulate leaf margins only at apical 1/5–1/7, almost entire margins of bracts on cupule and much longer nuts. The species is also similar to *Q. fleuryi* Hickel & A. Camus in having leaves glabrous on both surfaces with only an apically serrulate margin but differs in having shorter petioles, cupules enclosing 1/5 of the nut and much longer nuts. In addition, *Q. disciformis* Chun & Tsiang, and *Q. bella* Chun & Tsiang., previously known from China, are newly recorded from Ba Vi National Park, Vietnam.

## Keywords

Ba Vi National Park, DNA barcoding, Fagaceae, *Quercus*, Taxonomy, Vietnam, Xuan Lien Nature Reserve

## Introduction

*Quercus* L. comprises ca. 400–500 species (Nixon 1993, Valencia-A et al. 2016) and has been divided into two subgenera, *Quercus* subgenus *Cyclobalanopsis* (Oerst.) Schneider (ring-cup oaks) characterised by stigma capitate to subcapitate or discoid

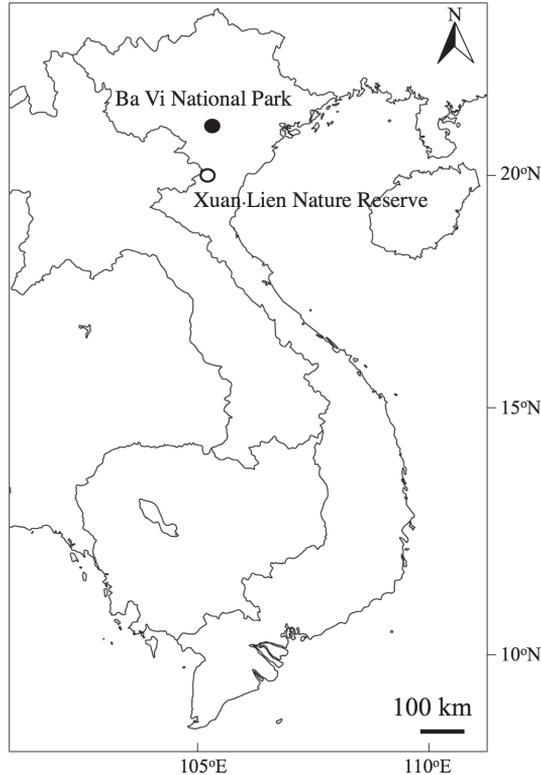
stigma, cupule bracts being connate or forming concentric or spiral rings and *Quercus* subgenus *Quercus* (scale-cup oaks) characterised by usually linear ampliate or broadly ampliated stigma, free and imbricate cupule bracts (Nixon 1993, Manos et al. 1999). In Vietnam, according to Ho (2003) and Ban (2005), a total of 43 *Quercus* species were recorded, amongst which 37 species belong to subgenus *Cyclobalanopsis* and six species belong to subgenus *Quercus*. Recently, the following two species were reported and the species of *Quercus* in Vietnam rose to 45 species: *Q. lineata* Blume of subgenus *Cyclobalanopsis* (Li et al. 2016) and *Q. trungkhanhensis* Binh & Ngoc of subgenus *Quercus* (Binh et al. in press).

To widen our knowledge on the Fagaceae of Vietnam, field surveys were undertaken by the authors for 13 conservation areas (national parks, nature reserves and conservation area) in Vietnam and a total of 105 *Quercus* samples were collected. Amongst them, during the field surveys in Xuan Lien Nature Reserve and Ba Vi National Park (Fig. 1), we discovered three unknown species of the subgenus *Cyclobalanopsis* which were not identical to any of the 38 species of *Cyclobalanopsis* previously recorded from Vietnam (Ho 2003, Ban 2005, Li et al. 2016, Binh et al. in press).

Xuan Lien Nature Reserve, Thuong Xuan District, Thanh Hoa Province, North Central Coast of Vietnam, was established in 1999 with a total area of 21,000 ha. Until now, 1,142 species of vascular plants belonging to 620 genera and 180 families have been recorded (Xuan Lien Nature Reserve 2017). In Fagaceae, 31 species including 17 *Lithocarpus* species (55%), 10 species of *Castanopsis* (32%) and four species of *Quercus* (13%) have been recorded (Xuan Lien Nature Reserve 2017). Ba Vi National Park, Ha Noi Capital, northern Vietnam was established in 1991 with a total area of 7,377 ha (Fig. 1). In this national park, located in the Ba Vi mountain range, 1,201 vascular plant species of 649 genera and 160 families including 19 species of Fagaceae are recorded (Ba Vi National Park 2008).

In this study, a new species is reported from Xuan Lien Nature Reserve and two species are newly recorded from Ba Vi National Park. A new species is described as *Quercus xuanlienensis* Binh, Ngoc & Bon. The two newly recorded species to the country are *Q. disciformis* Chun & Tsiang. and *Q. bella* Chun & Tsiang.

In addition to the morphological examination, DNA sequences and phylogenetic analyses are helpful for delimiting species (Hebert and Gregory 2005, Dick and Webb 2012). Here, DNA sequences of the three species were compared with those of 20 species in Vietnam to confirm that the three species are divergent and thus distinct from the other species. First, two DNA barcode regions were sequenced, the partial genes for the large subunit ribulose-1,5-bisphosphate carboxylase oxygenase (*rbcL*) and maturase K (*matK*) as basic DNA barcodes (CBOL Plant Working Group 2009). However, those sequences show limited divergence in the genus *Quercus* and thus multiple gene markers (Hubert et al. 2014, Simeone et al. 2016), RAD-seq (Cavender-Bares et al. 2015, Fitz-Gibbon et al. 2017) and MIG-seq (Suyama and Matsuki 2015, Binh et al. in review) have been used to determine phylogenetic relationships in *Quercus*. In particular, Binh et al. (in review) successfully used MIG-seq to determine the phylogenetic relationship in the *Quercus langbianensis* complex in Vietnam and revise its taxonomy. In this study, the authors



**Figure 1.** Collection sites of *Quercus xuanlienensis* Binh, Ngoc & Bon, *Quercus disciformis* Chun & Tsiang, and *Quercus bella* Chun & Tsiang.

compared the MIG-seq of *Q. xuanlienensis*, *Q. disciformis* and *Q. bella* with those of 18 *Quercus* species studied by Binh et al. (in review) and two additional species *Q. platycalyx* Hickel & A. Camus and *Q. quangtrienensis* Hickel & A. Camus that have cupules similar to *Q. disciformis* and *Q. bella*, to determine their identities and phylogenetic relationships.

## Materials and methods

### Morphological observations

The validity of a new species and the identities of newly recorded species were examined based on literature of the genus *Quercus* in Vietnam and its surrounding countries (Camus 1936–1954, Soepadmo 1972, Ho 2003, Huang et al. 1999, Ban 2005, Phengkklai 2008, Li et al. 2016, Binh et al. in press), authentic specimens including types by visiting the herbaria DLU, HN, FU, P and VNM and using images available on the web of JSTOR Global Plants (<https://plants.jstor.org/>) and Chinese Virtual Herbarium (<http://www.cvh.org.cn/>).

## DNA extraction

DNA was isolated from silica-gel dried leaf materials following the CTAB method (Doyle and Doyle 1987) with minor modifications, as in Toyama et al. (2016). Before the DNA extraction, dry leaf material was milled by QIAGEN TissueLyser to obtain fine powder and the powder was washed up to five times by 1 ml buffer (0.1 M HEPES, pH 8.0; 2% Mercaptoethanol; 1% PVP; 0.05 Ascorbic acid).

## DNA barcoding

DNA regions of the large subunit of ribulose-1,5-bisphosphate carboxylase oxygenase (*rbcL*) and maturase K (*matK*) were amplified and sequenced following the protocols of Kress et al. (2009) and Dunning and Savolainen (2010), respectively.

## Next generation DNA sequencing – MIG-seq

DNA products were used from 105 *Quercus* spp. as templates to amplify thousands of short sequences (loci) from a wide variety of genomes using primers designed for “multiplexed ISSR genotyping by sequencing” (MIG-seq, Suyama and Matsuki 2015). Then presence/absence of each locus in each sample was used for phylogenetic tree reconstruction regardless of whether it has SNP or not. According to the MIG-seq protocol of Suyama and Matsuki (2015) with minor modifications as in Binh et al. (in review), the 1st PCR, multiple non-repetitive regions from various inter-simple-sequence repeat (ISSR) are amplified from genomic DNA by multiplexed PCR with tailed ISSR primers. The 2nd PCR step was performed based on products from the 50 times dilution for each 1st PCR product with deionised water. Then, 3 µl of each 2nd PCR product was pooled as a single mixture library and purified. Subsequently, the Pippin Prep DNA size selection system (Sage Science, Beverly, MA, USA) was used to selected fragments in the size range 350–800 bp. A SYBR green quantitative PCR assay (Library Quantification Kit; Clontech Laboratories, Mountain View, CA, USA) was used to measure the concentration of the size-selected library with approximately 10 pM of libraries. Finally, 10 pM of libraries were used for sequencing on an Illumina MiSeq Sequencer (Illumina, San Diego, CA, USA), using a MiSeq Reagent Kit v3 (150 cycle, Illumina).

## Phylogenetic analyses

In MIG-seq, raw data from 105 samples were pretreated and quality control completed following Suyama and Matsuki (2015) as described in Binh et al. (in review). Subsequently, a list of loci obtained was used for the next steps. This list of loci was detected at least in one individual ( $1/105=0.01$ ) with the following settings: all samples belong to the

same population and threshold frequency of haplotype count in a population ( $r = 0.001$ , a threshold one-order higher than 0.01. Presence/absence (1/0) data of loci were used to compute a distance matrix, construct a neighbour-joining (NJ) tree and the reliability of the tree topology was examined by bootstrapping with 1000 replicates using PHYLIP ver. 3.695 (Shimada and Nishida 2017) as follows; 1000 times re-sampling with Seqboot, distance computation with Restdist, tree construction with NJ and consensus tree construction with Censense. In addition, FigTree v1.4.3 (<http://tree.bio.ed.ac.uk/software/figtree/>) was used to visualise the resulting tree. A phylogenetic tree for 105 samples including 43 *Quercus* species amongst 44 species previously recorded in Vietnam (data not shown) was constructed and subsequently reduced to 28 samples by focusing on the clades containing *Q. xuanlienensis*, *Q. disciformis*, *Q. bella* and the additional 20 *Quercus* species following Binh et al. (in review). A total of 19,916 loci were used for the final phylogenetic tree.

## Results

### Morphological comparison of a new species and two newly recorded species with similar species

The unknown species (*Quercus xuanlienensis*) collected from Xuan Lien Nature Reserve was not morphologically assignable to any of the species recognised in Vietnam and its surrounding countries. According to Flora of China (Huang et al. 1999) and Illustrated Flora of Vietnam (Ho 2003), *Q. xuanlienensis* is most similar to *Q. edithiae* in leaf size (7–15 × 3–5.8 cm), leaf base (cuneate), petiole length (1.5–2.8 cm long), number of secondary veins (8–11 pairs), cupule shape (bowl-shaped) and nut shape (ellipsoid to cylindrical-ellipsoid). However, *Q. xuanlienensis* is distinct from *Q. edithiae* in having a leaf margin serrated only along its upper 1/5–1/7 (vs. upper 2/3), entire margin of cupule bracts (vs. denticulate except basal 2 or 3 rings) and longer nut (5–6 cm long vs. 4–4.5 cm long) (Table 1). *Quercus xuanlienensis* is also morphologically similar to *Q. fleuryi* Hickel & A. Camus in leaf shape and texture, leaf margin serrulate only at apical 1/5–1/7, entire margin of cupule bracts, basally convex nuts, but *Q. fleuryi* (type: *Fleury 37831*, P [P00753925, P00753926]) showed much larger leaves (14–22 × 5–9 cm) than *Q. xuanlienensis* ((6–)8–11 × 3–4.5 cm)). In addition, *Q. xuanlienensis* is distinct from *Q. fleuryi* in having an ellipsoid bud (vs. ovate), shorter petiole (1.5–2 cm long vs. 2.5–4 cm long), smaller and bowl-shaped cupule, (1.3–1.7 cm high, 1.9–2.1 cm in diam. vs. campanulate to cylindrical, 3.6–3.7 cm high, 3.5 cm in diam.), fewer cupule bracts (7–8 rings vs. 10–13 rings), cupules covering 1/4 to 1/3 of a nut (vs. 2/3) and ellipsoid to cylindrical-ellipsoid (vs. ovoid to cylindrical-ellipsoid) and longer nuts (5–6 cm high, 2–2.3 cm in diam. vs. 3–4.5 cm high, 2–3 cm in diam.) (Table 1).

According to the key and descriptions in the Flora of China (Huang et al. 1999), the other two unknown taxa from Ba Vi National Park were identified as *Q. disciformis* and *Q. bella*. Excluding slightly thinner leaves and lower teeth, one species is identical with *Q. disciformis* in the following diagnostic characters: leaf blade oblong to obovate-elliptic (6–13 × 2.5–4 cm), margin serrate in the upper 2/3, glabrous on both surfaces when ma-

ture; lateral veins 11–13 pairs; petiole ca. 2 cm long; cupule discoid, rim flat when ripe, 3–4 cm in diam., covering base of the nut, scales arranged in 8–10 rings, margin of rings denticulate except apical 2 or 3 entire; nuts oblate 1.5–2 cm high, 2 cm in diam., apex flattened densely appressed hairy. Another species was identified as *Q. bella* having the following characteristics: leaf blade oblong-elliptic to lanceolate (8–15 cm × 2–3.5 cm), base slightly oblique, margin serrate in the upper 1/2; lateral veins 12 pairs of lateral veins; petiole 1–2 cm long; cupule discoid (ca. 0.5 cm × 2.5–3 cm), covering base of the nut, scales arranged in 6–8 rings, margin of rings irregular denticulate; nut oblate nut 1.5–2 cm high and 2.2–3 cm in diam.

### DNA barcoding and MIG-seq

The *rbcL* and *matK* sequences of *Q. xuanlienensis* showed 100% (627/627 bp) and 99% (907/910 bp) homologies with *Q. donnaiensis* and *Q. austrocochinchinensis*, respectively. The *rbcL* and *matK* sequences of *Q. disciformis* and *Q. bella* showed that 100% (696/696 bp) and 100% (833/833 bp) homologies with each other, respectively.

A phylogenetic tree, inferred using MIG-seq, showed that *Q. xuanlienensis*, *Q. disciformis* and *Q. bella* are not identical with any of the 20 species from Vietnam. The neighbour-joining (NJ) tree based on MIG-seq data for 28 sample of *Quercus* recognised two major clades using *Trigonobalanus* as an outgroup (Fig. 2). Clade 1 with 82% bootstrap value consists of three species of subgenus *Quercus* (*Q. lanata*, *Q. setulosa* and *Q. trungkhanhensis*) and Clade 2 with 99% bootstrap value consists of 20 species of subgenus *Cyclobalanopsis* including *Q. bella*, *Q. disciformis* and *Q. xuanlienensis*. These three species were clustered with *Q. quangtriensis*, *Q. neglecta* and *Q. platycalyx* and a clade of those six species was strongly supported (74% bootstrap value). Amongst the six species, *Q. xuanlienensis* was separated from the other five species forming a clade with a 74% bootstrap value. Four samples of *Q. disciformis* and three samples of *Q. bella* formed two distinct clades, each supported by 100% bootstrap value. *Quercus disciformis* was sister to *Q. bella* and the clade of those two species had an 84% bootstrap value.

### Discussion

The results of the NJ tree, based on MIG-seq data, showed that *Q. disciformis* is sister to but well differentiated from *Q. bella*. These two species were collected in Ba Vi National Park where they co-occur with similar in leaf and nut morphologies, but differ in the coverage of the cupule (Fig. 4, less than 1/8 in *Q. disciformis* vs. Fig. 5, basal 1/8 to 1/4 in *Q. bella*). According to the Flora of China (Huang et al. 1999), *Q. bella* is recorded from Guangdong, Guangxi and Hainan provinces, whereas *Q. disciformis* is distributed in SW Guangdong, Guangxi, Guizhou, Hainan and Hunan provinces. Ba Vi National Park is located in northern Vietnam, neighbouring Guangxi province and therefore the occurrences of *Q. disciformis* and *Q. bella* there are understandable.

**Table 1.** Morphological comparison amongst *Quercus xuanlienensis* Binh, Ngoc & Bon, sp. nov., *Quercus edithiae* Skan and *Quercus fleuryi* Hickel & A. Camus.

Characters	<i>Q. xuanlienensis</i>	<i>Q. edithiae</i> <sup>(1,2,5)</sup>	<i>Q. fleuryi</i> <sup>(3,4,5)</sup>
Buds shape	Ellipsoid	Ellipsoid to ovoid	Ovoid
Twigs	Tomentose then glabrous	Densely yellowish brown tomentose when young, later glabrous	Densely orange-brown tomentose when young, later glabrous
Stipules	Linear-lanceolate, 10–14 mm long	Caducous, not seen	Caducous, not seen
Leaf margin	Serrate on upper 1/5–1/7 of lamina	Serrate on the upper 2/3 of lamina	Undulate and serrulate on upper 1/6–1/7 of lamina
Leaf surface	Glabrous on both surfaces	Glabrous on upper surface, reddish brown pubescent on lower surface	Glabrous on both surfaces
Leaf base	Cuneate	Cuneate	Broadly cuneate
Leaf size	(6–)8–11(–15) × 3–4.5(–5) cm	7–15 × 3–5.8 cm	14–22 × 5–9 cm
Length of petioles	1.5–2 cm long	1.7–2.8 cm long	2.5–4 cm long
Number of secondary veins	8–11 pairs	9–10 pairs	10–12 pairs
Infructescence	0.8–1 cm long, each infructescence with (1 or) 2 acorns	0.8–1.5 cm long, each infructescence with (2 or) 3 acorns	0.8–1 cm long, each infructescence with (2 or) 3 acorns
Cupule shape and size	Bowl-shaped, 1.3–1.7 cm high, 1.9–2.1 cm in diam.	Bowl-shaped, 1.5–1.7 cm high, 2.3 cm in diam.	Campanulate to cylindrical, 3.6–3.7 cm high, 3.5 cm in diam.
Number of rings on cupule	7–8 rings	6–8 rings	10–13 rings
Margin of rings on cupule	Entire	Almost denticulate except basal 2 or 3 which are entire	Entire
Nut enclosure by cupule	Enclosing 1/5 of the nut	Enclosing 1/4 to 1/3 of the nut	Enclosing 2/3 of the nut
Nut shape and size	Ellipsoid to cylindrical-ellipsoid, 5–6 cm high, 2–2.3 cm in diam.	Ellipsoid to cylindrical-ellipsoid, 4–4.5 cm high, 2.1 cm in diam.	Ovoid to cylindrical-ellipsoid, 3–4.5 cm high, 2–3 cm in diam.
Base of the nut	Convex, 9–10 mm in diam.	Slightly convex, ca. 7 mm in diam.	Convex, ca. 12 mm in diam.

<sup>(1)</sup> From the material *Ford 623* (K)

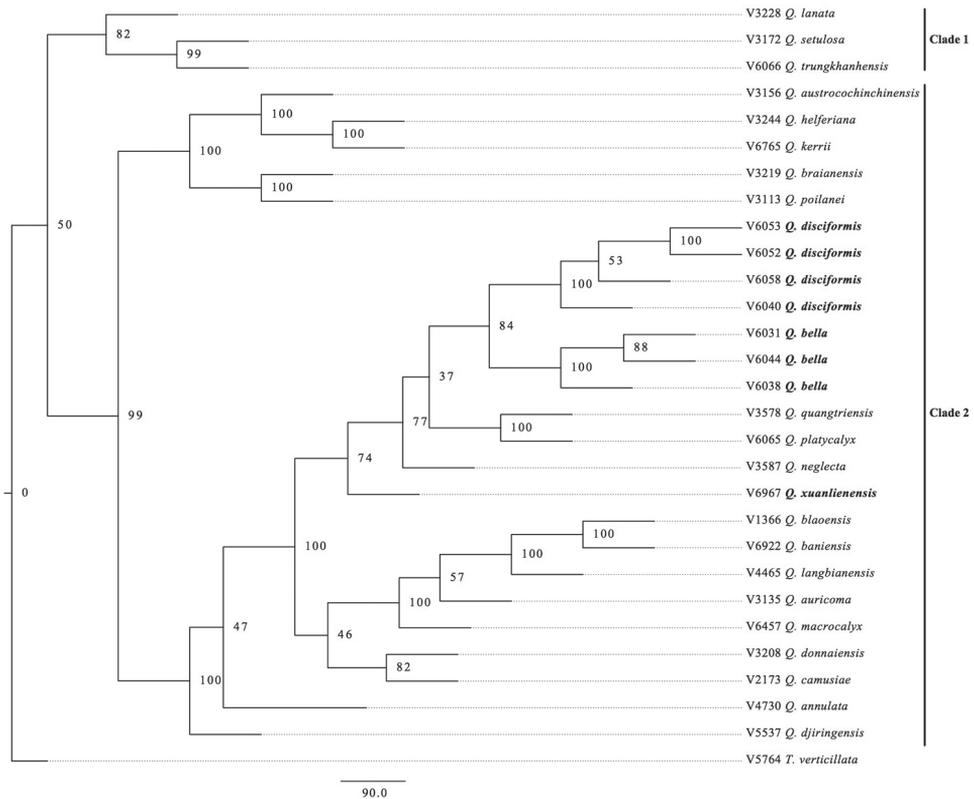
<sup>(2)</sup> From the original description in Hooker's *Icon. Pl.* 27: t. 2661 1901

<sup>(3)</sup> From the material *Fleury 37831* (P)

<sup>(4)</sup> From the original description in *Bull. Mus. Natl. Hist. Nat.* 29: 600 1923

<sup>(5)</sup> From the description in flora of China (Huang et al. 1999)

The two species are similar to *Q. platycalyx* and *Q. quangtriensis* in having oblong to oblong-elliptic leaves, usually serrate along leaf margins in the upper 1/2 to 2/3, glabrous on both surfaces when mature, and cupules covering less than 1/3 of the nut and oblate to ovoid nuts (Huang et al. 1999, Phengklai 2008, Ho 2003). The MIG-seq tree showed that those four species are related; the monophyly of a clade including



**Figure 2.** NJ tree of 28 samples of *Quercus* and one *Trigonobalanus* (outgroup) based on presence/absence data of 19,916 MIG-seq loci. Branches are labelled with bootstrap support (% of 1000 replicates).

the four species and *Q. neglecta* was supported by a 77% bootstrap value, although the support for the monophyly of the four species is weaker. The affinity of the four species and *Q. neglecta* was unexpected because *Q. neglecta* is an easily distinguished species having linear leaves and small nuts (Huang et al. 1999, Ho 2003).

The MIG-seq tree showed that *Q. xuanlienensis* is related to the above four species and *Q. neglecta* that is morphologically distinct from the other *Quercus* species. From the four species (*Q. disciformis*, *Q. bella*, *Q. quangtrienensis* and *Q. platycalyx*), *Q. xuanlienensis* is clearly distinguished by the leaf margin (leaf margin serrulate only at apical 1/5–1/7 in *Q. xuanlienensis* vs. serrate in upper 1/2 to 2/3 in the four species) and nut shape (ellipsoid to cylindrical-ellipsoid vs. oblate to ovoid). Thus, *Q. xuanlienensis* is separated as a distinct species from them.

Whereas *Q. edithiae* is morphologically most similar to *Q. xuanlienensis*, the type specimens of *Q. edithiae* collected from Hong Kong (type: Ford 623, K [K000832101, K000832102]) are morphologically distinct from *Q. xuanlienensis* in having distinct serrations, denticulate cupule bracts and smaller nuts and the description of *Q. edithiae* in Flora of China (Huang et al. 1999) agrees with the type specimen. The morphological differences between *Q. edithiae* and *Q. xuanlienensis* are as distinct as those

between related species of *Quercus* in Vietnam and its surrounding countries. Huang et al. (1999) recorded *Q. edithiae* in Guangdong, Guangxi, Hainan and Vietnam, but no specimen could be found of *Q. edithiae* collected from Vietnam in any herbarium in Vietnam or on the Chinese Virtual Herbarium website (<http://www.cvh.org.cn/>). Further studies are needed to confirm the occurrence of *Q. edithiae* itself in Vietnam.

The MIG-seq tree (Fig. 2) was very helpful in deriving the conclusions contained in this paper. As *Q. disciformis* and *Q. bella* are morphologically similar and were collected from the same locality, it was difficult to ascertain whether these are in fact two distinct species and not variants of a single species without the support of the MIG-seq data. Also, the separation of *Q. xuanlienensis* from the other species in Fig. 2 supported the conclusion that it is a new species. The authors also obtained sequences data of *rbcL* and *matK* but the informative content of those sequences was too low to resolve the relationships amongst such closely related species of *Quercus*. Difficulties were faced in determining the sequences of ITS for *Q. disciformis*, *Q. bella* and *Q. xuanlienensis*, most likely due to the low quality of the authors' samples. MIG-seq is applicable to low quality samples and provides finer resolution of the relationship amongst closely related species (Suyama and Matsuki 2015, Binh et al. in review). Further studies using MIG-seq would be fruitful to elucidate the diversity of *Quercus* in Vietnam, a centre of oak species richness in SE Asia.

## Taxonomic treatments

### *Quercus xuanlienensis* Binh, Ngoc & Bon, sp. nov.

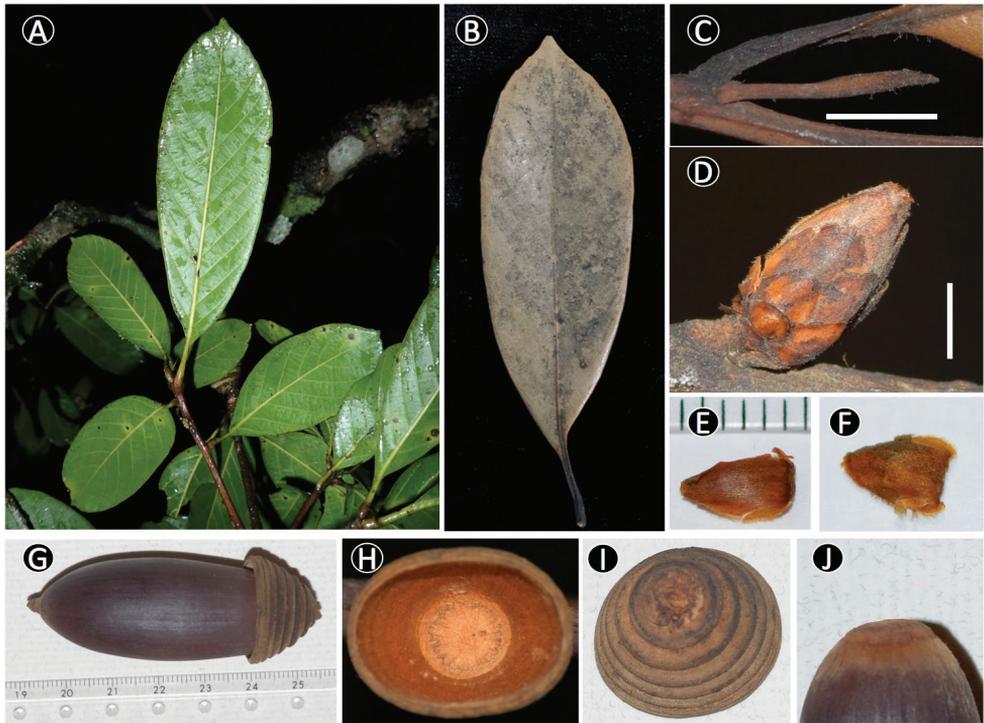
urn:lsid:ipni.org:names:77174819-1

Fig. 3

**Diagnosis.** *Quercus xuanlienensis* is morphologically similar to *Q. edithiae* of China and Vietnam in leaf size (7–15 × 3–5.8 cm), cuneate leaf base, petiole length (1.5–2.8 cm long), number of secondary veins (8–11 pairs), bowl-shaped cupule, ellipsoid to cylindrical-ellipsoid nut and basally convex nut but differs in leaf margin serrulate only at apical 1/5–1/7 (vs. serrate in the upper 2/3), entire bracts of cupule (vs. almost denticulate except basal 2 or 3 rings which is entire), cupule enclosing 1/5 of the nut (vs. enclosing 1/4–1/3 of the nut) and longer nut (5–6 cm long vs. 4–4.5 cm long).

**Type.** VIETNAM. Thanh Hoa Province, Thuong Xuan District, Xuan Lien Nature Reserve, in evergreen forest around waterfall, alt. 810 m, 19°52'46.7"N, 105°11'34.4"E, 6 Mar. 2017, *Binh HT, Ngoc NV, Bon TN V6967* (holotype KYO!; isotypes DLU!, FU!, P!, VNM!).

**Description.** Tree, ca. 18 m tall. Buds ellipsoid, ca. 9 mm long, ca. 4 mm in diam., scales imbricate, in 4–5 rows, ovate-triangular, ca. 3 × 2.5 mm, apex obtuse, margin ciliate, appressed whitish to yellowish brown hairy on both surfaces. Twigs glabrous when old, lenticellate. Stipules linear-lanceolate, 10–14 mm long, densely appressed hairy, glabrescent outside, glabrous inside. Leaves alternate; blade leathery, oblong-elliptic or obovate, (6–)8–11(–15) × 3–4.5(–5) cm, apex acuminate, acumen up to 0.6 cm long, base



**Figure 3.** *Quercus xuanlienensis* Binh, Ngoc & Bon. **A** Leafy twig **B** Adaxial side of mature leaf **C** Stipules **D** Bud **E, F** Inside and outside of bud scale **G** Mature fruit **H, I** Inside and outside of cupule **J** Basal scar of the nut. Scale bars: **C** 5 mm **D** 3 mm. Materials from *Binh et al.* V6967.

cuneate, margin recurved, serrulate in the upper 1/5–1/7, pale brown on the upper surface, yellowish brown to reddish brown on the lower surface when dry, glabrous on both surfaces; midribs ±flat on upper surface, prominent and distinct on lower surface, lateral veins 8–11 pairs, prominent on lower surface, at an angle of 40–45 degrees from midrib, straight and running into the margin, tertiary veins scalariform, indistinct on upper surface, prominent and distinct on lower surface; petioles 1–2 cm long, glabrous. Male and female inflorescences not seen. Infructescences axillary or terminal, erect, rachis 8–10 mm long, 4–5 mm in diam., glabrous, brownish red when fresh, blackish when dried. Fruits 6–6.5 cm high (including cupule), solitary or twin, sessile; cupules bowl-shaped, 1.3–1.7 cm high, 1.9–2.1 cm in diam., enclosing ca. 1/5 of the nut when mature, outside whitish to yellowish brown tomentose to glabrous, inside densely appressed yellowish brown hairy, wall ca. 1–2 mm thick, comprising of bracts, bracts arranged in 7–8 rings, margin of rings entire; nuts ellipsoid to cylindrical-ellipsoid, 5–6 cm high, 2–2.3 cm in diam., apex acute, densely appressed yellowish brown hairy around stylopodia, with stylopodia up to 4 mm long, basal scar 9–10 mm in diam., convex, to 3 mm high, glabrous.

**Distribution.** Vietnam. Thanh Hoa Province, Thuong Xuan District, Xuan Lien Nature Reserve.

**Ecology in Vietnam.** At present, only one individual was found in evergreen forest, at 810 m altitude.

**Etymology.** The specific epithet is derived from the district name of the type locality, Xuan Lien Nature Reserve, Thuong Xuan District, Thanh Hoa Province, North Central Coast of Vietnam.

**Phenology.** Fruiting specimens were collected in March.

**GenBank accession no.** Binh et al. V6967: LC331257 (*rbcL*), LC331254 (*matK*).

**Preliminary conservation status.** *Quercus xuanlienensis* is known for only one individual inside the protected area of Xuan Lien Nature Reserve. According to the criterion D of the IUCN Red List criteria (IUCN 2012), this species is qualified as Critically Endangered (CR).

***Quercus disciformis* Chun & Tsiang., J. Arnold Arbor. 28: 324 (1947)**

Fig. 4

*Cyclobalanopsis disciformis* (Chun & Tsiang) Y.C. Hsu & H.W. Jen, Acta Bot. Yunnan. 1: 148 (1979).

**Type.** CHINA. “Hsin-I Hsien, Ling-Tung Pao, Chung-Tung”, 3 Aug. 1931, C. Wang 31087 (holotype-IBK [catalogue no. IBK00081941, image!], isotype-IBSC [catalogue no. 0117316, image!]).

**Specimens examined in Vietnam.** Ha Noi, Ba Vi District, Ba Vi National Park, in evergreen forest: alt. 737 m, 21°04'33.88"N, 105°22'03"E, 12 Sept. 2016, Binh et al. V 6052, V6053, V6058 [fr.] (FU); alt. 1172 m, 21°03'34.1"N, 105°21'54.1"E, 11 Sep. 2016, Binh et al. V6040 [fr.] (FU).

**Distribution.** China (Guangdong, Guangxi, Guizhou, Hainan, Hunan) and Vietnam (Ba Vi National Park).

**Ecology in Vietnam.** In the field survey, only three individuals were found at an altitude of 737 m and one at 1172 m; in evergreen forest.

**Phenology.** Flowering from March to April, fruiting from August to September in China (Huang 1999). Fruiting in September in Vietnam.

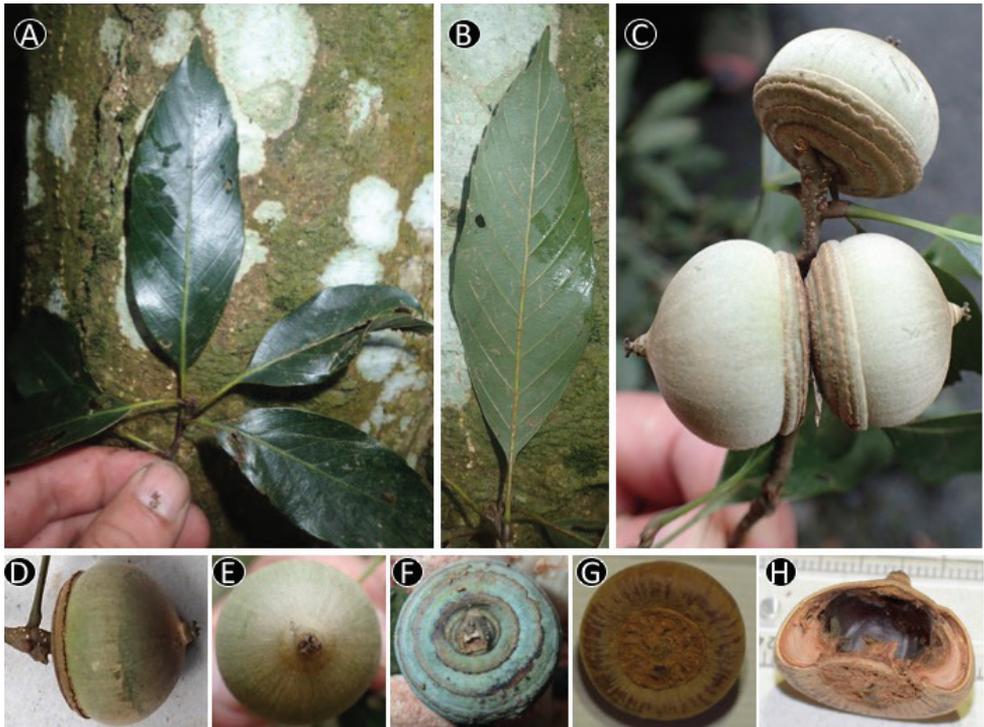
**GenBank accession no.** Binh et al. V6058: LC331258 (*rbcL*), LC331255 (*matK*).

**Preliminary conservation status.** *Quercus disciformis* is widely distributed from Guizhou to Guangdong and Hainan in China and not recorded as a threatened species in IUCN (2017). The Vietnamese population in Ba Vi National Park extends its distribution range, representing the south western limit. Given the situation, the population in Vietnam is locally important but the category Least Concern (LC) (IUCN 2012, Ban et al. 2007) would be appropriate for this species.

***Quercus bella* Chun & Tsiang., J. Arnold Arbor. 28: 326 (1947)**

Fig. 5

*Cyclobalanopsis bella* (Chun & Tsiang) Chun ex Y.C. Hsu & H.W. Jen., J. Beijing Forest. Univ. 15(4): 45 (1993).



**Figure 4.** Image of *Quercus disciformis* Chun & Tsiang. from Binh et al. V6058 (FU) **A** Leafy twig **B** Abaxial side of mature leaf **C–D** Infructescence and mature fruit **E** Nut **F** Cupule **G** Bottom of nut **H** Vertical section of nut.

**Type.** CHINA. “Fang-Cheng Hsien, Shi-Wan-Ta Shan”, alt. 200–250 m, in sparsely wooded ravine along stream on moist sites, 24 Mar. 1944, *S.H. Chun* 4772 (IBSC [catalogue no. 0039624, image!]).

**Specimens examined in Vietnam.** Ha Noi, Ba Vi District, Ba Vi National Park, in evergreen forest: alt. 600 m, 21°04'40.6"N, 105°22'17.2"E, 11 Sep. 2016, *Binh et al.* V 6044, V6038 [fr.] (FU); alt. 703m, 21°04'59.6"N, 105°22'03.6"E, 21 Sep. 2017, *Yahara et. al.* V6981 [fr.] (DLU, FU); alt. 1023 m, 21°03'33.7"N, 105°21'39.4"E, 11 Sep. 2016, *Binh et al.* V6031 [fr.] (FU).

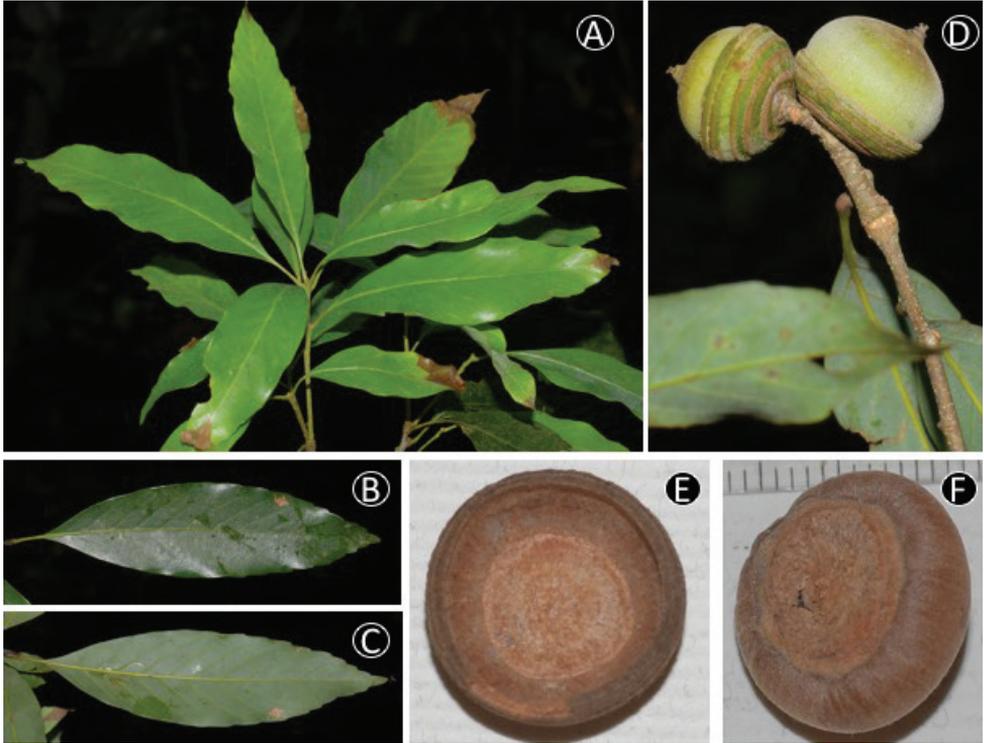
**Distribution.** China (Guangdong, Guangxi, Hainan) and Vietnam (Ba Vi National Park, Fig. 1).

**Ecology in Vietnam.** *Quercus bella* was found on the slopes in evergreen forests in Ba Vi National Park: at alt. 600–1172 m.

**Phenology.** Flowering from February to April, fruiting from October to December (Huang et al. 1999). Flowering and fruiting specimens were collected from Vietnam in September.

**GenBank accession no.** *Binh et al.* V6038: LC331259 (*rbcL*), LC331256 (*matK*).

**Preliminary conservation status.** *Quercus bella* was only previously known as an endemic species to China and distributed in Guangdong, Guangxi and Hainan. The



**Figure 5.** Image of *Quercus bella* Chun & Tsiang. **A** Leafy twig **B** Adaxial side of mature leaf **C** Abaxial side of mature leaf **D** Infructescence and mature fruit (**A–D** from *Yahara et al. V6981* (DLU, FU)) **E** Inside of cupule **F** Bottom of nut (**E–F** from *Binh et al. V6038* (FU))

species is not recorded as a threatened species in IUCN (2017). Although only three fruiting individuals of *Q. bella* were collected in Ba Vi National Park, more individuals are expected to occur there and the habitat in the Ba Vi National Park is currently well-protected from anthropogenic activities under the law. Thus, it is appropriate to place this species under the category Least Concern (LC) following IUCN Red List (IUCN 2012) and Vietnam Red Data book (Ban et al. 2007).

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## References

- Ba Vi National Park (2008) Plants of Ba Vi National Park. <http://vuonquocgiabavi.com.vn/he-thuc-vat-vqg-ba-vi> [In Vietnamese; Accessed 20 September, 2017]
- Ban NT (2005) Vietnam plant checklist, Vol. 2. Agriculture Publishers, Hanoi National University. [In Vietnamese]
- Ban NT, Ly DT, Tap N, Dung VV, Thin NN, Tien VN, Khoi KN (2007) Vietnam Red Data Book Part II. Plants. Natural Sciences and Technology Publishers, Hanoi. [In Vietnamese]
- Binh HT, Ngoc NV, Tai VA, Son HT, Tagane S, Yahara T (in press) *Quercus trungkhanhensis* (Fagaceae), a new species from Cao Vit Gibbon Conservation Area, Cao Bang Province, north-eastern Vietnam. *Acta Phytotaxonomica et Geobotanica*.
- Binh HT, Ngoc NV, Tagane S, Toyama H, Mase K, Mitsuyuki C, Strijk JS, Suyama Y, Yahara T (in review) A taxonomic study of *Quercus langbianensis* complex based on morphology, and DNA barcodes of classic and next generation sequences. *Phyto Keys*.
- Camus A (1936–1954) Les Chênes. Monographie du genre *Quercus* et Monographie du genre *Lithocarpus*. Paul Lechevalier Edition, Paris.
- Cavender-Bares J, González-Rodríguez A, Eaton DA, Hipp AA, Beulke A, Manos PS (2015) Phylogeny and biogeography of the American live oaks (*Quercus* subsection *Virentes*): a genomic and population genetics approach. *Molecular Ecology* 24(14): 3668–3687. <https://doi.org/10.1111/mec.13269>
- Dick CW, Webb CO (2012) Plant DNA barcodes, taxonomic management, and species discovery in tropical forests. In: Kress WJ, Erickson DL (Eds) *DNA Barcodes. Methods and Protocols* 858: 379–393. [https://doi.org/10.1007/978-1-61779-591-6\\_18](https://doi.org/10.1007/978-1-61779-591-6_18)
- Doyle JJ, Doyle JL (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.
- Dunning LT, Savolainen V (2010) Broad-scale amplification of *matK* for DNA barcoding plants, a technical note. *Botanical Journal of the Linnean Society* 164(1): 1–9. <https://doi.org/10.1111/j.1095-8339.2010.01071.x>
- Fitz-Gibbon S, Hipp AL, Pham KK, Manos PS, Sork VL (2017) Phylogenomic inferences from reference-mapped and de novo assembled short-read sequence data using RADseq sequencing of California white oaks (*Quercus* section *Quercus*). *Genome* 60(9): 743–755. <https://doi.org/10.1139/gen-2016-0202>
- Hebert PDN, Gregory TR (2005) The promise of DNA barcoding for taxonomy. *Systematic Biology* 54: 852–859. <https://doi.org/10.1080/10635150500354886>
- Ho PH (2003) An Illustrated Flora of Vietnam, Vol. 2. Young Publishers, Ho Chi Minh City. [In Vietnamese]
- Huang CJ, Zhang YT, Bartholomew B (1999) Fagaceae. In: Zhengyi W, Raven PH, Deyuan H (Eds) *Flora of China*. Volume 4, 333–369. [<http://www.eoras.org>]
- Hubert F, Grimm GW, Joussetin E, Berry V, Franc A, Kremer A (2014) Multiple nuclear genes stabilize the phylogenetic backbone of the genus *Quercus*. *Systematics and Biodiversity* 12(4): 405–423. <http://dx.doi.org/10.1080/14772000.2014.941037>
- IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1. Second edition. Gland, Switzerland and Cambridge, UK. [http://jr.iucnredlist.org/documents/redlist\\_cats\\_crit\\_en.pdf](http://jr.iucnredlist.org/documents/redlist_cats_crit_en.pdf) [accessed 10 December 2017]

- IUCN (2017) The IUCN Red List of Threatened Species. Version 2017-2. <http://www.iucnredlist.org> [Downloaded on 10 December 2017]
- Kress WJ, Erickson DL, Jones FA, Swenson NG, Perez R, Sanjur O, Bermingham E (2009) Plant DNA barcodes and a community phylogeny of a tropical forest dynamics plot in Panama. *Proceedings of the National Academy of Sciences of the United States of America* 106(44): 18621–18626. <https://doi.org/10.1073/pnas.0909820106>
- Li Q, Zhang J, Coombes A (2016) *Quercus lineata* (Fagaceae): new distribution records from China and Vietnam and its leaf anatomical features. *Phytotaxa* 266(3): 226–230. <https://doi.org/10.11646/21580>
- Linnaeus C (1753) *Species Plantarum*, 2. Stockholm.
- Manos PS, Doyle JJ, Nixon KC (1999) Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). *Molecular phylogenetics and evolution* 12(3): 333–349. <https://doi.org/10.1006/mpev.1999.0614>
- Nixon KC (1993) Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names. *Annales des Sciences Forestières* 50: 25s–34s. <https://doi.org/10.1051/forest:19930701>
- Phengkai C (2008) Fagaceae. *Flora of Thailand* 9(3): 179–410.
- Shimada MK, Nishida T (2017) A modification of the PHYLIP program: A solution for the redundant cluster problem, and an implementation of an automatic bootstrapping on trees inferred from original data. *Molecular Phylogenetics and Evolution* 109: 409–414. <https://doi.org/10.1016/j.ympev.2017.02.012>
- Simeone MC, Grimm GW, Papini A, Vessella F, Cardoni S, Tordoni E, Piredda R, Franc A, Denk T (2016) Plastome data reveal multiple geographic origins of *Quercus* Group *Ilex*. *PeerJ* 4: e1897. <https://doi.org/10.7717/peerj.1897> [eCollection 2016]
- Soepadmo E (1972) Fagaceae. *Flora Malesiana Series I, Volume 7(2)*. Noordho-Kol N.V., Djakarta, 265–403.
- Suyama Y, Matsuki Y (2015) MIG-seq: an effective PCR-based method for genome-wide single-nucleotide polymorphism genotyping using the next-generation sequencing platform. *Scientific Reports* 5: 16963. <https://doi.org/10.1038/srep16963>
- Toyama H, Tagane S, Chhang P, Nagamasu H, Yahara T (2016) Flora of Bokor National Park, Cambodia IV: A New Section and Species of *Euphorbia* Subgenus *Euphorbia*. *Acta Phytotaxonomica et Geobotanica* 67(2): 83–96.
- Valencia-A S, Rosales JLS, Arellano OJS (2016) A new species of *Quercus*, section *Lobatae* (Fagaceae) from the Sierra Madre Oriental, Mexico. *Phytotaxa* 269(2): 120–126. <http://dx.doi.org/10.11646/phytotaxa.269.2.5>
- Xuan Lien Nature Reserve (2017 onwards) Diversity of plants of Xuan Lien Nature Reserve. [http://xuanlien.org.vn/default.aspx?c=home&cl=vi&nid=Da\\_dang\\_loai\\_va\\_khu\\_he\\_thuc\\_vat&gid=120](http://xuanlien.org.vn/default.aspx?c=home&cl=vi&nid=Da_dang_loai_va_khu_he_thuc_vat&gid=120) [In Vietnamese; Accessed September 15, 2017]



# The taxonomic identity of three varieties of *Lecanorchis nigricans* (Vanilleae, Vanilloideae, Orchidaceae) in Japan

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## Abstract

To elucidate the taxonomy of the *Lecanorchis nigricans* Honda, 1931 species complex, the present study investigated the detailed morphology of three *L. nigricans* varieties in Japan. While *L. nigricans* var. *patipetala* Y.Sawa, 1980 and *L. nigricans* var. *yakusimensis* T.Hashim., 1990 have often been treated as synonyms of *L. nigricans* var. *nigricans*, the present study demonstrates that the three varieties are morphologically distinct. More specifically, *L. nigricans* var. *nigricans* only produces complete cleistogamous flowers and is distinct from the plants currently called “*L. nigricans*”, which are identical to the chasmogamous variety *L. nigricans* var. *patipetala*. The other chasmogamous variety *L. nigricans* var. *yakusimensis* can be easily distinguished from *L. nigricans* var. *patipetala* by its more spatulate tepals and higher cucullate lip. Therefore, the present study provides emended description of the three *L. nigricans* varieties based on type specimens and specimens collected from type localities. In addition, the isotype specimen of *L. nigricans* var. *patipetala* is designated as the lectotype because the holotype has been lost.

## Keywords

Japan, *Lecanorchis nigricans* var. *yakusimensis*, *Lecanorchis nigricans* var. *patipetala*, *Lecanorchis taiwaniana*, lectotypification, mycoheterotrophy, taxonomy

## Introduction

The genus *Lecanorchis* Blume, 1856 (Vanilleae, Vanilloideae, Orchidaceae) is a group of mycoheterotrophic plants that includes ca. thirty species and/or varieties (Hashimoto 1990; Szlachetko and Mytnik 2000; Govaerts et al. 2016; Suetsugu and Fukunaga 2016). Members of the genus are characterised by the presence of a calyculus, a cup-like structure located between the base of the perianth and the apex of the ovary (Hashimoto 1990) and are distributed across Southeast Asia, including India, Thailand, Laos, Vietnam, Malaysia, China, Taiwan, Japan, the Philippines, Indonesia, New Guinea and the Pacific Islands (Hashimoto 1990; Szlachetko and Mytnik 2000; Averyanov 2011).

Precise identification of *Lecanorchis* taxa is often hindered by the similar morphology and brief flowering periods (Hashimoto 1990; Averyanov 2005; Suddee and Pedersen 2011; Tsukaya and Okada 2013; Suetsugu and Fukunaga 2016; Suetsugu et al. 2016). In addition, important diagnostic characters are often lacking in herbarium specimens because the flowers of *Lecanorchis* members are easily dropped during preservation and the important diagnostic characters of some species have yet to be described in detail, especially for species that were first described many decades ago (reviewed by Suetsugu et al. 2016, 2017a, b). Therefore, adequate taxonomic studies of the genus have yet to be conducted (reviewed by Suetsugu et al. 2016, 2017a, b).

The taxonomic identity of *L. nigricans* Honda, 1931 has remained particularly unclear. The species was first described from Wakayama Prefecture (Kinki District, Japan; Honda 1931) and was subsequently reported from Taiwan, China, Thailand and Vietnam (Su 2000; Chen et al. 2009; Suddee et al. 2010; Hsu and Chung 2010; Vuong and Sridith 2016). Even though three *L. nigricans* varieties were described from Japan (Honda 1931; Sawa 1980; Hashimoto 1990), Yokota et al. (2016) defined the species in a broad sense, thereby synonymising *L. nigricans* var. *patipetala* Y. Sawa, 1980 and *L. nigricans* var. *yakusimensis* T. Hashim., 1990 as *L. nigricans* var. *nigricans*. However, it is possible that these treatments are based on the ambiguity of the original species description (Honda 1931; Sawa 1980; Hashimoto 1990) and that the species complex, in fact, comprises three entities.

To elucidate the taxonomy of the *L. nigricans* species complex, the present study investigated the detailed morphology of type specimens and specimens collected from type localities of three *L. nigricans* varieties in Japan. These findings revealed that the three varieties were morphologically distinct. More specifically, *L. nigricans* var. *nigricans* produces only complete cleistogamous flowers and is distinct from *L. nigricans* var. *nigricans sensu* Hashimoto 1990; Hashimoto et al. 1991; Nakajima and Ohba 2012; Yokota et al. 2016 (hereafter, the plants currently called “*L. nigricans*”), which is identical to the chasmogamous variety *L. nigricans* var. *patipetala* that was originally described from Kochi Prefecture (Shikoku District, Japan; Sawa 1980). In addition, the other chasmogamous variety *L. nigricans* var. *yakusimensis*, from Yakushima Island (Ryukyu Islands, Kagoshima Prefecture, Japan; Hashimoto 1990) can be distinguished from *L. nigricans* var. *patipetala* by its more spatulate tepals and higher cucullate lip. Therefore, the present study provides emended description of the three *L. nigricans* varieties based on type specimens and specimens collected from type localities.

## Materials and methods

### Morphological observation

In order to compare the morphologies of the three *Lecanorchis nigricans* varieties with previously recorded species, the authors reviewed the literature, conducted field sampling throughout Japan and examined both digitised plant specimens from online databases such as JSTOR Global Plants (<http://plants.jstor.org/>) and Plants of Taiwan (<http://tai2.ntu.edu.tw/specimeninfo.php>) and specimens from the following herbaria: TI, TNS, KYO, KPM, OSA, MBK, KOCH and KAG. Herbarium abbreviations follow Index Herbariorum (Thiers 2017, <http://sweetgum.nybg.org/science/ih/>). In total, at least 30 flowers were examined from 10 flowering plants to understand the morphological variations for each variety.

### DNA barcoding

For DNA isolation, the flowers of *L. nigricans* var. *nigricans*, *L. nigricans* var. *patipetala*, *L. nigricans* var. *yakusimensis* and their closely-related species *L. taiwaniana* S.S.Ying 1987 emend. Suetsugu, T.C. Hsu, S. Sawa, & Fukunaga 2016 were collected and desiccated in the field using silica gel (Table 1). DNA was extracted from these silica-dried plant materials, using the CTAB method (Wu et al. 2001). The rDNA internal transcribed spacer (ITS) region was amplified from the extracted DNA samples in 10 µL PCR mixtures that contained 2 µL extracted DNA, 0.05 µL TaKaRa Ex Taq Hot Start Version (Takara Bio, Japan), 10 µM of each primer (AB101 and AB102; Douzery et al. 1993), 0.25 µM of each dNTP and 1 µL 10× buffer, using an iCycler (BioRad, Japan) and the following conditions: initial denaturation at 94 °C for 5 min; followed by 30 cycles of 94 °C for 30 s, 55 °C for 30 s, and 72 °C for 1 min; followed by a final elongation at 72 °C for 7 min. The amplified PCR products were purified using EconoSpin (Gene Design, Inc.) columns and the subsequent samples were sent for sequencing to Eurofins Genomics (Ebersberg, Germany). The primers used for amplification were also used for sequencing.

**Table 1.** *Lecanorchis* spp. included in the current molecular analysis.

Taxon	Location	Collection date	Collection number	GenBank numbers
<i>L. nigricans</i> var. <i>nigricans</i>	Wakayama Pref., Kamitonda Town, Oka	20150819	H. Fukunaga s.n. OSA290835	LC315676
<i>L. nigricans</i> var. <i>patipetala</i>	Kochi Pref., Kochi City, Haruno	20150726	H. Fukunaga s.n. OSA290833	LC315674
<i>L. nigricans</i> var. <i>yakusimensis</i>	Kagoshima Pref., Yakushima Island, along Hanaage River	20150717	H. Yamashita s.n. OSA290834	LC315675
<i>L. taiwaniana</i>	Kochi Pref., Muroto City, Muroto Cape	20160816	H. Fukunaga s.n. OSA290836	LC315677

## Results and discussion

Even though Honda's original description of *Lecanorchis nigricans* was insufficient in that most diagnostic characteristics were overlooked, he noted that neither the species' sepals nor petals were open and that they, instead, were united, forming a cylindrical perianth tube (Honda 1931). This is quite different from the characteristics of the plants currently called "*L. nigricans*", whose flowers are widely open (Hashimoto 1990; Hashimoto et al. 1991; Nakajima and Ohba 2012; Yokota et al. 2016). Indeed, the analysis of type specimens and specimens collected from type localities revealed that the flowers of *L. nigricans* var. *nigricans* remain completely closed throughout their flowering period (Table 2; Figs 1–3; [https://www.youtube.com/watch?v=Y0SBE\\_J7bxo](https://www.youtube.com/watch?v=Y0SBE_J7bxo)). The cleistogamous variety of *L. nigricans* was only distributed in limited areas of Wakayama (type locality), Miyazaki, Kochi, Tokushima and Tokyo (Hachijo Islands). Therefore, the same name should not be used for both the plants currently called "*L. nigricans*", whose flowers are widely open and which is much more common throughout Japan (Hashimoto 1990; Hashimoto et al. 1991; Nakajima and Ohba 2012; Yokota et al. 2016). The chasmogamous variety of *L. nigricans* was initially described by Sawa (1980) as *L. nigricans* var. *patipetala*. It was found that there are no clear morphological differences amongst the plants currently called "*L. nigricans*", *L. nigricans* var. *patipetala* lectotype specimens and *L. nigricans* var. *patipetala* type locality specimens (Table 2; Figs 4–5). Therefore, the name *L. nigricans* var. *patipetala* should be used for the common chasmogamous variety of *L. nigricans* that is found throughout Japan, with the exception of the Ryukyu Islands.

Detailed morphological investigation revealed that *L. nigricans* var. *patipetala* could also be distinguished from *L. nigricans* var. *nigricans* by its larger perianth tube (14–17 mm vs. 11–14 mm), the shorter coloured area of its lip (ca. apical 1/3–1/5 vs. ca. apical 1/2–1/3), the shape of its lip apex in the natural situation (broadly rounded vs. acute), the status of lip hairs near apex (scarce, long and rarely branched multicellular hairs vs. dense, short and frequently branched multicellular hairs), the shape of the column (recurved vs. slightly recurved), the width of its petal base (narrow ca. 1.0–1.3 mm vs. relatively wide ca. 1.5–2.5 mm) and the shape of its anther cap (strongly bilobed vs. slightly bilobed; Table 2; Figs 1–5).

In addition, the other chasmogamous variety *L. nigricans* var. *yakusimensis* was described from Yakushima Island (Ryukyu Islands, Japan). However, even though pubescence at the ventral side of the column was highlighted as the variety's diagnostic character (Hashimoto 1990; Hashimoto et al. 1991), the column of *L. nigricans* var. *patipetala* also varies from glabrous to slightly hairy. Nonetheless, the column of *L. nigricans* var. *patipetala* is less hairy than that of *L. nigricans* var. *yakusimensis*. In addition, *L. nigricans* var. *yakusimensis* possesses more spatulate sepals and petals, as well as more highly cucullate lips, whereas *L. nigricans* var. *patipetala* possesses more oblong sepals and less cucullate lips. Furthermore, *L. nigricans* var. *yakusimensis* can be distinguished from *L. nigricans* var. *patipetala* by its wider anther caps (ca. 2.0 mm. vs. ca. 1.5 mm) and more recurved column. Thus, *L. nigricans* var. *yakusimensis* can

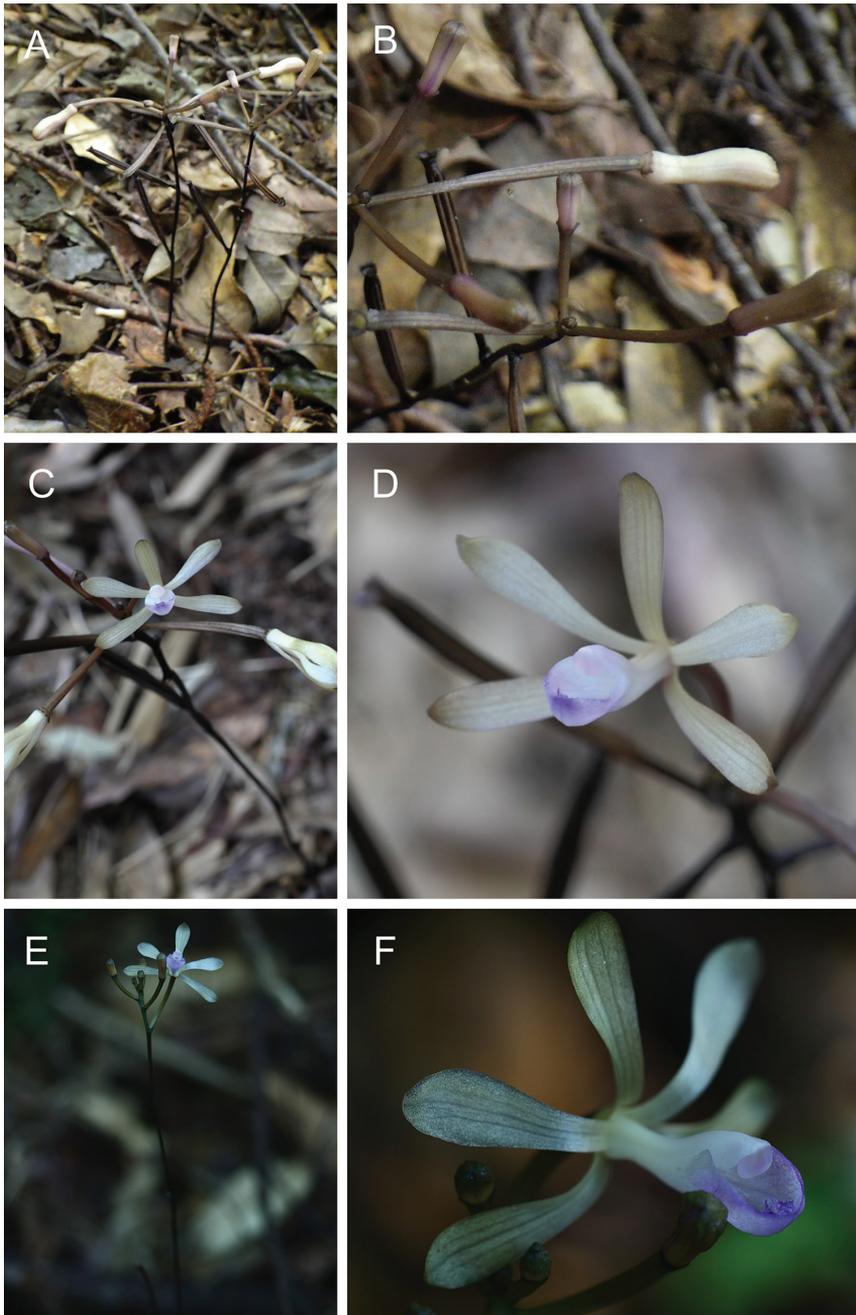
**Table 2.** Morphological characters of the three varieties of *Lecanorchis nigricans* and the morphologically similar *L. taiwaniana* and *L. tabugawaensis*.

Characters	<i>L. nigricans</i> var. <i>nigricans</i>	<i>L. nigricans</i> var. <i>patipetala</i>	<i>L. nigricans</i> var. <i>yakusimensis</i>	<i>L. tabugawaensis</i>	<i>L. taiwaniana</i>
Plant height	10–25(–30) cm	10–25(–30) cm	10–25(–30) cm	15–45 cm	15–45 cm
Rachis color in developing stage	purplish white	purplish white	purplish white	yellowish white	yellowish white
Rachis color in fruiting stage	black	black	black	brownish black	brownish black
Rachis length	2–8 cm	2–8 cm	2–8 cm	6–15 cm	(2–)6–15 cm
Internode length of upper half of rachis	1–3 mm	1–6(–10) mm	1–6(–10) mm	5–15 mm	5–15 mm
Floral condition	cleistogamous	chasmogamous	chasmogamous	chasmogamous	chasmogamous
Sepal and petal color	purplish white	purplish white	purplish white	yellowish white tinged with light purple	yellowish white tinged with light purple
Width of sepal and lateral petal	2.8–3.7 mm	3.0–3.8 mm	3.3–4.0 mm	2.0–2.5 mm	2.0–2.5(–3.0) mm
Shape of sepal and lateral petal	oblong-oblan- ceolate	oblong-oblan- ceolate	oblanceolate- spatulate	oblong	oblong
Lip shape	indistinctly 3-lobed	almost entire	almost entire and cucullate	almost entire	indistinctly 3-lobed
Colored area in lip	ca. apical 1/3–1/2	ca. apical 1/3–1/5	ca. apical 1/3	ca. apical more than 2/3	ca. apical 1/4–1/5
Proportion of the column fusion with lip	ca. 1/2	ca. 1/2	ca. 1/2	2/5–1/2	3/5–2/3
Column shape	slightly recurved	recurved	strongly recurved	straight	recurved
Apical part of the adaxial lip surface	dense, short and frequently branched hairs	scarce, long and rarely branched hairs	scarce, long and rarely branched hairs	glabrous	scarce, long and rarely branched hairs
Pubescence at basal part of column	glabrous	glabrous to slightly hairy	densely hairy	glabrous	densely hairy
Capsule color	black	black	black	bright brown	bright brown
Angle between capsule and inflorescence axis	70–90°	70–90°	70–90°	20–45°	20–45°

Data of the related species from Suetsugu et al. (2016) and Suetsugu and Fukunaga (2016)

be distinguished not only by its more hairy column, but also its tepals, lip, anther cap and column shape (Table 2; Figs 4–7).

As *L. nigricans* var. *yakusimensis* is more common than *L. nigricans* var. *patipetala* in both Yakushima and Taiwan (Suetsugu and Hsu, unpublished data), it is likely that the variety is also distributed on the other Ryukyu Islands. Thus, *L. oligotricha* Fukuy. 1942 that has been described from Iriomote Island (Ryukyu Islands), may actually be identical to *L. nigricans* var. *yakusimensis*, while *L. oligotricha* has been considered as a synonym of *L. nigricans* var. *nigricans*. Even so, the name *L. nigricans* var. *yakusimensis*



**Figure 1.** Photographs of three varieties of *Lecanorchis nigricans* in their natural habitats. **A** Flowering plant and **B** cleistogamous flowers of *Lecanorchis nigricans* var. *nigricans* in Oka, Kamitonda, Wakayama, Japan (its type locality). Photographed by Hirokazu Fukunaga **C** Flowering plant and **D** a flower of *Lecanorchis nigricans* var. *patipetala* in Haruno, Kochi, Japan. Photographed by Hisanori Takeuchi **E** Flowering plant and **F** a flower of *Lecanorchis nigricans* var. *yakusimensis* collected in Hanaage River, Yakushima, Japan (its type locality). Photographed by Hiroaki Yamashita.

is preferred because the taxon should be recognised as an intraspecific variety, instead of an independent species. In addition, it should be noted that some *L. nigricans* specimens from the Ryukyu Islands were misidentifications of *L. taiwaniana*. However, it is unlikely that *L. oligotricha* is synonymous with *L. taiwaniana*, owing to differences in sepal and petal shape, according to the protologue (Fukuyama 1942). Unfortunately, the type materials of *L. oligotricha* in KPM are poorly preserved and no mature flowers are available for dissection (Inoue et al. 1998). Therefore, further investigation of *L. oligotricha* specimens from the species' type locality will be critical to clarifying the species' taxonomic status.

Based on the findings of the present study, it is suggested that the two varieties *L. nigricans* var. *yakusimensis* and *L. nigricans* var. *patipetala* should be revived since the distinct morphological characteristics of the three varieties are clear and stable. It is also considered that the aforementioned differences amongst the three varieties are relatively minor and represent interspecific variation. The identical DNA barcode sequences of *L. nigricans*, *L. nigricans* var. *patipetala* and *L. nigricans* var. *yakusimensis* also support this conclusion, whereas the sequence divergence of the three *L. nigricans* varieties and *L. taiwaniana* (i.e. 5 substitutions) support the independent specific status of both *L. nigricans* and *L. taiwaniana*, even though the two are sometimes considered synonymous (e.g. Su 2000). Actually, *L. taiwaniana* and its closely-related species *L. tabugawaensis* Suetsugu & Fukunaga 2016 can easily be distinguished from the three varieties of *L. nigricans* by having taller inflorescences, longer and lighter coloured rachis, yellowish-white, narrower sepals and petals and brighter brown suberect capsules (Suetsugu and Fukunaga 2016; Suetsugu et al. 2016).

In addition, *L. nigricans* has recently been reported from China, Thailand and Vietnam (Su 2000; Chen et al. 2009; Suddee et al. 2010; Vuong and Sridith 2016). Vuong and Sridith (2016) noted that the specimens collected from Vietnam possessed character traits that were intermediates of those of *L. nigricans* and *L. taiwaniana*. The various morphological character of *L. nigricans* other than from Japan would actually imply that more than one taxon was placed under the name *L. nigricans* and that further clarification may be needed in these regions.

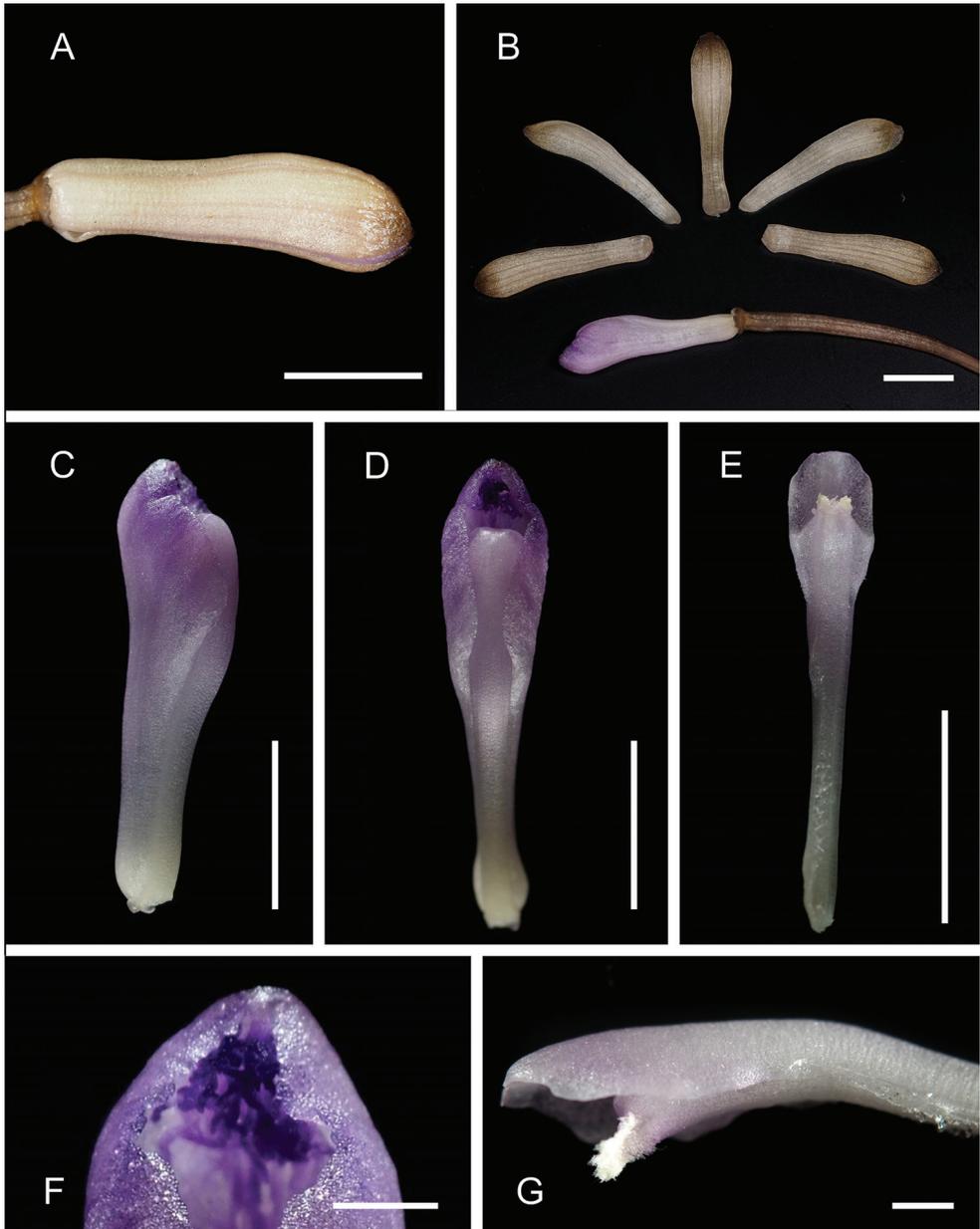
## Taxonomic treatment

### *Lecanorchis nigricans* Honda emend. Suetsugu & Fukunaga

Figs 2–3

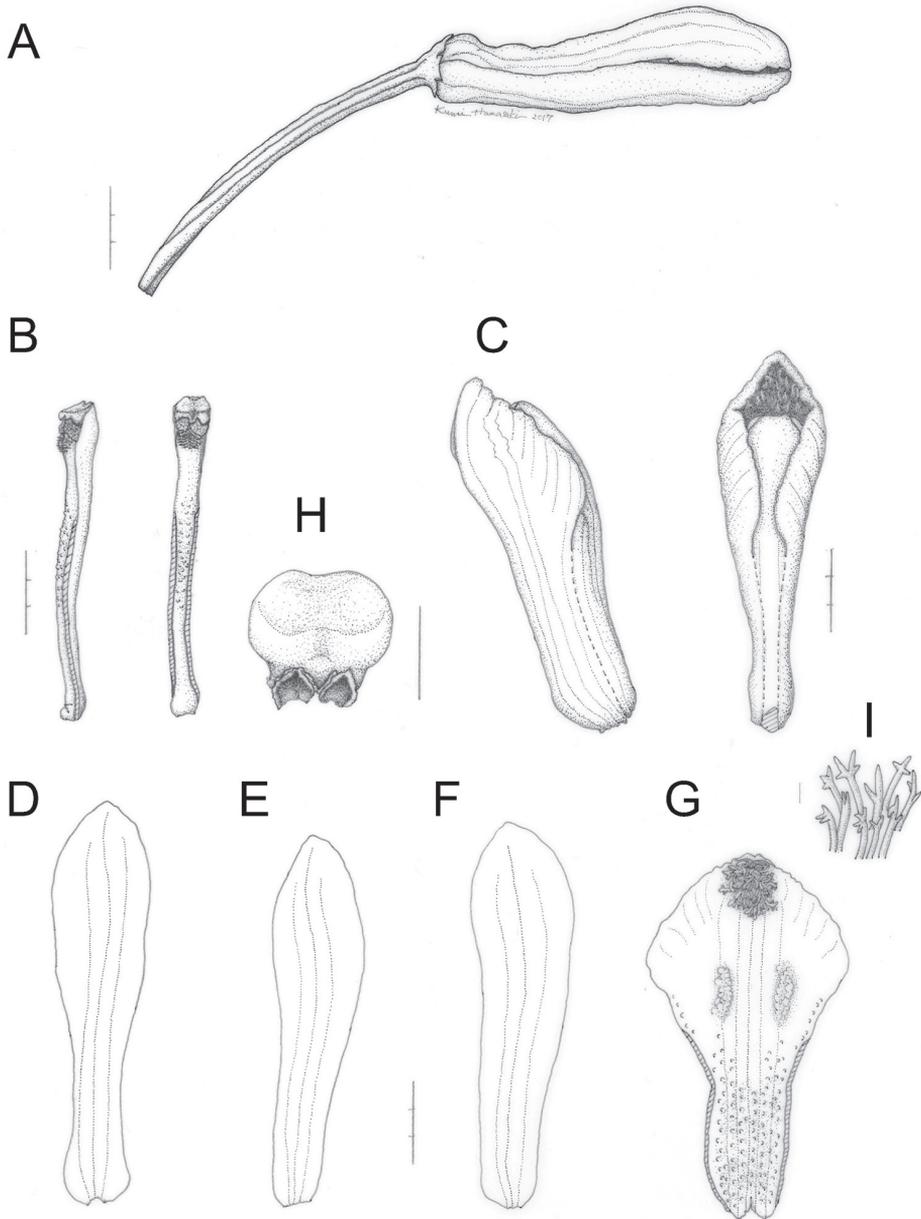
**Type.** JAPAN, Wakayama Pref., Nishimuro County, Iwata, Oka, date unknown 1931, *K. Kashiyama s.n.* (holotype TII!; Isotype TII!).

**Emended description.** Terrestrial, mycoheterotrophic herb. Inflorescence 10–25(–30) cm tall, solitary or branched at lower-half, white at flowering, black at fruiting, glabrous, ca. 0.8–2.0 mm in diam., with scale-like sheaths. Rhizome erect, J-shaped or complex, ligineous. Roots simple, radiate numerous, horizontally or down-



**Figure 2.** Dissected flowers of *Lecanorchis nigricans* var. *nigricans* collected in Konda, Kochi, Japan on 26 July 2015 (OSA). **A** Flower and pedicellate ovary **B** Dissected flower **C–D** Lip and column **E** Column **F** Hairs at anterior disc of lip **G** Glabrous status at the ventral side of the column. Scale bars: **A–E** 5 mm **F–G** 1 mm. Photographed by Takuto Shitara.

ward elongate to 20–30 cm long, yellowish brown. Rachis 2–8 cm, 3–15 flowered, internode length of upper-half of rachis, 1–3 mm. Floral bracts triangular, acute, 1.0–2.0 mm long. Pedicellate ovary ascending, 15–25 mm long. Flowers enclosed



**Figure 3.** *Lecanorchis nigricans* var. *nigricans* collected in type locality on 3 August 2016 (OSA). **A** Flower and pedicellate ovary **B** Column **C** Lip and column **D** Dorsal sepal **E** Lateral petal **F** Lateral sepal **G** Flattened lip **H** Anther cap **I** Hairs at anterior disc of lip. Scale bars: **A–G** 3 mm **H** 1 mm **I** 0.1 mm. Line drawings by Kumi Hamasaki.

or never opening. Sepals purplish white, linear, oblong-oblancoate, ca. 11–14 mm long, 3.0–3.7 mm wide, apex obtuse. Petals purplish white, linear, oblong-oblancoate, 13–14 mm long, 2.8–3.6 mm wide, apex obtuse. Lip spatulate, strongly 12–14

mm long, 3.2–3.9 mm wide in a natural situation, ca. 6.5–7.5 mm wide when flattened, disc with rather dense, short multicellular hairs which are often branched, near apex, or acute at apex in a natural situation. Column 10–12 mm long, 1.1–2.0 mm wide slightly recurved, fused with lip about 1/2 its length, ventrally glabrous or slightly puberulent; anther purplish white, ca. 1.5 mm wide. Capsule 17–30 mm long, cylindrical-fusiform, black, ascending at 70–90 degree angle from the axis. Flowering in late-June to mid-September.

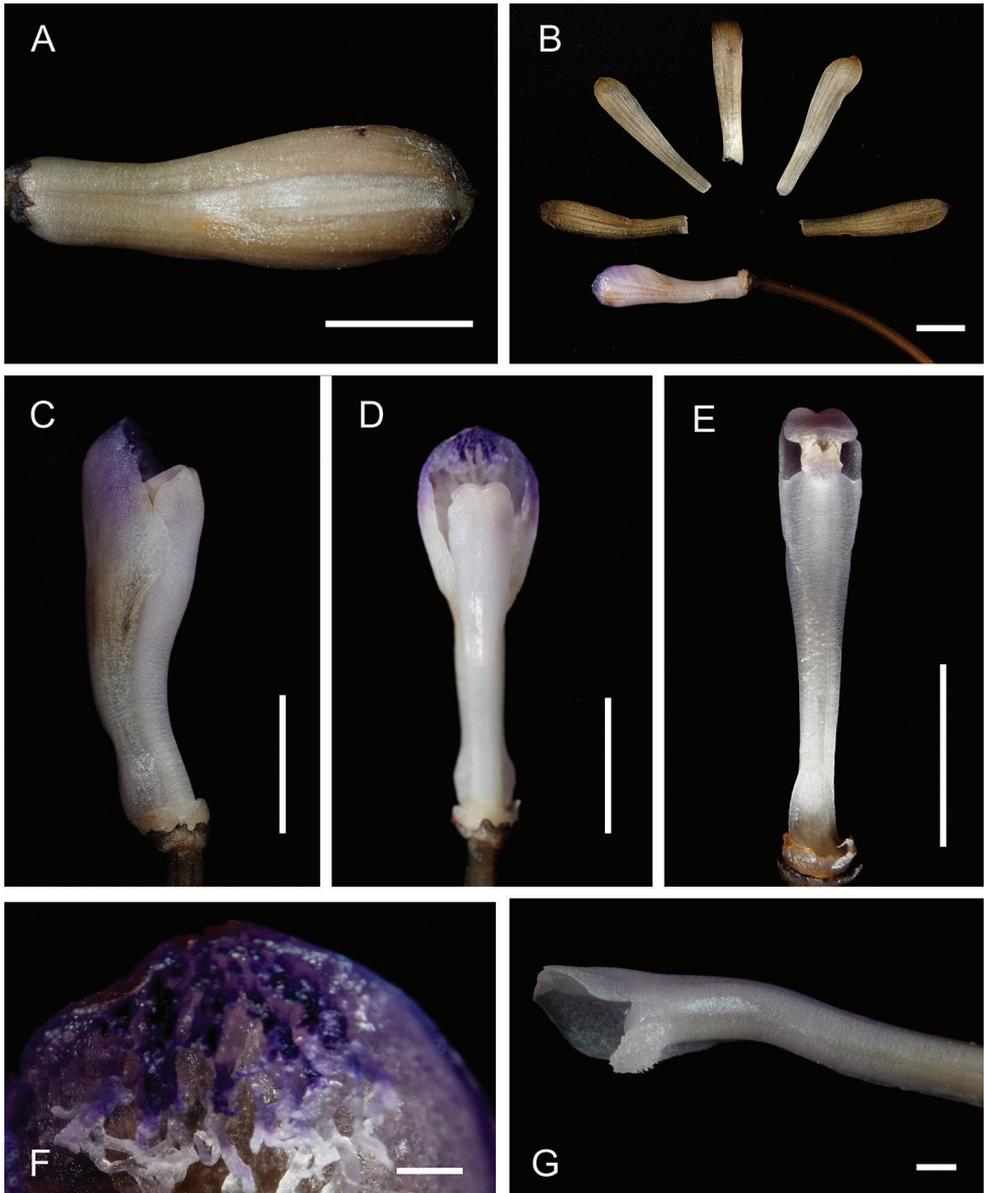
**Additional specimens examined.** JAPAN. Miyazaki Pref.: Nishimorokata County, Takaharu Town, 29 July 2016, *Nobuyuki Inoue s.n.* (OSA), JAPAN. Wakayama Pref.: Kamitonda Town, 3 Aug. 2016, *H. Fukunaga s.n.* (OSA, in spirit collection), Kamitonda Town, Oka 19 Aug. 2015, *H. Fukunaga s.n.* (MBK, in spirit collection), Nishimuro County, Iwata, Oka, 27 May 1929, *K. Kashiyama s.n.* (KYO), Nishimuro County, Iwata, Oka, 27 July 1929, *K. Kashiyama s.n.* (TI, KYO), Iwata, Oka, 13 July 1930, *K. Kashiyama s.n.* (KYO), Nishimuro County, Iwata, Oka, 14 July 1931, *K. Kashiyama s.n.* (TI), Nishimuro County, Iwata, Oka, 4 Aug. 1931, *K. Kashiyama s.n.* (TI), Nishimuro County, Iwata Village, August 1931, collector unknown (TSN), Nishimuro County, Iwata, Oka, 20 Sept. 1932, *K. Kashiyama s.n.* (KYO), Nishimuro County, Iwata, Oka, 20 Sept. 1933, *K. Kashiyama s.n.* (TI), Nishimuro County, Iwata, Oka, 1 Aug. 1933, *S. Kitasima s.n.* (KYO), Kamitonda Town, Oka 28 July 1984. *S. Kashiyama 911* (MBK, in spirit collection), JAPAN. Kochi Pref.: Kochi City, Zigokudani 29 July 1978. *Y. Sawa s.n.* (MBK, in spirit collection), Kochi Pref., Kochi City, Zigokudani, 8 Aug. 1978, *Yutaka Sawa O-86* (TI), Kochi City, Kouda, 26 July 2015, *Hirokazu Fukunaga s.n.* (OSA, in spirit collection), Kami County, Tosayamada Town, Aburaishi, 12 Aug. 1986, *Yutaka Sawa 1138* (TI), Kami County, Tosayamada Town, Aburaishi, 12 Aug. 1986, *Yutaka Sawa 1142* (TI), Kami City, Kahoku Town, 25 July 2016, *Hisanori Takeuchi s.n.* (OSA), JAPAN. Tokushima Pref.: Kaifu-County, Kainan Town, 18 July 1977. *T. Nakagawa 1043* (MBK), JAPAN. Tokyo Metropolis: Izu Islands, Hachijo Island. 6 Dec. 1940, *J. Ohchi s.n.* (TI), Izu Islands, Hachijo Island. 28 July 2016, *Masayuki Ishibashi s.n.* (OSA).

***Lecanorchis nigricans* Honda var. *patipetala* Y.Sawa emend. Suetsugu & Fukunaga**  
Figs 4–5

**Type.** JAPAN, Kochi Pref., Kochi City, Ikku, 5 Aug. 1979, *Y. Sawa O-101* (lectotype designated here, MBK-0022411)

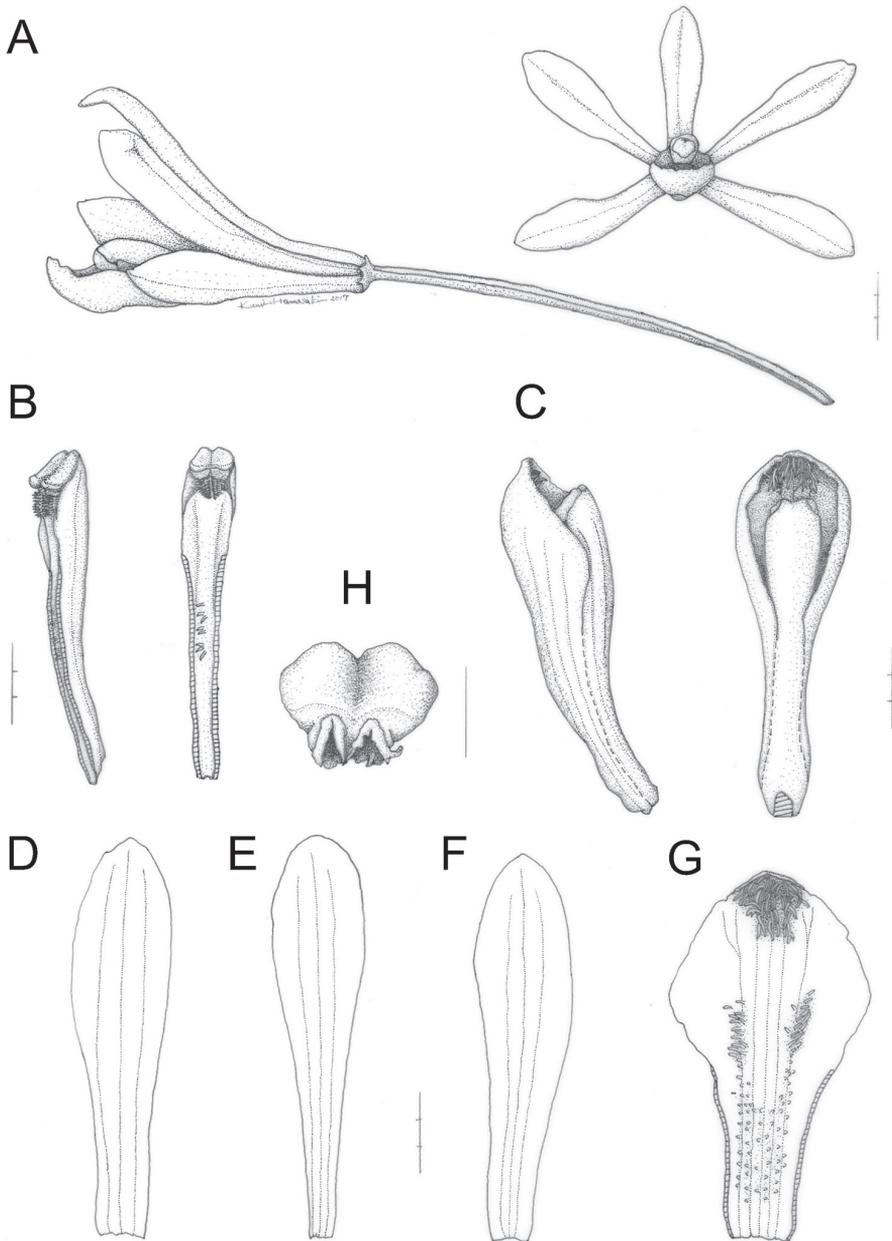
**Synonym.** *Lecanorchis nigricans* auct. non Honda (1931: 470): Hashimoto (1990:27), Hashimoto et al. (1991: 119), Nakajima and Ohba (2012: 141), Yokota et al. (2016: 248), syn. nov.

**Emended description.** Terrestrial, mycoheterotrophic herb. Inflorescence 10–25(–30) cm tall, solitary or branched at lower-half, purplish-white at flowering, black at fruiting, glabrous, ca. 0.8–1.5 mm in diam., with scale-like sheaths. Rhizome erect, J-shaped or complex, ligneous. Roots simple, radiate numerous, horizontally or down-



**Figure 4.** Dissected flowers of *Lecanorchis nigricans* var. *patipetala* collected in Haruno, Kochi, Japan on 26 July 2015 (OSA). **A** Flower and pedicellate ovary **B** Dissected flower **C–D** Lip and column **E** Column **F** Hairs at anterior disc of lip **G** Glabrous status at the ventral side of the column. Scale bars: **A–E** 5 mm **F–G** 0.5 mm. Photographed by Takuto Shitara.

ward elongate to 20–30 cm long, yellowish brown. Rachis 2–8 cm, 3–15 flowered, internode length of upper-half of rachis, 1–6(–10) mm. Floral bracts triangular, acute, 0.8–3.0 mm long. Pedicellate ovary ascending, 15–30 mm long. Flowers widely opening, ca. 2.5 cm in diameter. Sepals purplish white, linear, oblong-ob lanceolate, ca.



**Figure 5.** *Lecanorchis nigricans* var. *patipetala* collected in type locality on 28 July 2008 (OSA). **A** Flower and pedicellate ovary **B** Column **C** Lip and column **D** Dorsal sepal **E** Lateral petal **F** Lateral sepal **G** Flattened lip **H** Anther cap. Scale bars: **A–G** 3 mm **H** 1 mm. Line drawings by Kumi Hamasaki.

12–17 mm long, 2.7–3.4 mm wide, apex obtuse. Petals purplish white, linear, oblong-ob lanceolate, 13–17 mm long, 2.6–3.4 mm wide, apex obtuse. Lip shallowly spatulate, strongly 13–15 mm long, 4.0–4.5 mm wide in natural situation, ca. 6.0–7.0 mm

wide when flattened, disc with rather scarce, long multicellular hairs which are rarely branched, near apex. Column 10–13 mm long, 1.2–2.8 mm wide slightly recurved, fused with lip about 1/2 its length, ventrally glabrous or slightly puberulent; anther white, ca. 1.5 mm wide. Capsule 15–30 mm long, black, cylindrical-fusiform, ascending at 70–90 degree angle from the axis. Flowering in mid-July to mid-September.

**Note.** When describing *L. nigricans* var. *patipetala*, Sawa (1980) cited the specimens that he had collected from Ikku (Kochi Prefecture) on 5 August 1978. However, even though Sawa reported that the holotype specimen had been deposited in MBK and that the isotype specimens had been deposited in KYO and KOCH, no specimens fitting Sawa's description could be located, despite intensive surveys of MBK, KYO and KOCH. The only putative original specimen that was found was a specimen in MBK that was collected by Sawa from Ikku (Kochi Prefecture) on 5 August 1979. This specimen has already been treated as an isotype by the MBK curator. The status of the specimen is somewhat controversial since both the collection date (5 August 1979 vs. 5 August 1978) and collection number (*O-101* vs. *O-135*) differ from those of the *L. nigricans* var. *patipetala* protologue. However, the MBK specimen should still be recognised as an *L. nigricans* var. *patipetala* isotype, because the collection dates are similar enough that the difference could be regarded as a typing error. Actually, Hashimoto (1990), who investigated the *L. nigricans* var. *patipetala* holotype when the specimen was still preserved in MBK, cited the collection date as 5 August 1979 and collection number *O-101*. Actually, the collection number *O-101* was cited as a collection number for the *Gastrodia pubilabiata* holotype in the paper by Sawa (1980) that described both *L. nigricans* var. *patipetala* and *G. pubilabiata*. It is highly possible that the collection number for *L. nigricans* var. *patipetala* and *G. pubilabiata* was somehow reversed in the protologue. Therefore, in order to stabilise the taxonomic status of *L. nigricans* var. *patipetala*, the MBK isotype was designated as the lectotype, according to Articles 9.11 and 9.12 of the ICN (McNeill et al. 2012).

**Additional specimens examined.** JAPAN. Nagasaki Pref.: Fukuejima Island, Goto City, Kishiku Town, 24 July 2017, *Ueda Kouichi s.n.* (OSA, in spirit collection), Fukuejima Island, Goto City, Tomie Town, 21 July 2017 *Ueda Kouichi s.n.* (OSA, in spirit collection), JAPAN. Kochi Pref.: Kochi City, Engyouji, 4 Aug. 1979, *Yutaka Sawa O-95* (MBK), Kochi City, Ikku, 31 July 1978, *Yutaka Sawa O-83* (MBK), Kochi City, Ikku, 13 Aug. 1980, *Yutaka Sawa O-105* (MBK), Kochi City, Ikku, 5 Aug. 1980, *Yutaka Sawa O-103* (MBK), Kochi City, Haruno, 26 July 2015, *Hirokazu Fukunaga s.n.* (OSA, in spirit collection), Kochi City, Engyozi, 4 Aug. 1979, *Yutaka Sawa O-91* (TI), Kochi City, Engyozi, 31 July 1979, *Yutaka Sawa O-89* (TI), Kochi City, Engyozi, 31 July 1979, *Yutaka Sawa O-90* (TI), Kochi City, Ikku, 13 July 1980, *Shinichiro Sawa O-106* (TI), Kochi City, Ikku, 2 July 1983, *Yutaka Sawa 671* (TI), Kochi City, Ikku, 2 July 1983, *Yutaka Sawa 944* (TI), Kochi City, Ikku, 28 July 2007, *Hirokazu Fukunaga s.n.* (OSA, in spirit collection), Kochi City, Engyouji, 31 July 1979, *Yutaka Sawa s.n.* (MBK, in spirit collection), Kochi City, Engyouji, 4 Aug. 1979, *Yutaka Sawa s.n.* (MBK), Kochi City, Ikku, 5 Aug. 1978, *Yutaka Sawa O-102* (MBK), JAPAN. Mie Pref.: Ise City, Mt. Kamiji, 30 Oct. 1982, *Hiroshi Hara s.n.* (TI), Ise City, Mt. Kamiji, 23 July, *Chizuru Chuma s.n.* (TI), JAPAN. Aichi Pref.: Toyohashi City, Ooiwa Town, 11 Aug.

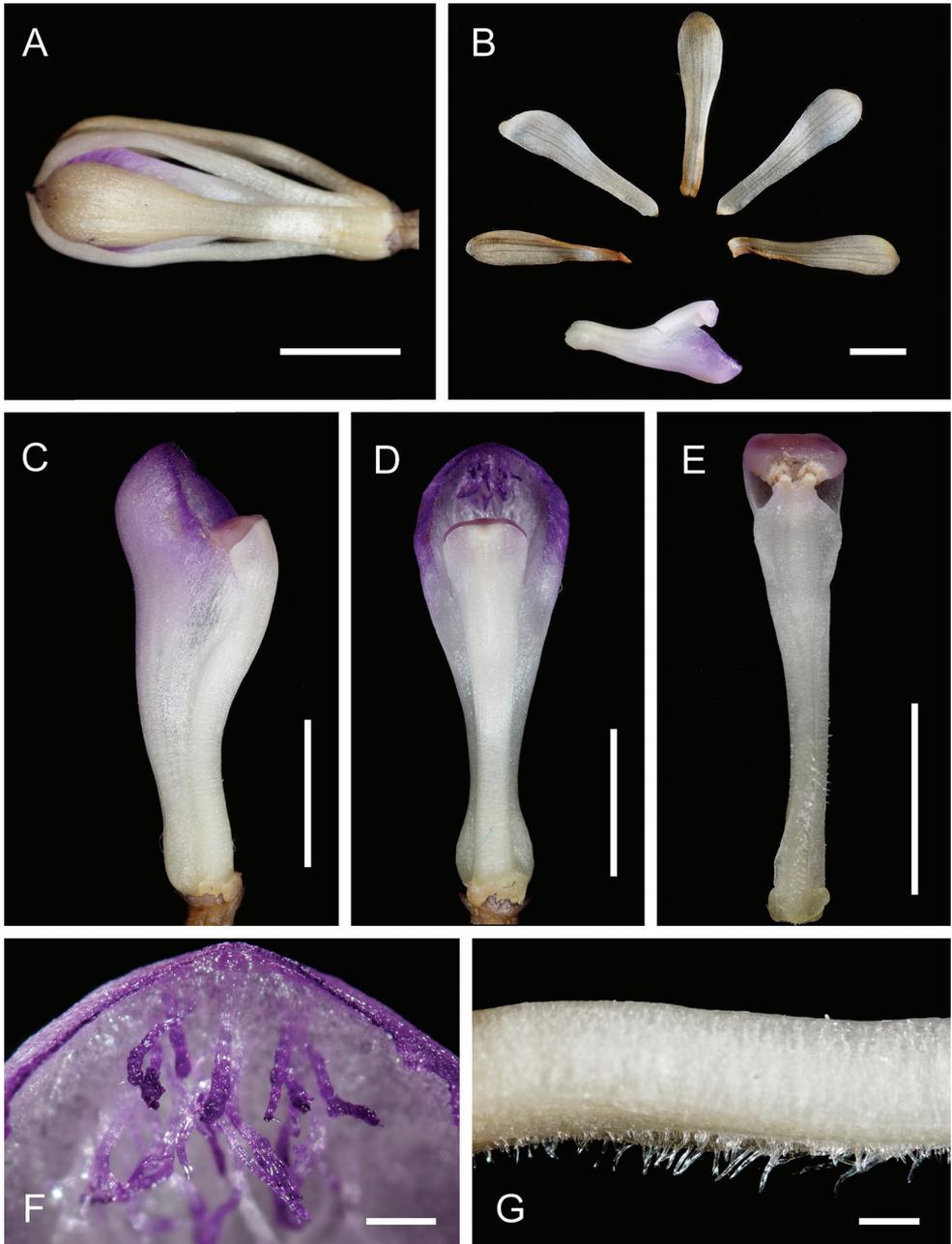
2000, *Yutaka Yoshida s.n.* (MBK, in spirit collection), JAPAN. Shizuoka Pref.: Inasa County, Hosoe Town, 31 Aug. 1981. *Yutaka Sawa* O-387 (MBK, in spirit collection), Inasa County, Hosoe Town, 31 Aug. 1981. *Yutaka Sawa* O-388 (MBK), Inasa County, Hosoe Town, along Hamanako, 9 Aug. 1981. *Isamu Yamashita* 387 (MBK), Osuka Town, Kawaramachi, 15 Aug. 1982. *Takao Sugino* 812 (MBK), Toyooka Village, Dairakuji, 13 Aug. 1982. *Takao Sugino* 819 (MBK), Mori Town, Daimon, 13 Aug. 1982. *Takao Sugino* 818 (MBK), Shimoda City, Mt. Nesugata, ca. 170 m alt, 12 Aug. 1989, *J. Kanda & Y. Hanei s.n.* (TNS), Iwata County, Toyooka Village, Dairakuji, 30 July 1982, *Yoshifusa Kurosawa* 58 (TSN), Iwata County, Toyooka Village, Dairakuji, 8 Aug. 1978, *Yoshifusa Kurosawa s.n.* (TSN), Hamamatsu City, Takizawa Town, Higashiyama, 9 Aug. 1981, *Isamu Yamashita* 377 (MBK), Atami City, Momoyama Town, 1 Sept. 1975, *Sunao Kikuchi s.n.* (KYO), Iwata City, Shikiji, 22 1979, *T. Tuyama s.n.* (TI, KYO), JAPAN. Kanagawa Pref.: Yokosuka City, *Saburo Takahashi s.n.*, 27 July 1989 (KPM), Tsukui County, Shiroyama Town, Ohdo, *F. Yamazaki s.n.*, 30 Aug. 1992 (TI), JAPAN. Tokyo Metropolis: Hachioji City, *Tsunao Asama s.n.*, date unknown, July 1981 (KPM), Hachioji City, *Hirokazu Fukunaga & Gen Gomi s.n.*, 23 Aug. 2008 (MBK, in spirit collection), JAPAN. Chiba Pref.: Kimitsu City, Toyofusa Island, *Shigeaki Fukushima s.n.*, 13 Aug. 2016 (OSA, in spirit collection), JAPAN. Chiba Pref., Abo County, Maruyama Town, 17 August 1989, *Joju Haginiwa JH015366* (TSN), JAPAN. Chiba Pref., Abo County, Maruyama Town, 17 Aug. 1989, *Joju Haginiwa JH015367* (TSN), JAPAN. Chiba Pref., Abo County, Maruyama Town, 17 Aug. 1989, *Joju Haginiwa JH015368* (TSN), Abo County, Maruyama Town, 17 Aug. 1989, *Joju Haginiwa JH015369* (TSN), Abo County, Maruyama Town, 17 Aug. 1989, *Joju Haginiwa JH015370* (TSN), Abo County, Maruyama Town, 17 Aug. 1989, *Joju Haginiwa JH015371* (TSN), Abo County, Maruyama Town, 17 Aug. 1989, *Joju Haginiwa JH015372* (TSN), Abo County, Maruyama Town, 17 Aug. 1989, *Joju Haginiwa JH038908* (TSN), Abo County, Maruyama Town, 17 Aug. 1989, *Joju Haginiwa JH038909* (TSN), Abo County, Maruyama Town, 17 Aug. 1989, *Joju Haginiwa JH040541* (TSN), JAPAN. Ibaraki Pref.: Hitachi City, Okubo Town, near Omegaoka Hospital, ca. 170 m alt, 25 Aug. 25. 1990, *T. Hashimoto s.n.* (TNS), Tsukuba City, Mt. Tsukuba, 7 Aug. 2007, *S. Matsumoto 070807-9* (TSN).

***Lecanorchis nigricans* Honda var. *yakusimensis* T.Hashim. emend. Suetsugu & Fukunaga**

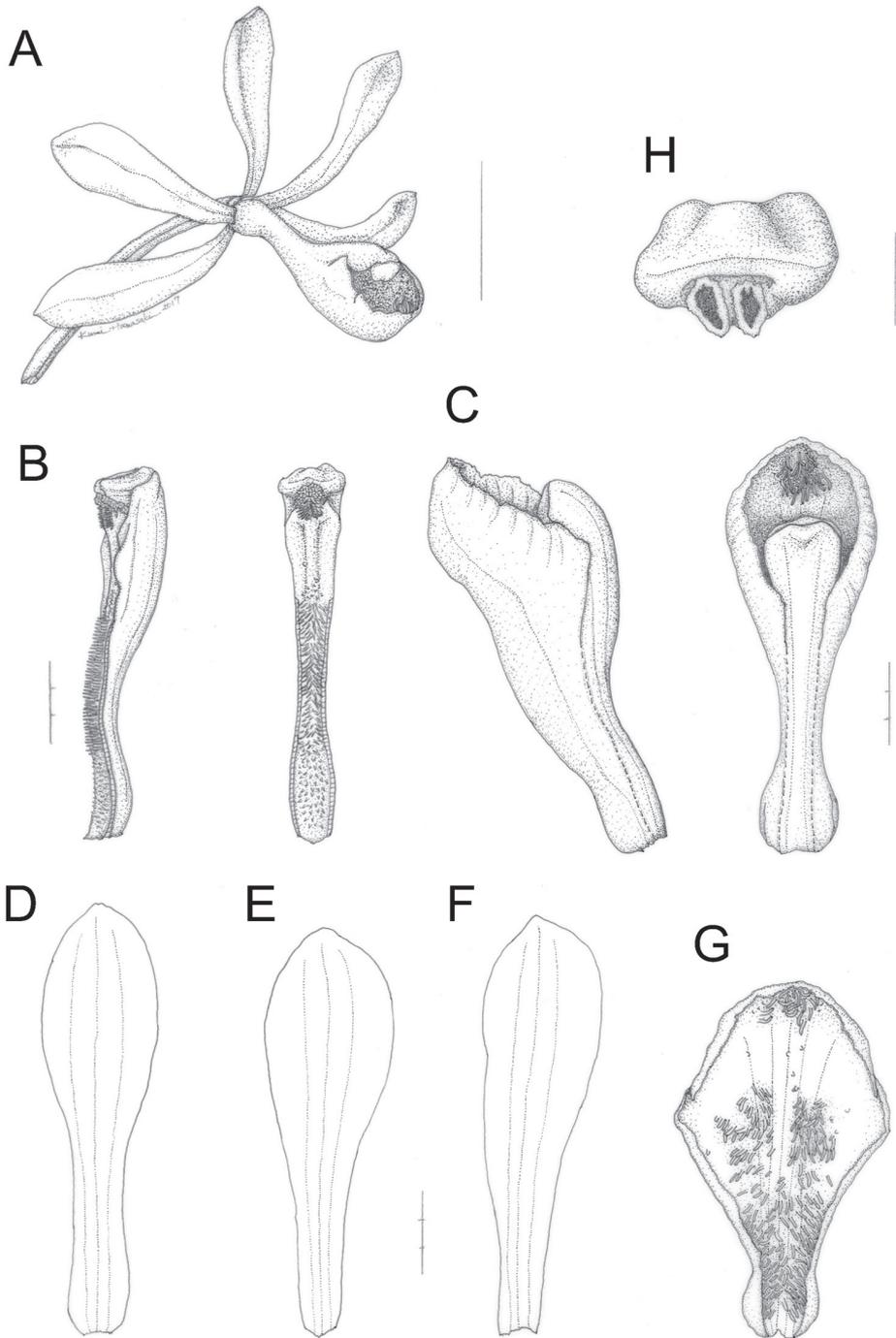
Figs 6–7

**Type.** Japan, Kagoshima Pref., Yakushima Island, along the Hanaage River, 21–27 July 1986, *Y. Hanei s.n.* (holotype TNS!).

**Emended description.** Terrestrial, mycoheterotrophic herb. Inflorescence 10–25(–30) cm tall, solitary or branched at lower-half, purplish-white at flowering, black at fruiting, glabrous, ca. 0.8–1.5 mm in diam., with scale-like sheaths. Rhizome erect,



**Figure 6.** Dissected flowers of *Lecanorchis nigricans* var. *yakusimensis* collected in type locality on 17 July 2015 (OSA). **A** Flower and pedicellate ovary **B** Dissected flower **C–D** Lip and column **E** Column **F** Hairs at anterior disc of lip **G** Pubescence at the ventral side of the column. Scale bars: **A–E** 5 mm **F–G** 0.5 mm. Photographed by Takuto Shitara.



**Figure 7.** *Lecanorchis nigricans* var. *yakusimensis* collected in type locality on 17 July 2015 (OSA). **A** Flower and pedicellate ovary **B** Column **C** Lip and column **D** Dorsal sepal **E** Lateral petal **F** Lateral sepal **G** Flattened lip **H** Anther cap. Scale bars: **A** 1 cm **B–G** 3 mm **H** 1 mm. Line drawings by Kumi Hamasaki.

J-shaped or complex, ligneous. Roots simple, radiate numerous, horizontally or downward elongate to 20–30 cm long, yellowish brown. Rachis 2–8 cm, 3–15 flowered, internode length of upper-half of rachis, 1–6(–10) mm. Floral bracts triangular, acute, 0.7–2.0 mm long. Pedicellate ovary ascending, 14–30 mm long. Flowers widely opening, ca. 2.5 cm in diameter. Sepals purplish white, linear, oblanceolate-spatulate, ca. 13–17 mm long, 3.3–4.0 mm wide, apex obtuse. Petals purplish white, linear, oblanceolate-spatulate, 13–17 mm long, 3.3–4.0 mm wide, apex obtuse. Lip spatulate to cucullate, strongly concave, 12–15 mm long, ca. 4.5 mm wide in natural situation, 7.5–8.0 mm wide when flattened, disc with rather scarce, long multicellular hairs which are rarely branched, near apex. Column 10–13 mm long, recurved, fused with lip about 1/2 its length, ventrally densely puberulent; anther purplish white, ca. 2.0 mm wide. Capsule 20–30 mm long, cylindrical-fusiform, black, ascending at 70–90 degree angle from axis. Flowering in mid-July to mid-September.

**Additional specimens examined.** JAPAN. Kagoshima Pref., Yakushima Island: along Hanaage River, 17 July 2015, *Hiroaki Yamashita s.n.* (OSA, in spirit collection), along Hanaage River, 27 July 2017, *Hiroaki Yamashita s.n.* (OSA, in spirit collection), along Osaki River, 17 July 2015, *Hiroaki Yamashita s.n.* (OSA, in spirit collection), along Nakase River, 17 July 2015, *Hiroaki Yamashita s.n.* (OSA, in spirit collection), Haruhira, 17 July 2015, *Hiroaki Yamashita s.n.* (OSA, in spirit collection), along Futamata River, Mt. Mochomu, 26 July 1991, *Yoshie Hanei s.n.* (TSN), along Futamata River, Mt. Mochomu, 26 July 1991, *Yoshie Hanei s.n.* (TSN), Kurio, 5 Aug. 1975, *Doi s.n.* (TSN).

## Acknowledgements

We thank the curators of TI, TNS, KYO, KPM, OSA, MBK, WMNH, KOCH and KAG for herbarium access. We also thank Drs. Yasen Mutafchiev, Tian-Chuan Hsu, Vladimir Ječmenica and Jun Yokoyama for their constructive comments on the earlier version of the manuscript. We also wish to express our sincere gratitude to the Board of Education of Kamitonda Town, Minoru Mizobuchi, Sachiko Tani, Hironobu Ozoe, Takatoshi Yamamoto, Ueda Koichi, Hiroaki Yamashita, Nobuyuki Inoue, Masayuki Ishibashi, Hisanori Takeuchi, Wataru Ohnishi, Shigeki Fukushima and Takuto Shitara for their continuing support during the field studies, providing specimens and pictures for this study. We are also grateful to Dr. Tian-Chuan Hsu for useful discussions on the taxonomic treatments. We gratefully acknowledge the sponsorship and the support of the New Technology Development Foundation 26-01, the Toyota Foundation and JSPS KAKENHI Grant Number 17H05016 (KS).

## References

Averyanov LV (2005) New orchids from Vietnam. *Rheedea* 15: 83–101.

- Averyanov LV (2011) The orchids of Vietnam. Illustrated survey. Pt. 3. Subfamily Epidendroideae (primitive tribes Neottieae, Vanilleae, Gastrodieae, Nervilieae). *Turczaninowia* 14: 15–100.
- Chen S, Cribb PJ, Gale SW (2009) *Lecanorchis*. In: Wu ZY, Raven PH, Hong DY (Eds) *Flora of China* vol. 25 (Orchidaceae). Science Press and Missouri Botanical Garden, Beijing & St. Louis, 171–172.
- Douzery EJP, Pridgeon AM, Kores P, Linder HP, Kurzweil H, Chase MW (1999) Molecular phylogenetics of Deseae (Orchidaceae): a contribution from nuclear ribosomal ITS sequences. *American Journal of Botany*. 86: 887–899. <https://doi.org/10.2307/2656709>
- Fukuyama N (1942) *Orchidaceae Liuliuenses Novae Vel Minus Cognitae*. I. *Transactions, Natural History Society of Formosa* 32: 241–244.
- Govaerts R, Bernet P, Kratochvil K, Gerlach G, Carr G, Alrich P, Pridgeon AM, Pfahl J, Campacci MA, Holland Baptista D, Tigges H, Shaw J, Cribb PJ, George A, Kreuz K, Wood JJ (2016) *World Checklist of Orchidaceae*. Facilitated by the Royal Botanic Gardens, Kew. [http://apps.kew.org/wcsp/namedetail.do?name\\_id=109178](http://apps.kew.org/wcsp/namedetail.do?name_id=109178) [Accessed on 31 January 2016]
- Hashimoto T (1990) A taxonomic review of the Japanese *Lecanorchis* (Orchidaceae). *Annals of the Tsukuba Botanical Garden* 9: 1–40.
- Hashimoto T, Kanda K, Murakawa H (1991) *Japanese Indigenous Orchids in Colour, Revised and Enlarged*. Ienohikari Association, Tokyo.
- Honda M (1931) *Nuntia ad Floram Japoniae XIV*. *Botanical Magazine Tokyo* 45: 469–471. <https://doi.org/10.15281/jplantres1887.45.469>
- Hsu TC, Chung SW (2010) *Supplements to the orchid flora of Taiwan (V)*. *Taiwania* 55: 363–369.
- Inoue K, Katsuyama T, Takahashi H, Akiyama M (1998) Recently rediscovered type materials of orchids described by Dr. Fukuyama and Dr. Masamune. *Journal of Japanese Botany* 73: 199–230.
- Nakajima M, Ohba H (2012) *Illustrations of Japanese orchids*. Bun-ichi Sogo Shuppan Co., Tokyo.
- Sawa Y (1980) Spontaneous orchids in the intermediate zone of Kochi Prefecture. *Research Reports of the Kochi University, Natural Science* 29: 59–71.
- Su HJ (2000) *Lecanorchis*. In: Huang TC (Ed.) *Flora of Taiwan (2<sup>nd</sup> edn) – Volume 5*. Department of Botany, National Taiwan University, Taipei, 932–936.
- Suddee S, Pedersen HA (2011) A new species of *Lecanorchis* (Orchidaceae) from Thailand. *Taiwania* 56: 37–41.
- Suddee S, Chantanaorrapint S, Tripetch P, Thainukul S (2010) New records in *Lecanorchis* Blume and *Vanilla* Plum. ex Mill. from Thailand, with keys to the Thai species. *Thai Forest Bulletin (Botany)* 38: 1–7.
- Suetsugu K, Fukunaga H (2016) *Lecanorchis tabugawaensis* (Orchidaceae, Vanilloideae), a new mycoheterotrophic plant from Yakushima Island, Japan. *PhytoKeys* 73: 125–135. <https://doi.org/10.3897/phytokeys.73.10019>
- Suetsugu K, Fukunaga H (in press) A new variety of the mycoheterotrophic plant *Lecanorchis triloba* (Orchidaceae) from Okinawa Island, Ryukyu Islands, Japan. *Acta Phytotaxonomica et Geobotanica*.
- Suetsugu K, Hsu TC, Fukunaga H, Sawa S (2016) Epitypification, emendation and synonymy of *Lecanorchis taiwaniana* (Vanilleae, Vanilloideae, Orchidaceae). *Phytotaxa* 265: 157–163. <https://doi.org/10.11646/phytotaxa.265.2.8>

- Suetsugu K, Hsu TC, Fukunaga H (2017a) Lectotypification of *Lecanorchis ohwii* (Vanilleae, Vanilloideae, Orchidaceae) with discussions of its taxonomic identity. *Phytotaxa* 309: 259–264. <https://doi.org/10.11646/phytotaxa.309.3.7>
- Suetsugu K, Hsu TC, Fukunaga H (2017b) The identity of *Lecanorchis flavicans* and *L. flavicans* var. *acutiloba* (Vanilleae, Vanilloideae, Orchidaceae). *Phytotaxa* 306: 217–222. <https://doi.org/10.11646/phytotaxa.306.3.4>
- Szlachetko DL, Mytnik J (2000) *Lecanorchis seidenfadenii* (Orchidaceae, Vanilloideae), a new orchid species from Malaya. *Annals of Botany Fennici* 37: 227–230.
- Thiers B (2017) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/> [Continuously updated]
- Tsukaya H, Okada H (2013) A new species of *Lecanorchis* (Orchidaceae, Vanilloideae) from Kalimantan, Borneo. *Systematic Botany* 38: 69–74. <https://doi.org/10.1600/036364413X662079>
- Vuong TB, Sridith K (2016) The phytogeographic note on the orchids flora of Vietnam: a case study from the Hon Ba Nature Reserve, Central Vietnam. *Taiwania* 61: 127–140.
- Wu ZH, Wang TH, Huang W, Qu YB (2001) A simplified method for chromosome DNA preparation from filamentous Fungi. *Mycosystema* 20: 575–577.
- Yokota M, Inoue K, Nakajima M, Ohba H (2016) Orchidaceae. In: Iwatsuki K, Boufford DE, Ohba H (Eds) *Flora of Japan*, Vol. IVb. Kodansha Publisher, Tokyo, 198–311.



# A new species of *Hypodematium* (Hypodematiaceae) from China

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## Abstract

*Hypodematium confertivillosum* J.X.Li, F.Q.Zhou & X.J.Li, **sp. nov.**, a new species of *Hypodematium* from Shandong, China, is described and illustrated. It is similar to *H. crenatum* (Forssk.) Kuhn & Decken and *H. glanduloso-pilosum* (Tagawa) Ohwi, but differs greatly from them by its abaxial fronds sparsely covered with rod-shaped glandular hairs, its adaxial fronds without rod-shaped glandular hairs and spore reniform, with verrucate processes, surface with distinct finely lamellar rugae ornamentation. The description, photographs and a key to *H. confertivillosum* as well as their notes are provided.

## Keywords

*Hypodematium confertivillosum*, *Hypodematium crenatum*, *Hypodematium glanduloso-pilosum*, spore ornamentation, SEM

## Introduction

Described in 1833, *Hypodematium* Kunze is the only genus of Hypodematiaceae Ching (Ching 1975). Iwatsuki (1964) reviewed the genus and recognised four species including one subspecies. Recently, more than 16 species of *Hypodematium*, mainly distributed in subtropical and temperate areas of Asia and Africa, have been established (Shing et al. 1999). China, with 12 species of *Hypodematium*, is regarded as the centre of distribution for this genus (Zhang and Iwatsuki 2013). The genus is characterised by

a distinctive swollen scaly stipe base and grows only on limestone habitat (Zhang and Iwatsuki 2013). Previous research on systematics and palynology of *Hypodematium* (Ching 1935, 1940, 1963, 1975, 1978a, b, Li et al. 1988, Shing et al. 1999, Zhou et al. 1999, Wang et al. 2010, Zhang and Iwatsuki 2013) provided an important background that allowed the recognition of the species new to science.

## Materials and methods

The voucher specimens of the new species were collected from Tashan mountain, China and deposited in PE (herbaria acronyms according to Thiers 2016).

Scanning electron microscopy (SEM) was used to document the micromorphology of spore and fronds. Samples were dehydrated and were then placed on aluminium stubs using double-sided adhesive tape and sputter coated with gold in a Hitachi E-1010 Ion Sputter Coater, following Wen and Nowicke (1999). The materials were subsequently observed and photographed under a SUPRATM55 scanning electron microscope.

## Taxonomy

*Hypodematium confertivillosum* J.X.Li, F.Q.Zhou & X.J.Li, sp. nov.

urn:lsid:ipni.org:names:77174973-1

**Diagnosis.** *Hypodematium confertivillosum* J. X. Li, F. Q. Zhou & X. J. Li is similar to *H. crenatum* (Forssk.) Kuhn & Decken and *H. glanduloso-pilosum* (Tagawa) Ohwi, from which it differs greatly by its abaxial fronds sparsely covered with rod-shaped glandular hairs, its adaxial fronds without rod-shaped glandular hairs and spore reniform, with verrucate processes, surface with distinct finely lamellar rugae ornamentation.

**Type.** China. Shandong Province: Linyi City, Fei County, Tashan Mountain, limestone rocks, 35°33'59.76"N, 117°51'29.51"E, 500–700 m a.s.l., 15 September 1982, J. X. Li 02025 (Holotype: PE, Isotype: SDCM). Figure 1.

**Description.** Plants 21–32 cm tall. Rhizomes creeping; densely scaly together with stipe base, scales reddish-brown, lustrous, linear-lanceolate, 10–12 × 1–2 mm, membranaceous, margin subentire, apex acuminate. Fronds approximate; stipe stramineous, 7–17 cm × 1–1.2 mm, nearly glabrous upward; laminae pentagonal, 12–17 × 12–14 cm, 3-pinnate-pinnatifid, base round-cordate, apex acuminate and pinnatifid; pinnae 10–12 pairs, slightly oblique, lower 2 pairs sub-opposite, 3–4 cm apart, upper pairs alternate; basal pinnae largest, deltoid-oblong, 10–11 × 8–8.5 cm, 2-pinnate-pinnatifid, base cordate, pinnae tapered; pinnules 6–8 pairs, anadromous, alternate, slightly oblique, acroscopic ones smaller, proximal basisopic pair largest, ovate-triangular, 5 × 2–3 cm, shortly stalked, base cuneate, pinnae tapered, pinnate-pinnatifid; ultimate pinnules oblong, 8–10 × 4–6 mm, apex obtuse, pinnatifid; lobe oblong, apex obtuse, margins obtuse-serrate; second and upper pairs of pinnae gradually shorter, lanceolate or oblong-lanceolate, 2-pinnate-pinnatifid, base rounded-cuneate or shal-

lowly cordate, with a short stalk, apex shortly acute. Veins obvious on both surfaces, pinnate, simple, ending at margin. Laminas chartaceous, fronds densely covered with long grey hairs adaxially, fronds abaxial surface, rachis and costae densely covered with long grey hairs and sparsely mixed with rod-shaped glandular hairs. Sori round, dorsal, 1–4 per segment; indusia reniform, pale grey, membranaceous, densely covered with grey hairs. Spores reniform, with verrucate processes, surface with distinct finely lamellar rugae ornamentation.

**Distribution.** This species is known only from the area around the type locality in Tashan, Shandong.

**Ecology.** Usually growing in limestone crevices of xeric areas.

**Discussion.** The perispore is an important trait for identifying species under the scanning electron microscopy (Liu and Li 1999) and it contributes to the discovery of some new species, for example *Dryopteris guanchica* (Jermy 1980). There are significant differences between the perispore of *H. confertivillosum* that has verrucate processes, surface with distinct finely lamellar rugae ornamentation, *H. crenatum* having curved long ridges, surface with fine striae ornamentation and *H. glanduloso-pilosum* having tuberculate-massive ornamentation, providing an important micromorphological basis for establishment of the new species *H. confertivillosum*. A comparison of *H. confertivillosum*, *H. crenatum*, and *H. glanduloso-pilosum* is given in Table 1 and Figure 2.

It is commonly believed that *Hypodematium*, a very special group, has different types of glandular hairs and non-glandular hairs, which is an important basis for the identification and classification of species of *Hypodematium* (Zhang and Iwatsuki 2013). *Hypodematium confertivillosum* fronds are sparsely covered with rod-shaped glandular hairs abaxially, but its adaxial fronds without rod-shaped glandular hairs; *H. crenatum* fronds are sparsely covered with acicular hairs adaxially, densely covered with long hairs abaxially and without rod-shaped glandular hairs on both surfaces. *Hypodematium glanduloso-pilosum* fronds are mixed, densely covered with acicular and rod-shaped glandular hairs adaxially and long hairs and rod-shaped glandular hairs abaxially. Therefore, the types of hair and the degree of density of different types of hair support the establishment of the new species of *H. confertivillosum*. A comparison of *H. confertivillosum*, *H. crenatum*, and *H. glanduloso-pilosum* is given in Table 2 and the taxonomic key below (adapted from Zhang and Iwatsuki 2013), and Figure 3.

#### Taxonomic key to the species of *Hypodematium*

- 1 Fronds not covered with rod-shaped glandular hairs adaxially ..... 2
- Fronds covered with rod-shaped glandular hairs and long grey hairs on both surfaces; perispore with tuberculate-massive ornamentation ... ***H. glanduloso-pilosum***
- 2 Fronds sparsely covered with rod-shaped glandular hairs abaxially; perispore with verrucate processes, surface with finely lamellar rugae ornamentation ..  
..... ***H. confertivillosum***
- Fronds not covered with rod-shaped glandular hairs abaxially; perispore with curved long ridges, surface with fine striae ornamentation ..... ***H. crenatum***

**Table 1.** Comparison of spore morphological features amongst three species of *Hypodematium*.

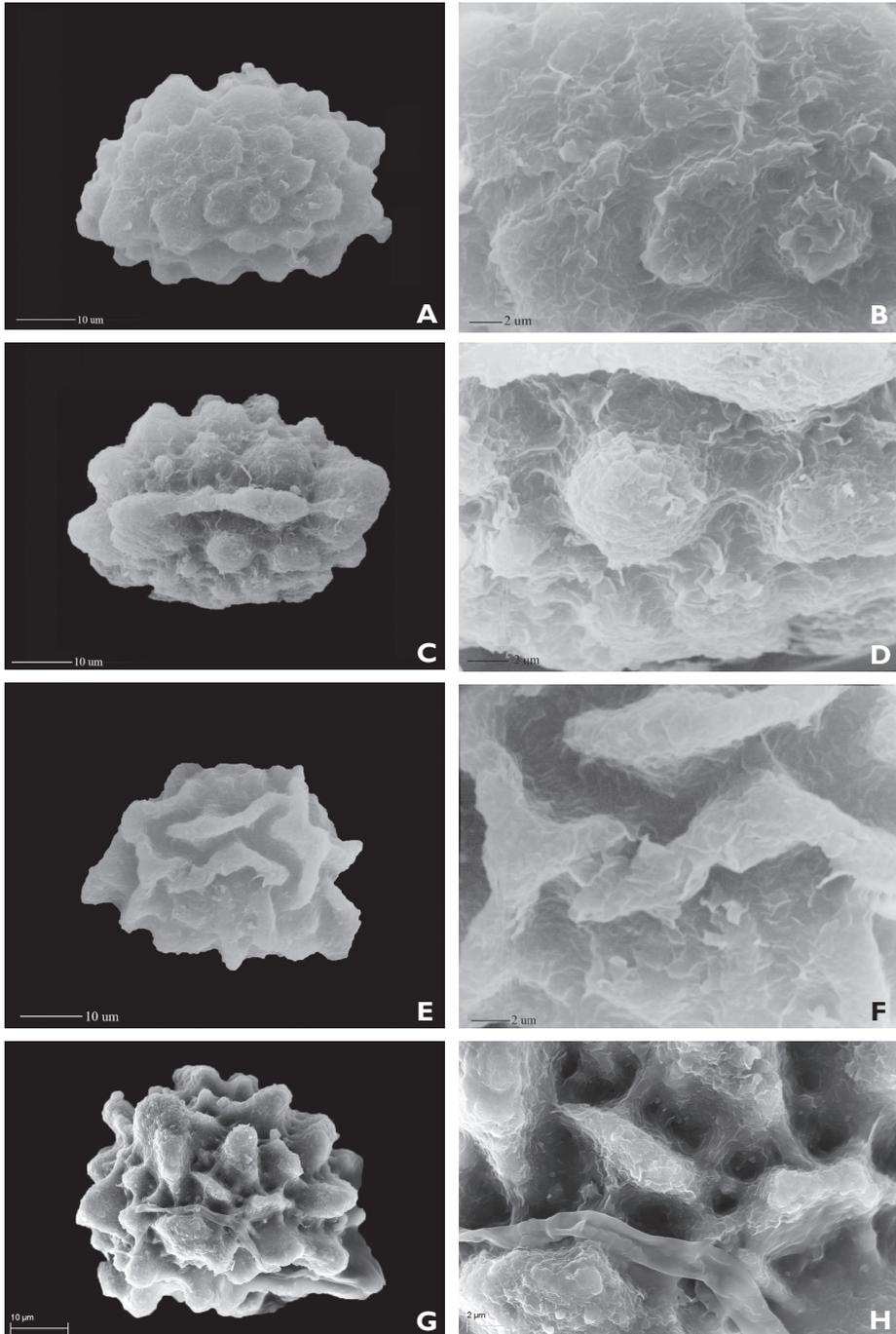
Species name	Size (µm)	Ornamentation of perispore SEM	Locality and voucher	Figure 2
<i>H. confertivillosum</i>	40.8×52.6	Verrucate processes, surface with finely lamellar rugae	Shandong J.X. Li 02025 PE	A–D
<i>H. crenatum</i>	46.1×50.3	Curved long ridges, surface with fine striae	Guangxi R.H. Zhou 0013-1 PE	E–F
<i>H. glanduloso-pilosum</i>	48.2×53.6	Tuberculate-massive	Shandong J.X. Li 96-035 SDCM	G–H

**Table 2.** Comparison of fronds and indusia in three species of *Hypodematium*.

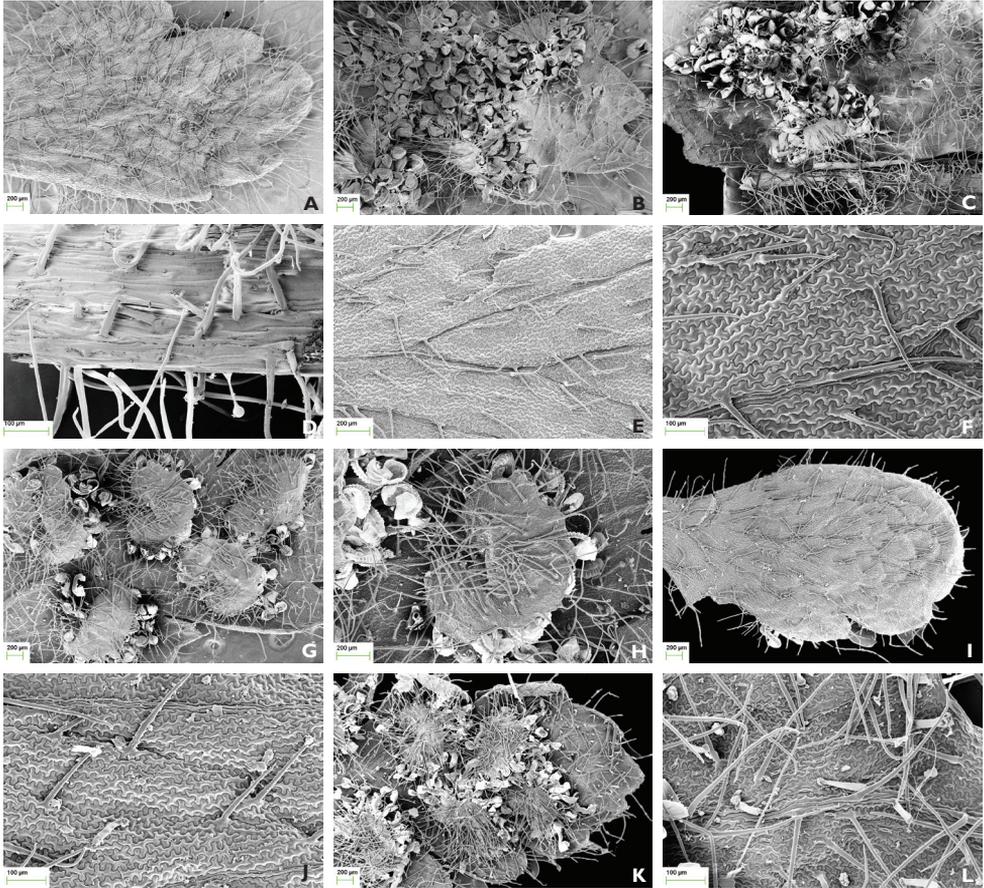
Species name	Adaxial fronds		Abaxial fronds		Rachis and costae		Indusia		Holotype, voucher and gatherer	Figure 3
	Non-glandular hairs	Glandular hairs	Non-glandular hairs	Glandular hairs	Non-glandular hairs	Glandular hairs	Non-glandular hairs	Glandular hairs		
<i>H. confertivillosum</i>	Densely covered with long grey hairs	Absent	Densely covered with long grey hairs	Sparsely rod-shaped glandular hairs	Densely covered with long grey hairs	Sparsely rod-shaped glandular hairs	Densely covered with long grey hairs	Sparsely rod-shaped glandular hairs	Holotype J. X. Li 02025	A–D
<i>H. crenatum</i>	Sparsely acicular hairs	Absent	Densely covered with long grey hairs	Absent	Densely covered with long grey hairs	Absent	Densely covered with long grey hairs	Absent	Voucher R. H. Zhou 0013-1	E–H
<i>H. glanduloso-pilosum</i>	Densely covered with acicular hairs	More rod-shaped glandular hairs	Densely covered with long grey hairs	Densely covered with rod-shaped glandular hairs	Densely covered with long hairs	Densely covered with rod-shaped glandular hairs	Densely covered with long grey hairs	Densely covered with rod-shaped glandular hairs	Voucher J. X. Li 96-035	I–L



**Figure 1.** *Hypodematium confertivillosum* J.X.Li, F.Q.Zhou & X.J.Li, sp. nov. **A** Habit **B** Sori on the abaxial surface of pinnules **C** Indusium with long hairs **D** Rhizome and stipe base scales **E** Long hairs from the abaxial surface of fronds **F** Rod-shaped glandular hairs from the abaxial surface of fronds **G** Hairs from the adaxial surface of fronds (Drawn by Y. B. Sun & J. X. Li).



**Figure 2.** Spore morphologies of three *Hypodematium* species (SEM). **A** Spore in equatorial view of *H. confertivillosum* (1500×) **B** Detail of spore in equatorial view of *H. confertivillosum* (5000×) **C** Spore in polar view of *H. confertivillosum* (1500×) **D** Detail of spore in polar view of *H. confertivillosum* (5000×) **E** Spore in equatorial view of *H. crenatum* (1500×) **F** Detail of spore in equatorial view of *H. crenatum* (5000×) **G** Spore in equatorial view of *H. glanduloso-pilosum* (1500×) **H** Detail of spore in equatorial view of *H. glanduloso-pilosum* (5000×).



**Figure 3.** The fronds and rachis of *H. confertivillosum*, *H. crenatum* and *H. glanduloso-pilosum* (SEM). **A** *H. confertivillosum* fronds densely covered with long hairs adaxially (30×) **B** *H. confertivillosum* fronds and indusia densely covered with long hairs and sparsely rod-shaped glandular hairs abaxially (30×) **C** *H. confertivillosum* fronds and costae densely covered with long hairs and sparsely rod-shaped glandular hairs abaxially (30×) **D** *H. confertivillosum* costae densely covered with long hairs and sparsely rod-shaped glandular hairs abaxially (160×) **E** *H. crenatum* fronds sparsely covered with acicular hairs adaxially (60×) **F** Close-up view of *H. crenatum* fronds covered with acicular hairs adaxially (140×) **G** *H. crenatum* fronds and indusia densely covered with long hairs abaxially (30×) **H** Close-up view of *H. crenatum* indusia covered with long hairs abaxially (60×) **I** *H. glanduloso-pilosum* fronds densely covered with acicular hairs and rod-shaped glandular hairs adaxially (30×) **J** Close-up view of *H. glanduloso-pilosum* fronds covered with acicular hairs and rod-shaped glandular hairs adaxially (140×) **K** *H. glanduloso-pilosum* fronds and indusia densely covered with long hairs and rod-shaped glandular hairs abaxially (30×) **L** Close-up view of *H. glanduloso-pilosum* fronds covered with long hairs and rod-shaped glandular hairs abaxially (140×)

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## References

- Ching RC (1935) On the genus *Hypodematium* Kunze. *Sunyatsenia* 3(1): 3–15. [pl. 2]
- Ching RC (1940) On natural classification of the family Polypodiaceae. *Sunyatsenia* 5(4): 201–268.
- Ching RC (1963) A reclassification of the family the Lypteridaceae from the mainland of Asia. *Acta Phytotaxonomica Sinica* 8(4): 289–335.
- Ching RC (1975) Two new fern families. *Acta Phytotaxonomica Sinica* 13(1): 96–98.
- Ching RC (1978a) The Chinese fern families and genera: systematic arrangement and historical origin. *Acta Phytotaxonomica Sinica* 16(3): 1–19.
- Ching RC (1978b) The Chinese fern families and genera: systematic arrangement and historical origin (Cont.). *Acta Phytotaxonomica Sinica* 16(4): 16–37.
- Iwatsuki K (1964) On *Hypodematium* Kunze. *Acta Phytotaxonomica et Geobotanica*. 21: 43–54.
- Jermy AC (1980) Biosystematic studies of *Dryopteris*. *Acta Phytotaxonomica Sinica* 18(1): 37–44.
- Li JX, Zhou FQ, Zhang YL (1988) Studies on the spore morphology of *Hypodematium* in China. *Proceedings of the International Symposium on Systematic Pteridology*: 269–272.
- Liu JX, Li YX (1999) Study on the spore morphology of *Cystopteris* Bernh from Beijing. In: Shing K-H (Ed.) Ching Memorial Volume. China Forestry Publishing House, 328–330.
- Shing KS, Chiu PS, Yao GH (1999) *Hypodematiaceae*. In: Shing KS (Ed.) *Flora Reipublicae Popularis Sinicae*, Vol. 4(1). Science Press, 151–191.
- Thiers B (2016) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>
- Wen J, Nowicke JW (1999) Pollen ultrastructure of *Panax* (the ginseng genus, Araliaceae), an eastern Asian and eastern North American disjunct genus. *American Journal of Botany* 86: 1624–1636. <https://doi.org/10.2307/2656799>
- Wang FG, Liu DM, Xing FW (2010) Two new species of *Hypodematium* (Hypodematiaceae) from limestone areas in Guangdong, China. *Botanical Studies* 51(1): 99–106.
- Zhou FQ, Gao CF, Zhang ZR, Li JX (1999) Studies on the morphology and anatomy of Hypodematiaceae from Shandong and its taxonomic significance. In: Shing K-H (Ed.) Ching Memorial Volume. China Forestry Publishing House, 357–369.
- Zhang GM, Iwatsuki K (2013) *Hypodematium* Kunze. *Flora of China*, Vol. 2-3. Science Press, Beijing & Missouri Botanical Garden Press, St. Louis, 535–539.

# Diagnostics, taxonomy, nomenclature and distribution of perennial *Sesuvium* (Aizoaceae) in Africa

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## Abstract

The taxonomy of perennial *Sesuvium* species in Africa has been poorly investigated until now. Previously five perennial species of *Sesuvium* were recognised in Africa (*S. congense*, *S. crithmoides*, *S. mesembryanthemoides*, *S. portulacastrum*, and *S. sesuvioides*). Based on the differing number of stamens, *S. ayresii* is accepted here as being distinct from *S. portulacastrum*. Field observations in Angola also led the authors to conclude that *S. crystallinum* and *S. mesembryanthemoides* are conspecific with *S. crithmoides*. A new subspecies, *Sesuvium portulacastrum* subsp. *persoonii*, is described from West Africa (Cape Verde, Gambia, Guinea-Bissau, Mauritania, Senegal). The molecular phylogeny indicates the position of *S. portulacastrum* subsp. *persoonii* within the “American lineage” as a part of the *Sesuvium portulacastrum* complex which needs further studies. A diagnostic key and taxonomic notes are provided for the six perennial species of *Sesuvium* found in Africa and recognised by the authors (*S. ayresii*, *S. congense*, *S. crithmoides*, *S. portulacastrum* subsp. *portulacastrum*, *S. portulacastrum* subsp. *persoonii*, *S. verrucosum* and the facultatively

short-lived *S. sesuvioides*). The distribution of *S. crithmoides*, previously considered to be endemic to Angola, is now confirmed for the seashores of Republic of Congo and DR Congo. The American species *S. verrucosum* is reported for the first time for Africa (the Macaronesian islands: Cape Verde and the Canaries). It is locally naturalised in Gran Canaria, being a potentially invasive species. These findings as well as new records of *S. verrucosum* from Asia and the Pacific Islands confirm its proneness to transcontinental introduction. Lectotypes of *S. brevifolium*, *S. crithmoides*, *S. crystallinum* and *S. mesembryanthemoides* are selected. The seed micromorphology and anatomy of the perennial African species is studied. Compared to the seeds of some annual African *Sesuvium* investigated earlier, those of perennial species are smooth or slightly alveolate. The aril is one-layered and parenchymatous in all species and usually tightly covers the seed. The aril detachments from the seed coat that form a white stripe near the cotyledon area easily distinguish *S. verrucosum* from other species under study.

### Keywords

Africa, Aizoaceae, molecular phylogeny, new subspecies, *Sesuvium*, Sesuvieae, Sesuvioideae, taxonomy

### Introduction

*Sesuvium* L. is one of the most widespread genera of Aizoaceae occurring in many subtropical and tropical regions of the world (Bohley et al. 2017). The perennial *Sesuvium* species often form mono- or oligodominant plant communities in coastal areas (e.g. Oliver 1871, Sauer 1982, Nellis 1994). *Sesuvium portulacastrum* (L.) L. is considered to be the species with the widest distribution pattern on all continents compared to the other representatives of the genus (Bogle 1970, Lonard and Judd 1997, Bohley et al. 2015). During the last decades the number of recognised species changed from eight (Bogle 1970) to twelve (Hartmann 1993) and reached fourteen after the inclusion of three American species of *Cypselea* Turpin (Bohley et al. 2017).

In its current circumscription, *Sesuvium* includes perennial or annual herbs with prostrate or ascending, often rooting at the nodes, glabrous or vesiculose stems (additionally with stout warts when dry; Sukhorukov et al. 2017); opposite, more or less succulent leaves with short or hardly visible petioles, which bear two semi-amplexicaulous, membranous or hyaline, entire or fimbriate, marginally concrescent stipules; axillary, bracteolate, pedicellate or sessile flowers; five, bi-coloured (green dorsally and pink or white ventrally) perianth lobes; five to numerous pink stamens; ovary consisting of two to five carpels; circumscissile capsule with the central column bearing 5–50 black or reddish, smooth or diversely sculptured seeds completely or partially covered with thin and hyaline aril.

*Sesuvium* is the type genus of subfamily Sesuvioideae (Lindley 1853, as “Sesuvieae”) which is characterised by stipulate or stipule-like leaf margins; bracteolate, perigynous flowers; externally sepaloid and internally petaloid perianth with the segments mostly apiculate on the back towards the apex, circumscissile capsule and seed usually covered by an aril (Hartmann 1993). Sesuvioideae is sister to all other Aizoaceae (Klak et al. 2003). Two major subclades were recognised within this subfamily: Sesuvioideae s.str. and *Tribulocarpus* S.Moore (Klak et al. 2003, Thulin et al. 2012). A recent study

found the monotypic *Anisostigma* Schinz to be closely related to *Tribulocarpus* (Klak et al. 2017a), which together are now recognised as the tribe Anisostigmateteae Klak (Klak et al. 2017b). The Sesuvioideae therefore now consists of two tribes, the Anisostigmateteae (two genera) and the Sesuvieae comprising *Sesuvium* (including *Cypselea*), *Trianthema* L. and *Zaleya* Burm.f. *Sesuvium* is divided into two subclades, the American lineage with  $C_3$  photosynthesis (*S. portulacastrum*, *S. verrucosum* Raf., *S. maritimum* (Walter) Britton, Sterns & Poggenb., as well as the species formerly included in *Cypselea*) and the African lineage comprising the native African species with a  $C_4$  photosynthetic pathway (Bohley et al. 2017). The species of each lineage are characterised by several types of leaf anatomy and are distinguished by the shape of the epidermal cells and by the mesophyll structure (Bohley et al. 2015). In the previous paper (Sukhorukov et al. 2017), the annual species of *Sesuvium* in Africa were revised. Instead of one (e.g. Jeffrey 1961, Hartmann 2002) or two (Bohley et al. 2017) species, four native species were accepted (*S. digynum* Welw., *S. hydaspicum* (Edgew.) Gonç., *S. nyasicum* (Baker) Gonç. and *S. sesuvioides* (Fenzl) Verd.) based on morphological and carpological characters. A new taxonomic treatment of the entire genus (Bohley et al. 2017) suggested the presence of five perennial species of *Sesuvium* in Africa: *S. congense* Welw., *S. crithmoides* Welw., *S. mesembryanthemoides* Wawra, *S. portulacastrum* and *S. sesuvioides* (also as a perennial species). All perennial taxa usually grow on the seashores of tropical Africa. One of them – *S. portulacastrum* – is considered to be a widespread species on the continent (Hutchinson and Dalziel 1927, Jeffrey 1961, Lonard and Judd 1997), whereas three others – *S. congense*, *S. crithmoides* and *S. mesembryanthemoides* – have been documented for Angola only (Welwitsch 1859, Oliver 1871, Bohley et al. 2017). However, Bohley et al. (2017) acknowledged that some of their taxonomic conclusions have been tentative and that further more detailed studies would be required to establish species limits within *Sesuvium* (e.g., *S. crithmoides*). Hereby, the results of such a study are published.

The authors' own field investigations, revision of relevant herbarium material and further taxonomic studies revealed a greater diversity of the perennial *Sesuvium* in Africa in contrast to the latest revision of the genus worldwide (Bohley et al. 2017). Additionally, the fine seed traits (micromorphology and anatomy) of perennial *Sesuvium* have been studied for the first time and some new samples have been added to the molecular analysis. Based on this, an improved taxonomy and phylogeny have been presented and the distribution of the perennial *Sesuvium* in Africa has been discussed.

## Methods

### Field studies and revision of the herbarium material

Field investigations were performed by the first author (AS) in Sal and Boa Vista Islands, Republic of Cape Verde (August 2015, January and September 2016) and in Namibia (March 2017); by Cláudia Baider in Mauritius (2017); by Marcos

Salas-Pascual (2016) and Filip Verloove (March–April 2017) in the Canary Islands (Spain) and by Cornelia Klak and Peter Bruyns in Angola (December 2016–January 2017). Additionally, the first author (AS) examined herbarium specimens in the herbaria B (on loan in Mainz, Germany), BM, BR, E, G, K, L (incl. U and WAG, but the African material in WAG was on loan), LE, LY, LYJB, M, MHA, MSB, MW, P, WIND; Filip Verloove identified the material in LPA; Cláudia Baider revised the specimens in MAU and Cornelia Klak in BOL, LUBA and PRE. In addition, some material of *Sesuvium portulacastrum* (leaves and seeds) collected by AS in Grenada (Lesser Antilles, Caribbean Islands) and Israel (as a cultivated plant in the Dead Sea area) was also used for anatomical and molecular studies.

To assess the conservation status of each taxon as per the IUCN Red List, past and present distribution data from herbarium specimens were collated. When the original specimen label did not give the precise location, a geographical point centred in the locality of the collection cited was used. This information was then assessed based on available ecological data or review of threats to allow insights into understanding the current population and distribution trends useful in defining the IUCN Red List Categories and Criteria (IUCN 2017). The extent of occurrence (EOO) and area of occurrence (AOO) were calculated using GeoCAT ver.  $\beta$ , with a cell of  $2 \times 2$  km<sup>2</sup> (Bachman et al. 2011). These assessments were not sent to the respective SSC IUCN groups prior to the publication of this article.

### Leaf anatomy

The leaves of *Sesuvium portulacastrum* subsp. *persoonii* were collected by AS in August 2015 in Cape Verde (Sal Island, near Santa Maria village) and soaked in a 70% alcohol solution. The sections were made by hand and stained with 0.2% aqueous toluidin blue. For the description of the leaf anatomy, the terminology by Bohley et al. (2015) was followed. The leaf structure was photographed with a Nikon DS-Vi1 camera (Nikon Corporation, Japan) at the Department of Higher Plants, Lomonosov Moscow State University.

### Seed morphology and anatomy

Seed micromorphology was observed using a scanning electron microscope (SEM) JSM–6380 (JEOL Ltd., Japan) at 15 kV after sputtercoating with gold-palladium in the laboratory of Electron Microscopy at Lomonosov Moscow State University. No dehydration of the seeds was required prior to SEM observation due to the absence of soft tissues (e.g. papillae or trichomes) on their surface.

The cross-sections of the seeds were prepared using a rotary microtome Microm HM 355S (Thermo Fisher Scientific, USA) and photographed with a Nikon DS-Vi1 camera (Nikon Corporation, Japan) at the Department of Higher Plants,

Lomonosov Moscow State University. Before sectioning, the seeds were soaked in water:alcohol:glycerin (1:1:1) solution, dehydrated in ethanol dilution series and embedded in the Technovit 7100 resin (Heraeus Kulzer, Germany).

The list of specimens used for SEM (perennial species) and anatomical investigations (both annual and perennial taxa) is given below. For seed morphology of the annual *Sesuvium* taxa, see Sukhorukov et al. (2017).

- Sesuvium ayresii* Marais: Ilot Marianne, 18 Jan 1975, *Lorence 1059* (K);  
*S. congense* Welw.: Angola, Lengue, 19 Dec 1932, *Grossweiler 9715* (BM); Angola, Porto Alexandre, Aug 1937, *H. Humbert 16375* (BM);  
*S. crithmoides* Welw.: Angola, Kabinda, 30 Nov 1957, *Lebrun 111905* (K); Angola, Luanda, 12 Jun 1858, *Welwitsch 2386* (BM000839897) as *S. crystallinum* Welw.;  
*S. dignum* Welw.: Angola, Mossamedes [Namibe], 8 May 1963, *A. De Menezes 409* (K);  
*S. hydaspicum* (Edgew.) Gonç.: Saudi Arabia, South Hijag, 29 Mar 1979, *J.S. Collenette 1153* (K);  
*S. nyasicum* (Baker) Gonç.: [Malawi] Nyassa [Lake Malawi], Monkey Bay, Aug 1896, *A. Whyte s.n.* (K000076291); Namibia, Hardap Region, 2 Mar 2017, *A. Sukhorukov s.n.* (MW);  
*S. portulacastrum* (L.) L. subsp. *portulacastrum*: 1) [Mexico, Colima State] Revillagigedo Island, 23 Mar 1932, *J.T. Howell 8353* (K); 2) Grenada, St.-George's, 1 Dec 2016, *A. Sukhorukov 684* (MW);  
*S. portulacastrum* (L.) L. subsp. *persoonii* Sukhor.: Senegal, St. Louis, 23 Jul 1960, *J.D. Kesby 20* (K); Cape Verde, Sal Island, Santa Maria, 30 Aug 2015, *A. Sukhorukov 59* (MW);  
*S. sesuvioides* (Fenzl) Verd.: Angola, Mossamedes [Namibe], Praia Amelia, 28 Dec 1955, *E.J. Mendes 1172* (BM);  
*S. verrucosum* Raf.: USA, California, San Joaquin co., 4 Jul 1934, *E. Lee 963* (H1283635); USA, Nevada, Pershing co., 31 Aug 2000, *A. Thielim 13396* (M).

## DNA extraction and PCR

Total DNA was extracted from silica gel-dried or fresh material of *S. portulacastrum* (collected in Israel and Grenada), *S. portulacastrum* subsp. *persoonii* (Cape Verde) and *S. nyasicum* (Namibia). The DNA from fresh material was extracted according to Krinitsina et al. (2015) and that from dry leaves was extracted using DiamondDNA Plant kit (DiamondDNA, Russia) with further purification using AMPure Beads (Beckman Coulter, USA) (for details see Krinitsina et al. 2015).

The nuclear ITS region (internal transcribed spacer 1, 5.8S ribosomal RNA gene and internal transcribed spacer 2) and three plastid regions (*rps16* gene intron, *atpB-rbcL* intergenic spacer, *trnL-trnF* intergenic spacer) were sequenced. PCR amplifications were carried out in a Thermal Cycler T100 (Bio-Rad, USA) using primers and cycler programmes listed in Table 1. The reaction mix (25 µl) contained 10 ng of DNA,

**Table 1.** Primers and cycler programmes used for the molecular analysis.

Marker	Primer sequences and combination	Reference	Cycler programmer
ITS	ITS5 5'-GGA AGT AAA AGT CGT AAC AAG G-3' / ITS4 5'-TCC TCC GCT TAT TGA TAT GC-3'	White et al. 1990	95 °C for 15 min, 5 cycles of amplification (95 °C for 30 s, 53 °C–49 °C for 1 min (–1 °C per cycle), 72 °C for 1 min), 30 cycles of amplification (95 °C for 15 s, 50 °C for 30 s, 72 °C for 40 s), 72 °C for 5 min
<i>rps16-intron</i>	rps16 F 5'-GTG GTA GAA AGC AAC GTG CGA CTT-3' / rps 16 intr R 5'-CTT GTT CCG GAA TCC TTT ATC-3'	rps16 F and rps16 R (Oxelman et al. 1997); rps16 int F and rps 16 intr R (Bohley et al. 2015)	95 °C for 15 min, 35 cycles of amplification (95 °C for 1 min, 50 °C–65 °C (increasing by 0.3 °C per cycle) for 1 min, 72 °C for 4 min), 72 °C for 5 min
	rps16 int F 5'-GTA TGT TGC TGC CAT TTT TGA AAG G-3' / rps16 R 5'-TCG GGA TCG AAC ATC AAT TGC AAC-3'		
<i>atpB-rbcL</i> spacer	atpB-rbcL F 5'-GAA GTA GTA GGA TTG ATT CTC-3' / atpB-rbcL R 5'-CAA CAC TTG CTT TAG TCT CTG-3'	Golenberg et al. 1993	95 °C for 15 min, 35 cycles of amplification (95 °C for 20 s, 56 °C for 30 s, 72 °C for 60 s), 95 °C for 20 s, 56 °C for 80 s, 72 °C for 8 min
<i>trnL-F</i>	Tab C 5'-CGA AAT CGG TAG ACG CTA CG-3' / Tab D 5'-GGG GAT AGA GGG ACT TGA AC-3'	Tab C, Tab D and Tab F (Taberlet et al. 1991); trnL-F inter F (Bohley et al. 2015)	95 °C for 15 min, 35 cycles of amplification (95 °C for 1 min, 50 °C–65 °C (increasing by 0.3 °C per cycle) for 1 min, 72 °C for 4 min), 72 °C for 5 min
	trnL-F inter F 5'-GGA CGA GAA TGA AGA TAG ACT C-3' / Tab F 5'-ATT TGA ACT GGT GAC ACG AG-3'		

1 µM of each primer, 200 µM of each dNTP and 0.5 U hot start TagF polymerase (AmpliSens, InterLabService, Russia). PCR products were checked on 1.2% agarose gels and purified using AMPure Beads (Beckman Coulter, USA) according to the manufacturer's protocol. AMPure Beads suspension was mixed with a solution containing PCR-product at the ratio 1.2:1 (for ITS and *atpB-rbcL* primer pairs) or 1.4:1 (for all other primer pairs). The sequencing was performed at Genome centre, Engelhardt Institute of Molecular Biology (Moscow, Russia) on Applied Biosystems 3730 DNA Analyser using ABI PRISM® BigDye™ Terminator v.3.1 Cycle Sequencing Kit.

## Sequence alignment and phylogenetic reconstruction

The raw forward and reverse sequences were checked and combined in BioEdit sequence alignment editor v. 7.0.5.3 (Hall 1999). The sequences were aligned using Muscle algorithm and MEGA6.0 software package ([www.megasoftware.net](http://www.megasoftware.net); see Tamura et al. 2013). Two data sets were assembled: (1) consisting of three chloroplast markers and (2) the nuclear (ITS) gene region. These data sets were first analysed separately and then in combination using the Maximum Likelihood (ML) method in MEGA 6.0 (Tamura et al. 2013) and Bayesian Inference (BI) in BEAST (Bouckaert et al. 2014). A bootstrapping of 1,000 replicates for ML analysis was processed to estimate the confidence probabilities on each branch of the phylogenetic trees constructed. An initial tree (ML) for the heuristic search was obtained by applying the Neighbour-Joining method to a matrix of pairwise distances estimated using the Maximum Composite Likelihood approach. All positions containing gaps were treated as missing data. Bayesian analyses were run for 20,000,000 generations with four MCMC chains in two independent runs. The first 2,000,000 samples from each run were discarded as burn-in. Convergence was assessed by comparing standard deviation of split frequencies between different runs (MCMC Trace Analysis Tool (Tracer) version v1.6.0; Rambaut et al. 2014). For ML and BI analyses, optimal models of molecular evolution for combined matrices were identified using jModelTest2 (Darriba et al. 2012) (optimal model is GTR + G). Voucher information and GenBank accession numbers are listed in Table 2.

## Results and discussion

### Leaf anatomy

The leaf anatomy of a new subspecies *S. portulacastrum* subsp. *persoonii* (Fig. 1) was investigated.

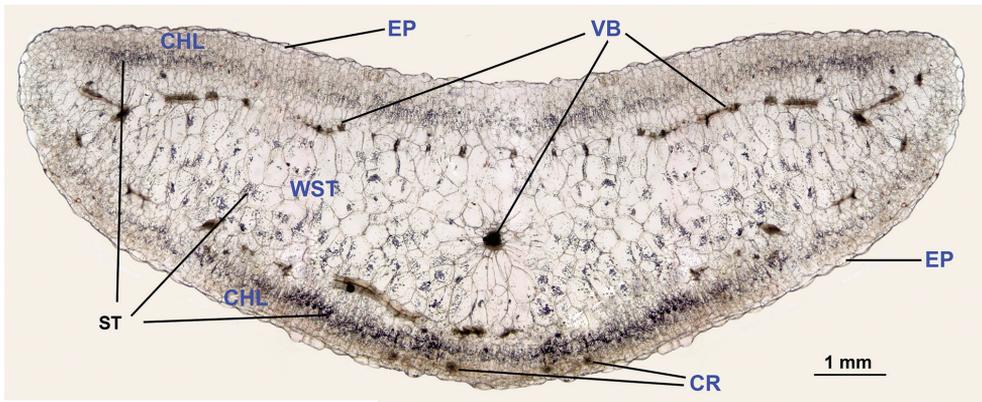
*Description:* Leaves terete, of lenticular shape in cross-sections, very succulent, leaf thickness ~4.2 mm; epidermis of the adult leaves mamillate (with slightly convex outer cell walls); hypodermis absent; mesophyll with palisade and water storage cells; palisade cells forming chlorophyll-containing tissue arranged in 3–7 layers below the epidermis (~0.6–0.7 mm from each leaf side), with abundant druses; the cells of innermost palisade layer and adjacent cells of water storage tissue with abundant starch grains (looking like dark stripes: Fig. 1); water storage cells arranged in numerous layers; one or rarely two main vascular bundles in the centre of the leaf are present, with numerous lateral vascular bundles.

The anatomical structure of the leaves of *S. portulacastrum* subsp. *persoonii* is similar to that of *S. portulacastrum* (type subspecies) described by Bohley et al. (2015). The difference between the “*Tribulocarpus* type” (e.g. *Sesuvium maritimum*, *S. verrucosum*,

**Table 2.** Voucher information and GenBank accession numbers for perennial *Sesuvium* species and outgroups included in the phylogenetic analysis. The newly sequenced samples are highlighted in bold.

Species	Voucher information (country, year, herbarium acronym and number)	GenBank accession number			
		<i>rps 16</i> intron	<i>atpB-rbcL</i> intergenic spacer	<i>trnL-trnF</i> intergenic spacer	ITS
<i>Sesuvium congense</i>	Angola, 2009 (PRE849008.8)	KJ848244.1	KJ848148.1	KJ848291.1	KJ848196.1
<i>S. crithmoides</i>	Angola, 2009, (PRE849042.0)	KJ848247.1	KJ848151.1	KJ848294.1	KJ848199.1
<i>S. humifusum</i> (ex- <i>Cypselea humifusa</i> )	USA (MJG014141)	KJ848241.1	KJ848145.1	KJ848288.1	KJ848193.1
<i>S. hydaspicum</i>	Burkina Faso, 1996 (MO055896)	KJ848230.1	KJ848136.1	KJ848277.1	KJ848181.1
<i>S. hydaspicum</i>	Burkina Faso, <i>Madsen 5264</i> (S)	–	–	–	AJ937561.1
<i>S. maritimum</i>	Mexico, 1999 (BRIT)	–	–	–	KJ848178.1
<i>S. maritimum</i>	USA, Louisiana, <i>Thomas et al. 103258</i> (NY)	–	–	–	AJ937562.1
<i>S. maritimum</i>	USA, Texas, <i>Walker 1673</i> (NY)	–	–	–	AJ937563.1
<i>S. maritimum</i>	USA, [North Carolina], 1998 (BRIT)	KJ848228.1	KJ848134.1	KJ848275.1	KJ848179.1
<i>Sesuvium</i> sp.	Namibia, 1996 (MO5667010)	–	–	–	KJ848190.1
<i>Sesuvium</i> sp.	Angola, 2009 (PRE849020)	KJ848246.1	KJ848150.1	KJ848293.1	KJ848198.1
<b><i>S. nyasicum</i></b>	<b>Namibia, 2017, <i>Sukhorukov s.n.</i> (MW)</b>	<b>MG209774</b>	<b>MG209769</b>	<b>MG209777</b>	<b>MG495932</b>
<b><i>S. portulacastrum</i></b>	<b>Israel, Dead Sea, <i>Sukhorukov s.n.</i> (MW)</b>	<b>MG209775</b>	<b>MG209772</b>	<b>MG762002</b>	<b>MG461526</b>
<b><i>S. portulacastrum</i></b>	<b>Grenada, St.-George's, 2016, <i>Sukhorukov 684</i> (MW)</b>	<b>MG209776</b>	<b>MG209771</b>	<b>MG209779</b>	–
<i>S. portulacastrum</i>	Morocco, 2012 (MJG014142)	KJ848232.1	KJ848138.1	KJ848279.1	KJ848183.1
<i>S. portulacastrum</i>	Saint Kitts and Nevis, 1994 (MO5158713)	KJ848236.1	KJ848141.1	KJ848284.1	KJ848188.1
<i>S. portulacastrum</i>	Mexico, 2010 (MJG014143)	KJ848240.1	KJ848144.1	KJ848287.1	KJ848192.1
<i>S. portulacastrum</i>	USA, Florida, 2013 (MJG014144)	KJ848243.1	KJ848147.1	KJ848290.1	KJ848195.1
<i>S. portulacastrum</i>	Taiwan, 2003 (MO6268738)	–	–	–	KJ848185.1
<i>S. portulacastrum</i>	Venezuela (ex cult., <i>Thiede s.n.</i> (HBG))	–	–	–	AJ577758.1
<i>S. portulacastrum</i>	Bolivia, 1998 (MO5903990)	–	–	–	KJ848184.1
<i>S. portulacastrum</i>	India, anonym (RK402)	–	–	–	FJ784241.1
<i>S. portulacastrum</i>	India, [without herbarium voucher]	–	–	–	KC185421.1
<i>S. portulacastrum</i>	India, anonym (AUFMS260)	–	–	–	KF848298.1
<b><i>S. portulacastrum</i> subsp. <i>personii</i></b>	<b>Cape Verde, Sal Island, <i>Sukhorukov 59</i> (MW)</b>	<b>MG209773</b>	<b>MG209770</b>	<b>MG209778</b>	<b>MG495933</b>
<i>S. sesuvioides</i>	Namibia, 1988 (HBG910260)	KJ848231.1	KJ848137.1	KJ848278.1	KJ848182.1
<i>S. sesuvioides</i>	Angola, 2009 (PRE8499750)	KJ848245.1	KJ848149.1	KJ848292.1	KJ848197.1
<i>S. sesuvioides</i>	Namibia, <i>Van Slageren &amp; Brand MSJB020</i> (WAG)	–	–	–	AJ937583.1
<i>S. verrucosum</i>	USA, [California], 1999 (BRIT)	KJ848229.1	KJ848135.1	KJ848276.1	KJ848180.1

<i>S. verrucosum</i>	Mexico, 2004 (MEXU 1237208)	KJ848237.1	KJ848142.1	KJ848285.1	KJ848189.1
<i>S. verrucosum</i>	USA, [Nevada], 2013 (MJG014145)	KJ848242.1	KJ848146.1	KJ848289.1	KJ848194.1
<i>S. verrucosum</i>	Saudi Arabia, <i>Fayed s.n.</i> (UBT)	–	–	–	AJ937564.1
<i>S. verrucosum</i>	United Arab Emirates, Dubai, <i>Hartmann &amp; Hartmann 34761</i> (HBG)	–	–	–	HE585045.1
<i>S. verrucosum</i>	Mexico, 1998 (MEXU1231179)	–	–	–	KJ848191.1
<i>Portulaca oleracea</i> (outgroup)	South Korea, Jeollanam-do prov., Gisan-ri, 2013 (JKTM1000081)	–	–	–	KM051437.1
<i>Phytolacca dioica</i> (outgroup)	Garden material, South Africa, 2002, <i>Klak 988</i> (BOL)	AJ532733.1	AJ532612.1	KM261955.1	–



**Figure 1.** Leaf anatomy of *S. portulacastrum* subsp. *personii*. Abbreviations: **CHL** chlorenchyma **EP** epidermis **CR** crystals (druses) **ST** starch grains in the palisade cells **VB** vascular bundles **WST** water storage tissue. Scale bar: 1 mm.

some individuals of *S. portulacastrum* with papillate leaves) and the “*Sesuvium portulacastrum* type” (glabrous forms of *S. portulacastrum* and *S. maritimum*) appears to lie only in the presence or absence of papillae (bladder cells) on the leaf epidermis (Bohley et al. 2015). Therefore, the authors propose to unite these two types of leaf anatomy into the “*Sesuvium portulacastrum* type”.

### Flower, fruit and seed characters

The position of the ovary in *Sesuvium* is considered superior (e.g. Jeffrey 1961, Adamson 1962, Bogle 1970, Gonçalves 1995) or semi-inferior (Ferren 2003). Sometimes the flowers are described as perigynous (Hartmann 2002, Hassan et al. 2005b, Bohley et al. 2017), but this term does not describe the insertion of the ovary as compared to other floral parts. In fact, the connate part of the tepals forms a true hypanthium, with concrescence of the lower parts of the filaments with the inner surface of the flower

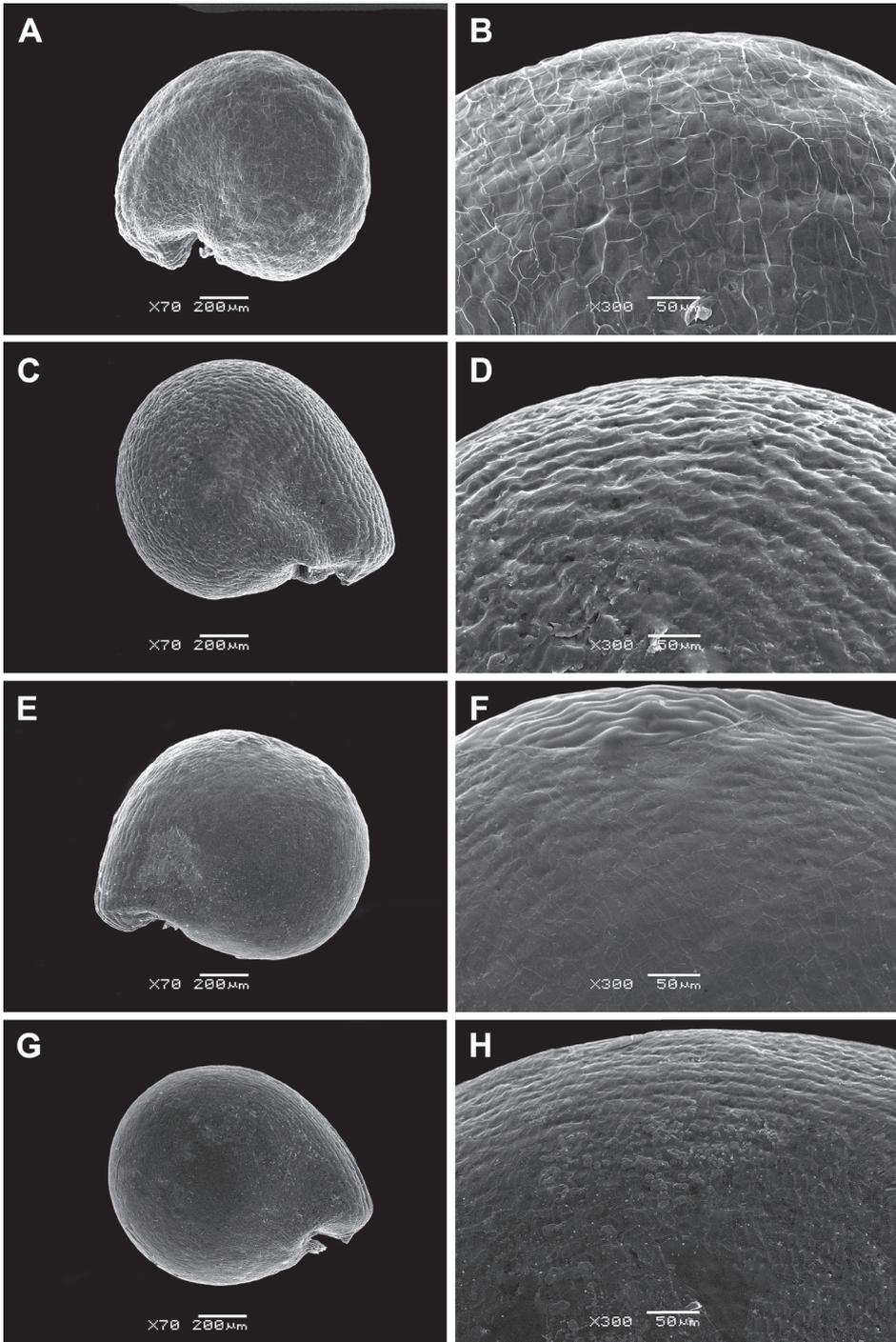
cup. The insertion of the stamens seems to be near the top of the hypanthium. However, the ovary itself is situated above the point where the other floral parts are inserted and it should therefore be considered superior as in other Sesuvioideae (Bogle 1970). The perigynous flowers and superior position of the ovary are very characteristic traits for the Sesuvioideae as the basal-most lineage within the Aizoaceae.

The fruit in *Sesuvium* is a circumscissile capsule. The capsule is usually shorter than or rarely almost equal to the tepals, especially in some annual species. The reproductive diaspore type is a seed. The mode of seed dispersal in *Sesuvium* has not yet been investigated, but it was suggested that the seeds might be dispersed by water (Marais 1990, Tomlinson 2016). Taking into account the coastal habitats where almost all perennial species of the genus are found, this assumption seems to be reasonable. All plant parts of perennial *Sesuvium* in coastal areas are grazed by cattle (Burkill 1985) and thus endozoochory may also be an important mode for dispersal. The thick seed coat protects the embryo against long-lasting water impact or digestion, as in many other species of Caryophyllales with similar dispersal facilities requiring embryo protection (e.g. Netolitzky 1926, Sukhorukov 2008, Sukhorukov and Zhang 2013, Sukhorukov et al. 2015).

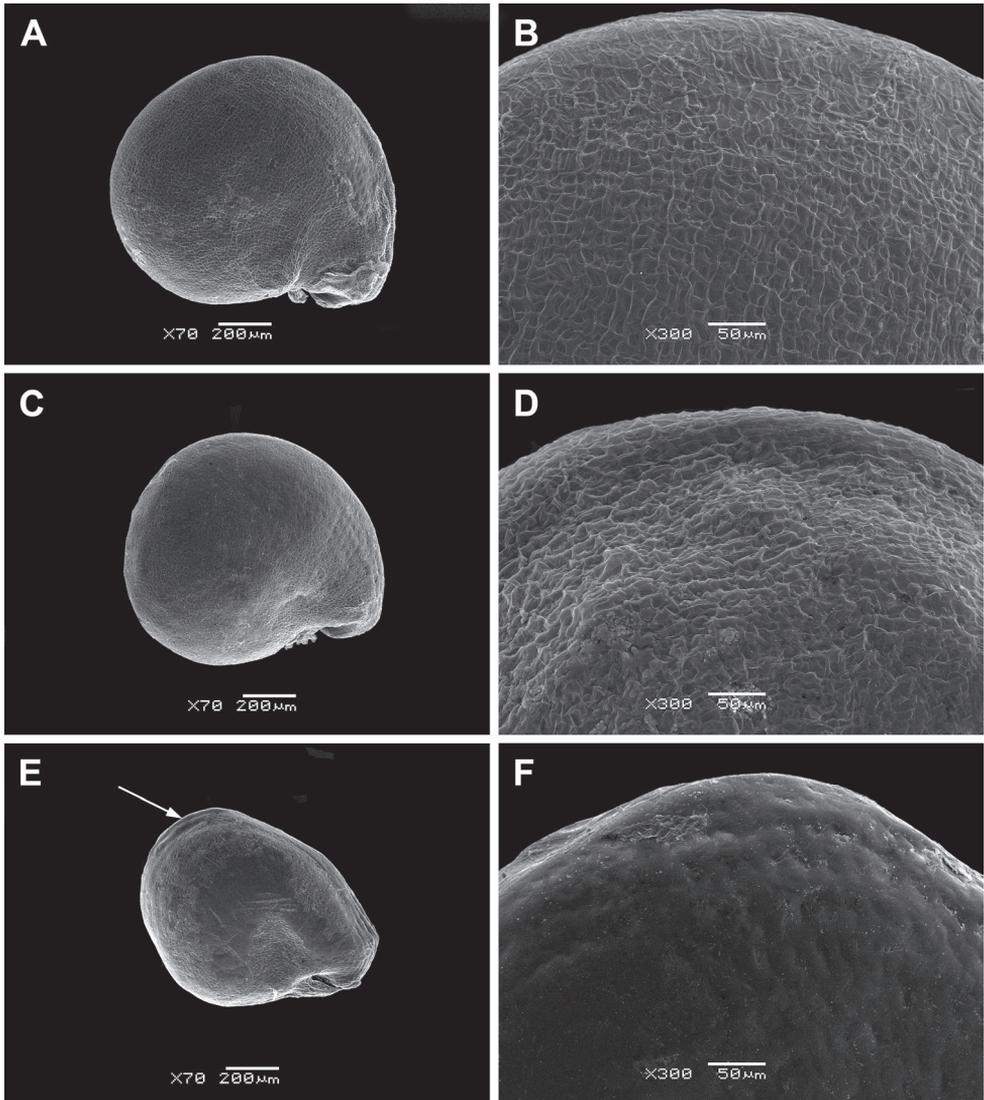
The seeds of all perennial *Sesuvium* under study are roundish, 0.9–1.1 mm in diameter and slightly flattened (Figs 2 and 3). The aril is one-layered, whitish, ca. 1–2  $\mu\text{m}$  thick in cross-section and consists of thin-walled cells. It tightly adheres to the seed coat. However, *S. verrucosum* is distinguished by the small detachments of the aril from the seed coat forming a distinctive fold in the cotyledon area (Fig. 3E). The aril usually covers the seed completely (Figs 2, 3A–D), but in some seeds of *S. portulacastrum*, it is only partially present. An aril covering up to half the seed surface is not common in *S. portulacastrum* (or any other *Sesuvium*) mentioned by Hassan et al. (2005a). The presence of a tiny aril apparently does not provide any protective function and its role in seed dispersal or germination is unclear.

The seed coat of perennial *Sesuvium* is smooth or slightly wavy, often with small, radially elongated striae. Hardly noticeable pits were found only in *S. verrucosum* (Fig. 3F). In cross-section, the testal layer is much thicker than the 1–3 endotegmal layers. In almost all species, the testa thickness ranges from (25–)30 to 50  $\mu\text{m}$  (Fig. 4), but the testa of a *S. portulacastrum* specimen from Grenada studied for comparison was found to measure between 70 and 80  $\mu\text{m}$ . The outer periclinal wall of the testa cells is clearly thicker than the inner periclinal wall and the protoplast is usually clearly visible. The walls and protoplast of the testa cells are completely filled with tannins, especially the external areas of the outer cell walls, which appear dark brown. The “stalactites” in the outer cell walls are not prominent in comparison to other representatives of the core Caryophyllales (Takhtajan 1991, Sukhorukov and Zhang 2013, Sukhorukov et al. 2015). The thickness of the tegmen layers is 2–8  $\mu\text{m}$  (each layer has an average thickness of 3  $\mu\text{m}$ ). The embryo is annular and the perisperm is copious.

There are no significant differences in seed structure between perennial and annual *Sesuvium* species growing in Africa. However, the seed-coat testa of some annual African *Sesuvium* (*S. hydaspicum* and especially *S. nyasicum*) has wrinkle- or ridge-like

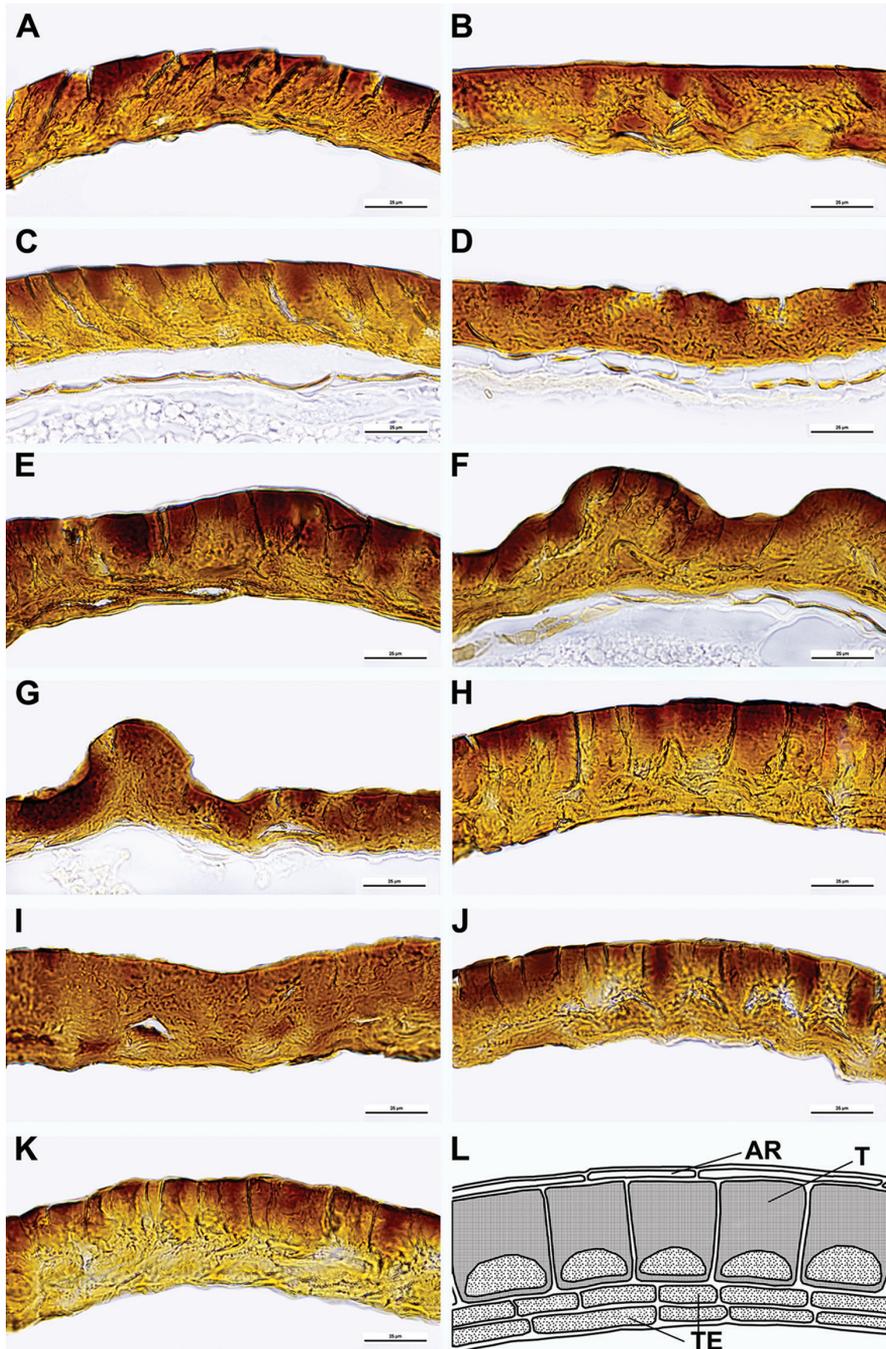


**Figure 2.** SEM micrographs of *Sesuvium* seeds (covered with an aril). **A, B** *S. ayresii* **C, D** *S. congense* **E, F** *S. crithmoides* **G, H** *S. crystallinum* (now merged with *S. crithmoides*). Magnification: **A, C, E, G**: 70 $\times$ ; **B, D, F, H**: 300 $\times$ .



**Figure 3.** SEM micrographs of *Sesuvium* seeds (covered with an aril). **A, B** *S. portulacastrum* subsp. *persoonii* **C, D** *S. portulacastrum* subsp. *portulacastrum* **E, F** *S. verrucosum*. Magnification: **A, C, E**: 70×; **B, D, F**: 300×. Arrow on image E indicates the detachment of the aril from the seed coat forming a distinctive fold in the cotyledon area.

outgrowths (Sukhorukov et al. 2017). In all other species, the seeds are smooth, except for the annual North American *Sesuvium trianthemoides* Correll with rugose seed ornamentation (Correll 1966). This species is known only from the type locality and the character of the seed ornamentation could be of taxonomic importance to distinguish it from other related species (Ferren 2003). These investigations show that the easily visible detachment of the aril from the seed coat, appearing as a patch near the coty-



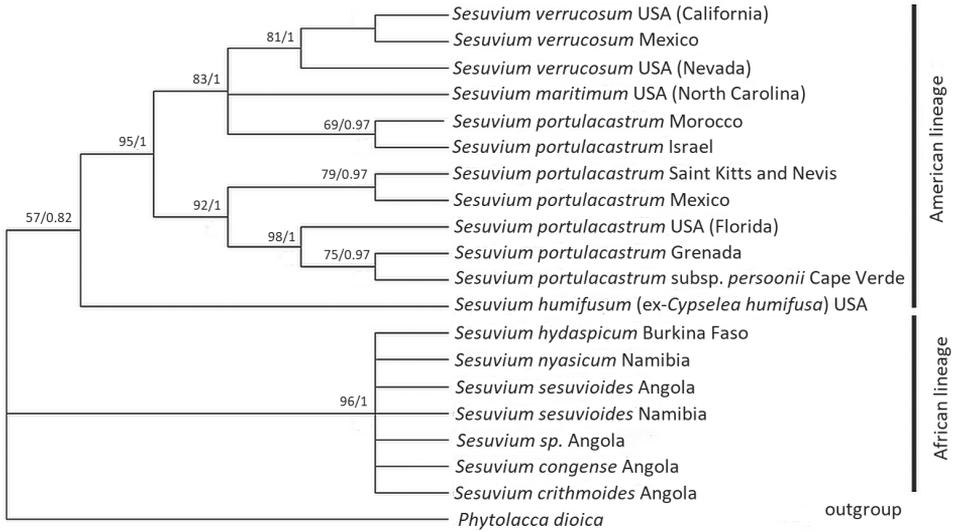
**Figure 4.** Seed anatomy of annual and perennial *Sesuvium* species in Africa: **A** *S. ayresii* **B** *S. congense* **C** *S. crithmoides* **D** *S. crystallinum* (now merged with *S. crithmoides*) **E** *S. digynum* **F** *S. hydaspicum* **G** *S. nyasicum* **H** *S. portulacastrum* subsp. *personii* **I** *S. portulacastrum* subsp. *portulacastrum* **J** *S. sesuvioides* **K** *S. verrucosum* **L** schematic drawing of the seed structure. Scale bar: 25 µm. Abbreviations (image **L**): **AR** seed aril; **T** testa; **TE** tegmen.

ledon area, clearly distinguishes *S. verrucosum* from other taxa encountered in Africa. This character is added to the diagnostic key as a taxonomically important trait. Apart from *S. verrucosum*, this peculiarity is also observed in the North American annual *S. maritimum* and South American *S. parviflorum* DC., a forgotten name of a species that is often identified as *S. portulacastrum* or *S. sessile* Pers. (Sukhorukov et al., in prep.). *S. verrucosum* and *S. maritimum* appear closely related to each other according to the molecular data (Bohley et al. 2015). Other American species previously considered within the genus *Cypselea* and recently transferred to *Sesuvium* based on the molecular phylogeny (Bohley et al. 2017) – *Sesuvium humifusum* (Turpin) Bohley & G.Kadereit, *S. megianum* (K.Müll.) Bohley & G.Kadereit and *S. rubriflorum* (Urb.) Bohley & G.Kadereit – have much smaller, reddish seeds with a thin seed coat (Sukhorukov, pers. observ.). The seeds of these three species (–0.2 mm across) are amongst the smallest in the large “Globular Inclusion” clade (core Caryophyllales: Cuénoud et al. 2002) along with tiny seeds of some Molluginaceae (Sukhorukov et al., in press).

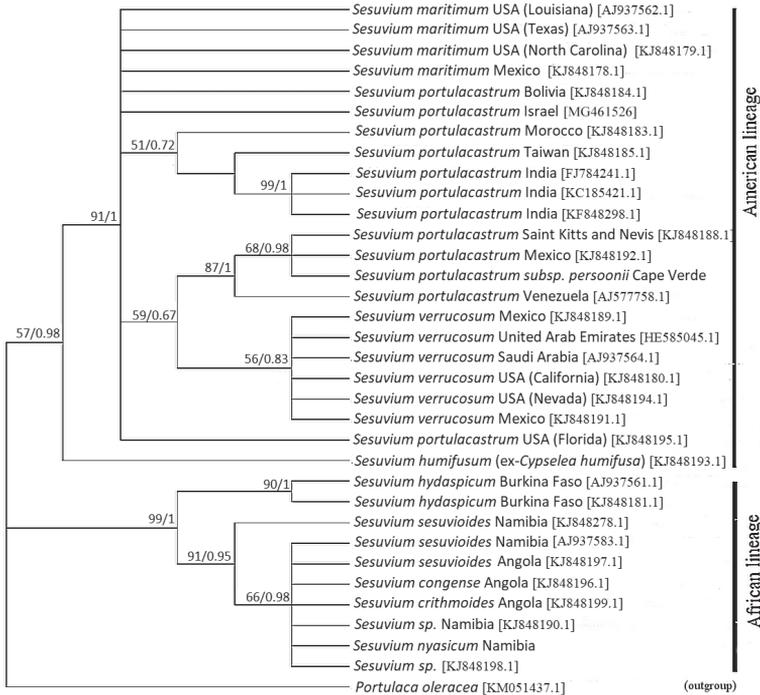
Many African taxa with an annual or perennial life history (*S. congense*, *S. crithmoides*, *S. crystallinum*, *S. digynum*, *S. sesuvioides*) possess an indistinctly striate seed surface (Figs 2 and 3; see also Sukhorukov et al. (2017)). Smooth seeds of *Sesuvium sesuvioides* or indistinctly wrinkled seeds of *S. digynum* have relatively thin (20–30 µm) testa. However, thickness varies considerably in *S. hydaspicum* (from 20 to 50 µm) and especially in *S. nyasicum* (from 20 to 100 µm) due to the presence of protruding “wrinkles” originating from the testa. The testa is thinner between the wrinkles and much thicker in wrinkled areas.

## Molecular phylogeny

Several new samples were added to the molecular phylogeny including *S. nyasicum*, *S. portulacastrum* and the new subspecies *S. portulacastrum* subsp. *persoonii*. In both ITS and chloroplast trees (Figs 5 and 6), as well as in the combined tree (Fig. 7), *Sesuvium* is divided into two clades referred to as the “African” and the “American” lineages (Bohley et al. 2015). Although the relationships within the “African lineage” are still not resolved, this clade contains the species native to Africa. In contrast, the “American lineage” consists of the species originating in America, including samples of *S. portulacastrum* collected in Asia and Africa. In all trees, *Sesuvium portulacastrum* is not monophyletic. The African *Sesuvium portulacastrum* subsp. *persoonii* is nested within the “American lineage” as a part of the *Sesuvium portulacastrum* complex, either as a sister lineage to *S. portulacastrum* (the sample from Grenada) in the chloroplast tree (Fig. 5) or amongst the Central American samples of *Sesuvium portulacastrum* complex (Fig. 6). Due to its well-defined distribution range, this new taxon with clearly petiolate, shorter and thicker leaves is considered here as a subspecies of *S. portulacastrum*. However, the taxonomic status of *S. portulacastrum* subsp. *persoonii* needs further studies for the following reasons: (1) the lack of material from the Indian subcontinent, especially *S. repens* Willd. and *S. portulacastrum* (s.l.) from the Americas, Africa (e.g. *S. ayresii*) and Southeast Asia, precludes recognition



**Figure 5.** Phylogenetic relationships of perennial *Sesuvium* species from ML analysis of combined plastid sequences (rps 16 intron, trnL-trnF, atpB-rbcL, 1377 bp in total). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. ML bootstrap support/BI posterior probabilities are specified at the branch nodes (not shown when <50%).



**Figure 6.** Phylogenetic relationships of perennial *Sesuvium* species from ML analysis of ITS sequences. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. ML bootstrap support/BI posterior probabilities are specified at the branch nodes (not shown when <50%).



**Figure 7.** Phylogenetic relationships of perennial *Sesuvium* species inferred from combined analysis of plastid (rps 16 intron, trnL-trnF, atpB-rbcL) and ITS sequences. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. ML bootstrap support/BI posterior probabilities are specified at the branch nodes (not shown when <50%).

of the exact relationships of all taxa within the large “American lineage” and (2) *Sesuvium portulacastrum* is still considered a highly variable species distributed worldwide (Bohley et al. 2017). However, some “strange” forms of this species in Asia (especially in the large biogeographical region of Malesia) are present in the European herbaria in a very limited quantity and were not included in the molecular analysis. The preliminary morphological studies (Sukhorukov et al., in prep.) suggest that at least two species need to be reinstated to species rank (*S. parviflorum* DC. and *S. microphyllum* Willd.) and some new taxa from South and Central America are yet to be described.

### Taxonomy of perennial *Sesuvium* in Africa

One American species (*S. verrucosum*) and one new subspecies (*S. portulacastrum* subsp. *personii*) are added to the taxonomic list of *Sesuvium* in Africa. The authors also propose to merge *S. crystallinum* with *S. crithmoides*. According to the latest investigations in Angola, *S. sesuvioides* previously considered as an annual species (e.g.

Gonçalves 1970, Sukhorukov et al. 2017) can be a facultatively short-lived perennial herb. In total, six perennial species in Africa (*S. ayresii*, *S. congense*, *S. crithmoides*, *S. portulacastrum*, *S. verrucosum* and the facultatively short-lived *S. sesuvioides*) and one subspecies of *S. portulacastrum* mentioned above have been accepted.

### Diagnostic key to perennial *Sesuvium* in Africa

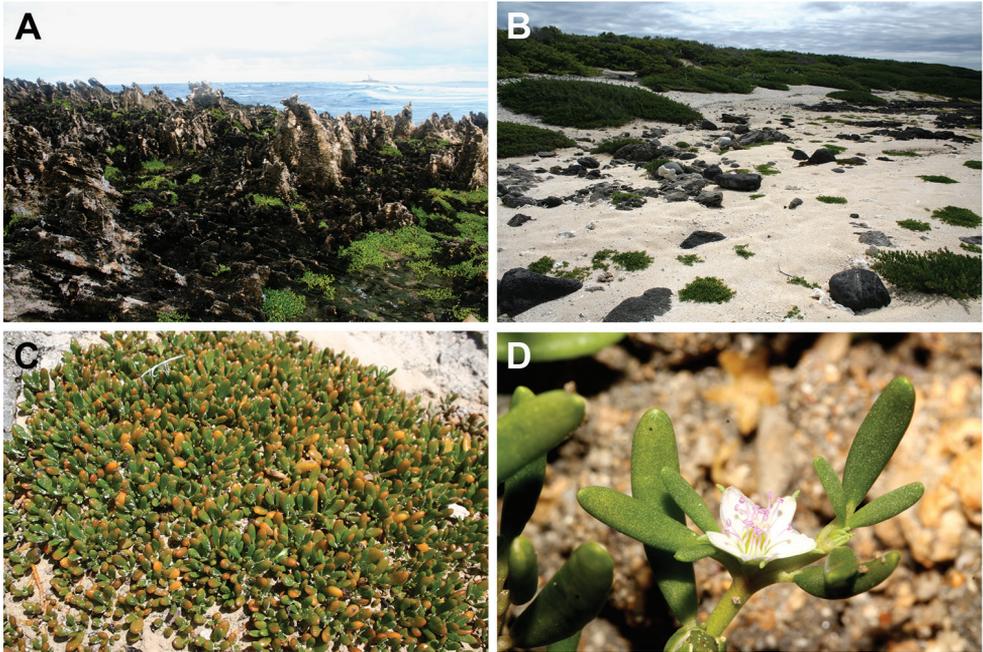
- 1 Stems and leaves densely papillate (plants grayish); flowers sessile or with short (up to 3 mm) pedicels.....**2**
- Stems and leaves glabrous (younger leaves may be papillate); flower sessile or pedicellate (pedicels up to 15 mm) .....**4**
- 2 Each flower surrounded by 4(–6) bracteoles..... ***S. crithmoides***
- Each flower with 2 bracteoles.....**3**
- 3 Old stems stout, hardened; leaves linear to lanceolate (lower leaves often spatulate); perianth cup (concurrent part of the segments) roundish; aril tightly adherent to the seed coat..... ***S. congense***
- Old stems not hardened; leaves oblong; perianth cup turbinate; aril peeling off the seed coat near the cotyledon area (appearing as a white fold) ..... ***S. verrucosum***
- 4 Leaves up to 25(28) mm long; flowers sessile or shortly pedicellate (pedicels up to 3.5 mm) .....**5**
- Leaves usually longer; pedicels 7–12(20) mm long.....**6**
- 5 Perennial; leaves terete or semi-terete; flowers sessile or shortly pedicellate (pedicels up to 3.5 mm), white or pink..... ***S. ayresii***
- Short-lived perennial or annual; leaves conduplicate; flowers sessile, mauve ....  
.....***S. sesuvioides***
- 6 Ramification not rampant; leaves clearly petiolate (petioles 5–10 mm long), usually less than three times longer than wide (all blades including those of upper leaves ovoid or oblong, 20–40 × 10–15 mm), and very fleshy (3–9 mm thick)..... ***S. portulacastrum* subsp. *persoonii***
- Ramification rampant; leaves shortly petiolate (petioles up to 3 mm long), more than three times longer than wide (all blades oblong-spatulate or oblanceolate, 20–60 × 5–10(12) mm) and thinner (1.5–4 mm) .....  
..... ***S. portulacastrum* subsp. *portulacastrum***

### Synopsis of perennial *Sesuvium* in Africa

***Sesuvium ayresii* Marais, Kew. Bull. 32(2): 483 (1978)**

Fig. 8

**Holotype.** MAURITIUS [main island], Fort William, Sep 1860, *Ph.B. Ayres s.n.* (K000076290! iso – LE!).



**Figure 8.** *Sesuvium ayresii*: **A** the only species growing on the islet (Ile aux Fous, Mauritius, 1 August 2007) **B** clumps on sandy beach (Ilot Gabriel, Mauritius, 6 August 2007) **C** an individual clump on calcarenite (Ile de la Passe, Mauritius, 3 February 2007) **D** close-up of a flower (Rivulet Terre Rouge Bird Sanctuary, Mauritius, 1 September 2017). Photographs by F.B.V. Florens.

**Description.** The description of *S. ayresii* was provided by Marais (1978). The most indicative characters of this species are small (up to 25–28 mm long, but usually smaller) terete or semi-terete leaves and (sub)sessile flowers (see Marais 1978, Hartmann 2002). Additionally, Marais (1978) reported a smaller number of stamens (12–20) that have never been observed in *S. portulacastrum* (stamens more than 30). The smaller seed size (~1 mm) of *S. ayresii* compared with *S. portulacastrum* (Marais 1978) seems to be an insignificant diagnostic trait. Leaf shape and leaf size are very variable, sometimes within a given individual.

**Ecology.** *Sesuvium ayresii* usually grows on coral rocks, basalts or calcarenites (Marais 1978), but it also can be encountered on sandy seashores, like many other species of the genus. The records of *Sesuvium* from the calcarenite islets of Les Bénitiers (Johnston 1894) and Rochers des Oiseaux (Johnston 1895) probably belong to *S. ayresii*. *Sesuvium ayresii* is reported as the only member of the genus in the Mascarenes (Marais 1990).

**Additional specimens examined** (Fig. 14). MAURITIUS [main] Island: Gris Gris, [no date, before 1932], *Vaughan 653* (MAU 0017795); Rocky coast near Rivière des Anguilles, 8 Dec 1962, *Edgerley s.n.* (MAU 0017801); Post Lafayette, east coast, 11 Jan 1973, *Lorence 189* (K, MO324309); estuary of Black River, 10 Sep 1981, *L. Averyanov 446* (MHA); Mer Rouge, 13 Mar 2004, *Pynee et al. s.n.* (MAU

0012461); Cap Malheureux, 26 Apr 2004, *Pynee s.n.* (MAU 0017803); Albion, 10 Nov 2011, *Pynee s.n.* (MAU 0009004); Rivulet Terre Rouge Bird Sanctuary, 01 Sep 2017, *Baider CB 2729* & *V. Florens* (MAU 0023815); Mauritius [islets] Island: Gunner's Quoin or Quoin de Mire, 1871, *Horne 129* (K); 06 Aug 2007, *Baider CB 677* & *V. Florens* (MAU 0023819); 07 Aug 2007, *Baider CB 701A* & *V. Florens* (MAU 0023820); 07 Aug 2007, *Baider CB 701B* & *V. Florens* (MAU 0023821); Ile de la Passe, 26 Oct 1888, *Johnston s.n.* (E00651982); 29 Nov 2003, *Baider CB 588* & *V. Florens* (MAU 0023826); Ile aux Fouquets, 4 Nov 1962, *Rountree s.n.* (MAU 0017798); Ilot Marianne, east coast, 13 May 1956, *Vaughan s.n.* (MAU 0017796); 18 Jan 1975, *D. Lorence 1059* (K, MAU 0017800); 28 Nov 2007, *Baider CB 551* & *V. Florens* (MAU 0023822); 31 Jul 2007, *V. Florens s.n.* (MAU 0023823); Ilot Sancho, south coast, 15 Aug 1974, *D. Lorence 943* (K, MAU 0017799); Ile D'Ambre, 21 Dec 2003, *Baider CB 783A* & *V. Florens* (MAU 0023827); 21 Dec 2003, *Baider CB 783B* & *V. Florens* (MAU 0023828); Ilot Bernache, 21 Dec 2003, *Baider CB 814* & *V. Florens* (MAU 0023829); Ilot Gabriel or Gabriel Islet, 20 Apr 2006, *Pynee s.n.* (MAU 0017804, MAU 0017805), 06 Aug 2007, *Baider CB 1942*, *V. Florens* & *D. Hammond* (MAU 0023825); Ile aux Fous, 01 Aug 2007, *V. Florens* & *D. Hammond s.n.* (MAU 0023824); Rodrigues [main] Island: Plaine Coral, Jul 1970, *Cadet RO218/2604* (MAU 0017807); 1874, *Balfour s.n.* (E00651981, K); Rodrigues [islets] Island: Frigate Island, Jan 1963, *Staub s.n.* (MAU 0017806); Ile Gombrani, 10 Jan 2004, *Baider CB 932* & *V. Florens* (MAU 0023817); Ile aux Crabes, 13 Jan 2004, *Baider CB 1036* & *V. Florens* (MAU 0023818); Ile aux Cocos, 15 Jan 2004, *V. Florens s.n.* (MAU 0023816).

**General distribution.** Endemic to the Mascarenes.

**Conservation status.** The species should be considered Near Threatened (NT) according to the IUCN red list criteria (IUCN 2017). This assessment is based on the species' EOO of 24,241 km<sup>2</sup> and AOO of 68 km<sup>2</sup>; together with other factors including the species' habitat being restricted to seashores affected by salt spray, fragmentation of the populations and a high probability of losing sites in the near future due to habitat transformation (construction of hotels, improvement of seashores by removal of vegetation, dumping of refuse in the coastal belt), especially on mainland Mauritius. Only a few of the populations are located in areas with some degree of protection such as Nature Reserves or National Parks (one on Rodrigues; nine on Mauritius), most of them being on small islets. Some records are over 50 years old and need to be updated to determine any decline in its geographic distribution. Competition with invasive alien plants seems not to be a serious problem for this species, although sea-level rise is reducing the area of suitable habitat.

***Sesuvium congense* Welw. in Oliver, Fl. Trop. Afr. 2: 586 (1871)**

**Lectotype** (Gonçalves 1965): [ANGOLA, Bengo Province] Dist. Ambriz, Habit. freq. [ent] in rupestribus et glareosis ad ostia flum. Onço in Mossul [Ambriz Municipality,

frequent in mountainous and gravelly places along the estuary of the river Onço in Mosul] fl. & fr. Nov 1853, *Welwitsch* 2382 (LISU214650 – photo! isolectotypes – BM000839899!, BM001209754! K000076293! LE!, P04602200!)

**Nomenclatural notes.** A specimen in LISU has been wrongly stated to be the holotype by Gonçalves (1965) and then by Bohley et al. (2017). Indeed, the sheets of *S. congense* with the same label and collection number are present in several herbaria, as are many other specimens of Welwitsch’s material from Angola (Albuquerque et al. 2009). No specimens and herbarium were cited in the protologue (Welwitsch in Oliver 1871) except the location “Lower Guinea, Congo [Angola as a part of Kongo Kingdom], Ambriz”. The lectotype selected here is in accordance with Art. 9.9 of ICN (McNeill et al. 2012). The synonymisation of *S. congense* with *S. portulacastrum* (Adamson 1962) is incorrect.

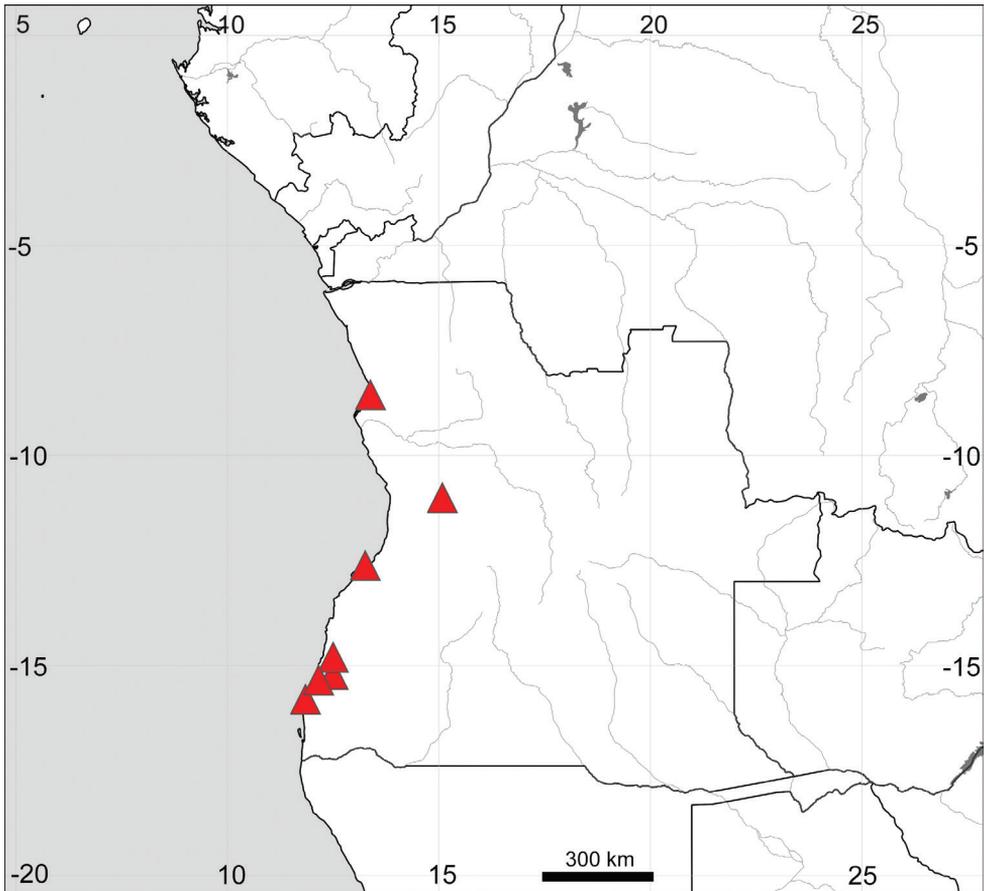
The epithet “congense” probably refers to the “Kingdom of Kongo”, a West African kingdom that united the territories of northern Angola (incl. Bengo and Zaire provinces) and the western part of DR Congo, as well as portions of Republic of Congo and Gabon.

**Description.** The morphological description of the species is provided in Oliver (1871), Gonçalves (1970) and Bohley et al. (2017). This species is sometimes confused with branched *S. sesuvioides* (especially when the upper parts of the branches are collected) with similar smooth seeds. In contrast to *S. congense* or related *S. crithmoides*, *S. sesuvioides* is glabrous, with turbinate or balustriform flowers (without a rounded perianth cup).

**Additional specimens examined.** ANGOLA: **Benguela prov.:** Lengue, 19 Dec 1932, *Grossweiler* 9715 (BM); 20 km W of Benguela, Baía Azul, 1 Apr 1973, *P. Bamps & S. Martins* 4372 (BR0000013827366); 74 km S of Benguela along road to Cuio, 74 m alt., 25 Dec 2016, *C. Klak* 2557 (BOL); **Namibe prov.:** Maiombo river, Oct 1859, *Welwitsch* 2395 (BM); Mossamedes [Namibe], valley of Rio Mukungo, Aug 1937, *H. Humbert* 16407 (BM); Mossamedes [Namibe], Porto Alexandre, 26 May 1937, *A.W. Exell & F.A. Mendonça* 2294 (BM); Mossamedes [Namibe], Porto Alexandre, Aug 1937, *H. Humbert* 16375 (BM); ca. 22 km NE of Namibe, 18 Jan 2009, *Winter* 7683 (PRE); road to Baba from Lucira road, 23 Jan 2009, *Winter* 7779 (PRE); Namibe, 9.7 km S of airport turn-off, 23 Jan 2009, *Winter* 7762 & 7766 (PRE); 27 km E of Namibe, 252 m, 19 Dec 2016, *C. Klak* 2554 (BOL).

**General distribution** (Fig. 9). Coastal sandy areas in Angola, from Bengo to Namibe provinces, recorded at altitudes between 74 and 252 m a.s.l. (Gonçalves 1965).

**Conservation status.** *Sesuvium congense* has an estimated EOO of 54,340 km<sup>2</sup> (which would place the species in LC) and AOO of 36 km<sup>2</sup> (which would place it in EN). However, it is unknown if the species persists in some of these localities. The size of its populations and their threats are little known, but the populations on the seashore and near rivers are probably impacted by development and agriculture. Therefore, the species, at this point in time, should be considered Data Deficient (DD) according to the IUCN Red List Criteria (IUCN 2017).



**Figure 9.** Distribution map of *Sesuvium congense*.

***Sesuvium crithmoides* Welw., Ann. Conselho Ultramar. ser. 1: 586 (1859)**

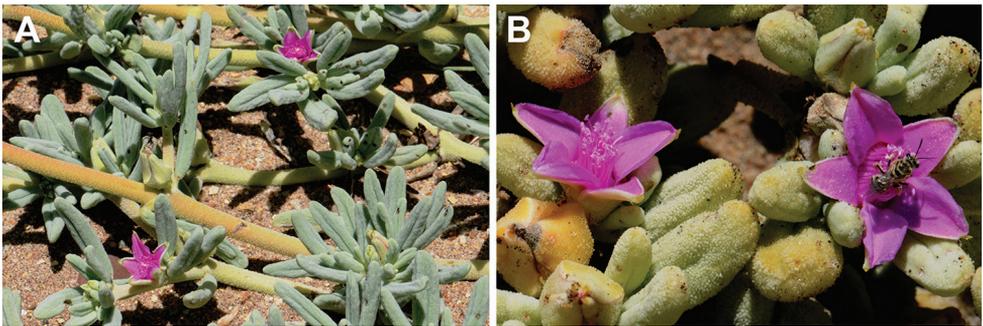
Figs 10, 11

**Lectotype** (designated here by Sukhorukov). ANGOLA, distr. Loanda [Luanda], in arenosis maritimis de Ilha de Loanda [on sandy seashores of Loanda Island], 12 Jun 1858, *Welwitsch 2386* (BM000839897! specimen on the left; isolectotypes – BM001209752! BM001209753! K000076292! P04602195! COI00070549! [photo seen], LISU031837! [photo seen]).

**Note.** Welwitsch collected this new species in 1854 and 1858 from several neighbouring locations in Luanda Province. All examined sheets were labelled with the same collector's number (2386) and the location of the lectotype specimen is close to that mentioned in the protologue (Barra do Dande settlement, ca. 30 km N of Luanda). Surprisingly, none of the authentic specimens contained the name of Barra do Dande (Welwitsch 1859) and the species itself was not mentioned in a subsequent treatment of the genus (Welwitsch in Oliver 1871).



**Figure 10.** General view of *Sesuvium crithmoides* (incl. *S. crystallinum*) on the dunes of Rio dos Flamingos, Angola. Photographs by C. Klak and P.V. Bruyns (December 2016).



**Figure 11.** Parts of the plant of *Sesuvium crithmoides*: **A** reproductive shoots **B** close-up view of flowers. Photographs by C. Klak and P.V. Bruyns (at the mouth of Rio dos Flamingos, south of Namibe, Angola, December 2016).

–*Sesuvium mesembryanthemoides* Welw., Ann. Conselho Ultramar. ser. 1: 557 (1859), nomen nudum

**Note.** Welwitsch (1859) mentioned the name *Sesuvium mesembryanthemoides* (nomen nudum) for the first time, but did not describe the plant morphologically (“Uma nítida espécie de *Sesuvium*” [a distinct species of *Sesuvium*]). He probably supposed that it was conspecific with *S. crithmoides*, which was described in the same article (Welwitsch 1859). As mentioned above, all sheets of *S. crithmoides* and *S. mesembryanthemoides* (nomen), collected by Welwitsch, have the same collection number (2386).

=*Sesuvium mesembryanthemoides* Wawra in Wawra & Peyr., *Sitzungsber. Acad. Wien, Math.-Nat.* 38: 564 (1860).

**Lectotype** (designated here by Sukhorukov). [ANGOLA] Benguela, *Dr Wawra 210* (LE!).

**Note.** Interestingly, Wawra collected the same species in Angola independently from Welwitsch and used the same epithet “*mesembryanthemoides*” for his new *Sesuvium*. Unfortunately, the original sheets of *S. mesembryanthemoides* Wawra cited in the protologue (“in littore maris prope Benguelam, *Wawra 210*”: Wawra and Peyritsch 1860) were destroyed in B, W or WU (Bohley et al. 2017; Johannes Walter, pers. comm.). Wawra and Peyritsch (1860) reported the presence of four to six bracteoles in the flowers of *S. mesembryanthemoides* and it therefore evidently differs from *S. congense* (with similar narrow leaves), which has flowers with two bracteoles only. Bohley et al. (2017) have designated the lectotype of *S. mesembryanthemoides* Wawra in the herbarium LISU (with isoelectotypes in BM, BR, C, COI, K, LE) based on Welwitsch’s specimens (“Mossamedes [Namibe], seashore, 1 Jul 1859, *Welwitsch 2389*”). However, the material collected by Welwitsch in Namibe province of Angola is not mentioned in the protologue of *S. mesembryanthemoides* Wawra and does not belong to the original material. Therefore, this lectotypification cannot be accepted. A lectotype using a Wawra’s specimen (syntype) seen in LE has been selected.

=*Sesuvium crystallinum* Welw. in Oliver, *Fl. Trop. Afr.* 2: 586 (1871).

**Lectotype** (designated here by Sukhorukov): [ANGOLA] Mossamedes [Namibe], hab.[itat] in arenosis maritimis pr.[ope] Mossamedes [on sandy seashores near Mossamedes], Jul 1859, *Welwitsch 2389* (BM000839898! isoelectotypes – C, COI, G! K! LE! LISU).

Two locations (“Mossamedes” and “Benguela”) were indicated in the protologue. The lectotype of *Sesuvium crystallinum* is selected here from the specimens collected by Welwitsch with the number 2389 which were located in different herbaria including LISU (“holotype” in Bohley et al. (2017); not correctable to “lectotype” under Art. 7.10).

**Taxonomic and nomenclatural notes.** The type material of *S. crithmoides* comprises the plant fragments with narrow (linear or lanceolate) leaves reaching 8 cm in length. The leaf length and shape is a single character used for its delimitation from the closely related *S. crystallinum* (Gonçalves 1970) and *S. mesembryanthemoides* Wawra (Bohley et al. 2017). Both species are considered to have shorter (up to 5 cm) and broader leaves. However, the authentic material and protologue of *S. mesembryanthemoides* clearly state that this plant was described as a remarkable species with subtriquetrous-terete (narrow) leaves (Wawra in Wawra and Peyritsch 1860). Therefore, the use of *S. mesembryanthemoides* as a priority name against *S. crystallinum* (Hartmann 2002, Figueiredo and Smith 2008, Bohley et al. 2017) with broader and shorter leaves cannot be accepted. In all characters, including leaf length and shape, *S. crithmoides* and *S. mesembryanthemoides* are clearly conspecific.

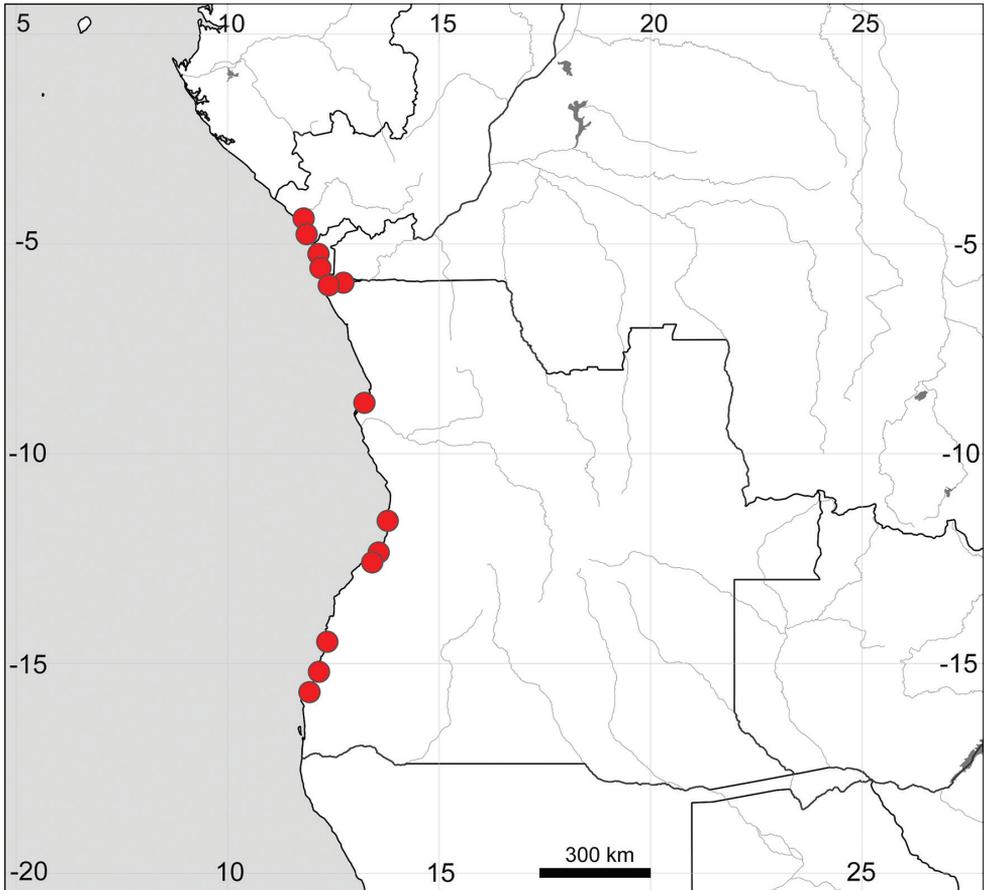
The authors propose to merge the broad-leaved individuals (*S. crystallinum*) with *S. crithmoides* for the first time. Observations by the authors in Angola (C. Klak and P. Bruyns) did not confirm the separate existence of “short-leaved” or “long-leaved” plants. Other morphological and carpological characters are the same in both *S. crithmoides* and *S. crystallinum*. Only *S. crithmoides* (Winter 7786 (PRE) from Baba, Angola) was included in the molecular analysis (Bohley et al. 2017).

*Sesuvium crithmoides* was considered as an endemic to Angola, although with possible records in coastal areas of the DR Congo (Bohley et al. 2017). One collection of *S. crithmoides* from the DR Congo (see also Hauman 1951, sub *S. mesembryanthemoides*) has been found and was also identified for the Republic of Congo for the first time (previously wrongly labelled as *Sesuvium portulacastrum*). All specimens seen from the Republic of Congo or the DR Congo have long and narrow leaves.

**Additional specimens examined.** ANGOLA: **Benguela prov.:** Benguela, [without date] *H. Vanderyst* 13141 (BR0000013827410); near Benguela, Lobito Bay, 1 Sep 1906, *H. Bolus* 12453 (BOL); S of Benguela, seashore at Cuio village, 25 Dec 2016, *C. Klak* 2558 (BOL); **Cabinda prov.:** Landana, 9 Aug 1895, *A. Dewevre* 231 (BR0000013827380), Landana, 15 Aug 1913, *Bequaert* 616 (BR000000871151); Cabinda, Sumba village, 30 Nov 1957, *Lebrun* 11195 (BR0000013827441; K); **Cuanza Sul prov.:** Praia de Sousa, 11°36'S 13°47'E, 3 Feb 1975, *J.D. Ward* 82 (K, WIND); **Luanda prov.:** Luanda, *Welwitsch* 2380 (LE), the same place, 13 Sep 1955, *J. Lebrun* 10905 (BR0000013827403); **Namibe prov.:** Cabo Negro, Sep 1859, *Welwitsch* 2387 (BM); Cabo Negro, Aug 1937, *H. Humbert* 16391 (BM); the same place, 15 Apr 1973, *P. Bamps et al.* 4519 (BR0000013827465); Mossamedes [Namibe city], 1937, *L.W. Carrisso and F. Sousa* 218 (BM); Mossamedes, 21 Sep 1955, *J. Lebrun* 10926 (BR0000013827472); Baba, 23 Jan 2009, *P.J.D. Winter* 7786 (LUBA, PRE); seashore at mouth of Rio dos Flamingsos, 17 Dec 2016, *C. Klak* 2551 (BOL); DEMOCRATIC REPUBLIC OF CONGO: **Kongo Central prov.:** Banana, [without date] *Gillet s.n.* (BR0000013827434); [Nature Reserve] Luki-Mayumbe, 1959, *Flamigni* 10773 (BR0000013827427); REPUBLIC OF CONGO (new records): Kouilou, 5 Sep 1962, *L. Makany* 63 (P04602222); Djeno Region [Pointe-Noire], 26 Jan 1966, *C. Farron* 4795 (P04602197 & P04602199); Pointe-Noire, Dec 1958, *J. Koechlin* 5528 (P04602193).

**General distribution** (Fig. 12). Angola, Democratic Republic of Congo, Republic of Congo. *Sesuvium crithmoides* has been introduced to USA (Georgia, Glynn county, Brunswick, on ballast, 15 Aug 1902, *R.M. Harper* 1524 (BM!); see also Small (1933)), probably as casual and not naturalised species (Ferren 2003). The specimen seen also has long and narrow leaves.

**Conservation status.** *Sesuvium crithmoides* has an estimated EOO of 177,271 km<sup>2</sup> and AOO of 56 km<sup>2</sup>. It was found to be common in two localities in Angola (*C. Klak* 2551 & 2558), where it grows within 50 metres of the sea. Sources of disturbance include vehicles driven along the beach, which was observed near Namibe city. However, vehicles are even now rather few in Angola and much of the southern, very arid Angolan coastline is still relatively pristine. Due to its large EOO and low threat level, the authors therefore recommend this species to be classified as Least Concern (LC) according to the IUCN Red List Criteria (IUCN 2017).



**Figure 12.** Distribution map of *Sesuvium crithmoides*.

*Sesuvium portulacastrum* (L.) L., *Syst. Nat.*, ed. 10(2): 1058 (1759).

≡ *Portulaca portulacastrum* L., *Sp. Pl.* 1: 446 (1753).

**Lectotype** (Wijnands 1983). Hermann (1698), *Icon.* 212 [112, a typographic error], as “*Portulaca corassavica* ...”.

Two subspecies of *S. portulacastrum* growing in Africa have been accepted.

*Sesuvium portulacastrum* subsp. *portulacastrum*

Fig. 13

= *Sesuvium brevifolium* Schumach. & Thonn. in Schumacher, *Beskr. Guin. Pl.*: 233 (1827).

**Lectotype** (designated here by Sukhorukov): Danish Gold Coast, Guinea [probably SE Ghana], *P.E. Isert s.n.* (C10004542! [photo seen]).



**Figure 13.** Parts of the plant of *Sesuvium portulacastrum* subsp. *portulacastrum*: **A** vegetative shoots **B** reproductive shoots. Photographs by M. Salas-Pascual (Gran Canaria, Canary Islands, Spain, July 2017).

The lectotype is chosen due to inclusion of two elements in the protologue (Schumacher 1827), a specimen cited and a drawing (Table 216, Fig. 1).

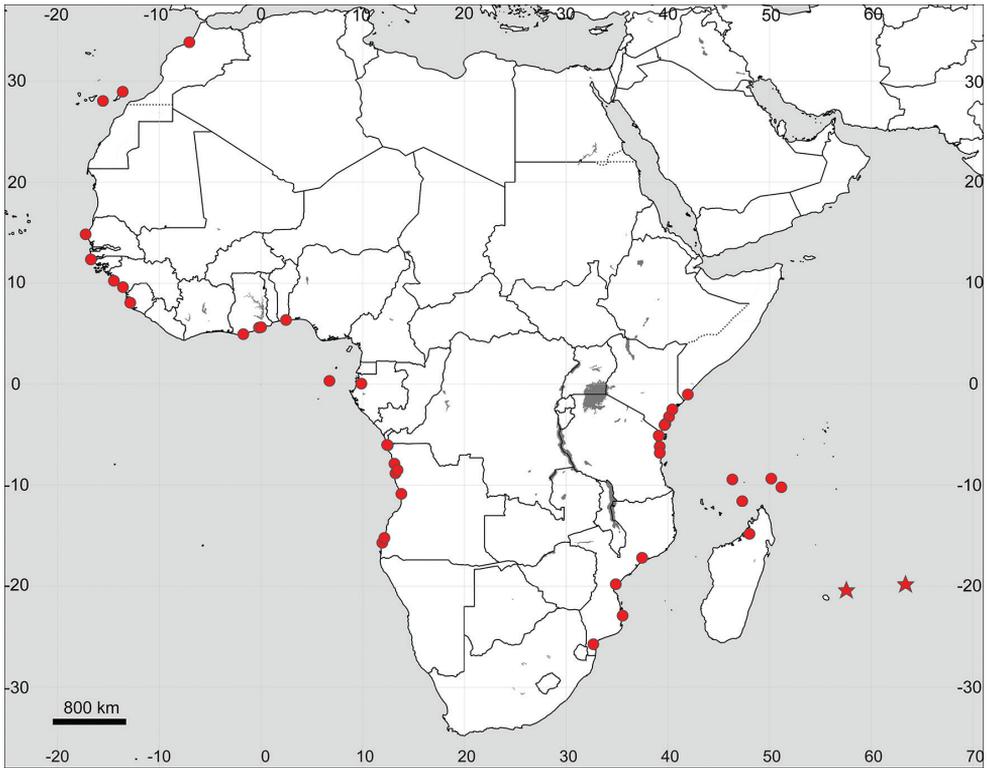
**Taxonomic notes.** The autonomous subspecies is of American origin and is known in many parts of tropical Africa and other continents, especially in regions with a hot and humid climate. According to the lectotypification undertaken by Wijnands (1983), the “true” *S. portulacastrum* is present in Central America (including the Caribbean Islands). The following characters distinguish this subspecies: rampant ramification, glabrous stems and adult leaves with mamillate epidermis, petioles up to 3 mm, oblong-spatulate leaves of 20–60 × 5–10(12) mm and 1.5–4 mm thick, conspicuous (7–12 mm) pedicels, flowers 10–15 mm in diameter and slightly elongated seeds. This description makes sense, because the species is non-uniform in its morphological characters (e.g. leaf length, presence of papillae on stems and leaves, seed ornamentation) and is corroborated by the molecular phylogeny (Bohley et al. 2017). Although *S. portulacastrum* is considered to have numerous synonyms (Bohley et al. 2017), at least some of them need further studies due to the presence of morphological differences, e.g. *S. microphyllum* Willd. (Caribbean Islands), *S. sessile* Pers. (South America?) or populations growing in Southeast Asia. In addition, *Sesuvium* is represented in Central America by at least six taxa (Sukhorukov et al., in prep.) and two of them have to be described as new species.

From humid coastal parts of West Africa, only one perennial species was described, *S. brevifolium* Schumach. & Thonn. (Schumacher 1827). This species has spatulate or oblong leaves with very short petioles, the characters being typical of *Sesuvium portulacastrum*. For this reason, *S. brevifolium* is merged with *S. portulacastrum* subsp. *portulacastrum*, this being in agreement with other accounts (Hooker 1849, Welwitsch in Oliver 1871, Bohley et al. 2017).

The autonomous subspecies of *S. portulacastrum* is distributed along the sea shores of many parts of tropical and subtropical Africa (Exell 1944, Jeffrey 1961, Gonçalves 1979, Gilbert 1993, Friedmann 1994, Sosef et al. 2006, Lisowski 2009, Acebes-Ginováes et al. 2010) and it seems to be present in almost all regions of Africa except South Africa. The causes of such invasion to seashore communities in Africa or in other

regions of the Old World are not clear. It can be partially explained by the cultivation of *S. portulacastrum* in some areas for ornamental purposes, but mostly by transportation of its seeds in the sand ballast of ships sailing between America and other parts of the world in the 15<sup>th</sup>–17<sup>th</sup> centuries. The examination of the herbarium specimens indicates that *S. portulacastrum* was sometimes collected in the same places as native *Sesuvium* (*S. congense* or *S. crithmoides*), e.g. on seashores of Kongo-Central province (DR Congo) and Angola.

**Additional specimens examined.** ANGOLA: Luanda, Praia do Bispo, Dec 1858, *Welwitsch 2385* (BM); [Bengo prov.] Ambriz, [no date] *Welwitsch 2383* (K); [Bengo prov.] Dande River, 17 Sep 1955, *J. Lebrun 10908* (BR0000013828103); Mossamedes [Namibe], 10 Jan 1956, *E.J. Mendes 1250* (BM); [Namibe prov.] Cabo Negro, 15 Apr 1973, *P. Bamps et al. 4522* (BR0000013828097, K, LE); Kwanza Sul prov., 10°51'S 13°48'E, 2 Feb 1975, *C.J. Ward and J.D. Ward 68* (K); BENIN: Cotonou beach, 22 Mar 1970, *L.A. Assi 11134* (G); DEMOCRATIC REPUBLIC OF CONGO: [Kongo Central prov.] Banana, 16 Jul 1915, *Bequaert 8014* (BR0000013828165); Bula-Bemba, 2 Sep 1958, *J. Wagemans 1982* (BR0000013828172); GABON: Estuaire prov., 22 Feb 1985, *A.M. Louis 1728* (BR0000013828028); GHANA: Sekondi, 3 Oct 1925, *H. Howes 980* (K); nr Tema harbor, 20 Sep 1960, *J.O. Ankrab 20547* (K); Accra, 12 Aug 1958, *J. Lebrun 11334* (BR0000013828042); Greater Accra Region, Ambassador Beach, 26 Feb 1977, *A.J.M. Leeuwenberg 11123* (BR0000013828035); GUINEA: Conakry, Aug 1954, *H. Jacques 7002* (LE); [Boké Region] Boffa pref., Bel-Air, 5 Feb 1979, *S. Lisowski 51828* (BR0000013827567); GLORIOSO ISLANDS: Iles aux Crabes (*C. Fontaine*, obs.; image seen!); KENYA: Kilifi distr., Malindi, 3 Dec 1961, *R. Polhill and S. Paulo 895* (BR0000013828059, K, P04602215); Mikindani distr., Mtwara, 12 Mar 1963, *H.M. Richards 17861* (K); Mombasa, 13 Dec 1969, *Bally 13736* (G); Tana River distr., Tana delta, Shekiko Camp, 25 Apr 1990, *S.A. Robertson 6121* (K); MADAGASCAR: [no exact location and date] herb. *Petit-Thouars s.n.* (P04600013); MOROCCO: Skhirat, 10 Jun 1937, *J. Gattefosse 138* (G, P05196618); MOZAMBIQUE (selected specimens): Delagoa [Maputo] Bay, 1890, *H. Junod 258* (G); Komati river, 15 Jul 1922, *C.E. Moss 7040* (BM); Lorenzo Marques, 31 Aug 1959, *R. Watmaugh 313* (M); Maputo, 3 Jun 1970, *M.F. Correia and A. Marques 1630* (E00651988); Sofala province, Beira, 26 Feb 1972, *M.F. Correia and A. Marques 2812* (M); Maputo, 8 Mar 1979, *P.A. Schäfer 6707* (K); Inhambane prov., Massinga, Pomene, 20 Jun 1980, *J. de Koning 8197* (WAG1408388); Maganja da Costa, Praia Maraga, 15 Nov 1996, *A.R. Torre and M.F. Correia 14693* (BR0000013828134, M); [Massinga distr.] Pomene, 24 Sep 1980, *P.C.M. Jansen 7521* (BR0000013828110); SÃO TOMÉ & PRÍNCIPE: São Tomé [Island], Apr 1916, *A. Cortesão s.n.* (BM); SENEGAL: [Oussouye Dept.] Basse Casamance National Park, Kabrousse, 22 Dec 1976, *C. Van den Berghen 1582* (BR0000013827519); [Cap Vert Peninsula] Lake Retba, 20 Dec 1984, *D. Thoen 7367* (BR0000013827526); SEYCHELLES: Aldabra Island, 26 Feb 1968, *F.R. Fosberg 49547* (L1693568); Aldabra, South Island, Grand Cavalier, 11 May 1972, *D. Wood 1686* (E00651983); Farquhar Group, Farquhar Island, 2 Feb 1972, *Frazier*



**Figure 14.** Distribution map of *Sesuvium ayresii* (stars) and *S. portulacastrum* subsp. *portulacastrum* (circles, mapped only for Africa).

121 (K); Farquhar Group, St Pierre Island, 4 Oct 1941, *P.O. Wiehe 1681* (MAU 0023813, MAU 0023814); SIERRA-LEONE: Samu chiefdom, 22 Mar 1930, *R.R. Glanville 251* (BM, K); SOMALIA: Kodei village, 1°1'S 41°58'E, 29 Jun 1983, *J.B. Gillett et al. 5116* (K); SPAIN: Canary Islands (selected specimens): Lanzarote, Playa Honda, 24 Mar 2011, *F. Verloove 9276* (BR); La Laja beach, Las Palmas de Gran Canaria, 28°03'38.70"N, 15°25'12.28"W, 31 Jul 2017, *M. Salas-Pascual s.n.* (MW); Beach of El Águila, San Bartolomé de Tirajana, 27°46'38.80"N, 15°31'38.50"W, 31 Jul 2017, *M. Salas-Pascual s.n.* (MW); El Veril beach, San Bartolomé de Tirajana, 27°45'36.78"N, 15°33'50.77"W, 31 Jul 2017, *M. Salas-Pascual s.n.* (BR, MW); Edge of the Charca de Maspalomas, San Bartolomé de Tirajana, 27°44'24.96"N, 15°35'43.79"W, 31 Jul 2017, *M. Salas-Pascual s.n.* (MW); TANZANIA: Tanga, Tanga Bay, 4 Nov 1929, *Greenway 1853* (K); Zanzibar, Marahubi Beach, 22 Apr 1961, *H. Faulkner 2814* (BR0000013828073); Dar es Salam, 26 Aug 1968, *M. Batty 284* (K); TUNISIA: pers. comm. R. El Mokni (photo!).

**General distribution.** The subspecies seems to be widely distributed on the seashores of the tropics, but some populations from tropical America and SE Asia are distinct in their morphological characters. The distribution of *Sesuvium portulacastrum* subsp. *portulacastrum* in Africa is presented in Fig. 14.

***Sesuvium portulacastrum* subsp. *persoonii* Sukhor., subsp. nov.**

urn:lsid:ipni.org:names:77174974-1

*Sesuvium pedunculatum* sensu Sieber (in herb.) non Pers.

**Diagnosis.** Differs from the autonymous subspecies by the absence of rampant ramification, clearly petiolate leaves (petioles 5–10 mm long) that are usually less than three times as long as wide (all blades including those of upper leaves ovoid or oblong, 20–40 × 10–15 mm) and 3–9 mm thick.

**Holotype.** Republic of Cape Verde, Sal Island, 2 km W of Santa Maria town, 16.590246, -22.924272, sandy depressions near the sea, 30 Aug 2015, *A.P. Sukhorukov* 59 (MW0595660! iso – BR, G, K).

**Description.** Sprawling glabrous perennial herb (the shoots are often partially buried by sand and appear to be separate plants) with ramification not rampant; stems rooted or not, roundish, greenish or more often red (Fig. 15A, B), 3–5 mm in diameter, ascendent (not creeping); leaves opposite, petiolate; petioles 5–10 mm, reddish or green, broadened basally, leaf blades oblong, 20–40 mm long (the leaves on the shortened shoots are smaller), 10–15 mm wide, 3–9 mm thick, entire, green or reddish (Fig. 15C); flowers solitary in the leaf axils (each node bears one flower from one of the opposite leaves), ~10 mm in diameter, with two hyaline glabrous bracteoles; pedicels 3–5 mm, accrescent at fruiting stage up to 10(15–20) mm long; perianth bifid, apically acutish, green abaxially and pink adaxially (Fig. 15D), without prominent red glands at the tip of the segments; stamens ~50, pink, slightly shorter than perianth, filaments 5 mm long, anthers 0.4–0.6 mm long; ovary turbinate, with (2)3–4 stigmas; seeds ~20, black, roundish, ~1 mm across, completely covered with a funicular aril; seed surface smooth or slightly uneven.

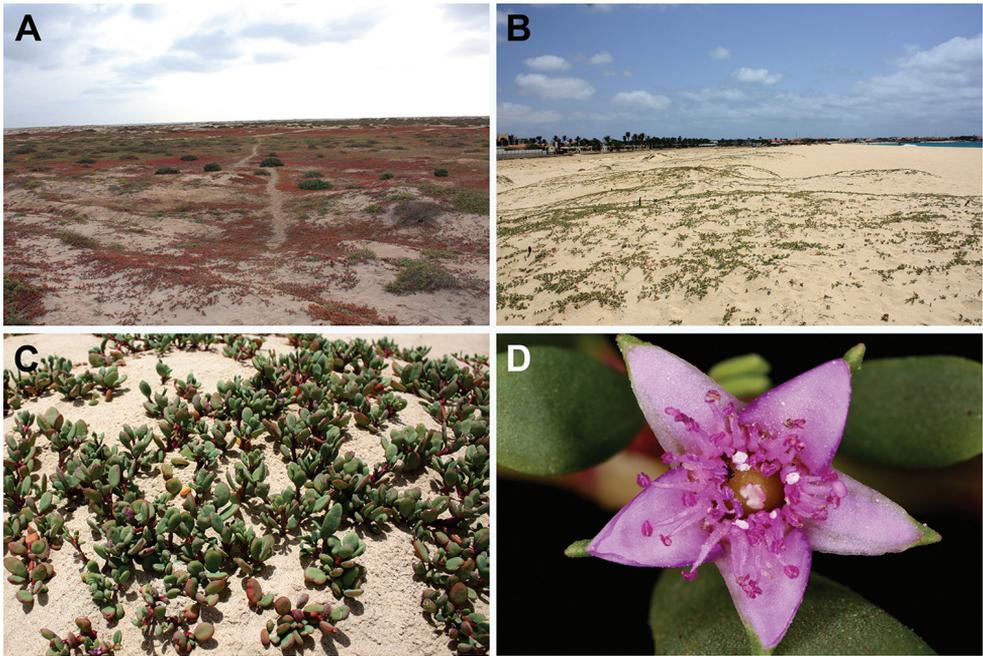
**Etymology.** The subspecies is named after Christiaan Hendrik Persoon (1761–1836), botanist and mycologist, who described several *Sesuvium* species.

**Ecology.** Sandy beaches near the sea and seasonally flooded, saline plains on the landward side of the coastal dune belt.

**Flowering and fruiting.** All year round, but most abundantly from September to May (at least in the Cape Verde Islands).

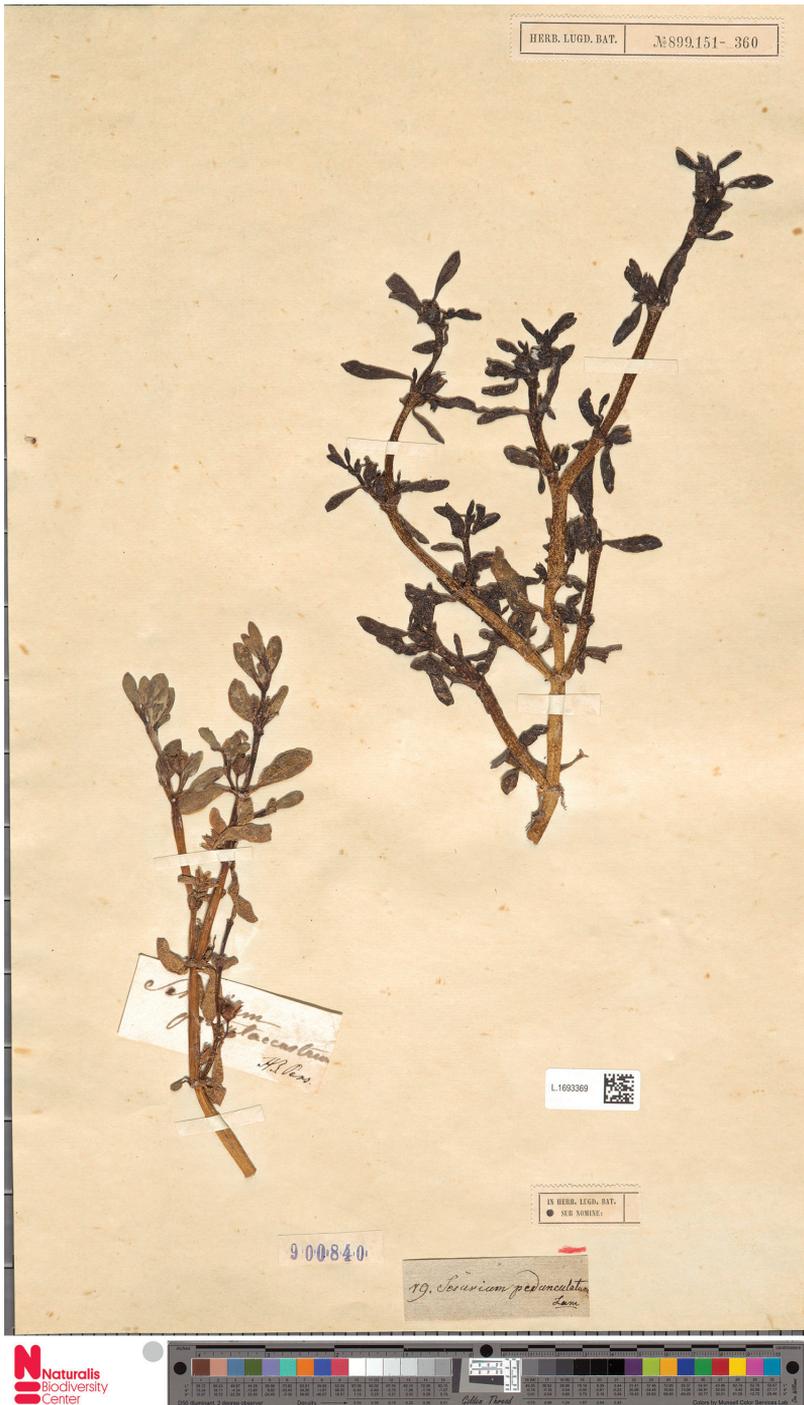
**Taxonomic and nomenclatural notes.** Franz Wilhelm Sieber labelled his *Sesuvium* collections from Senegal as *S. pedunculatum* Pers. The use of this name for the African material is very confusing but explained here.

The name was published by Persoon (1806), who provided a very short diagnosis mentioning pedicellate flowers (not petiolate leaves!) and noted that the species originates from India. It is assumed that Persoon probably did not see the plant in the wild. A specimen was found in the De Candolle herbarium (G-DC) that contains three fragments of different origin: two fragments of *S. portulacastrum* from the Caribbean and one fragment of Sieber's collection from Senegal (1825) named *S. pedunculatum*. However, the material kept at G-DC is not a type of *S. pedunculatum*, but only one of the duplicates sent by Sieber to different herbaria.



**Figure 15.** *Sesuvium portulacastrum* subsp. *persoonii*: **A** general view of the plant (of red colour) in saline depressions near the seashore, together with the subshrub *Arthrocaulon franzii* **B** *S. portulacastrum* subsp. *persoonii* on the seashore dunes **C** closer look at an individual **D** close-up of the flower. Photographs by A. Sukhorukov (**A–C** Sal Island, Cape Verde, August 2015) and A. Konstantinova (**D** Sal Island, Cape Verde, January 2016).

In Leiden (L), where the largest collection of Persoon’s types is deposited, one sheet with two different plant fragments and without any information about their locality (L1693369) was found with the label “*Sesuvium pedunculatum* Lam.” (!) (Fig. 16). Lamarck’s authorship of this species is clearly wrong (see Lamarck 1817: 141). The plant fragment on the left side of the herbarium sheet shows typical characteristics of the leaf shape found in *S. portulacastrum* subsp. *persoonii*, but it is named by Ch. H. Persoon as *S. portulacastrum*. The right fragment on the sheet belongs to the anonymous subspecies of *S. portulacastrum*. According to Persoon’s identification, his new species (*S. pedunculatum* Pers.) is indeed a synonym of the typical *S. portulacastrum* that has been recorded in India at least since the 17<sup>th</sup> century, probably as an alien species (BM, K and L). *Sesuvium pedunculatum* was treated as a variety under *S. portulacastrum* (as *S. portulacastrum* var. *pedunculatum*) by Cambessedes (in Saint-Hilaire 1829), who described this variety from temperate South America (!) as “les fleurs sont un peu plus grandes, et portées sur des pédoncules longs de deux à trois lignes” [the flowers are slightly larger, with the pedicels two to three lines long]. Furthermore, the synonymisation of *S. pedunculatum* and *S. portulacastrum* is confirmed by reference of Persoon (Persoon 1806) to the very clear drawing in Lamarck (1793) showing the shoot, flowers and fruits of typical *S. portulacastrum*. This image in Lamarck (1793)



**Figure 16.** A specimen kept in Leiden (L1693369) and probably seen by Persoon, containing both *Sesuvium portulacastrum* subsp. *portulacastrum* (right) and *S. portulacastrum* subsp. *personii* (left) from different locations (America and West Africa, respectively).

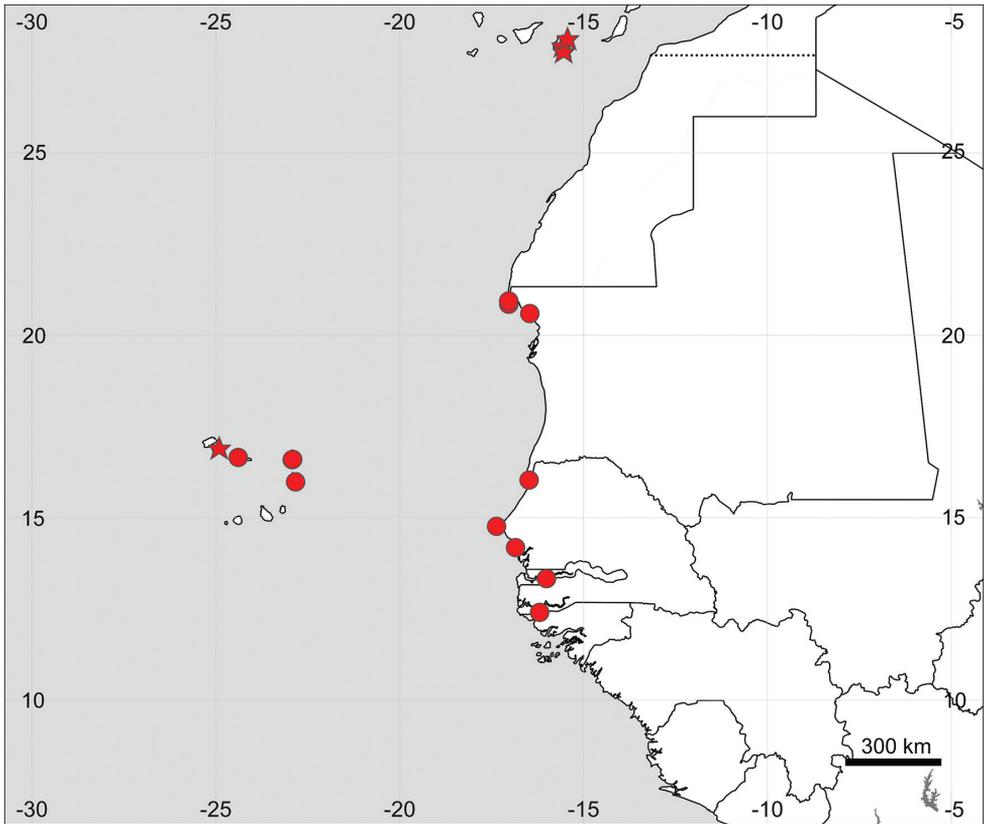
was chosen as the lectotype of *S. pedunculatum* by Hartmann (2002) and it is treated by her as a synonym of *S. portulacastrum*. Her opinion was accepted by Bohley et al. (2017). The authors also agree with Hartmann (2002) and Bohley et al. (2017) about the merger of *S. pedunculatum* with *S. portulacastrum* [subsp. *portulacastrum*].

*Sesuvium portulacastrum* subsp. *persoonii* is morphologically similar to *S. repens* Willd., a species found in coastal areas of the Indian subcontinent (E! G! K!). Both species possess distinctly petiolate leaves, but the latter species has much smaller (usually up to 20 mm long) leaves and shortly pedicellate flowers (pedicels at fruiting stage up to 6 mm long). *Sesuvium portulacastrum* always has tapered leaves with indistinct petioles up to 3 mm long. Additionally, the leaf thickness in *S. portulacastrum* subsp. *persoonii* varies from 3 to 9 mm and the leaves are especially thick (terete, almost roundish) in plants growing in saline depressions. In contrast to that, *S. portulacastrum* subsp. *portulacastrum* plants seen in the wild or in cultivation possess thinner (1.5–4 mm) leaves, in accordance with previous measurements (Bohley et al. 2017). Besides, plants with clearly petiolate leaves (*S. repens* and *S. portulacastrum* subsp. *persoonii*) have never been found in the Americas.

**Additional specimens examined** (Fig. 17). CAPE VERDE: São Nicolau Island, Praia Branca, 1851, *C. Bolle s.n.* (E00651990); Sal Island, Santa Maria, 19 Oct 1934, *M. Dinklage 3192* (BM, BR0000013828158); Sal Island, 1934, *A. Chevalier 44288* (P04602231); Boa Vista Island, Santa Monica beach, 15.981955, -22.831910, 10 Jan 2016, *A. Sukhorukov s.n.* (MW); GAMBIA: [Upper River Region] Keneba, Sep 1952, *D.S. Bertram s.n.* (K); GUINEA-BISSAU: Cacheu Region, S. Domingos sector, Candemba, 15 Apr 1997, *M.A. Diniz & A.E. Gonçalves 1777* (K); MAURITANIA: [Dakhlet Nouadhibou Region] Cape Arguin, Dalmas, 5 May 1895, herb. *E. Drake 6* (P04602228); Cansado, 1901, *A. Gruvel s.n.* (P04602226); Port Etienne [Nouadhibou], 12 Apr 1908, *anonym s.n.* (P04602227); SENEGAL: [without exact location] 1825, *Sieber 19* (E000651984; G00660404; K; LE; M; P05196607); [without exact location and year] *Sieber 112* (LE); [without exact location] 1859, *Perrotet 366* (G); St. Louis, 1902, *A. Chevalier 3469* (P04602206); Dakar, Hann beach, common, 23 May 1947, *J.T. Baldwin 5754* (K); St. Louis, 23 Jul 1960, *J.D. Kesby 20* (K); St. Louis, 14 Nov 1984, *P. Bamps 7642* (BR0000013827533); Poumekhor, saline depression, common, 2 Feb 1966, *J. Audru 3200* (P04602214); Joal-Fadiouth, 25 Jun 1973, *P. Geissler 6538* (G).

**General distribution.** The authors are still not sure whether this overlooked subspecies is native to West Africa. Plants with such habit are known from the seashores near Chennai, India (Anand Kumar, pers. comm., with an image sent to AS), but are not represented in any herbaria. One sheet from “Peninsula Indiae Orientalis” (herb. *Wight 963*, L1693577) corresponds to the African specimens of *S. portulacastrum* subsp. *persoonii* (labelled as “*S. portulacastrum* var.”) in leaf shape.

Reports of the occurrence and frequency of *S. portulacastrum* subsp. *persoonii* in West Africa until the early 20<sup>th</sup> century are inconsistent. The first reference for West Africa originates from Forster (1789, sub *S. portulacastrum*) who cited it for Santiago Island (Cape Verde Archipelago). Schmidt (1852) thought that this record was



**Figure 17.** Distribution map of *Sesuvium portulacastrum* subsp. *persoonii* (circles) and *S. verrucosum* (stars).

doubtful, because this plant was not mentioned by other travellers. However, Hooker (1849) reported *Sesuvium* as a common plant on seashores of the adjacent Senegal. F.W. Sieber was the first to collect the specimens of *S. portulacastrum* subsp. *persoonii* (collections from Senegal in early 19<sup>th</sup> century, identified as *S. pedunculatum*). Other specimens, named as *S. portulacastrum* and collected in mid-19<sup>th</sup> century in Cape Verde (São Nicolau Island) and Senegal (without exact location), are stored in the herbaria E and G, respectively. *Sesuvium portulacastrum* subsp. *persoonii* (under the names *S. pedunculatum* or *S. portulacastrum*) had not been reported amongst the most common plants in the checklists for West African plants until the early 20<sup>th</sup> century (e.g. Engler 1910). Chevalier (1920) cited *Sesuvium portulacastrum* subsp. *persoonii* (sub *S. portulacastrum*) for West Africa (Mauritania and Senegal), with subsequent records for Santiago and Sal Islands (Cape Verde), where it grows spontaneously on the seashores and in saline depressions (Chevalier 1935). M. Dinklage (collections from 1934, kept at BM!) noted the common and abundant *Sesuvium* populations on sandy beaches in Santa Maria village (Sal Island, Cape Verde). Recently, *S. portulacastrum* subsp. *persoonii* has been reported for several islands of Cape Verde Archipelago: Boa

Vista, Mayo, Sal, Santiago and São Vicente (Gilli 1976, Gonçalves 1995, Arechavaleta et al. 2005, all as *S. portulacastrum*).

All populations of perennial *Sesuvium* seen by the first author (AS) in Cape Verde belong to *S. portulacastrum* subsp. *persoonii*. It is common at least in the southern part of Sal Island on the sandy beaches and seasonally flooded saline depressions by the seashores near Santa Maria and in pristine landscapes in Boa Vista (e.g., Santa Monica beach in the southern part of the island). In Sal Island, *S. portulacastrum* subsp. *persoonii* is often a characteristic species of such habitats together with other dominant plants of coastal communities, such as *Arthrocaulon franzii* (Sukhor.) Pirainen & G.Kadereit ( $\equiv$  *Arthrocnemum franzii* Sukhor.), *Suaeda vermiculata* Forssk. ex J.F.Gmel., *Tetraena fontanesii* (Webb & Berthel.) Beier & Thulin ( $\equiv$  *Zygophyllum fontanesii* Webb & Berthel.) and *Cistanche phelipaea* (L.) Cout. Based on the specimens seen, it is concluded that *Sesuvium portulacastrum* subsp. *persoonii* is present on the seashores and saline depressions in (semi)arid territories of West Africa (Cape Verde, Gambia, Guinea-Bissau, Mauritania and Senegal) as a geographically separated form of *S. portulacastrum*.

**Conservation status.** *Sesuvium portulacastrum* subsp. *persoonii* is common on sandy inland plains on Sal and Boa Vista islands (Cape Verde). Herbarium labels refer to it as a very characteristic plant of seashore communities in Senegal. Currently the construction of new buildings close to the coast is drastically damaging the natural landscapes, especially on Cape Verde Archipelago (Romeiras et al. 2016, Sukhorukov and Nilova 2016) and may negatively affect the number of populations. However, at present, as there is doubt about the origin of this new subspecies (if it is native to the region), it should not be assessed for the IUCN Red List until more data is available.

***Sesuvium sesuvioides* (Fenzl) Verdc., Kew Bull. 12(2): 349 (1957)**

Fig. 18

$\equiv$  *Diplochonium sesuvioides* Fenzl in Endl., Nov. Stirp. Dec.: 58 (1839).

Lectotype (Sukhorukov & al. 2017): [S Africa, in rupestribus ad Garipum fluvium lateris coloniae occidentalis, alt. 500 ft., without date] [on the rocks near Gariep [Orange] river close to the west of the colony] Drège 2938 (K000076286!; iso – LE!);

$\equiv$  *Halimus sesuvioides* (Fenzl) Kuntze, Revis. Gen. Pl. 1: 263 (1891) as “*Halimum sesuvioides*”.

**Description.** The differences between *S. sesuvioides* and related annual African taxa were provided in Sukhorukov et al. (2017). Here, it is noted that *S. sesuvioides* is a facultatively perennial herb and, for that reason, it is also included in the list of perennial species (as in Bohley et al. 2017).

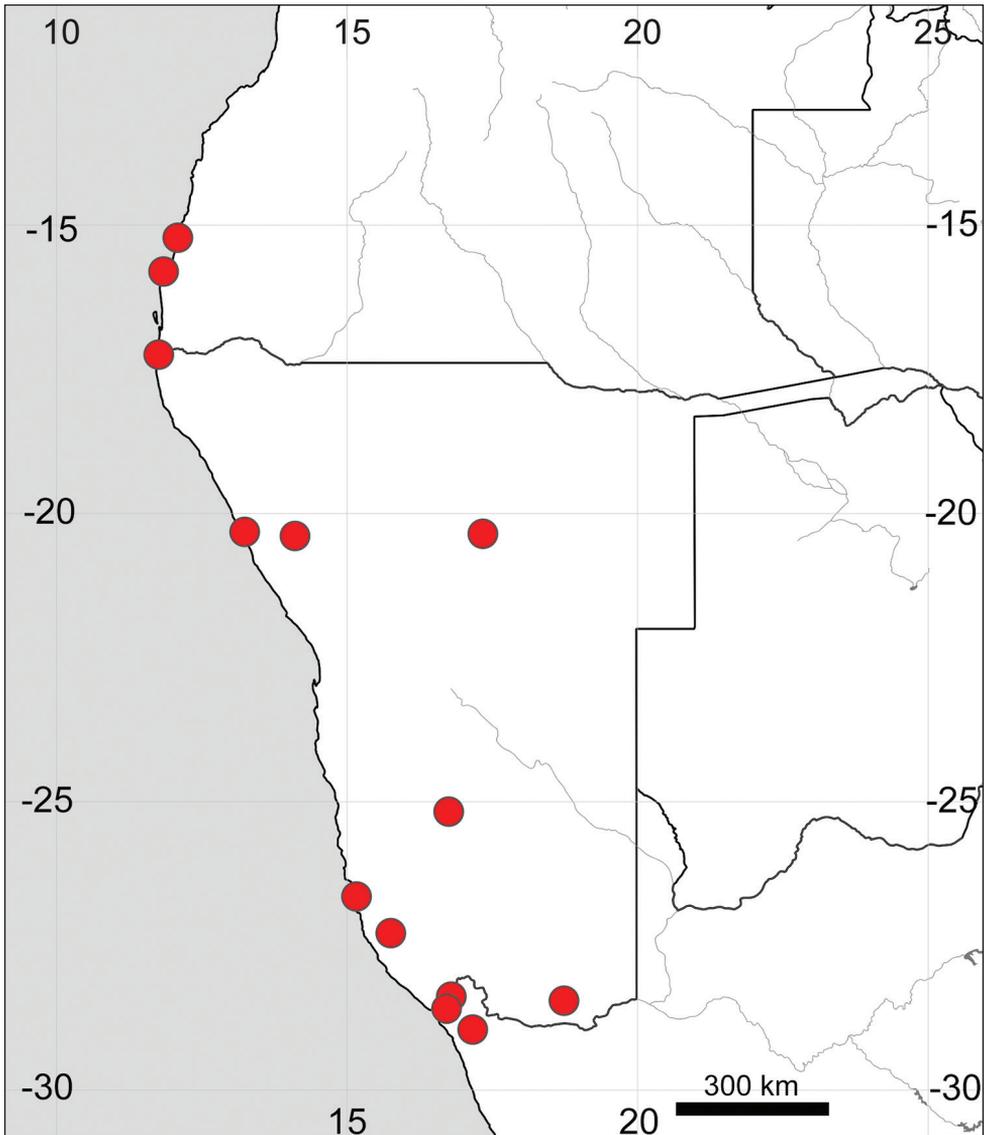
**General distribution.** The distribution of *S. sesuvioides* was mapped in Sukhorukov et al. (2017), but the presence of this species was erroneously indicated in the



**Figure 18.** General view of *Sesuvium sesuvioides* plants at Rio dos Flamingos, Angola. Photographs by C. Klak and P.V. Bruyns (December 2016).

eastern part of South Africa, due to a misapplication of the name “Kleifontein”. The record from Kleifontein (24 Oct 1922, *Dinter 4151*, BM!) indeed belongs to the small village located south of Maltahöhe (Hardap Region, Namibia) and not to the village in Gauteng province (South Africa) mentioned by Sukhorukov et al. (2017). The authors came to this conclusion after tracing the journeys of Kurt Moritz Dinter, who only visited Namibia (it was known at the time as “South-West Africa”: Glen and Germishuizen 2010). Likewise, the lectotype specimen was not collected at Garpia river near Swellendam, Western Cape (as indicated in Sukhorukov et al. (2017)), but on the banks of the Orange River (or Gariap River, spelled by Drège as “Garip”), where *S. sesuvioides* is frequently found. Therefore the records of *S. sesuvioides* from Gauteng and the Western Cape provinces (Sukhorukov et al. 2017) are erroneous. In South Africa, the distribution pattern of *S. sesuvioides* is restricted to the Richtersveld and the lower Orange River valley (Northern Cape province). Records in Namibia and Angola are from the Namib desert (Sukhorukov et al. 2017, see also Fig. 19).

*Sesuvium sesuvioides* has a large geographical distribution with an estimated EOO of 501,893 km<sup>2</sup>, but its AOO is only 60 km<sup>2</sup> (which would place it in EN). Many localities, especially in Namibia, are in desert areas and are presumably under little threat. Some populations collected in the past are likely to be in protected areas today. However, the current size of the populations is unknown. Therefore, the species should be considered as Data Deficient (DD) according to the IUCN Red List Criteria (IUCN 2017).



**Figure 19.** Distribution map of *Sesuvium sesuvioides*.

***Sesuvium verrucosum* Raf., New Fl. [Rafinesque] 4: 16 (1836).**

**Neotype** (Bohley et al. 2017). [USA] “Salt River”, leg. Nutt.[all] (P00680440!); epitype (“A.C. Sanders 23186”, BRIT, n.v.)

**Nomenclatural notes.** It is still doubted whether *Sesuvium verrucosum* (Rafinesque 1836) is the oldest name for this taxon. Three older names—*Sesuvium revolutifolium* Ortega from Cuba (Ortega 1797), *S. revolutum* Pers. and *S. sessile* Pers. (Persoon 1806), both of unknown origin—may be conspecific with *S. verrucosum*. However, the

description of both *S. revolutum* and *S. sessile* is very short and poor and no original material could be traced. The protologue of *S. revolutifolium* completely matches the habit of *S. verrucosum*, but it is not sure whether the plants from North America are identical to those from Cuba. *Sesuvium revolutifolium*, *S. sessile* and *S. revolutum* have been synonymised with *S. portulacastrum* by Bohley et al. (2017), but the nomenclature of all three species needs further study.

**Description.** The most indicative characters of this species are: 1) perennial life history, 2) presence of abundant papillae on stems and leaves, 3) sessile turbinate flower buds and capsules and 4) clearly expressed detachments of the aril from the seed coat. Usually, the stems are rooting; however Ferren (2003) and Baldwin et al. (2012) described *S. verrucosum* as a non-rooting plant (probably applicable to younger plants, as observed in the specimen from Cape Verde listed below). For detailed morphological description, see Fadaie et al. (2006) and Bohley et al. (2017).

**Examined specimens.** CAPE VERDE: São Vicente Island, near Baía das Gatas, 6 Sep 1986, *W.F. Prud'homme van Reine SV3* (L1693699); SPAIN (CANARY ISLANDS): Gran Canaria (selected specimens): San Bartolomé de Tirajana, Cauce del Barranco del Toro, Junto a la depuradora, 11 Dec 2003, *B. Navarro, J. Naranjo, B. Vilches, I. Santana, M. Soto, O. Saturno s.n.* (LPA20044; sub *S. portulacastrum*); San Agustín, Barranco del Toro near the beach, dry riverbed and beach, very common, 30 Mar 2017, *F. Verloove 12825* (BR, LPA, MW).

**General distribution.** *Sesuvium verrucosum* is widely distributed in North Mexico and the southern part of the USA (Ferren 2003). Outside of its native range in the New World, it is reported as an introduced species in South-West Asia: Bahrain (Verdcourt 1985; see also specimens at BM! E! and K!), the eastern part of Saudi Arabia (Miller 1996; specimens at E!, K!), Iran (Fadaie et al. 2006) and United Arab Emirates (collections from Sharjah, 2009, K!). As indicated on the sheets from Bahrain (collected by M. Cornes and A.M. Alder, 1983–1985, E!), *S. verrucosum* is a widespread species in irrigated areas and loamy sands. In Saudi Arabia, it is invasive in diverse inland plant communities including wastelands and salt pans (Miller 1996).

One record has to be added for Syria: small young plants with only a few flowers and flower buds (Syria, Adra, desert, 27 Mar 1931, *R. Gombault 1998*, P04583848!), previously reported as *S. mesembryanthemoides* (Bohley et al. 2017). Surprisingly, *S. verrucosum* was found in other regions of the world as well (re-identifications of AS): (1) North Vietnam (Tonkin, Hải Phòng, sandy seashores, Jul 1908, *Ch. D'Alleizette 2723*, L1693583!, a new record for Southeast Asia) and (2) Hawaii [USA], Oahu, 10 Aug 1967, *D. Herbst 523* (L0717044!). Both specimens were initially identified by the collectors as *S. portulacastrum*.

Here, neophytic *S. verrucosum* is reported for the first time from Macaronesia (Fig. 17), i.e. from São Vicente (Cape Verde) and Gran Canaria (Canary Islands, Spain). In Gran Canaria, the species is well-established and dominant in a dried-out riverbed and extends to the beach and young dunes (Fig. 20). So far, *S. verrucosum* has not been recorded in other suitable habitats in the area (pers. obs. by Marcos Salas-Pascual in 2016 and Filip Verloove in March and April 2017) and it remains unknown how the species was introduced. Due to the evident invasive character of this species, it may be found in other African countries.



**Figure 20.** *Sesuvium verrucosum*: A green-leaved plants, B red-leaved plants. Photographs by F. Verloove (Gran Canaria, Canary Islands, Spain, spring 2017).

## Conclusion

The taxonomic diversity of perennial *Sesuvium* in Africa is greater than previously thought. Some species have a broad distribution pattern in tropical Africa. *Sesuvium verrucosum* is here considered as a naturalised alien species at least in the Canaries. The micromorphology and anatomy of the seeds in perennial African *Sesuvium* are similar, in contrast to that in annual species of the genus. However, the seeds of American *Sesuvium verrucosum* (as well as *S. maritimum* and *S. parviflorum*) demonstrate a peculiarity in seed morphology (detachment of the aril from the seed coat in the area of the cotyledons).

The recent results of morphological and molecular phylogenetic studies (Hassan et al. 2005b, Bohley et al. 2017, Sukhorukov et al. 2017; present paper; Sukhorukov et al., in prep.) suggest that at least seventeen *Sesuvium* species should be accepted: *S. ayresii*, *S. congensis*, *S. crithmoides*, *S. digynum*, *S. edmonstonei*, *S. humifusum*, *S. hydaspicum*, *S. maritimum*, *S. mezianum*, *S. nyasicum*, *S. parviflorum*, *S. portulacastrum* (divided into two subspecies), *S. repens*, *S. rubriflorum*, *S. sesuvioides*, *S. trianthemoides* and *S. verrucosum*. The *Sesuvium portulacastrum* complex needs further investigations.

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## References

- Acebes-Ginováés JR, León-Arencibia MC, Rodríguez-Navarro ML, Del Arco MJ, García-Gallo A, Pérez de Paz PL, Rodríguez O, Martín-Osorio VE, Wildpret W (2010) Pteridophyta, Spermatophyta. In: Arechavaleta M, Rodríguez S, Zurita N, García A (Eds) Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres). Gobierno de Canarias, Santa Cruz de Tenerife, 119–172.
- Adamson RS (1962) The South African species of Aizoaceae: XII. *Sesuvium*, *Trianthema* and *Zaleya*. Journal of South African Botany 28(3): 243–253.
- Albuquerque S, Brummitt RK, Figueiredo E (2009) Typification of names based on the Angolan collections of Friedrich Welwitsch. Taxon 58(2): 641–646. <http://www.jstor.org/stable/27756901>
- Arechavaleta M, Zurita N, Marrero MC, Martín JL (Eds) (2005) Lista preliminar de especies silvestres de Cabo Verde (hongos, plantas y animales terrestres). Gobierno de Canarias, Santa Cruz de Tenerife.
- Bachman S, Moat J, Hill AW, de Torre J, Scott B (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. ZooKeys 150: 117–126. <https://doi.org/10.3897/zookeys.150.2109>
- Baldwin BG, Goldman DH, Keil DJ, Patterson R, Rosatti TJ, Wilken DH (2012) The Jepson Manual: Vascular plants of California. University of California Press, Berkeley, Los Angeles, London.
- Bogle AL (1970) The genera of Molluginaceae and Aizoaceae in the southeastern United States. Journal of the Arnold Arboretum 51: 431–462. <https://doi.org/10.5962/bhl.part.7046>
- Bohley K, Joos O, Hartmann H, Sage R, Liede-Schumann S, Kadereit G (2015) Phylogeny of Sesuvioideae (Aizoaceae) – Biogeography, leaf anatomy and the evolution of C<sub>4</sub> photosynthesis. Perspectives in Plant Ecology, Evolution and Systematics 17: 116–130. doi: 10.1016/j.ppees.2014.12.003
- Bohley K, Winter PJD, Kadereit G (2017) A revision of *Sesuvium* (Aizoaceae, Sesuvioideae). Systematic Botany 42(1): 124–147. <https://doi.org/10.1600/036364417X694575>

- Bouckaert R, Heled J, Kuhnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ (2014) BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 10(4): e1003537. <https://doi.org/10.1371/journal.pcbi.1003537>
- Burkill HM (1985) *The useful plants of West Tropical Africa*, 2<sup>nd</sup> ed., Vol. 1 (Families A–D). Royal Botanic Gardens Kew, London.
- Chevalier A (1920) *Exploration botanique l’Afrique occidentale Française*, Vol. 1. Paul Lechevallier, Paris.
- Chevalier A (1935) Les Iles du Cap Vert. Géographie, biogéographie, agriculture. Flore de l’Archipel. *Revue de botanique appliquée et d’agriculture coloniale* 15(170): 733–1090. <https://doi.org/10.3406/jatba.1935.5553>
- Correll DS (1966) Some additions and corrections to the flora of Texas – III. *Rhodora* 68: 420–428.
- Cuénoud P, Savolainen V, Chatrou LW, Powell M, Grayer RJ, Chase MW (2002) Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid rbcL, atpP, and matK DNA sequences. *American Journal of Botany* 89: 132–144. <https://doi.org/10.3732/ajb.89.1.132>
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9(8): 772. <https://doi.org/10.1038/nmeth.2109>
- Engler A (1910) *Die Pflanzenwelt Afrikas insbesondere seiner tropischen Gebiete*, Vol. 1, part 5. Wilhelm Engelmann Verlag, Leipzig.
- Exell AW (1944) *Catalogue of the vascular plants of S. Tomé (with Principe and Annobon)*. British Museum (Natural History), London.
- Fadaie F, Attar F, Ghahreman A (2006) A new record of Aizoaceae (*Sesuvium verrucosum* Raf.) for the flora of Iran. *Iranian Journal of Botany* 12(1): 87–88.
- Ferren WR (2003) *Sesuvium*. In: *Flora of North America Editorial Committee (Eds) Flora of North America, North of Mexico*, Vol. 4. Oxford University Press, New York, Oxford, 80–81.
- Figueiredo E, Smith GF (Eds) (2008) *Plants of Angola* [Strelitzia 22]. South African National Biodiversity Institute, Pretoria.
- Forster G (1789) *Plantae Atlanticae ex insulis Madeira, Sti Iacobi, Adscensionis, Stae Helenae et Fayal reportatae*. *Commentationes Societatis Regiae Scientiarum Gottingensis* 9: 46–74.
- Friedmann F (1994) *Flore des Seychelles*. Dicotylédones. Orstom Editions, Paris.
- Gilli A (1976) Die Veränderung der Flora der Kapverdischen Inseln in den letzten 124 Jahren. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 115: 34–39.
- Gilbert MG (1993) Aizoaceae. In: Thulin M (Ed.) *Flora of Somalia*, Vol. 1. The Royal Botanic Gardens Kew, London, 111–117.
- Glen HF, Germishuizen G (2010) *Botanical exploration of southern Africa*, 2<sup>nd</sup> ed. [Strelitzia 26] South African National Biodiversity Institute, Pretoria.
- Golenberg EM, Clegg MT, Durbin M, Doebley J, Ma DP (1993) Evolution of a noncoding region of the chloroplast genome. *Molecular Phylogenetics and Evolution* 2: 52–64. <https://doi.org/10.1006/mpev.1993.1006>
- Gonçalves ML (1965) Subsídios para o conhecimento da flora de Angola – I. *Garcia de Orta* 13: 377–382.

- Gonçalves ML (1970) Aizoaceae. In: Exell AW, Fernandes A, Mendes EJ (Eds) *Conspectus florum Angolensis. Rosaceae-Alangiaceae*, Vol. 4. Oficinas Gráficas da Imprimarte, Lisbon, 302–333.
- Gonçalves ML (1979) Aizoaceae. In: Mendes EJ (Ed.) *Flora de Moçambique*, Vol. 83. Aizoaceae. Junta de Investigações Científicas do Ultramar, Lisbon, 1–13.
- Gonçalves ML (1995) Aizoaceae. In: Paiva J, Martins ES, Diniz MA, Moreira I, Gomes I, Gomes S (Eds) *Flora de Cabo Verde*, Vol. 12. IICT & INIDA, Lisbon & Praia, 1–17.
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hartmann HEK (1993) Aizoaceae. In: Kubitzki F, Rohwer JG, Bittrich V (Eds) *The families and genera of vascular plants*, Vol. 2: Flowering Plants, Dicotyledons: Magnoliid, Hamamelid and Caryophyllid Families. Springer, New York, 37–69. [https://doi.org/10.1007/978-3-662-02899-5\\_6](https://doi.org/10.1007/978-3-662-02899-5_6)
- Hartmann HEK (2002) *Illustrated handbook of succulent plants: Aizoaceae F–Z*. Springer, Berlin, Heidelberg, New York.
- Hassan NS, Meve U, Liede-Schumann S (2005a) Seed coat morphology of Aizoaceae–Sesuvioideae, Gisekiaceae and Molluginaceae and its systematic significance. *Botanical Journal of the Linnean Society* 148: 189–206. <https://doi.org/10.1111/j.1095-8339.2005.00407.x>
- Hassan NS, Thiede J, Liede-Schumann S (2005b) Phylogenetic analysis of Sesuvioideae (Aizoaceae) inferred from nrDNA internal transcribed spacer (ITS) sequences and morphological data. *Plant Systematics and Evolution* 255: 121–143. <https://doi.org/10.1007/s00606-0050357-x>
- Hauman L (1951) Aizoaceae. In: Robyns W (Ed.) *Flora du Congo Belge et du Ruanda–Urundi*, Vol. 2. INEAC Publ., Brussels, 100–117.
- Hermann P (1698) *Paradisus batavus, continens plus centrum plantarum affabre aere insisas et descriptionibus illustratas*. Elsevier, Leiden.
- Hooker WJ (1849) *Niger Flora; or, an enumeration of the plants of Western Tropical Africa*. Bailliere, London.
- Hutchinson JL, Dalziel J (1927) *Flora of West Tropical Africa*, Vol. 1. Crown Agents, London.
- IUCN (2017) *Guidelines for Using the IUCN Red List Categories and Criteria, Version 13*. IUCN, Gland, Switzerland. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf> [accessed 7 Nov 2017].
- Jeffrey C (1961) Aizoaceae. In: Hubbard CE, Milne-Redhead E (Eds) *Flora of Tropical East Africa* [no volume number]. Crown Agents, London, 1–35.
- Johnston HH (1894) Report on the flora of Les Bénitiers, Mauritius. *Transactions and Proceedings of the Botanical Society of Edinburgh* 59: 331–335.
- Johnston HH (1895) Report on the flora of the out-lying islands in Máhebourg Bay, Mauritius. *Transactions and Proceedings of the Botanical Society of Edinburgh* 59: 1–36.
- Klak C, Khunou A, Reeves G, Hedderson T (2003) A phylogenetic hypothesis of the Aizoaceae (Caryophyllales) based on four plastid DNA regions. *American Journal of Botany* 90(10): 1433–1445. <https://doi.org/10.3732/ajb.90.10.1433>
- Klak C, Hanáček P, Bruyns PV (2017a) Out of southern Africa: Origin, biogeography and age of the Aizoioideae (Aizoaceae). *Molecular Phylogenetics and Evolution* 109: 203–216. <https://doi.org/10.1016/j.ympev.2016.12.016>

- Klak C, Hanáčec P, Bruyns PV (2017b) Disentangling the Aizoioideae: New generic concepts and a new subfamily in Aizoaceae. *Taxon* 66: 1147–1170. <https://doi.org/10.12705/665.9>
- Krinitsina AA, Zaika MA, Speranskaya AS, Sukhorukov AP, Sizova TV (2015) A rapid and cost-effective method for DNA extraction from archival herbarium specimens. *Biochemistry (Moscow)* 80(11): 1478–1484. <https://doi.org/10.1134/S0006297915110097>
- Lamarck JB (1793) *Tableau encyclopédique et méthodique des trois règnes de la nature*. Botanique, Vol. 2. Panckoucke, Paris.
- Lamarck JB (1817) *Encyclopédique Méthodique*. Botanique, Vol. 5 (Supplement). Agasse, Paris.
- Lindley J (1853) *The vegetable kingdom; or, the structure, classification, and uses of plants*, 3<sup>rd</sup> ed. Bradbury & Evans, London.
- Lisowski S (2009) *Flore (Angiospermes) de la République de Guinée*, Vol. 1 (Text). Jardin Botanique National de Belgique, Meise.
- Lonard RI, Judd FW (1997) The biological flora of coastal dunes and wetlands. *Sesuvium portulacastrum* (L.) L. *Journal of Coastal Research* 13(1): 96–104. <http://www.jstor.org/stable/4298595>
- Marais W (1978) A new Mascarene *Sesuvium* (Aizoaceae). *Kew Bulletin* 32(2): 483. <https://doi.org/10.2307/4117120>
- Marais W (1990) 104. Aizoacées. In: Bosser J, Cadet T, Guého J, Marais W (Eds) *Flore des Mascareignes*. Mauritius Sugar Industry Research Institute, L'Institut Français de Recherche Scientifique and The Royal Botanic Gardens Kew, Mauritius, Paris, London, 1–13.
- McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, Prado J, Prud'homme van Reine WF, Smith GF, Wiersema JH, Turland NJ (2012) International code of nomenclature for algae, fungi, and plants (Melbourne Code) adopted by the eighteenth International Botanical Congress Melbourne, Australia, July 2011. Koeltz Scientific Books, Königstein.
- Miller AG (1996) Aizoaceae. In: Miller AG, Cope TA (Eds) *Flora of the Arabian Peninsula and Socotra*, Vol. 1. University Press, Edinburgh, 155–168.
- Nellis DW (1994) *Seashore plants of South Florida and the Caribbean*. Pineapple Press, Sarasota.
- Netolitzky F (1926) Anatomie der Angiospermen-Samen. In: Linsbauer K (Ed.) *Handbuch der Pflanzenanatomie*, Abt. 2, 2(10). Bornträger, Berlin, 1–364.
- Oliver D (1871) *Flora of Tropical Africa*, Vol. 2 (Leguminosae to Ficoideae). Reeve & Co, London.
- Ortega CG (1797) *Novarum, aut rariorum plantarum horti regii botanici Matritensis descriptionum decades, cum nonnullarum iconibus*. Typ. Ibarrriana, Madrid.
- Oxelman B, Lidén M, Berglund D (1997) Chloroplast rps16 intron phylogeny of the tribe Sileneae (Caryophyllales). *Plant Systematics and Evolution* 206: 393–410.
- Persoon CH (1806) *Synopsis Plantarum: seu Enchiridium botanicum, complectens enumerationem systematicam specierum hucusque cognitarum*, Vol. 2, part 1. Cramer, Paris.
- Rafinesque CS (1836) *New flora and botany of North America*, Part 4. [Printed for the author and publisher], Philadelphia.
- Rambaut A, Suchard MA, Xie D, Drummond AJ (2014) *Tracer v1.6*. <http://beast.bio.ed.ac.uk/Tracer>

- Romeiras MM, Catarino S, Gomes I, Fernandes C, Costa JC, Cauapé-Costells J, Duarte MC (2016) IUCN Red List assessment of the Cape Verde endemic flora: towards a global strategy for plant conservation in Macaronesia. *Botanical Journal of the Linnean Society* 180(3): 413–425. <https://doi.org/10.1111/boj.12370>
- Saint-Hilaire A de (1829) *Flora Brasiliae Meridionalis*, Vol. 2. Belin, Paris.
- Sauer JD (1982) *Cayman Island seashore vegetation: a study in comparative biogeography*. University of California Press, Berkeley, Los Angeles, London.
- Schmidt JA (1852) Beiträge zur Flora der Cap Verdischen Inseln: mit Berücksichtigung aller bis jetzt daselbst bekannten wildwachsenden und kultivierten Pflanzen: nach eigenen Untersuchungen und mit Benutzung der gewonnenen Resultate anderer Reisenden [Additions to the flora of Cape Verde Islands, with a consideration of all known native and cultivated plants based on the own investigations and results of other travelers]. Mohr, Heidelberg.
- Schumacher FC (1827) *Beskrivelse af Guineiske planter: som ere fundne af Danske botanikere, især af etatsraad Thonning*. Popp, Copenhagen.
- Small JK (1933) *Manual of the southeastern flora: being descriptions of the seed plants growing naturally in Florida, Alabama, Mississippi, eastern Louisiana, Tennessee, North Carolina, South Carolina and Georgia*. [Printed by the author], New York.
- Sosef MSM, Wieringa JJ, Jongkind CCH, Achoundong G, Azizef Issembé Y, Bedigian D, van den Berg RG, Breteler FJ, Cheek M, Degreef J, Faden RB, Goldblatt P, van der Maesen LJG, Ngok Banak L, Niagadourma R, Nzabi T, Nziengui B, Rogers ZS, Stévert T, van Valkenburg JLCH, Walters G, de Wilde JJFE (2006) Checklist of Gabonese vascular plants. National Botanic Garden of Belgium, Meise.
- Sukhorukov AP (2008) Fruit anatomy of *Anabasis* (Salsoloideae, Chenopodiaceae). *Australian Systematic Botany* 21(6): 431–442. <https://doi.org/10.1071/SB08013>
- Sukhorukov AP, Mavrodiev EV, Struwig M, Nilova MV, Dzhililova KK, Balandin SA, Erst A, Krinitsyna AA (2015) One-seeded fruits in the core Caryophyllales: their origin and structural diversity. *Plos One* 10(2): e0117974. <https://doi.org/10.1371/journal.pone.0117974>
- Sukhorukov AP, Nilova MV (2016) A new species of *Arthrocnemum* (Salicornioideae: Chenopodiaceae-Amaranthaceae) from West Africa, with a revised characterization of the genus. *Botany Letters* 163(3): 237–250. <https://doi.org/10.1080/23818107.2016.1185033>
- Sukhorukov AP, Verloove F, Alonso MA, Belyaeva IV, Chapano C, Crespo MB, El Aouni MH, El Mokni R, Maroyi A, Shekede MD, Vicente A, Dreyer A, Kushunina M (2017) Chorological and taxonomic notes on African plants, 2. *Botany Letters* 164(2): 135–153. <https://doi.org/10.1080/23818107.2017.1311281>
- Sukhorukov AP, Zhang M (2013) Fruit and seed anatomy of *Chenopodium* and related genera (Chenopodioideae, Chenopodiaceae/Amaranthaceae): Implications for evolution and taxonomy. *Plos One* 8(4): e61906. <https://doi.org/10.1371/journal.pone.0061906>
- Sukhorukov AP, Zhang M-L, Kushunina M, Nilova MV, Krinitsyna A, Zaika MA, Mazei Yu (in press) Seed characters in Molluginaceae (Caryophyllales): implications for taxonomy and evolution. *Botanical Journal of the Linnean Society*.
- Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.
- Takhtajan AL (Ed.) (1991) *Anatomia seminum comparativa*, Vol. 3. Nauka, Leningrad.

- Tamura K, Stecher G, Peterson D, FilipSKI A, Kumar S (2013) MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. <https://doi.org/10.1093/molbev/mst197>.
- Thulin M, Thiede J, Liede-Schumann S (2012) Phylogeny and taxonomy of *Tribulocarpus* (Aizoaceae): a paraphyletic species and an adaptive shift from zoochorous trample burrs to anemochorous nuts. *Taxon* 61(1): 55–66.
- Tomlinson PB (2016) *The botany of mangroves*, 2<sup>nd</sup> ed. Cambridge University Press, Padstow.
- Verdcourt B (1985) An introduced *Sesuvium* (Aizoaceae) in Arabia. *Kew Bulletin* 40(1): 208.
- Wawra H, Peyritsch J (1860) *Sertum benguelense*. *Sitzungsberichte der Kaiserlichen Academie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 38: 543–586.
- Welwitsch F (1859) Apontamentos phytogeográficos sobre a flora da província de Angola na África equinocial. *Anais do Conselho do Ultramarino, ser. 1*: 527–593.
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) *PCR Protocols: a guide to methods and applications*. Academic Press, New York, 315–322.
- Wijnands DO (1983) *The Botany of the Commelins*. Balkema, Rotterdam.

# Taxonomic revision of *Pachyptera* (Bignoniaceae, Bignoniaceae)

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## Abstract

*Pachyptera* DC. is a small genus of neotropical lianas included in tribe Bignoniaceae (Bignoniaceae). The genus has a complicated taxonomic history but currently includes species distributed from Belize to Southern Amazon. *Pachyptera* is characterised by four main synapomorphies, namely, a papery peeling bark, prophylls of the axillary buds organised in a series of three, patelliform glands arranged in lines in the upper portions of the calyx and corolla tube. Furthermore, members of the genus also have stems with four phloem wedges in cross-section and conspicuous extrafloral nectaries between the interpetiolar region and at the petiole apex, although these characters are also shared with other genera of tribe Bignoniaceae. Here, we present a taxonomic revision of *Pachyptera*, which includes a complete list of synonyms, detailed morphological descriptions of species and an identification key, as well as information on the habitat, distribution and phenology, nomenclatural notes, taxonomic comments and illustrations of all the species. In addition, we designate three lectotypes, propose one new combination, raise one variety to species status and describe a new species. After these adjustments, a *Pachyptera* with five well-defined species is recognised.

## Keywords

Amazon, Flora, *Pachyptera kerere*, Neotropics, Taxonomy

## Introduction

*Pachyptera* DC. (Bignoniaceae, Bignoniaceae) includes neotropical lianas that are distributed from Belize to central Brazilian Amazon, with most species restricted to wet Amazonian forests (Lohmann and Taylor 2014). The genus has a complicated taxonomic history, including a difficult generic circumscription and several poorly defined taxa. Here, a new systematic treatment of *Pachyptera* is proposed and five species are recognised using an integrative approach that includes data derived from a recent molecular phylogeny (Francisco and Lohmann 2017, Francisco and Lohmann submitted), coalescent approaches (Francisco and Lohmann submitted) and new morphological studies.

This new classification recognises a monophyletic genus that is characterised by four morphological synapomorphies, namely, a papery peeling bark, prophylls of the axillary buds organised in a series of three (Lohmann and Taylor 2014), peltiform glands arranged in lines on the upper portions of the calyx and corolla tube (Lohmann 2006, Lohmann and Taylor 2014). In addition, stems with four phloem wedges in cross-section, conspicuous extrafloral nectaries on the interpetiolar region and at the petiole apex also help to identify members of the genus (Lohmann and Taylor 2014).

## Taxonomic history

*Pachyptera* was originally described by de Candolle (1845), who characterised the genus by a compressed capsule and seeds with coriaceous wings. The genus originally included six species, four of which [i.e. *P. umbelliformis* DC., *P. striata* DC., *P. dasyantha* DC. and *P. perrottetii* DC.] are synonyms of *Tanaecium pyramidatum* (Rich.) L.G. Lohmann, while *P. puberula* DC. is a synonym of *Dolichandra uncata* (Andrews) L.G. Lohmann. Only *P. foveolata* DC. remains in *Pachyptera*, although as a synonym of *Pachyptera kerere* (Aubl.) Sandwith.

Nearly five decades after being described, *Pachyptera* was synonymised into *Adenocalymma* Mart. ex Meisn by Baillon (1891) based on the broad and thick capsule shared amongst members of these genera. Subsequently, Bureau and Schumann (1896 [1897]) transferred *P. foveolata* to *Adenocalymma* section *Pachyptera*, which was characterised by villous anthers and plate-shaped glands arranged in lines outside the corolla tube, right below the lobes. At the same time, *P. kerere* was transferred to *Adenocalymma* section *Hanburyophyton* together with four species of *Mansoa*, i.e. *A. alliaceum* (Lam.) Miers, *A. asperulum* Bureau & K. Schum., *A. splendens* Bureau & Schum. [= *Mansoa difficilis*] and *A. lanceolatum* Miers. *Pachyptera* was subsequently segregated from *Adenocalymma* by Sprague and Sandwith (1932) and restored to generic rank, as a monotypic genus that only included *P. foveolata*.

*Pachyptera foveolata*, as circumscribed by Sprague and Sandwith (1932), consisted of a species complex that included individuals with white to crimson flowers. While the authors themselves recognised the difficulties associated with the recognition of such a diverse species, the restricted sampling prevented them from analysing the breadth of

morphological variation included in this group and the recognition of a single species. Five years later, Sandwith (1937) noted that Aublet's epithet "kerere" was the correct name for *P. foveolata* and proposed the new combination *Pachyptera kerere*. Dugand (1955) also noted the high variation found in flower traits of specimens of *Pachyptera kerere* and described the new variety *P. kerere* var. *erythraea* Dugand. The variety *P. kerere* var. *erythraea* differs from *P. kerere* var. *kerere* in the red corolla (vs. white in *P. kerere* var. *kerere*). Gentry (1977) subsequently noted that *P. kerere* var. *kerere* and *P. kerere* var. *erythraea* also differed in the sub-exserted to exserted anthers (vs. included anthers in *P. kerere* var. *kerere*), campanulate corolla with 11–15 mm in diameter (vs. sub-bilabiate corolla with 3–7 mm in diameter in *P. kerere* var. *kerere*) and leaf blade puberulous (vs. leaf blade glabrous in *P. kerere* var. *kerere*), which led him to raise *P. erythraea* (Dugand) A.H. Gentry to species rank.

Although *Bignonia incarnata* Aubl. was described in the same work as *Bignonia kerere* Aubl. (1775), the close relationship between those two taxa was not noted. In fact, *Bignonia incarnata* was thought to be morphologically similar and perhaps more closely related to *Cydista aequinoctialis* (L.) Miers by various authors (see Sandwith 1937). Nearly two decades later, Gentry (1973) noted the similarity between individuals of *B. incarnata* and *P. kerere*, which led him to treat *B. incarnata* as a variety of *P. kerere*, i.e. *Pachyptera kerere* var. *incarnata* (Aubl.) A.H. Gentry. At the same time, Gentry (1973) reduced *Pseudocalymma* [= *Mansoa*] into *Pachyptera* due to the shared trifid tendrils, white to red or purple flowers, interpetiolar gland-fields, 3-colpate pollen and deciduous bracts. In this work, three species of *Pseudocalymma* were transferred to *Pachyptera* [*P. alliacea* (Lam.) A.H. Gentry, *P. hymenaea* (DC.) A.H. Gentry, and *P. standleyi* (Steierm.) A.H. Gentry], all of which are currently placed in *Mansoa*.

Gentry (1979) and Gentry and Tomb (1979) used new palynological data as a basis to merge *Pachyptera* and *Hanburyphython* Bureau ex Warm. in *Mansoa* DC., resulting in seven new combinations: *M. alliacea* (Lam.) A.H. Gentry, *M. erythraea* (Dugand) A.H. Gentry, *M. hymenaea* (DC.) A.H. Gentry, *M. kerere* var. *kerere* (Aubl.) A.H. Gentry, *M. kerere* var. *incarnata* (Aubl.) A.H. Gentry, *M. parvifolia* (A.H. Gentry) A.H. Gentry, and *M. standleyi* (Steierm.) A.H. Gentry. In addition, a new species was described, *Mansoa ventricosa* A.H. Gentry, a taxon known from the type specimen plus one additional material whose placement was uncertain.

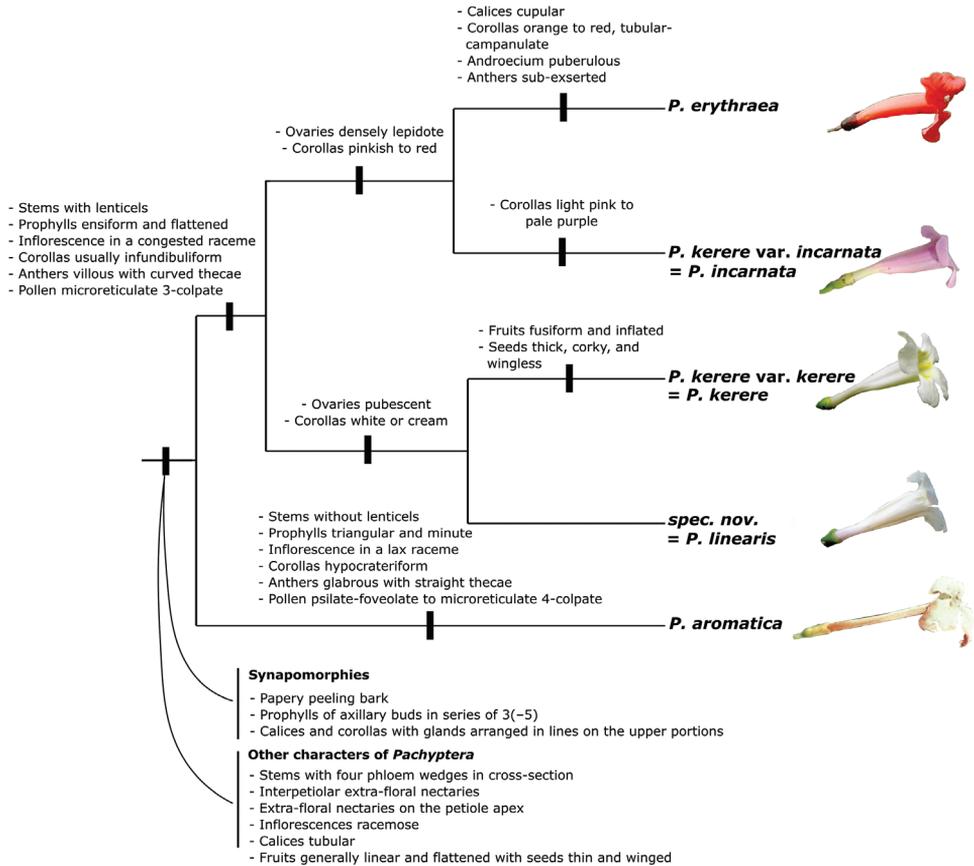
### Phylogenetic based classifications of *Pachyptera*

While the taxonomic confusion between *Mansoa* and *Pachyptera* remained for several years, molecular phylogenetic data (Lohmann 2006) indicated that *Mansoa* and *Pachyptera* are distantly related, while the monotypic *Leucocalantha* Barbosa Rodrigues is closely related to *Pachyptera*. *Leucocalantha* was described based on the long and white corollas that resembled the Asian genus *Millingtonia* L.f. (Oroxyleae, Bignoniaceae). The genus only included *Leucocalantha aromatica* Barb. Rodr., which is

characterised by white, pubescent and hypocrateriform corolla tubes and glands at the apices of the petioles and corollas. While the close relationship between *Leucocalantha* and *Pachyptera* was initially surprising, a careful morphological study recovered multiple morphological features shared between these taxa (e.g. stems with four phloem wedges in cross-section, corollas with glands arranged in lines on the upper portions of the tube and racemose inflorescences). This observation led to the re-establishment of *Pachyptera* and the inclusion of *Leucocalantha* into *Pachyptera* in a revised generic classification of the whole tribe Bignonieae (Lohmann and Taylor 2014). Under this classification, *Pachyptera* included four species, i.e. *P. aromatica* (Barb. Rodr.) L.G. Lohmann, *P. erythraea* (Dugand) A.H. Gentry, *P. kerere* and *P. ventricosa* (A.H. Gentry) L.G. Lohmann. This circumscription was based on morphological observations for all taxa and a molecular phylogenetic framework of the whole tribe Bignonieae that sampled half of the species of *Pachyptera* (Lohmann 2006); two rare and morphologically complicated species (i.e. *P. erythraea* and *P. ventricosa*) were not sampled in the phylogeny, raising their generic placement into question.

A recent phylogenetic and morphological study of *Pachyptera* (Francisco and Lohmann 2017) sampled all species recognised by Lohmann and Taylor (2014). In this phylogeny, *Pachyptera ventricosa* was more closely related to *Mansoa* than to other species of *Pachyptera*, which led to the reestablishment of *Mansoa ventricosa* (Francisco and Lohmann 2017). In addition, this study also provided further support for the inclusion of *P. aromatica* and *P. erythraea* into *Pachyptera*. As such, *Pachyptera* was recognised as a monophyletic genus comprising three species. However, the infra-specific classification of the *P. kerere* species complex remained uncertain. More specifically, it remained dubious whether *P. erythraea* and *P. kerere* var. *incarnata* should be treated as separate species or varieties of *P. kerere*.

A more comprehensive phylogenetic study of the genus (Francisco and Lohmann submitted) sampled multiple individuals of all three species of *Pachyptera* recognised by Francisco and Lohmann (2017) and used coalescent approaches to verify species limits. This study identified five evolutionary units that are characterised by distinct morphological features and ecological traits (Fig. 1). Within this phylogenetic framework, *P. aromatica* is sister to the remaining species of the genus. This species is characterised by a series of morphological autapomorphies such as stems without lenticels, prophylls of axillary buds triangular and minute, inflorescence in lax racemes, corolla hypocrateriform, anthers glabrous with straight thecae and pollen glabrous psilate-foveolate to microreticulate 4-colpate. The remaining species of the genus are divided into two main clades, the first of which includes *P. erythraea* and *P. kerere* var. *incarnata* (= *P. incarnata*), both of which are characterised by pinkish to red corollas, with ovaries densely lepidote. *Pachyptera incarnata* is easily distinguished by the light pink to pale purple corollas (vs. orange to red in *P. erythraea*), calyx tubular (vs. cupular in *P. erythraea*), corolla infundibuliform (vs. corolla tubular-campanulate in *P. erythraea*), androecium glabrous (vs. androecium puberulous in *P. erythraea*), anthers included (vs. anthers sub-exserted in *P. erythraea*) and ovaries not-bisulcate (vs. bisulcate in *P. erythraea*). The second clade includes *P. kerere* var. *kerere* (= *P. kerere*) and a



**Figure 1.** Schematic diagram summarising phylogenetic relationships within *Pachyptera*, with morphological characters mapped on the diagram. Names of the terminal taxa indicate the taxon in which these species were previously included. The taxonomic updates proposed here are also indicated. Relationships depicted follow Francisco and Lohmann (submitted).

new species described here (*P. linearis* Francisco & L.G. Lohmann), both characterised by white to cream coloured corollas, with ovaries pubescent (Fig. 1). *Pachyptera kerere* is separated from *P. linearis* by the fruit fusiform (vs. linear in *P. linearis*) and the seeds inflated, thick, corky and wingless (vs. seeds flattened, thin, membranaceous and winged in *P. linearis*).

## Distribution

Almost all *Pachyptera* species are found in the Amazon rainforest. Only *P. kerere* is widely distributed while all other species have restricted distributions. *Pachyptera kerere* is frequent throughout the Amazon and also distributed in Central America from Panama

to Belize. *Pachyptera aromatica* is restricted to the Brazilian Amazon. *Pachyptera erythraea* is endemic to the middle Magdalena River Valley of Colombia, while *P. incarnata* is endemic to Eastern Amazon. *Pachyptera linearis* is known only by a few collections from Venezuela and Colombia.

## Habitats

Species of *Pachyptera* occur in wet *terra-firme* forests, generally close to water bodies or riverbanks and are also found in flooded forests such as the Brazilian *igapó*. The majority of *Pachyptera* species has seeds with thin wings that are wind dispersed, while *P. kerere* has thick, corky and wingless seed adapted to water dispersal (Gentry 1976). Water dispersal arose several times independently in tribe Bignonieae, mostly from wind-dispersed ancestors (Gentry 1983, 1990, Lohmann 2004). Shifts between dispersal syndromes may have driven the speciation of *P. kerere* (Francisco and Lohmann submitted).

## Reproductive biology

*Pachyptera* includes great diversity of floral morphology that is associated with different pollination syndromes. *Pachyptera aromatica* has white, hypocrateriform corollas and nocturnal anthesis (Barbosa Rodrigues 1891). The flowers of this species are classified as “*Tanaecium* type” and fit the hawkmoth pollination syndrome (Gentry 1974). *Tanaecium* type flowers evolved multiple times within Bignonieae (Alcantara and Lohmann 2010) and are found in *Tanaecium* and *Bignonia nocturna* (Barb. Rodr.) L.G. Lohmann. *Pachyptera erythraea*, on the other hand, have orange to red flowers that are tubular campanulate, with sub-exserted anthers. These flowers are classified as “*Martinella* type” and are likely pollinated by hummingbirds (Gentry 1974).

*Pachyptera incarnata*, *P. kerere* and *P. linearis* share infundibuliform and dorso-ventrally compressed corollas, with two longitudinal ridges in the throat that form yellow nectar guides, as well as included anthers. *Pachyptera incarnata* has light pink to pale purple flowers, while *P. kerere* and *P. linearis* have white to cream flowers. These flowers are classified as “*Anemopaegma* type” and are pollinated by large to medium-sized bees, mainly euglossine and anthophorids (Gentry 1974).

## Etymology

*Pachyptera* is a Latin derived name that means “with thick wings” (from Latin: pach = thick, aptera = without wings). This characteristic is found in the type species of the genus, *Pachyptera kerere*.

## Morphology

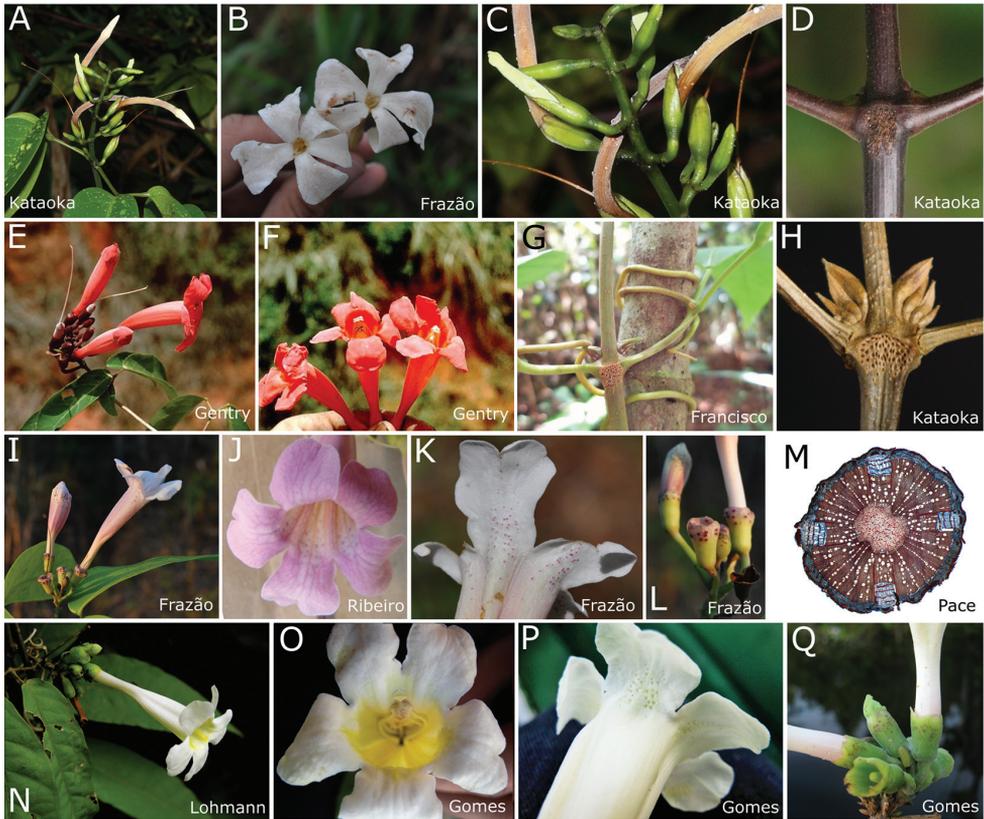
*Habit.* All species of *Pachyptera* are lianas, although seedlings are initially herbaceous and free standing until ca. 80 cm (grow vertically).

*Stems.* The stems of *Pachyptera* exhibit four phloem wedges in cross-section, a type of cambial variation also found in *Adenocalymma*, *Martinella*, *Cuspidaria*, *Fridericia* and *Tanaecium* (Lohmann 2006, Lohmann and Taylor 2014). Moreover, the pith of the stem of *Pachyptera* is solid although a few specimens of *P. aromatica* also show a slightly hollow pith, a condition only known from *Stizophyllum* and *Pleonotoma* within tribe Bignoniaceae (Lohmann and Taylor 2014). Cylindrical to tetragonal stems are found in *Pachyptera*, sometimes within a single individual. Young stems are usually cylindrical, becoming tetragonal in more advanced stages of development. Tetragonal stems are only found in stems  $\geq 6$  cm<sup>2</sup> of *P. aromatica* but are also found in stems with a smaller diameter in other species of the genus (Francisco personal observation). Stem surface is striated and frequently bears lenticels (except in *P. aromatica*). The peeling bark is a morphological synapomorphy of the genus (Lohmann 2006, Lohmann and Taylor 2014).

*Prophylls of the axillary buds.* Prophylls of the axillary buds, referred to as “pseudostipules” in the past (e.g. Gentry 1980), exhibit several shapes and are useful generic characters within Bignoniaceae (Lohmann and Taylor 2014). Species of *Pachyptera* usually have multiple flattened and ensiform prophylls of the axillary buds (triangular and minute in *P. aromatica*, Fig. 5B), arranged in 3(–5) series (Fig. 2H). Sometimes the prophylls are so minute in *P. aromatica* that only the larger prophyll series is visible to the naked eye (Fig. 2D). The supra-numerary prophylls are an exclusive morphological synapomorphy of *Pachyptera* (Fig. 2G, H).

*Extrafloral nectaries.* Extrafloral nectaries (i.e. EFNs) are useful generic and species level markers within Bignoniaceae, aiding the identification of sterile materials (Seibert 1948, Lohmann and Taylor 2014). EFNs produce sugar that attracts ants which, in turn, have an important protective role against herbivores (Gentry 1974, Nogueira et al. 2015). In *Pachyptera*, EFNs are composed of large groups of patelliform glands located between the interpetiolar region (Fig. 2D, G, H) and at the petiole apex, right below the junction with the petiolules. Interpetiolar gland fields are also found in other Bignoniaceae genera (e.g. *Fridericia*, *Lundia*, *Tanaecium*) and have evolved multiple times within the tribe (Nogueira et al. 2013, Lohmann and Taylor 2014). On the other hand, clusters of patelliform glands located on petioles and petiolules are rare in Bignoniaceae and only known from a few species (e.g. *Tanaecium pyramidatum* and *Mansoa standleyi*).

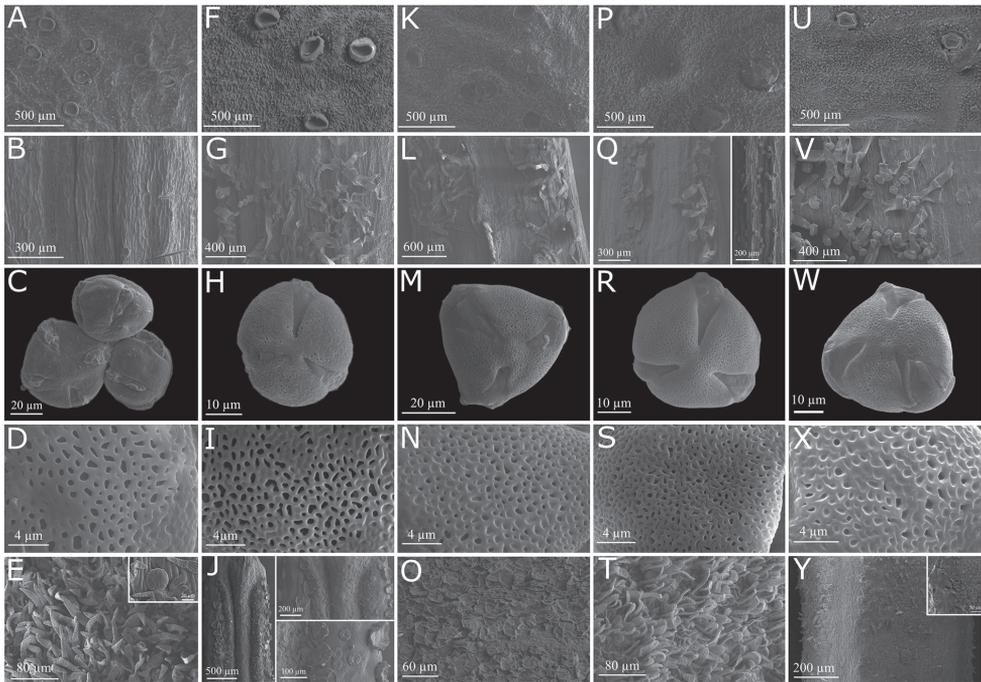
*Leaves and tendrils.* As with most representatives of Bignoniaceae, leaves of *Pachyptera* are 2-3-foliolate, with the terminal leaflet replaced by a trifid tendril. Tendrils are often deciduous, leaving a tiny scar in the position of tendril detachment. Leaflets can be quite variable in shape, varying even within a single species. Leaflet asymmetry is striking in the group and can help in its identification.



**Figure 2.** Sample of morphological features of *Pachyptera*. **A–D** *Pachyptera aromatica*: **A** Inflorescence **B** Frontal view of flowers **C** Detail of inflorescence and flowers, showing calyx partition **D** Interpetiolar region of stem with extrafloral nectaries (EFNs) and prophylls of the axillary buds 3-seriated, triangular and minute **E–F** *P. erythraea*: **E** Inflorescence **F** Frontal view of flowers **G–L** *P. incarnata*: **G** Stem with tendril surrounding a tree **H** Interpetiolar region of stem with EFNs and prophylls of the axillary buds flattened, ensiform and seriated **I** Inflorescence **J** Frontal view of flower **K** Pink patelliform glands on flower lobes **L** Detail of calyx **M–Q** *P. kerere*: **M** Stem cross-section with four phloem wedges **N** Inflorescence **O** Frontal view of flower **P** White patelliform glands on flower lobes **Q** Detail of calyx.

*Inflorescences.* The inflorescence of *Pachyptera* is a simple raceme that can originate from the apical and axillary buds, producing terminal and axillary inflorescences respectively. Racemes can be lax, with a well-developed central axis, ca. 6–24 cm in *P. aromatica* (Fig. 2A, C) or reduced, with a short central axis (< 4.8 cm long) in all other species of the genus (Fig. 2E, I, N). In *Pachyptera*, inflorescence bears ca. 6–30 flowers, although only 1–2 flowers open at a time.

*Calyx.* The calyx of *Pachyptera* is tubular (cupular in *P. erythraea*) with grouped patelliform glands on the upper half (Figs 2M–N, 3A, F, K, P, U), a synapomorphy of the genus. Even though this feature evolved multiple times within the tribe (Lohmann 2006; Lohmann and Taylor 2014), each evolutionary event led to a different gland type and arrangement and the calyx glands found in *Pachyptera* have a unique mor-

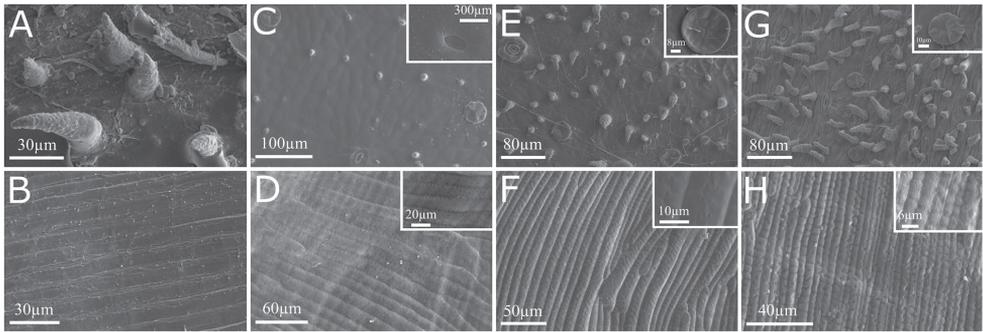


**Figure 3.** Vertical lines show calyx with patelliform glands, region of stamen insertion, pollen grains, detail of pollen exine and ovary surface variation in all species of *Pachyptera*, respectively. **A–E** *P. aromatica* **F–J** *P. erythraea* **K–O** *P. incarnata* **P–T** *P. kerere* **U–Y** *P. linearis*.

phology and arrangement within the tribe. These patelliform glands are conspicuous, sometimes wine-coloured (Fig. 1M) and thought to play an important role against nectar robbers (Gentry 1974).

**Corollas.** More than half of *Pachyptera* species have infundibuliform and dorso-ventrally compressed corollas (Fig. 2I, N), with internal yellow nectar guides (Fig. 2F, O) and a villous portion where stamens and staminodes are included (Fig. 3G, L, Q, V). The corolla tube shape of *P. erythraea* is slightly modified and expands above the short basal constriction and becomes tubular-campanulate (Figs 2E–F, 8B). On the other hand, *P. aromatica* exhibits an extraordinary and distinctive morphology, showing a corolla hypocrateriform, not compressed (Fig. 2A–B), without nectar guides that are glabrous internally (Fig. 3B). Corolla colour is useful for species identification, ranging from white to red (see Figs 1, 2). All species display nectaries on the upper portion of the corolla tube and base of the corolla lobes that exude large globules of colourless and viscous liquid (Fig. 2K, P), likely associated with ant-plant interactions. This feature is a morphological synapomorphy of the genus (Lohmann 2006; Lohmann and Taylor 2014).

**Androecium.** As with most members of Bignoniaceae, *Pachyptera* has four didynamous stamens and one staminode. Filaments are usually glabrous but puberulous in *P. erythraea*. The anthers are generally included, but sub-exserted in *P. erythraea* (Fig. 2F).



**Figure 4.** Vertical lines show fruit and seed surface, respectively. **A–B** *P. aromatica* **C–D** *P. incarnata* **E–F** *P. kerere* **G–H** *P. linearis*.

The densely villous anthers, with curved thecae, are diagnostic of the majority of *Pachyptera* species (Fig. 2F, O). Only *P. aromatica* has glabrous anthers with straight thecae. Villous anthers are an important feature of *Pachyptera* (except *P. aromatica*), only shared with *Lundia*.

*Pollen.* Pollen has been shown to represent a useful trait for generic delimitation within the Bignoniaceae (Gentry and Tomb 1979). Members of *Pachyptera* generally have microreticulate 3-colpate pollen (Fig. 3H, M, R, W), a condition also found in *Lundia*, *Pleonotoma* and *Tanaecium* (Gentry and Tomb 1979). However, *P. aromatica* has psilate-foveolate to microreticulate 4-colpate pollen grains (Fig. 3C–D).

*Gynoecium.* Members of *Pachyptera* have capitate, elliptic and ovate stigmas. While the style and stigma are always glabrous, the ovary is pubescent (Fig. 3E, T, Y) or lepidote (Fig. 3J, O). As with most representatives of Bignoniaceae, *Pachyptera* has bilocular ovaries, with two ovules per locule and axillary placentation. All species have well-developed nectar discs.

*Fruits.* Fruits are coriaceous to woody septical capsules, with two valves. The capsule is linear and flattened in most species (fusiform and inflated in *P. kerere*), puberulous, lepidote, covered with patelliform glandular trichomes and without lenticels (Fig. 4A, C, E, G). Each valve has an inconspicuous longitudinal midline (conspicuous and raised in *P. kerere*).

*Seeds.* The seeds of *Pachyptera* are mostly oblong, thin, chartaceous to coriaceous, with membranaceous and hyaline wings, except from *P. kerere* in which seeds are irregularly circular and obcordate, thick, corky and wingless. Seed surface has provided excellent information for the systematics of various plant groups (Barthlott 1981). The seed surface of *Pachyptera* species is striated, with a distinctive secondary sculpture in each species. More specifically, the seed surface of *P. aromatica* is striated and smooth, while the seed surface of *P. incarnata* is striated with randomly distributed micropores and the seed surface of *P. kerere* is striated with two pairs of medium micropores on each striation. In *P. linearis*, the seed surface is striated, with the striations being regularly interrupted by lateral rays (Fig. 4B, D, F, H). The seed surface of *P. erythraea* is unknown.

## Material and methods

*Species delimitation.* Molecular phylogenetic data (Francisco and Lohmann submitted) was used to aid species delimitation. While it is understood that not all species need to be monophyletic, species are evolutionary lineages that reach a status of reciprocal monophyly in advanced stages of the speciation process (de Queiroz 2007; Funk and Olmstead 2003). As such, independent evolutionary units that share a unique combination of features are treated here as separate species, following Cracraft (1983).

*Morphological descriptions.* Morphological descriptions of all species of *Pachyptera* were based on extensive fieldwork and on the analysis of multiple herbarium specimens. The authors examined 378 specimens deposited in the following herbaria: A, B, COL, ESA, F, G, HB, HERBAM, HRCB, HUA, IAN, INPA, K, LINN, MBM, MG, MICH, MO, NY, NX, P, R, RB, RBR, S, SPF, SP, SPSF, UEC, UFACPZ, US, VEN and WU (acronyms following Thiers 2015). Images or the actual specimens of all type materials were also analysed. Fieldwork was conducted between 2014 and 2015, in the Brazilian states of Amazonas, Pará and Roraima, the centre of diversity of *Pachyptera*. Specimens collected during field expeditions were deposited at SPF and MO. All accepted names are listed alphabetically, with nomenclatural discussions and citations following McNeill et al. (2012).

Morphological descriptions and measurements were conducted on dried specimens and fresh materials following the terminology of Lohmann and Taylor (2014), with additional terms from Radford (1974), Gentry and Tomb (1979), Hesse et al. (2009), Hickey (1979), Nogueira et al. (2013) and Weberling (1992). Rare conditions are shown within parentheses. Calyx, corolla and ovary surfaces, fruit coat, pollen surface and seed coat were analysed from representative specimens of each taxon using scanning electron microscopy (SEM) (Appendix 1). The selected structures were mounted on stubs and sputter-coated with gold. Micrographs were obtained on a Zeiss DSM 970 scanning electron microscope.

*Distribution maps and examined specimens.* Distribution maps were prepared using QGIS 2.16.3 (QGIS Development Team 2016). A list of examined specimens was prepared and listed alphabetically using the R package monographaR (Reginato 2016) implemented in R (R Development Core Team 2017).

## Taxonomic treatment

### *Pachyptera* DC., Prodr. 9: 175. 1845

*Pachyptera* DC., Prodr. 9: 175. 1845. Type: *Pachyptera foveolata* DC. (lectotype, designated by Sandwith [1932: 84]) [= *Pachyptera kerere* (Aubl.) Sandwith]

*Sererea* Raf., Sylva Tellur. 107. 1838. Type: *Sererea heterophylla* (Willd.) Raf., Sylva Tellur. 107. 1838. *nom. illeg. superfl.* [= *Pachyptera kerere* (Aubl.) Sandwith]

*Leucocalantha* Barb. Rodr., Vellozia, ed. 2. 1: 46, tab. 7. 1891. Type: *Leucocalantha aromatica* Barb. Rodr., Vellozia. ed. 2. 1: 47, tab. 7. 1891.

**Description.** *Liana*; stems with four phloem wedges in cross-section, solid (hollow in some specimens of *P. aromatica*), cylindrical to tetragonal, striated, with lenticels (without in *P. aromatica*), with interpetiolar extrafloral nectaries, with a continuous (discontinuous) and transversal interpetiolar ridge, with a papery peeling bark, lepidote, puberulous becoming glabrescent with age; prophylls of the axillary buds 3(–5) seriated (a single series visible to the naked eye in some specimens of *P. aromatica*), flattened and ensiform (triangular and minute in *P. aromatica*). *Leaves* 3-2-foliolate with the terminal leaflet replaced by a trifid tendril; blades discolorous (concolor), chartaceous to coriaceous, usually asymmetric (symetric in some specimens of *P. aromatica*), apex mucronulate, glabrous to puberulous, with simple trichomes covering veins (throughout surface), lepidote, with patelliform trichomes throughout the lamina, venation pinnate, secondary venation brochidromous, tertiary venation percurrent, margin entire, flat or sub-revolute; petioles striated, apices articulated, glabrous to puberulous, lepidote, patelliform glands distributed at petiole apices; petiolules with unequal lengths, striated, apices not-pulvinated (pulvinated in *P. aromatica*), puberulous, lepidote, lateral petiolules shorter than the apical ones. *Inflorescence* axillary or terminal, a few-flowered raceme, congested (lax in *P. aromatica*); axis puberulous, lepidote, patelliform glands grouped at the axis; pedicel puberulous, lepidote; bracts and bracteoles caducous, scarcely evident, puberulous, lepidote. *Calyx* tubular (cupular in *P. erythraea*), coriaceous, smooth, glabrous internally, puberulous externally, lepidote, patelliform glands grouped at the upper portion. *Corolla* white to cream (orange to red in *P. erythraea* and light pink to pale purple in *P. incarnata*), with yellow nectar guides, infundibuliform, (hypocrateriform in *P. aromatica* and tubular-campanulate in *P. erythraea*), straight, dorso-ventrally compressed (not compressed in *P. aromatica*), membranaceous, tube puberulous externally, lepidote, glabrous internally, but villous at the region of insertion of stamens and staminode (glabrous in *P. aromatica*); lobes imbricate, with a pair of patelliform glands arranged in lines externally, lepidote internally. *Androecium* didynamous, included in two heights, with one staminode, glabrous (puberulous in *P. erythraea*); anthers white, becoming darkish with age, included (sub-exserted in *P. erythraea*), villous (glabrous in *P. aromatica*), basifixed, connective thick, round (acute in *P. aromatica*), with thecae divergent, curved forward (straight in *P. aromatica*); pollen 3 colpate, microreticulate (4 colpate, psilate-foveolate-microreticulate in *P. aromatica*). *Gynoecium* glabrous; ovary cylindrical, not-sulcate (bisulcate in *P. erythraea*), smooth, pubescent, (densely lepidote in *P. erythraea* and *P. incarnata*); ovules arranged in two series per locule, placentation axial; stigma glabrous; nectar disc well developed, glabrous. *Capsule* linear, flattened (fusiform, inflated in *P. kerere*), coriaceous to woody, smooth, puberulous, lepidote, with patelliform glandular trichomes throughout, in higher densities at the margins of valves, without lenticels, each valve with an inconspicuous longitudinal midline (conspicuous and raised in *P. kerere*), calyx caducous; seeds oblong, thin, not-corky (irregularly circular, obcordate, thick and corky in *P. kerere*), chartaceous to coriaceous, glabrous, smooth, striated, winged (wingless in *P. kerere*), with membranaceous (chartaceous) and hyaline wings.

**Nomenclatural note.** *Sererea* Raf. was described to accommodate one species, *Sererea heterophylla* Raf., using a wrong spelling. However, *Sererea heterophylla* (Willd.) Raf. was actually based on *Bignonia heterophylla* Willd., a superfluous name for *Bignonia kerere* Aubl.

**Number of species, distribution and habitat.** *Pachyptera* comprises five species found in wet and flooded forest vegetation from Belize to Bolivia and Brazil.

### Key to species of *Pachyptera*

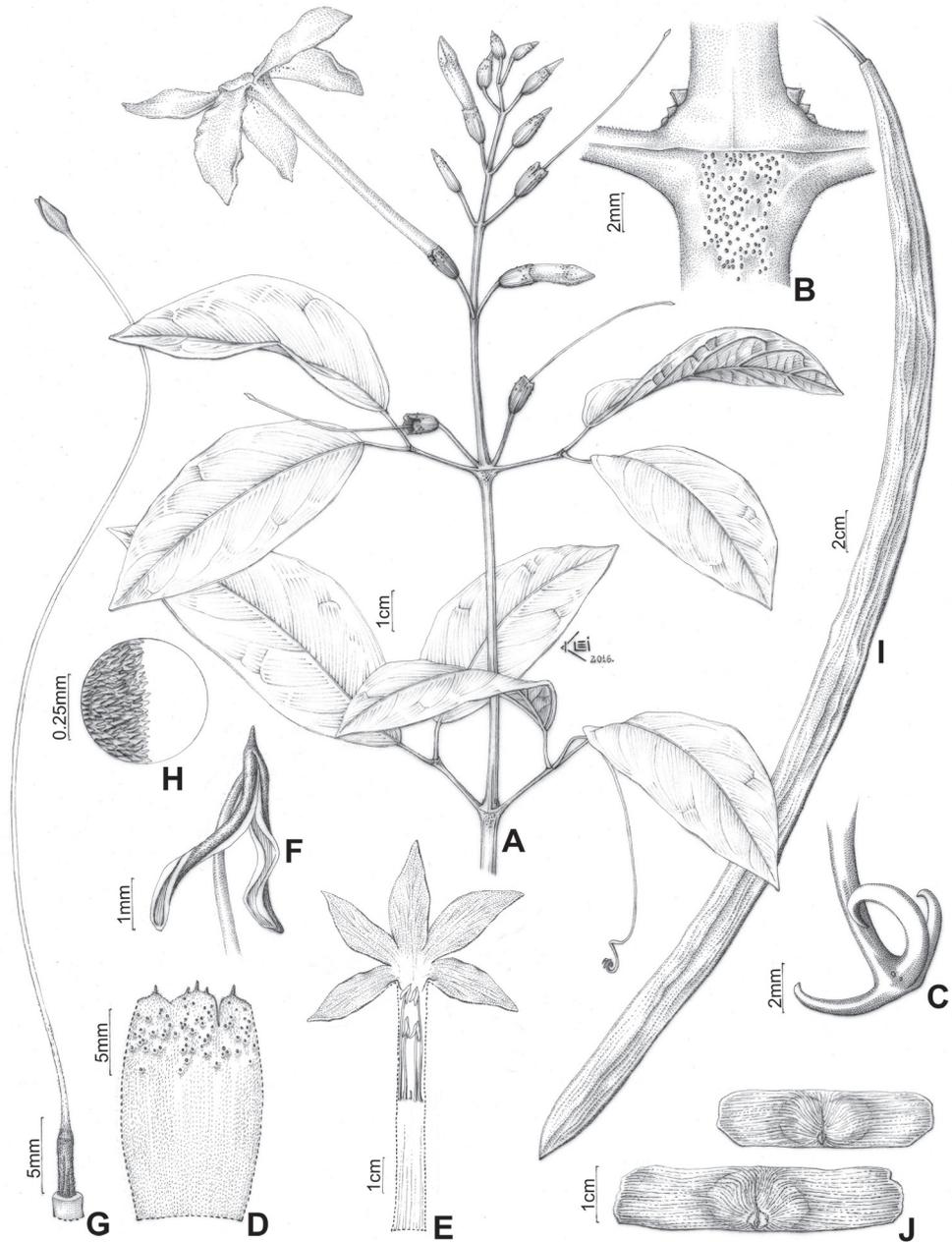
- 1 Stems cylindrical (if tetragonal, then only on older portions), without lenticels; prophylls of the axillary buds triangular and minute; corolla hypocrateriform ..... *P. aromatica*
- Stems tetragonal (if cylindrical, then only on younger portions), with lenticels; prophylls of the axillary buds ensiform and flattened; corolla infundibuliform or tubular-campanulate ..... **2**
- 2 Corolla light pink to pale purple or orange to red; ovary densely lepidote ..... **3**
- Corolla white to cream; ovary pubescent ..... **4**
- 3 Calyx reddish-wine throughout, cupular; corolla orange to red, tubular campanulate; stamens sub-exserted; capsule linear, 34.0–41.0 cm long,  $\geq 2.7$  cm wide ..... *P. erythraea*
- Calyx green, light pink at the apex, tubular; corolla light pink to pale purple, infundibuliform; stamens included; capsule linear, 10.5–42.6 cm long,  $\leq 2.6$  cm wide ..... *P. incarnata*
- 4 Ovary densely pubescent; capsule fusiform, inflated, each valve with a conspicuous midline; seeds thick, corky and wingless ..... *P. kerere*
- Ovary sparsely to moderately pubescent; capsule linear, flat, each valve with an inconspicuous midline; seeds thin, coriaceous and winged ..... *P. linearis*

### 1. *Pachyptera aromatica* (Barb. Rodr.) L.G. Lohmann, Ann. Missouri Bot. Gard. 99(3): 456. 2014

Fig. 5

*Pachyptera aromatica* (Barb. Rodr.) L.G. Lohmann, Ann. Missouri Bot. Gard. 99(3): 456. 2014. *Leucocalantha aromatica* Barb. Rodr., Vellozia. ed. 2. 1: 47, tab. 7. 1891. *Pachyptera aromatica* (Barb. Rodr.) L.G. Lohmann, Cat. Pl. Fung. Brasil 1: 770. 2010, *nom. nud.* Type: Brazil. Amazonas: in capoeiras prope Manáos, in Rio Negro, July, fl., B. Rodrigues 633. Lectotype (designated here): tab. 7, in Vellozia. 1891, excluding the pollen image.

**Description.** *Liana*; stems solid (hollow), cylindrical (tetragonal when  $\geq 6$  cm<sup>2</sup> diameter), vinaceous, with greyish striations, without lenticels; prophylls of axillary buds 3-seriated (a single series visible to the naked eye in some specimens), triangular and



**Figure 5.** *Pachyptera aromatica*: **A** Flowering branch **B** Interpetiolar region with extra-floral nectaries (EFNs) and prophylls of the axillary buds 3-seriated, triangular and minute **C** Trifid trentil **D** Open calyx (external view) **E** Open flower showing the androecium **F** Upper portion of stamen showing glabrous filament, glabrous anther and acute connective **G** Gynoecium **H** Detail of ovary surface showing pubescent indument (L.H. Fonseca 327, SPF) **I** Fruit linear and flattened **J** Seeds wings (T.B. Croat 11085, MO).

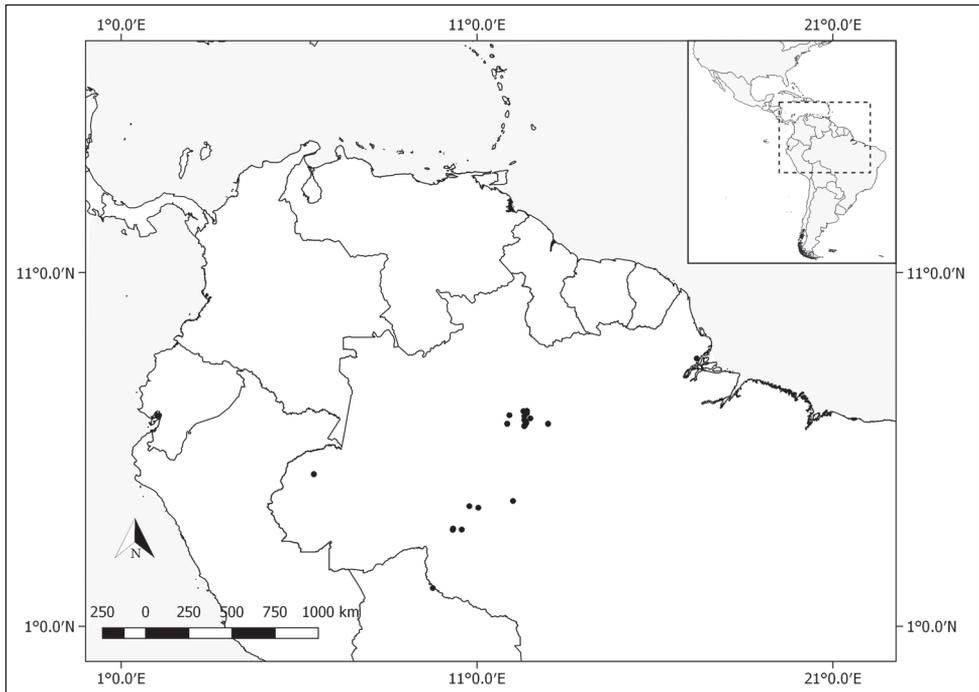
minute. *Leaves* with blades discolorous, chartaceous to coriaceous, elliptic, obovate or ovate-lanceolate, asymmetric (symmetric), apex acuminate or caudate, base cuneate, obtuse or rounded, lateral blades 5.3–19.8 × 2.0–8.0 cm, apical blades 9.0–19 × 3.8–9.0 cm; petioles cylindrical, (0.3–)1.0–6.0 cm long; petiolules often pulvinated, lateral petiolules 0.5–6.0 cm long, apical petiolules 3.0–8.5 cm long. *Inflorescence* a lax raceme, 6–24 cm long; pedicel 0.5–1.8 cm long; bracts 0.4–2.1 mm long; bracteoles cymbiform or lanceolate, 0.7–0.8 mm. *Calyx* green, tubular, sub-bilabiate, 5-denticulate (truncate), 1.0–1.8 × 0.3–0.6 cm. *Corolla* white, hypocrateriform, 6.3–12.2 cm long, 0.4–1.0 cm of diameter at the tube mouth; lobes elliptic or obovate, 1.9–4.0 × 1.1–1.9 cm. *Androecium* with the longer stamens 14.0–23.1 mm long, the shorter stamens 11.0–19.7 mm long, glabrous; anthers glabrous, included, with thecae straight, 3.8–6.2 × 0.3–0.6 mm; pollen 4-colpate, psilate-foveolate-microreticulate. *Gynoecium* ca. 5.4 cm long; ovary 2.7–4.8 × 1.0–1.2 mm, cylindrical, not-sulcate, smooth, moderately to densely pubescent, with simple and dentritic trichomes, sparsely lepidote, with glandular peltate trichomes, without patelliform glandular trichomes; stigma ovate, 2.3 × 1.6 mm; nectar disc 0.3–1.4 × 1.3–2.1 mm. *Capsule* linear, flattened, 33.1–95.0 × 1.0–2.0 cm, each valve with an inconspicuous longitudinal midline; seeds oblong, 4.0–5.5 × 1.0–1.6 cm, thin, not-corky, chartaceous, striated, secondary sculpture smooth, winged, with membranaceous (chartaceous) and hyaline wings.

**Distribution.** *Pachyptera aromatica* grows in wet forest vegetation in the Brazilian Amazon (Amapá, Amazonas, Rondônia). Fig. 6.

**Phenology.** This species flowers from June to January. Fruits were collected in January, March and July through November.

**Nomenclatural note.** Like Lohmann and Taylor (2014), it was not possible to locate the holotype of *P. aromatica* during multiple visits to the RB, where the holotype was thought to be deposited. It was also not possible to locate any isotypes of any of the collections visited, indicating that the types of *P. aromatica* were likely lost, just like several other type materials collected by Barbora Rodrigues in the Amazon (Mori and Ferreira 1987). As such, we here designate the illustration used in the original description of this species as the lectotype.

**Taxonomic comments.** *P. aromatica* is characterised by cylindrical (tetragonal when  $\geq 6$  cm<sup>2</sup> diameter) and vinaceous stems with greyish striations, interpetiolar extrafloral nectaries, triangular and minute prophylls of the axillary buds 3-seriated and white and hypocrateriform corollas (Figs 2A–D, 5A). This species was originally described within a monotypic genus due to its unusual morphology (Barbosa Rodrigues 1891), but was later transferred into *Pachyptera* based on a combination of morphological and molecular phylogenetic data (Lohmann and Taylor 2014). *Pachyptera aromatica* is sister to the remaining species of the genus (Fig. 1; Francisco and Lohmann 2017, Francisco and Lohmann submitted). The phylogenetic placement of *P. aromatica* corroborates its placement within *Pachyptera* and helps to explain the unusual morphology of this taxon. Selection exerted by differ pollinators may help to explain the floral differences amongst *P. aromatica* and its close relatives. *Pachyptera aromatica* also has a series of other unusual features in the genus such as the poorly developed,



**Figure 6.** Distribution of *Pachyptera aromatica*.

triangular and minute prophylls of the axillary buds (vs. well developed, flattened and ensiform prophylls of all other species of *Pachyptera*), glabrous region of stamen and staminode insertion (vs. villous region of stamen and staminode insertion of all other species of *Pachyptera*), glabrous anthers with straight thecae (vs. villous anthers with curved thecae of all other species of *Pachyptera*) and white hypocrateriform corollas (vs. white to red infundibuliform or tubular-campanulate corollas of all other species of *Pachyptera*) (Fig. 5A–B, E–F).

**Specimens examined. BRAZIL. Amapá:** Macapá, Margem de campo, 31 Oct 1980, fl., B. Rabele 1003 (MG). **Amazonas:** Humaitá, near river Livramento, 6 Oct 1934, fr., B.A. Krukoff 6845 (NY, K); Humaitá, Basin of Rio Madeira, on Rio Livramento, 1 Jan 1982, fl., B.A. Krukoff 12511 (INPA); Iranduba, Estrada entre Novo Airão e Manacapuru, 2°54'46.6"S, 60°57'58.8"W, fl., L.H. Fonseca 327 (SPF); Itacoatiara, Rio Solimões, West of Itacoatiara, brazilnut plantation, EPILOC360, 3°00'S 58°45'W, 100 m, 15 Jan 1990, fr., A.H. Gentry 69107 (MO); Manaus, Mar 1907, fr., M. Labroy 1906 (P); *Ibid.*, 30 July 1929, fl., A. Sucre s.n. (R, RB); *Ibid.*, 30 July 1929, fl., fr., A. Ducke s.n. (MO); *Ibid.*, 31 July 1929, fl., A. Ducke 22698a (P, R); *Ibid.*, 8 Aug 1931, fr., A. Ducke s.n. (R); *Ibid.*, 8 Nov 1931, fr., A. Ducke 22698b (P); Manaus, BR-17, Km 3, 26 Aug 1955, fl., L.F. Coelho INPA1731 (INPA); *Ibid.*, BR-17, km 3, 30 Aug 1955, fl., F.C. Mello s.n. (INPA); *Ibid.*, ca. 80 km N de Manaus, Distrito Agropecuário da SUFRAMA, Rodovia BR 174, km 64, depois 21 km leste na ZF3, Fazenda Porto Alegre, 1 Jan 1962, st., M.H. Nee s.n. (INPA); *Ibid.*, Campos Sales,

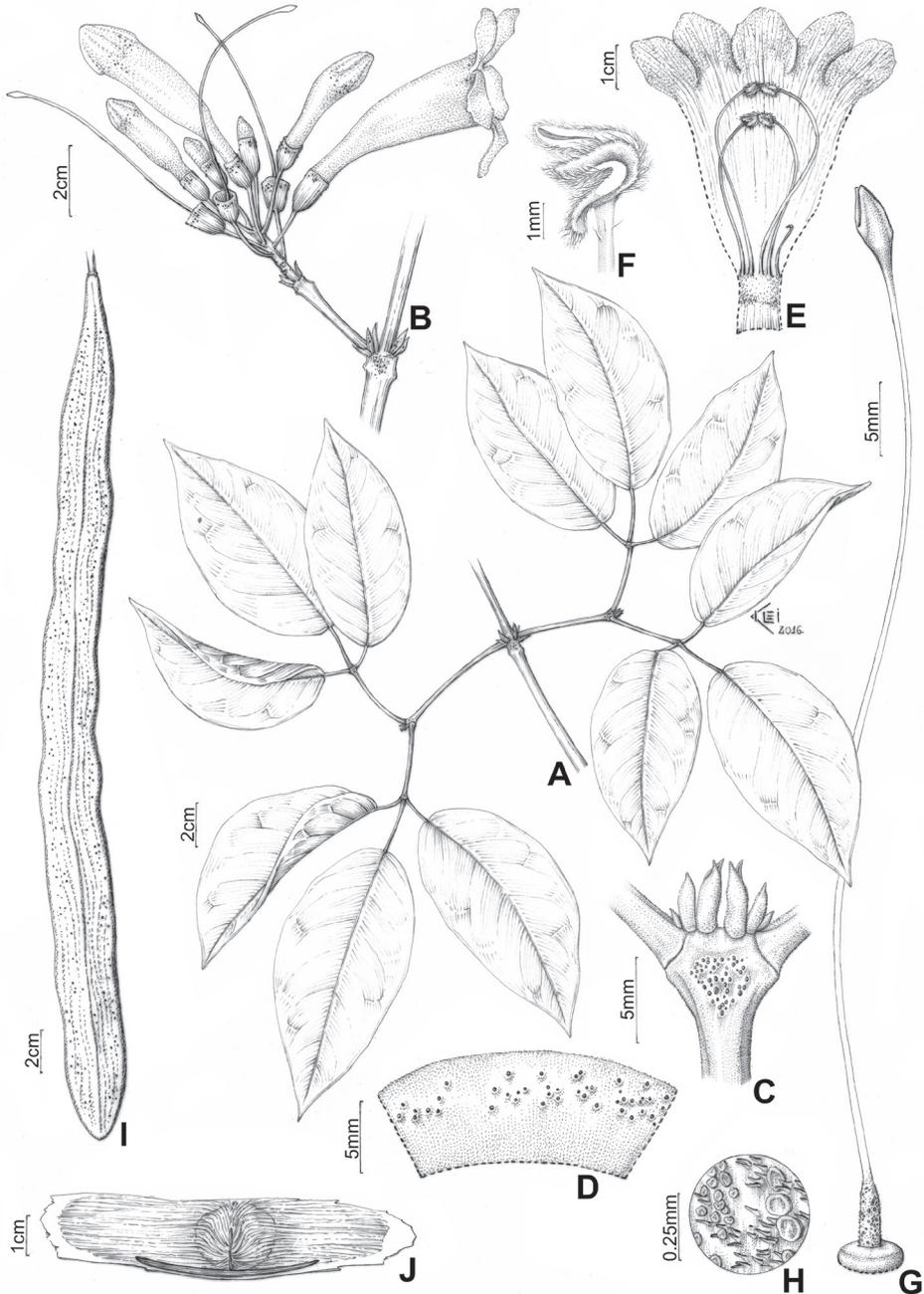
margem do Igarapé do Buião, 28 Sept 1954, fl., J.C. Almeida INPA137 (INPA); *Ibid.*, Estrada BR-17, 30 Aug 1955, fl., C.M. Francisco s.n. (MG), Luís s.n. (MG); *Ibid.*, Estrada da Forquilha, Margem do igarapé da cachoeira Alta, 22 Aug 1955, fl., J.C. Chagas INPA1701 (INPA); *Ibid.*, Estrada do Aleixo, km 11 past INPA, 2 Dec 1974, fl., A.H. Gentry 13022 (INPA, MO); *Ibid.*, Estrada do igarapé do Tabatinga, 17 Sept 1963, fl., W.A. Rodrigues 5476 (INPA); *Ibid.*, Estrada do Passarinho, 6 Aug 1962, fl., W.A. Rodrigues 4578 (INPA, SPF); *Ibid.*, Ground of INPA at Manaus, 5 Apr 1974, st., A.H. Gentry 11201 (MO), A.H. Gentry 11207 (MO); *Ibid.*, Igarapé do Buião, 15 Oct 1962, st., W.A. Rodrigues 4693 (MO, US); *Ibid.*, Igarapé do Franco, 29 Aug 1957, fl., J.C. Almeida INPA5722 (INPA); *Ibid.*, Loco Cachaeira Grande, 4 July 1943, fl., A. Ducke 239 (NY, K); *Ibid.*, Margem da estrada do Paredão, 3 Aug 1955, fl., J.C. Almeida INPA1540 (INPA); *Ibid.*, Margem do Igarapé do Buião, 19 Aug 1955, fl., J.C. Almeida INPA1687 (INPA); *Ibid.*, Mauazinho, Industrial development, 2°18'57.6"S, 60°04'58.8"W, 50-60 m, 4 Aug 1987, fl., S. Tsugaru B-690 (NY); *Ibid.*, Outskirts of Manaus, road to INPA, boat landing, behind airport, 26 Nov 1974, fr., A.H. Gentry 12862 (INPA, MO, R); *Ibid.*, s.d. fl., Ule U. 4217 (HB, MO); *Ibid.*, Sede do Inpa, Aleixo, depostio do Oficina, 10 July 1972, fl., M. Silva 1024 (INPA, MO); *Ibid.*, Wedge of Rio Negro, a few km N of Manaus, 26 Nov 1974, st., A.H. Gentry 12888 (INPA, MO); *Ibid.*, Rio Negro, Aug 1900, fl., U. Ule 5217 (K); *Ibid.*, Rio Preto da Eva, 2-5 km N of Manaus-Itacoatiara Road at km 79 near Río Preto da Eva, 24 Nov 1974, fl., A.H. Gentry 12832 (MO); *Ibid.*, Road toward Río Negro, 10 km N from Manaus on Estrada Aleixo, 21 Nov 1974, st., A.H. Gentry 12778 (MO, R); *Ibid.*, Rodovia BR-174 Manaus-Presidente Figueiredo, sentido norte., 02°47'53.97"S, 60°02'13.12"W, 87 m, 23 Sept 2016, fl., E. Kataoka 349 (SPF); *Ibid.* (BR-174), próximo a entrada da Reserva de Campinarana do INPA., 2°35'23.76"S, 60°02'2.26"W, 88 m, 23 Sept 2016, fr., A. Frazão 313 (SPF); *Ibid.*, Reserva Florestal Adolpho Ducke 02°53'S, 59°58'W, 15 July 1995, fl., M.J.G. Hopkins 1570 (SPF); *Ibid.*, 15 July 1995, fl., M.J.G. Hopkins 1574 (NYBG); *Ibid.*, 2 Sept 1962, st., A.P. Duarte 7048 (RB); *Ibid.*, Estrada da entrada, 15 Feb 1995, st., M.J.G. Hopkins 1543 (INPA, SPF); *Ibid.*, Nova Prainha, SB-20-ZA, Ponto 02, 10 Sept 1976, st., J.A. Souza INPA61048 (INPA); *Ibid.*, área interna da Reserva Ducke, planta na trilha LO2 entre 1050 e 1100 metros, no interior do gride PPBIO, 15 Oct 2012, st., A. Nogueira 190 (SPF); *Ibid.*, Planta fichada: 2966-24, 15 July 1995, fl., L.G. Lohmann 28 (INPA, SPF); *Ibid.*, próxima a sede da reserva, na área de platô, 02°55'49.0"S, 59°58'23.2"W, 100 m, 5 May 2015, st., C.S. Gerolamo 9 (SPF); *Ibid.*, km 26 on Manaus-Itacoatiara road, 2°18'S, 59°54'W, 80 m, 19 Jan 1990, fl., A.H. Gentry 69308 (MO); *Ibid.*, 23 Nov 1974, st., A.H. Gentry 12815 (INPA, MO); *Ibid.*, Km 16, 3 Dec 1974, fl., A.H. Gentry 13056 (MO); *Ibid.*, km 55, 24 Oct 1963, fr., E. Oliveira 2790 (IAN); *Ibid.*, km 26, 30 Sept 1976, st., J.A. Souza INPA61920 (INPA); *Ibid.*, 1 Jan 1976, st., J.A. Souza s.n. (INPA); *Ibid.*, 15 July 1976, st., J.A. Souza INPA71829 (INPA); *Ibid.*, 21 July 1976, st., J.A. Souza INPA71832 (INPA); *Ibid.*, 25 May 1976, st., J.A. Souza INPA71839 (INPA); *Ibid.*, 3 Aug 1976, st., J.A. Souza INPA71828 (INPA); *Ibid.*, 6 Aug 1976, J.A. Souza INPA71827 (INPA); Novo Airão, Estação Ecológica Anavilhanas, 2°32'08.0"S, 60°50'49.0"W, 9 Oct 2006,

fl., L.G. Lohmann 794 (SPF). **Rondônia:** Porto Velho, 11 Sept 1963, fl., B. Maguire 56679 (MO); *Ibid.*, Guaporé, 1 June 1952, fl., G.A. Black 52-14674 (IAN); *Ibid.*, Rio Madeira, Aug 1936, fl., A. Ducke 35624 (MO, RB, US); *Ibid.*, Aug 1936, fl., A. Sucre s.n. (RB); Rio Cuieras, 2 km below mouth of Rio Brancinho, 11 Sept 1973, fl., G.T. Prance 17773 (INPA, MO, NY). *Ibid.*, Sub-base do Projeto RADAM, aeroporto internacional local, 3 Sept 1975, fl., C.D.A. Mota 18 (INPA); *Ibid.*, Sub-base do Projeto RADAM, aeroporto internacional local, 3 Sept 1975, fr., C.D.A. Mota 26 (INPA); s.loc., 1 Jan 1972, fr., B. Maguire s.n. (INPA).

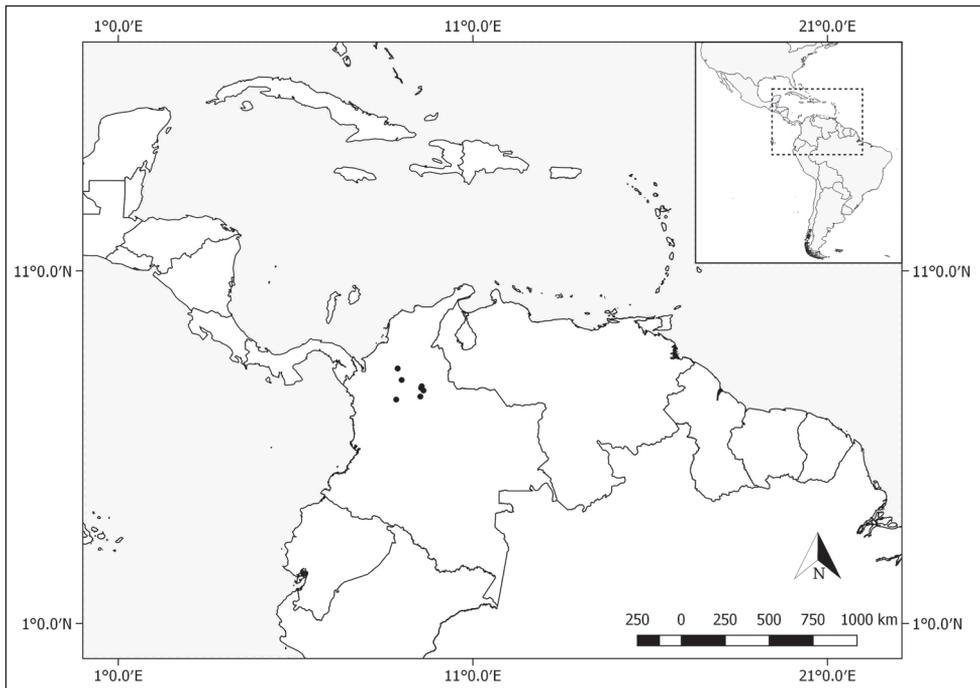
**2. *Pachyptera erythraea* (Dugand) A.H. Gentry, *Phytologia* 35(3): 186, fig. 2A. 1977**  
Fig. 7

*Pachyptera erythraea* (Dugand) A.H. Gentry, *Phytologia* 35(3): 186, fig. 2A. 1977.  
*Pachyptera kerere* var. *erythraea* Dugand, *Caldasia* 7(31): 16. 1955. *Mansoa erythraea* (Dugand) A. Gentry, *Ann. Missouri Bot. Gard.* 66(4): 782. 1979 [1980].  
Type: Colombia. Santander: 10 leguas al S.E. de Barranca Bermeja, a 9 km de la margen izquierda del Río Opón, 200 m., 26 Aug. 1954, fl., R. Romero-Castañeda 4727 (holotype, COL000004375!).

**Description.** *Liana*; stem solid, tetragonal (cylindrical when young), green or brown, with greyish striations, lenticellate; prophylls of axillary buds 3(-4)-seriated, flattened and ensiform. *Leaves* with blades discolorous, chartaceous, elliptic, ovate-lanceolate, asymmetric, apex caudate, base cordate, oblique, lateral blades 11.0–19.2 × 4.7–8 cm, apical blades 12.0–12.3 × 5.7–6.2 cm; petioles semi-cylindrical, 3.8–6.5 cm long; petiolules not pulvinate, lateral petiolules 1.3–2.4 cm long, apical petiolules 2.5–4.1 cm long. *Inflorescence* a congested raceme, 2.2–4.5 cm long; pedicel 1.8–2.6 cm long; bracts 1.2–1.3 × 0.5–0.9 mm long; bracteoles cymbiform or triangular, 0.4–0.8 mm. *Calyx* reddish-wine, cupular, truncate, minutely 5-lobed, 0.9 × 0.7–0.9 cm. *Corolla* orange to red, tubular-campanulate, 8.5–8.7 cm long, ca. 2.2 cm of diameter at the tube mouth; lobes rounded (sub-circular), 1.8 × 1.4–1.6 cm. *Androecium* with the longer stamens 44.8–49.3 mm long, the shortest stamens 34.6–39.3 mm long, sparsely puberulous at the dorsal portion of the apex; anthers villous, sub-exserted, with thecae curved forward, 2.0–2.6 × 0.6–1.4 mm; pollen 3-colpate, microreticulate. *Gynoecium* ca. 6.6 cm long; ovary 3.1–3.9 × 1.3–1.6, cylindrical, bisulcate, smooth, sparsely puberulous at grooves, with simple trichomes, moderately lepidote, with patelliform glandular trichomes distributed in two vertical lines parallel to the grooves, glandular peltate trichomes forming a vertical line of transition between internal and external grooves and mixing with simple trichomes within the grooves; stigma elliptic, 3.8 × 1.9–2.1 mm; nectar disc ca. 2.4 × 3.8 mm. *Capsule* linear, flattened, 34.0–41.0 × 2.7–3.0 cm, each valve with an inconspicuous longitudinal midline; seeds oblong, 7.5–9.8 × 2.0–2.1 cm, thin, not-corky, chartaceous to woody, striated, secondary sculpture not seen, winged, with membranaceous and hyaline wings.



**Figure 7.** *Pachyptera erythraea*: **A** Branchlets with four leaves **B** Inflorescence **C** Interpetiolar region showing extra floral nectaries and prophylls of axillary buds 3-seriated, flattened and ensiform **D** Open calyx (external view) **E** Open flower showing the androecium with anthers united by the villous indument **F** Upper portion of stamen, showing villous and curved thecae **G** Gynoecium **H** Detail of the lepidote ovary indument, with simple trichomes and glandular peltate, and patelliform trichomes (M. Weir 72, K) **I** Linear and flattened fruit **J** Seed wings (A.H. Gentry 20050, MO).



**Figure 8.** Distribution of *Pachyptera erythraea*.

**Distribution.** *Pachyptera erythraea* is endemic to wet forest vegetation from the Magdalena River Valley in northern Colombia (Antioquia, Santander). Fig. 8.

**Phenology.** Flowers collected in January, March and July to December. Two fruiting collections are known, one collected in July and the other in September.

**Taxonomic comments.** *Pachyptera erythraea* is distinguished by the orange to red corollas (vs. white, light pink to pale purple in all other species), cupular calyces (vs. tubular in all other species) and sub-exserted anthers (vs. included anthers in all other species). Moreover, *P. erythraea* is the sole species of *Pachyptera* with tubular-campanulate corollas. The fruit of *P. erythraea* is flat, without a visible longitudinal midline. The seeds are thin and winged, similar to those of *P. incarnata* and *P. linearis*. *Pachyptera erythraea* is closely related to *P. incarnata*, with which it shares a moderately to densely lepidote ovary (Fig. 1). However, these species are separated by the bi-sulcate ovary, with glandular peltate and patelliform trichomes arranged in vertical lines in *P. erythraea* vs. the non-sulcate ovary, fully covered by glandular peltate trichomes in *P. incarnata*.

**Specimens examined. COLOMBIA. Antioquia:** Caucasia, along road to Nechi 24 km from Caucasia-Planeta Rica road, Hacienda Costarica, margin of primary forest and trees remaining in cleared pasture, 8°03'36.0"N, 75°04'48.0"W, 60 m, 21 Mar 1987, fl., J.L. Zarucchi 4887 (HUA, K, MO); *Ibid.*, 21 Mar 1987, fl., J.L. Zarucchi 4862A (MO); Zaragoza, Carretera a Zaragoza entre Carralao y Angostura, 70 m, 13 Jan 1989, fl., G. Ramiro Fonnegra 2580 (HUA); Rio Magdalena, July 1868, fl., M. Weir 72 (K). **Santander:** Barranca Bermeja, 10 leguas al SE de Barranca Bermeja,

7°03'36.0"N, 73°51'36.0"W, 200 m, 26 Aug 1954, fl., R. Romero-Castañeda 4727 (COL, MO); *Ibid.*, 12 leguas al SE de Barranca Bermeja, orilla derecha del rio Opón, 200 m, 4 Oct 1954, fl., R. Romero-Castañeda 4979 (COL); *Ibid.*, 2 km S. of Llanitas, 19 km N. of Barranca Bermeja, 7°03'36.0"N, 73°51'36.0"W, 160 m, 24 July 1975, fl., A.H. Gentry 15369 (MO); 11-13 km N of Barranca Bermeja on road to Puerto, 07°09'19"N, 73°50'28"W, 160m, 24 July 1975, fl., A.H. Gentry 15372 (MO); Campo Capote, Magdalena Valley, campo Capote, 30 km E of Carare, 6.61, -73.91, 300 m, 29 Sept 1977, fr., A.H. Gentry 20050 (MO); El Centro, 3 km S. of El Centro on road to Yarima, 200 m, 25 July 1975, fl., fr., A.H. Gentry 15402 (MO).

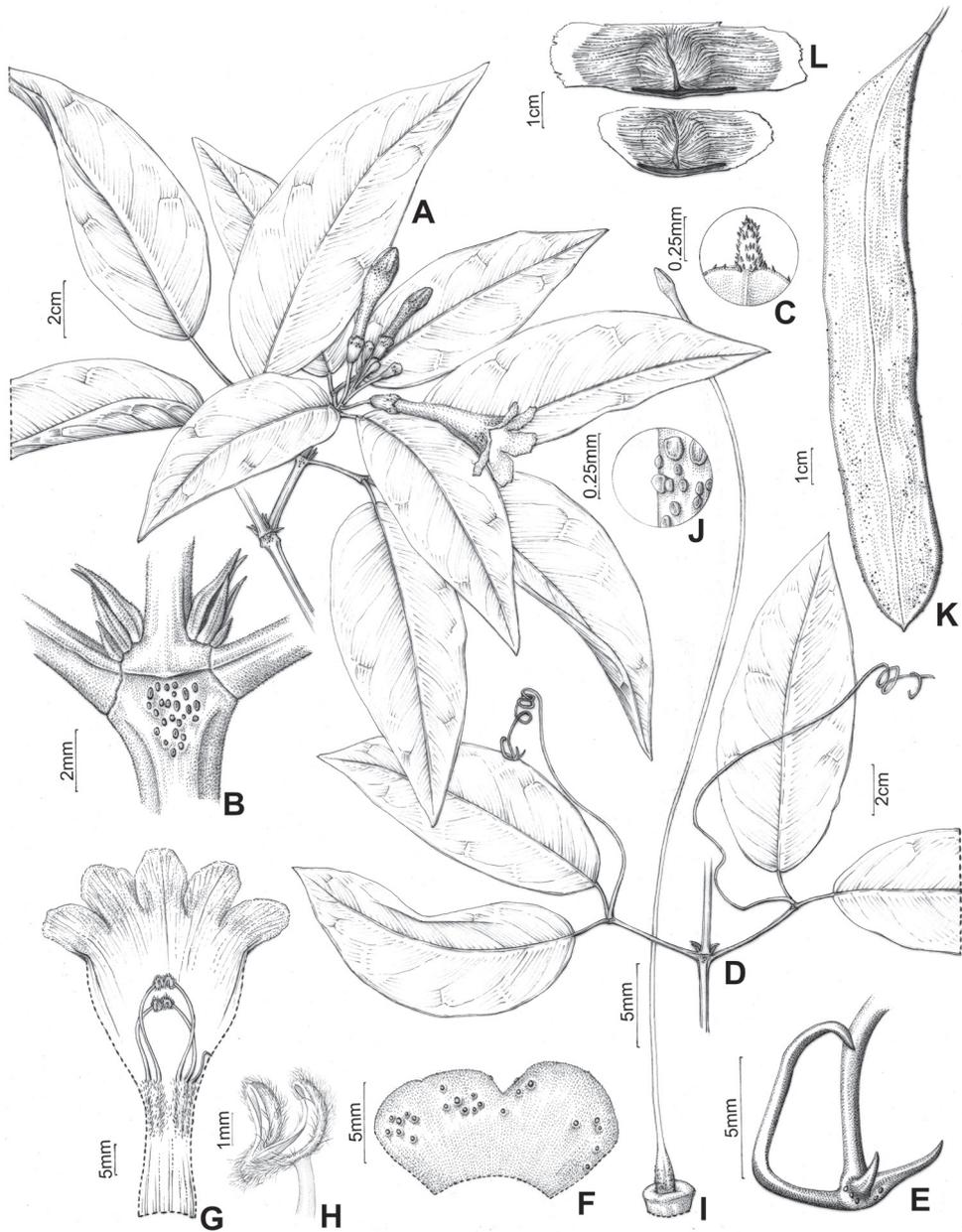
### 3. *Pachyptera incarnata* (Aubl.) Francisco & L.G. Lohmann, comb. nov.

urn:lsid:ipni.org:names:77175179-1

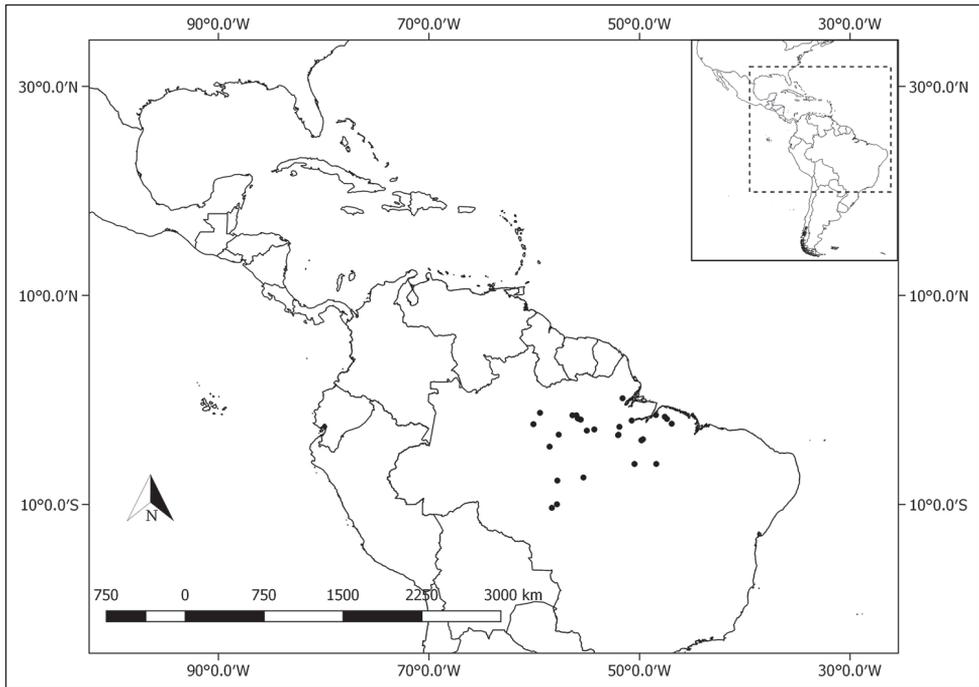
Fig. 9

*Bignonia incarnata* Aubl., Hist. Pl. Guiane. 2: 645, tab. 261, 262, fig. 1–8. 1775. *Bignonia incarnata* Aublet sec. Splitg., Tijdschr. Nat. Geschied 9: 7. 1842. *nom. nud.* *Cydista incarnata* Miers, Proc. Roy. Hort. Soc. London. 3: 192. 1863. *nom. nud.* *Pachyptera kerere* var. *incarnata* (Aubl.) A.H. Gentry, Brittonia 25(3): 235. 1973. *Mansoa kerere* var. *incarnata* (Aubl.) A.H. Gentry, Ann. Missouri Bot. Gard. 66(4): 783. 1979 [1980]. Type: French Guiana. s.loc., s.d., (fl., fr), J.B.C.F. Aublet s.n. Lectotype (designated here): tab. 261 and 262, in Hist. Pl. Guiane 1775.

**Description.** *Liana*; stems solid, tetragonal (cylindrical when young), green or brown (reddish), with greyish striations, lenticellate; prophylls of axillary buds 3(–5)-seriated, flattened and ensiform. *Leaves* with blades discolorous (concolor), chartaceous to coriaceous (membranaceous), elliptic, obovate or ovate-lanceolate, asymmetric, apex acute, acuminate or caudate (retuse), base cordate, oblique, lateral blades 2.6–21.1 × 1.9–9.2 cm, apical blades 5.7–20 × 2.6–7.6 cm; petioles semi-cylindrical, 0.8–5.5 cm long, petiolules not puvinated, lateral petiolules 0.8–5.5 cm long, apical petiolules 1.4–4.4 cm long. *Inflorescence* a congested raceme, 0.8–3.5 cm long; pedicel 0.5–1.3(–7.5) cm long; bracts 0.8–2.5 × 0.7–0.9 mm long; bracteoles cymbiform or filiform, 0.2–0.7 mm. *Calyx* green, light pink at apex, tubular, bilabiate, minutely 5-lobed or truncate, 0.4–1 × 0.4–0.6 cm. *Corolla* light pink to pale purple, infundibuliform, 2.9–7.6 cm long, 0.7–1.9 cm of diameter at the tube mouth; lobes rounded (sub-circular), 0.3–1.5 × 0.4–1.3 cm. *Androecium* with the longer stamens 23.4–17.0 mm long, the shorter stamens 10.0–15.7 mm long, glabrous; anthers villous, included, with thecae curved forward, 2.6–3.1 × 0.5–0.5 mm; pollen 3-colpate, microreticulate. *Gynoecium* 3.0–5.0 cm long; ovary 1.8–2.9 × 0.7–0.91, cylindrical, not-sulcate, smooth, glabrous, densely lepidote, with glandular peltate trichomes, rarely with some patelliform glandular trichomes; stigma capitate or ovate, 0.8–3.5 × 0.5 mm; nectar disc 0.8– 1.0 × 1.7–1.8 mm. *Capsule* linear, flattened, 10.5–42.6 × 1.4–2.6 cm, each valve with an inconspicuous longitudinal midline; seeds oblong, 4.0–7.0 × 1.3–2.8 cm, thin, not-corky,



**Figure 9.** *Pachyptera incarnata*: **A** Flowering branch **B** Interpetiolar region with EFNs and prophylls of axillary buds 3-seriate, flattened and ensiform **C** Mucronulate leaflet apex **D** Branchlets trifoliolate with terminal leaflet replaced by trifold tendrils **E** Trifold tendril **F** Calyx external view **G** Open flower showing the androecium with anthers united **H** Stamen with villous and curved thecae **I** Gynoecium **J** Ovary surface lepidote, with glandular peltate trichomes (J.N.C. Francisco 103, SPF) **K** Fruit linear flattened capsule **L** Seeds wings (J.N.C. Francisco 122, SPF).



**Figure 10.** Distribution of *Pachyptera incarnata*.

chartaceous to sub-coriaceous, striated, secondary sculpture with randomly distributed micropores, winged, with membranaceous and hyaline wings.

**Distribution.** This species is found in wet forest vegetation in Brazil (Amazonas, Mato Grosso, Pará, Rondônia) and French Guiana. Fig. 10.

**Phenology.** *Pachyptera incarnata* flowers in February to May and July to December. Fruiting material has been collected in April, May, July to October and December.

**Etymology.** The specific epithet “*incarnata*” refers to the corolla colour referred by Aublet as “of flesh”.

**Nomenclatural note.** This species was first described by Aublet (1775) as *Bignonia incarnata*. Gentry (1973) treated *B. incarnata* as a variety of *P. kerere* due to the shared racemose inflorescences, corolla infundibuliform, villous anthers and prophylls of the axillary buds 3-seriated. Gentry (1973) distinguished the two varieties based on differences in the fruit and seed morphology. More specifically, *P. kerere* var. *kerere* included the individuals with inflated fruits, corky and wingless seeds, while *P. kerere* var. *incarnata* included the individuals with flattened fruits, thin and winged seeds. Despite the floral similarity between these two species, *P. incarnata* is phylogenetically more closely related to *P. erythraea*, with which it shares a densely lepidote ovary and flattened and linear fruits (Fig. 1). Based on the authors’ new molecular phylogeny (Francisco and Lohmann submitted) and morphological data, this taxon is raised back to species-level,

following Aublet (1775). As it was not possible to locate original material, the original illustration is here designated as the lectotype.

**Taxonomic comments.** *Pachyptera incarnata* is characterised by the infundibuliform and light pink to pale purple corolla with ovary densely lepidote. The capsule is linear, flattened and coriaceous, with pink patelliform glandular trichomes throughout the surface and has an inconspicuous longitudinal midline. Seeds are oblong, thin, chartaceous to sub-coriaceous, winged, with membranaceous and hyaline wings.

**Specimens examined.** **BRAZIL. Amapá:** Campaipí, Embrapa reserve and vicinity, 0°10'N, 51°37'W, 3 Sept 1983, fl., S.A. Mori 15783 (MG, MO). **Amazonas:** Manaus, 31 Aug 1931, fl., A. Ducke 24091 (R); *Ibid.*, estrada do Aleixo, near Manaus, turn off to Río Negro at km 11 past INPA, 2 Dec 1974, fl., A.H. Gentry 13027 (MO); *Ibid.*, INPA boat landing behind Manaus airport, Río Negro, 15 Dec 1974, fr., A.H. Gentry 13323 (MO); *Ibid.*, across from Guarara factory, 20 Apr 1974, fl., D.G. Campbell P22008 (MO); Presidente Figueiredo, Balbina, Rebio Uatumã, grade do PPBio, 6 Oct 2006, fr., J.R. Carvalho-Sobrinho 1078 (INPA). **Mato Grosso:** Aripuanã, MT-420, beira do rio, 10°15'00.0"S, 59°07'12.0"W, 11 July 1997, fl., G.F. Árbocz 4256 (ESA); Juruena, beira do Rio Juruena, floresta aluvial, 10°18'36.0"S, 58°19'48.0"W, 10 July 1997, fl., V.C. Souza 18583 (ESA); Nova Bandeirantes, estrada Iporã, 255 m, 22 July 2015, fl., fr., R.S. Ribeiro 78 (SPF). **Pará:** Belterra, Floresta Nacional do Tapajós, estrada para comunidade de Jamaraguá, km 72, 02°55'15.9"S, 55°01'39.4"W, 114 m, 16 Sept 2015, fl., J.N.C. Francisco 89 (SPF); estrada do Mocambo, IPEAN, 02 May 1969, fl., J.M. Pires 12075 (IAN, MO); Irituia, Rio Irituia, varzea S. Miguel do Guamá, 29 Oct 1948, fl., G.A. Black 48-3355 (IAN); Itaituba, estrada Santarém-Cuiabá, BR 163, km 794, 7°25'S, 55°20'W, 12 May 1983, fl., I.L. Amaral 1248 (MO); Marabá, Marabu, Serra Norte, Carajás, 7°42'36.0"S, 57°48'36.0"W, 01 Aug 1983, fl., M. Silva 1604 (MO, UEC); Óbidos, beira do Lago Curumu, floresta de várzea, 01°51'37.3"S, 55°38'47.3"W, 24 m, 23 Sept 2015, fl., J.N.C. Francisco 130 (SPF); Óbidos, lago Maria Teresa, floresta de várzea, 01°52'37.7"S, 55°35'28.7"W, 14 m, 23 Sept 2015, fl., J.N.C. Francisco 121 (SPF); *Ibid.*, 01°52'38.2"S, 55°35'27.4"W, 14 m, 23 Sept 2015, fr., J.N.C. Francisco 122 (SPF); Oriximiná, Floresta Nacional de Saracá-Taquera, próximo ao alojamento Pioneiros de pesquisadores, floresta de terra firme, 01°27'56.6"S, 56°22'43.8"W, 71 m, 27 Sept 2015, fl., J.N.C. Francisco 151 (SPF); *Ibid.*, Porto Trombetas, rejeitos, Linha 69, beira de floresta, 1°45'36.0"S, 55°51'36.0"W, 09 Dec 1987, fl., O.H. Knowles 1120 (INPA); *Ibid.*, Porto Trombetas, Serra Assas, descampado, 21 Oct 1987, fl., O.H. Knowles 1106 (INPA); Palestina do Pará, fazenda Andorinha sede 2, início da mata do rio Gameleira, 6°06'36.0"S, 48°24'36.0"W, 160 m, 18 Apr 2004, fr., G. Pereira-Silva 8765 (CEN); Parauapebas, Serra dos Carajás, Platô N2, vegetação de canga, 7 Mar 2010, fl., L.C.B. Lobato 3870 (MG); *Ibid.*, à margem da estrada Raymundo Mascarenhas, 8 Feb 1990, fl., J.B.P. Rocha 701 (IAN); Portel, 1°57'36.0"S, 50°45'00.0"W, 21 Oct 1955, fl., L. Williams 18222 (IAN, MO); Porto Trombetas, Mineração Rio do Norte, 1991, fr., Evando 542 (INPA); Santarém, beira da PA-370, próxima à guarita da Usina Hidrelétrica Curuá-Uma, floresta de terra firme, 02°49'21"S, 54°17'58.9"W, 49 m, 19 Sept 2015, fl., J.N.C. Francisco 103 (SPF); *Ibid.*, ramal

próximo à Usina Hidrelétrica Curuá-Uma, solo areno argiloso, floresta de terra firme, 02°48'45.2"S, 54°18'08.8"W, 47 m, 19 Sept 2015, fl., J.N.C. Francisco 105 (SPF); São Miguel do Guamá, Rio Guamá, beira do rio, igapó, 21 Aug 1948, fl., fr., Dardano 48-3092 (IAN); Senador José Porfírio, margem direita do Rio Xingu, capoeira de terra firme, 02°34'00"S, 51°55'00"W, 3 Dec 1991, fr., G. Santos 282 (MG); Tucuruí, área de desmatamento, 1 Sept 1983, fl., F.E. Miranda 362 (NY); *Ibid.*, BR-422, Km 45, Breu Branco, margem do rio Tocantins, 5 Nov 1983, fl., J. Ramos 1011 (INPA); *Ibid.*, estrada para o lago 31 de março, 30 Aug 1983, fl., J. Revilla 8397 (NY); *Ibid.*, margens da PA-149 até ca. Km 50, 22 Aug 1983, fr., J. Revilla 8326 (NY); Viseu, Serra do Piriá, à 13km de Açaiteua, 4 Dec 1993, fl., J. Sales 1539 (MG); Vitória do Xingu, 3°19'32"S, 52°00'16"W, 1 Aug 2015, fl., R.V. Pyramo PSACF\_EX06147 (RB); V *Ibid.*, 3°22'4"S, 52°02'23"W, 12 Aug 2015, fl., B.R. Silva PSACF\_EX06201 (RB).

#### 4. *Pachyptera kerere* (Aubl.) Sandwith, *Recueil Trav. Bot. Néerl.* 34: 219. 1937.

Fig. 11

*Bignonia kerere* Aubl., *Hist. Pl. Guiane* 2: 644, tab. 260. 1775, excluding the fruit description and tab. 263. *Bignonia heterophylla* Willdenow, *Sp. Pl.* 3: 298. 1800 [1801]. *nom. superfl. illeg. Sererea heterophylla* (Willd.) Rafinesque, *Sylva Tellur.* 107. 1838. *nom. superfl. illeg. Adenocalymma kerere* (Aubl.) Bureau & K. Schum. *Fl. Bras.* 8(2): 119. 1891. *Adenocalymma stridula* Miers, *Ann. Mag. Nat. Hist. ser.* 3 7: 392. 1861. *nom. illeg., Petastoma kerere* (Aubl.) Schnee in. Pittier, *Cat. Fl. Venez.* 2: 404. 1947. *Mansoa kerere* (Aubl.) A. Gentry, *Ann. Missouri Bot. Gard.* 66(4): 783. 1979 [1980]. Type: French Guiana. Cayenne, s.d., fl., J.B.C.F. Aublet s.n. (holotype, BM000992379!).

*Pachyptera foveolata* DC., *Prodr.* 9: 175. 1845. *Adenocalymma foveolatum* (DC.) Bail- lon, *Hist. Pl.* 10: 7, fig. 9–16. 1891. *Adenocalymma foveolatum* (DC.) K. Schu- mann, *Nat. Pflanzenfam* 4(3b): 214, fig. 89 F–G. 1894. *nom. superfl. illeg. Adeno- calymma foveolatum* (Bureau) Bureau & K. Schumann, *Fl. Bras.* 8(2): 109. 1896. *nom. illeg.* Type: French Guiana, s.loc., 1819–1821, fr., M. Poiteau s.n. (lectotype, designated by Sprague and Sandwith 1929, p. 84: G-DC [G00014105]!).

*Adenocalymma brachybotrys* DC., *Prod.* 9: 202. 184. Type: French Guiana. s.loc., 1821, fl., G.S. Perrottet s.n. (holotype, P03578200!).

*Adenocalymma symmetricum* Rusby, *Descr. S. Amer. Pl.* 122. 1920. Type: Venezuela. Lower Orinoco, 1896, fl., Rusby & Squires s.n. (holotype, NY00313053!).

*Bignonia benensis* Britton ex Rusby, *Bull. Torrey Bot. Club* 27: 70. 1900. Type: Bolívia. Junction of Beni and Madre de Dios rivers, Aug. 1886, fl, H.H. Rusby 1143. (lecto- type, designated here, NY00313133!; isotype, MICH01115822!, NY00313132!, US00603898!, US00125816!).

*Tanaecium zetekii* Standley, *Contr. Arnold Arbor* 5:140. 1933. Type: Panamá. Barro Colorado Island, 3 Feb 1932, fl., R.H. Woodworth 363. (holotype, F651874!; isotype, A00093244!, MO807829!, US00125783!).

**Description.** *Liana*; stems solid, tetragonal (cylindrical in younger portions), green or brown, with greyish striations, lenticellate; prophylls of axillary buds 3(–5)-seriated, flattened and ensiform. *Leaves* with blades discolorous (concolor), membranaceous to chartaceous (coriaceous), elliptic, obovate or ovate-lanceolate, asymmetric, apex acute, acuminate or caudate, base cordate, oblique, lateral blades 4.4–22.5 × 2.1–14.3 cm, apical blades 5.2–22.5 × 2.0–11.5 cm; petiole semi-cylindrical, 0.3–6.9 cm long, petiolules not puvinated, lateral petiolules 0.3–6.0 cm long, apical petiolules 0.8–6.0 cm long. *Inflorescence* a congested raceme, 0.6–4.8 cm long; pedicel (0.2–)0.5–5.7(–7.5) cm long; bracts 1.1–2.4 mm long; bracteoles cymbiform or filiform, 0.4–2.3 × 0.5–0.8 mm. *Calyx* green, sometimes with purplish apex, tubular, bilabiate or sub-bilabiate, truncate, minutely 5-lobed, 0.5–1.2 × 0.4–0.9 cm. *Corolla* white to cream, infundibuliform, 4.0–9.5 cm long, 0.9–2.5 cm of diameter at the tube mouth; lobes rounded (sub-circular), 0.6–1.9 × 0.5–1.8 cm. *Androecium* with the longer stamens 18.0–29.1 mm long, the shorter stamens 11.9–20.3 mm long, glabrous; anthers villous, included, thecae curved forward, 1.9–3.1 × 0.3–1.0 mm; pollen 3-colpate, microreticulate. *Gynoecium* 3.2–6.0 cm long; ovary 1.8–3.6 × 0.8–1.6, cylindrical, not-sulcate, smooth, densely pubescent, with simple and dentritic trichomes, sparsely lepidote, with glandular peltate trichomes, without patelliform glandular trichomes; stigma capitate or ovate, 1.6–3.1 × 0.9–3.5 mm; nectar disc 0.4–1.9 × 0.5–4.0 mm. *Capsule* fusiform, inflated (slightly flattened), 8.0–26.0 × 1.5–3.6 cm, each valve with a conspicuous and raised longitudinal midline; seeds irregularly circular and obcordate, 2.8–4.4 × 1.4–3.0 cm, thick, corky, striated, secondary sculpture with two pairs of medium micropores on each striation, wingless.

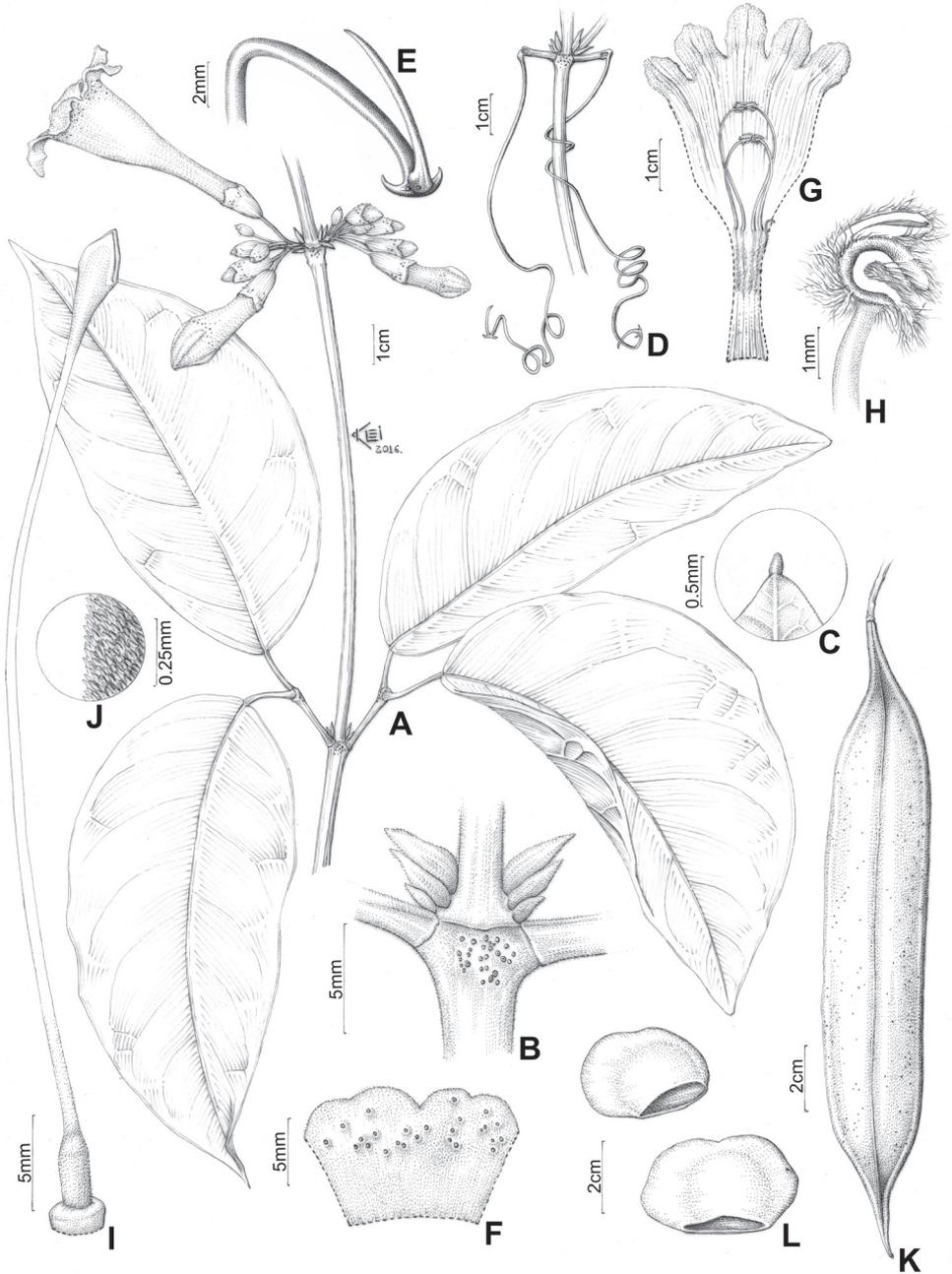
**Distribution.** This species is typically found in wet and often flooded forest vegetation in Belize (Toledo), Costa Rica (Limón, Puntarenas), Guatemala (Izabal), Honduras (Atlántida, Cólón), Nicaragua (Atlántico Sur, San Juan), Panama (Bocas del Toro, Colón, Darién, Panama), Bolívia (Beni), Brazil (Acre, Amapá, Amazonas, Maranhão, Mato Grosso, Pará, Rondônia, Roraima), Colombia (Amazonas, Antioquia, Bolívar, Chocó), French Guiana (Cayenne), Guyana (Cuyuni-Mazaruni, Upper Demerara-Berbice, Venezuela), Peru (Amazonas, Huánuco, Loreto, Madre de Dios), Suriname and Venezuela (Amazonas, Apure, Bolívar, Delta Amacuro). Fig. 12.

**Phenology.** This species flowers and fruits throughout the year.

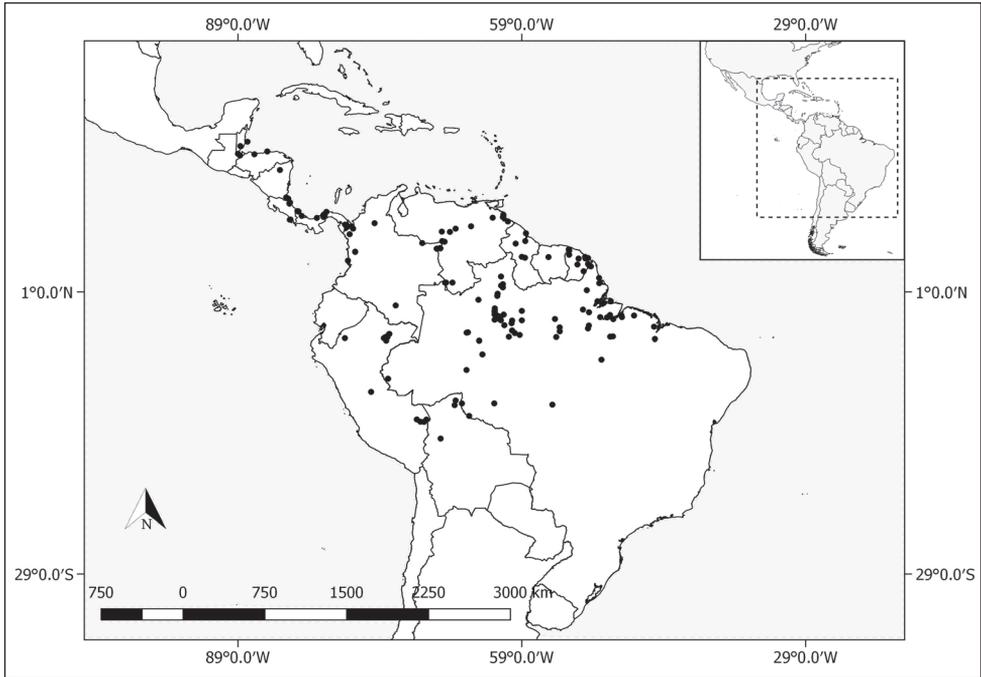
**Etymology.** The specific epithet is derived from vernacular name “kérére” or “té-rére” adopted by the indigenous group Galibis, from French Guiana, who use this plant as rope material.

**Nomenclatural note.** The original description of this species by Aublet (1775) included a mistake in the fruit illustration and description, which consists of the description of *Amphilophium magnollifolium* (Kunth) L.G. Lohmann instead.

*Bignonia benensis* was described by Britton (1990) based on a collection by *Rusby 1143*. This material cannot be considered a holotype because it was not cited in the protologue. Two related specimens are deposited at NY and US and one at MICH. Although there are two materials deposited at NY, only one is original material. The other specimen is a duplicate that was originally deposited at the College of



**Figure 11.** *Pachyptera kerere*: **A** Flowering branch **B** Interpetiolar region with EFNs and prophylls of axillary buds 3-seriated, flattened and ensiform **C** Apice of the leaflet mucronulate **D** Branchlets with terminal leaflet replaced by trifid tendril **E** Trifid tentril **F** Calyx external view **G** Open flower showing the androecium with anthers united **H** Stamen with villous and curved thecae **I** Gynoecium **J** Ovary surface pubescent (J.N.C. Francisco 41, SPF) **K** Fruit fusiform and inflated, with a conspicuous and raised longitudinal midline on valve (T.B. Croat 11085, MO) **L** Seeds corky and wingless (R.A.A. Oldeman B-1449, MO).



**Figure 12.** Distribution of *Pachyptera kerere*.

Pharmacy Herbarium, where Britton worked. Materials from this herbarium were only later incorporated into the NY collection along with other items. Therefore, the specimen originally deposited at NY (NY313133) is here designated as lectotype.

**Taxonomic comments.** *Pachyptera kerere* is easily recognised by the infundibuliform, white to cream corollas, with densely pubescent ovary. The fusiform, woody, inflated (sometimes slightly flattened) fruit, with a conspicuous and raised longitudinal midline, is very distinctive. The seeds are irregularly circular and obcordate, corky and wingless.

*Pachyptera kerere* shares infundibuliform corollas with *P. incarnata* and *P. linearis*. However, *P. kerere* can be differentiated by the densely pubescent ovary (vs. sparsely pubescent ovary of *P. linearis* and densely lepidote ovary in *P. incarnata*). Furthermore, *P. kerere* is easily separated from *P. incarnata* by the white corolla (vs. light pink to pale purple corolla of *P. incarnata*).

**Specimens examined.** **BELIZE.** Belize: Mile 5 3/4, Northern Highway, 7 June 1974, fl., J.D. Dwyer 12737 (MO). Stann Creek: 16°50'N, 88°30'W, May 1901, fl., fr., E.J.F Campbell 95 (K). **Toledo:** Maya Mountains foothill, Solomon Camp, vicinity of the junction of Richardson Creek and Bladen Branch, 16°31'48.0"N, 88°45'00.0"W, 80 m, 5 Mar 1987, fl., G. Davidse 32046 (MO). **COSTA RICA.** **Limón:** Parque Nacional Tortuguero, Estación Agua Fría, alrededores de la casa-estación, vegetación secundaria y relictos de vegetación primaria, 10°24'36"N, 83°33'36"W, 40 m, 24 Oct 1987, fl., R. Robles 1121 (MO); *Ibid.*, Estación Cuatro Esquinas, 800 m al Sur de la casa-estación, a orillas de la Laguna de Tortuguero,

10°30'36.0"N, 83°30'00.0"W, 2 m, 29 Nov 1987, fr., R. Robles 1391 (MO); Puerto Viejo de Talamanca, along road in vicinity of beach between Punta Cocles and Punta Uva, E of Puerto Viejo de Talamanca, 9°37'48"N, 82°42'36"W, 0–5 m, 6 Nov 1984, fl., M.H. Grayum 4411 (MO); Rio Gandoca, Refugio Gandoca-Manzanillo Low-lying coastal swamps and forests, Gandoca (slightly to N of trail from Mata de Limón), 9°36'N, 82°36'W, 0 m, 27 Jan 1987, fl., M.H. Grayum 8032 (MO); Talamanca, Sixaola, Gandoca, finca Cangrejo, Anai, 9°34'45"N, 82°36'20"W, 10 m, 24 Mar 1995, fr., G. Herrera 7551 (K). **Puntarenas:** Cantón de Osa, cuenca Térraba-Sierpe, Chocuaaco, 8°43'50"N, 83°27'17"W, 150 m, 29 Dec 1996, fl., R. Aguilar 4824 (MO); Golfo Dulce, Reserva Forestal Golfo Dulce Aguabuena, sector sur, 08°42'00"N, 83°31'12"W, 50 m, 15 Jan 1992, fl., R. Aguilar 818 (MO). **GUATEMALA. Izabal:** Dartmouth, between Dartmouth and Morales toward Lago Izabel, Montana del Mico, 15°30'36.0"N, 88°46'48.0"W, 35 m, 7 Apr 1940, fl., fr., J.A. Steyermark 39022 (F, MO); Puerto Barrios, near Rio Pargueña, 38–40 km N of Puerto Ayacucho, 25 May 1939, fl., P.C. Standley 73082 (F). **HONDURAS. Atlantida:** Esparta, 41.5 km E of Tela on the Tela-Ceiba Hwy then ca. 6 km N along old timber road. In remaining patches of primary forest, 15°39'N, 87°16'W, 100 m, 24 Apr 1994, fl., fr., A.E. Brant 2917 (MO). **Colón:** Rio Guaimoreto, 1.8 mi strip on the north bank of rio Guaimoreto between old bridge and opening of Laguna Guaimoreto 4.5 NE of Trujillo on old road to Castilla, 15°57'30"N, 85°54'30"W, 0 m, 10 July 1980, fl., J.G. Saunders 453 (MO); Trujillo, 1.8 mi strip on the north bank of rio Guaimoreto between old bridge and opening of Laguna Guaimoreto 4.5 mim, NE of Trujillo on old road to Castilla, 15°57'N, 85°54'W, 0 m, 19 June 1980, fl., J. Saunders 397 (MO). **NICARAGUA. Atlántico Sur:** Rio Pijibaye, 11°27'N, 83°54'W, 10–20 m, 18 Feb 1995, fl., fr., R. Rueda 3216 (MO). **Río San Juan:** Municipio de San Juan del Norte, Reserva Indio-Maíz, entre San Juan del Norte y la Finca de Chepelió, 50 m, 8 July 2002, fl., R. Rueda 16901 (MO). **PANAMA. Bocas del Toro:** Water Valley, vicinity of Chiriqui Lagoon, 23 Nov 1940, fl., H. von Wedel 1754 (MO). **Colón:** Chagres, Isthmus of Panama, 26 Mar 1850, fl., A. Fendler 206 (K); Portobello, ridge top, 1–3 miles W of Portobello, 7 Sept 1971, fl., A.H. Gentry 1766 (MO); premontane wet forest along Road S1 as it climbis the hill 1 Km SE of Camp Pina, 6 km WNW of Gatun Dam, 125 m, 21 Dec 1973, fl., M. Nee 8948 (MO); Western most part of province, site of proposed copper mine (INMET), Tailings Area, lowland forest on steep slopes, 8°53'50"N, 80°39'44"W, 40 m, 15 Apr 2009, fl., G. McPherson 20983 (MO). **Darién:** Rio Cupe, Rio Tuirá between Boca de Cupe and mouth of Rio Pucro, 7°54'N, 77°30'W, 0 m, 12 Jan 1975, fl., A.H. Gentry 13528 (MO); Yavisa, Rio Chucunaque, 0–1 hour above Yaviza, near sea level, 8°10'48.0"N, 77°40'48.0"W, 0 m, 8 Jan 1975, fl., A.H. Gentry 13477 (MO). **Panama:** Barro Colorado Island, Canal Area, cove north of dock, 2 July 1970, fr., T.B. Croat 11085 (MO); Barro Colorado Island, Canal Zone, shore line N of Smithsonian Laboratory Harbour towards Salud Point, 9. 16°, menos 79. 84°, 28 Feb 1964, fl., F. Ehrendorfer 6400-22 (WU); *Ibid.*, Shoreline, 24 Jan 1968, fl., fr., J.D. Dwyer 8450 (F); *Ibid.*, tip of Pearson Trail Peninsula S & W to 3rd large cove, 09°10'07"N, 79°51'31"W, 0–5 m, 7 May 1968, fr., T.B. Croat 5406

(MO). **BOLIVIA. Beni:** Riberlata, ca. 3 km SW of Riberalta on road to Hamburgo (crossing of Río Beni), várzea forest, heavily disturbed, 11°01'48.0"S, 66°06'00.0"W, 230 m, 20 Sept 1981, fl., J.C. Solomon 6349 (MO); Vaca Díez, Cachuela Esperanza Río Beni, 12 Sept 1985, fl., M. Moraes 550 (MO). **BRAZIL. s.loc., s.d., fl., s.inf. s.n. (B). Acre:** Porto Walter, Along Rio Juruá-Mirim, ca. 3 hrs by boat, above its mouth at Rio Juruá, 11 Nov 2001, fl., P. G. Delprete 7688 (NY). **Amapá:** Macapá, canteiro do Museu Macapá, 30 June 1981, fl., Verônica 17 (RBR); Rio Araguari, 1°10'48.0"N, 52°07'48.0"W, 22 July 1951, fr., R.L. Fróes 27540 (IAN, MO); Rio Calcoene, 16 Nov 1901, fl., W.A. Ducke s.n. (K, MO); Rio Puchacá afluente do Vila Nova, 15 Feb 1961, fl., A.G. Andrade 855 (R). **Amazonas:** Anavilhanas, Rio Negro, May 1980, fl., M. Gouling 66a (MG, MO); *Ibid.*, s.d., fl., M. Gouling 2120 (MG, MO); Autaz-Mirim, igapó do Curi, 20 Mar 1973, fl., fr., A.A. Loureiro INPA37554 (INPA); *Ibid.*, Lago do Purupuru, igapó, 17 Mar 1973, fl., fr., A.A. Loureiro s.n. (INPA); Careiro, Lago do Castanho, igapó, 7 June 1972, fr., M. Honda INPA36004 (INPA); Itaubarana, Rio Purus region, Rio Ipixuna, 15 km downstream from Itaubarana (30 km from Tapaua), igapó, 5°38'0"S, 63°10'0"W, 19 Jan 1986, fl., G. Gottsberger 115-19186 (MO); Itaubarana, Rio Purus region, Rio Ipixuna, 15 km downstream from Itaubarana (30 km from Tapaua), igapó, 5°38'0"S, 63°10'0"W, 23 Jan 1986, fl., G. Gottsberger 16-23186 (MO); Janauacá, Lago do Castanho, 7 June 1972, fr., M. Honda INPA36004 (INPA); Manaus, bank of Rio Negro and Rio Amazonas near Manaus, 4 Apr 1974, fl., fr., A.H. Gentry 11191 (MO); *Ibid.*, Campus do INPA, Séde do INPA, estrada do Aleixo, km 3, capoeira, solo argiloso, 5 Aug 1973, fl., P.N. Conceição 5 (INPA); *Ibid.*, estrada do Igarapé do Mariano, capoeira fechada, 23 Apr 1958, fl., fr., J.C. Almeida INPA6383 (INPA); *Ibid.*, Igarapé do Binda, 19 Jan 1955, fl., J.C. Chagas 606 (K); *Ibid.*, terra úmida, 2°18'36.0"S, 60°04'48.0"W, 19 Jan 1955, fl., J.C. Almeida INPA606 (INPA); Novo Airão, margem do Rio Negro, mata de igapó, 01°54'21.0"S, 61°20'08.9"W, 21 m, 12 May 2015, fl., M. Beyer 324 (SPF); *Ibid.*, 1°40'07.0"S, 61°25'00.1"W, 13 m, 12 May 2015, fl., M. Beyer 332 (SPF); *Ibid.*, Estação Ecológica Anavilhanas, 2°31'48.0"S, 60°50'24.0"W, 5 Feb 2007, fl., L.G. Lohmann 836 (SPF); Presidente Figueiredo (entorno), beira do Rio Uatumã, abaixo do Ramal da Morena, 1°00'S, 59°00'W, 24 Feb 2007, fl., C.E. Zartman 6349 (INPA, SPF); *Ibid.*, beira do Rio Uatumã, abaixo do ramal da Morena, 24 Feb 2007, fr., C.E. Zartman 6333 (INPA); *Ibid.*, Balbina, 2°01'48.0"S, 60°01'12.0"W, 13 Aug 2008, fl., F.F. Melo 532 (INPA); Rio Ituxi, Boca du Curuquete, Rio Purus, 10 July 1971, fl., G.T. Prance 14036 (INPA); Rio Negro between Rio Quinini and Moreira, sandy river bank, 13 Oct 1971, fl., G.T. Prance 15178 (INPA); *Ibid.*, Parana do Jacaré, 2°01'48.0"S, 60°01'12.0"W, 24 June 1992, fl., S.A. Mori 22470 (MO); São Francisco, Rio Negro, Paraná do Camanaú até Ponta do Canta Galo, 1°41'24.0"S, 61°16'12.0"W, 25 Apr 1973, fl., fr., M.F. Silva 1092 (INPA); Solimões, boca do Tefé, capoeira, 27 Sept 1904, fl., A. Ducke MG6821 (INPA); Tefé, Lago Tefé, northwest shore, igapó habitat, sandy, flooded lakeshor, 11 Dec 1982, fl., T. Plowman INPA126243 (INPA); Xiborema, solo argiloso, mata de várzea, 1 Jan 1957, fl., L.F. Coêlho s.n. (INPA). **Maranhão:** Lago Verde, fazenda São Francisco, 11Km N of Km 337 of BR 316, forest with Orbignya

Palm, 4°0'S, 44°56'W, 25 Sept 1980, fr., D.C. Daly D264 (MG); Palmeirândia, 17 Dec 2006, fl., C.M. Vieira 72 (IAN). **Mato Grosso:** Colíder, canteiro de obras da UHE Colíder, terra firme, 10°58' 48.0"S, 55°46'12.0"W, 258 m, 6 June 2011, fl., C.R.A. Soares 3594 (HERBAM, NX); near Tabajara, upper Machado River region, Nov 1931, fl., B.A. Krukoff 1517 (K, NY, P). **Pará:** Aguá, Rio Irucú, mata de várzea, 1992, fl., fr., U.R. Maciel 1971 (MG); *Ibid.*, Rio Marajozinho, mata de várzea, 1992, fl., U.R. Maciel 1793 (MG), U.R. Maciel 1823 (MG); Almeirim, Distrito de Monte Dourado, coletas ao longo do Rio Jari, 0°51'00"S, 52°32'00"W, 68 m, 4 July 2010, fl., R.C. Forzza 5994 (RB); Altamira, Rodovia Transamazônica (BR-230), margem do Rio Xingú, antes da travessia da Balsa, lado esquerdo da rodovia, sentido Altamira - Marabá, 03°07'34.4"S, 51°42'03.2"W, 5 m, 30 Nov 2005, fl., R.G. Udulutsch 2708 (HRCB, MBM, SPF, UNESPRC); Aveiro, Flona do Tapajós, Rio Cupari, 12 May 2011, fl., M.A. Braga 77 (RB); Belém, Campus of IPEAN, 6 Dec 1974, fl., A.H. Gentry 13075 (MO); Belterra, caminho para Pindobal, 29 Oct 1947, fl., G.A. Black 47-1861 (IAN, K); Chaves, Ilha Mexiana, Faz. Nazareth, 18 Sept 1901, fl., M. Guedes s.n. (MO); estrada entre S. Miguel e Río Caracuru, varzea, capoeira, 17 Jan 1969, fl., N.T. Silva 1654 (K, MO); Furo Macujubirm, 30 Aug 1901, fl., M. Guedes s.n. (MO); Ilha de Marajó, Rio Gipuru, 00°15'S, 50°30'W, 24 Oct 1987, fl., H.T. Beck 178 (F, MO); Melgaco, na Ilha do Marajó, Río Mapari, afluente do Río Tajapurú, 29 Nov 1991, NA, G. Santos 226 (MO); Óbidos, capoeira, 5 Aug 1902, st., W.A. Ducke s.n. (K, MO); Ourém, capoeira, 4 Dec 1903, fl., R.S. Rorb s.n. (MG); Paraupebas, Reserva Biológica da Serra dos Carajás, Companhia Vale do Río Doce, área da planta piloto, mina de exploração de ferro-N4, 500 m, 20 Nov 1991, fr., G. Santos 183 (G, MO); Piriá, Bank of Rio Piriá, N of km 90, 28 Oct 1965, fl., G.T. Prance 1736 (IAN, K, MO); Rio Mojú, 1 June 1954, fl., G.A. Black 54-16283 (K); Río Tocentius, reg. de S. Joazim de Itaquara, 18 Dec 1960, fr., E. Oliveira 1243 (IAN, MO); Santarém, 1877-78, fl., M. Jobert 857 (P); São Sebastião da Boa Vista, estrada de acesso a Vila Cocal, 2 Sept 1992, fl., C.A. Santos 31 (MG); Senador Jose Porfirio (Sozel), margem direita do Rio Xingu, 02°34'00"S, 51°55'00"W, 3 Dec 1991, fr., G. Santos 287 (MO); Tucuruí, Breu Branco, igapó às margens do rio Tocantins, 14 Oct 1983, fl., J. Revilla 8681 (NY, SPF); *Ibid.*, Breu Branco, margem do rio Tocantins, 12 Sept 1983, fl., F.E. Miranda 576 (NY); Vitória do Xingu, Rio Xingu, Sítio Pimental, 2°52'48.0" S, 52°00'36.0"W, 15 Jan 2012, fl., C.S. Rosario s.n. (MBM). **Rondônia:** Costa Marques, às margens do rio Caltário, 28 Oct 1996, fr., L.C.B. Lobato 2398 (MG); Pacáas Novos, Rio Pacáas Novos, 3 Aug 1968, fl., G.T. Prance 6759 (INPA, K, MO, R). **Roraima:** Caracará, Rio Branco, 0°56'46.4"S, 61°52'32"W, 36 m, 15 May 2015, fl., A. Frazão 149 (SPF); *Ibid.*, 0°36'14"N, 61°35'43"W, 50 m, 20 Mar 2012, fl., G. Martinelli 17395 (RB); *Ibid.*, paraná abalaô, 0°56'49"N, 60°58'14"W, 34 m, 27 Mar 2012, fl., fr., M. Nadruz 2647 (RB); *Ibid.*, próximo ao encontro com o Rio Negro, 1°22'24.5"S, 61°51'59.7"W, 34 m, 16 May 2015, fl., A. Frazão 153 (SPF); *Ibid.*, Parque Nacional do Viruá, margem do Rio Branco, igapó, 01°40'29.0"N, 61°11'24.6"W, 42 m, 26 Sept 2014, fl., J.N.C. Francisco 41 (SPF); *Ibid.*, próximo da sede do Parque, floresta de terra firme, 01°29'23.3"N, 61°00'09.1"W, 68 m, 24 Sept 2014, fl., J.N.C. Francisco 40 (SPF);

*Ibid.*, 01°29'24.9"N, 61°00'11.4"W, 67 m, 24 Sept 2014, fl., J.N.C. Francisco 39 (SPF); Igarapé Água Boa, Río Mucajai between Pratinha and Río Apiau, 22 Jan 1967, fl., G.T. Prance 4012 (INPA, K, MO, R, US); Rorainópolis, Rio Branco, 00°43'46.3"S, 61°51'24.0"W, 32 m, 14 May 2015, fl., V. Thode 424 (SPF); *Ibid.*, Ponto 11, 0°56'24.0"S, 61°50'24.0"W, 22 m, 14 May 2015, fl., fr., A. Frazão 136 (SPF); *Ibid.*, boca do Rio Branco com o Rio Negro, 1°23'8"S, 61°52'46"W, 40 m, 25 Apr 2014, fl., R.C. Forzza 8094 (RB); *Ibid.*, 1°23'8"S, 61°52'46"W, 40 m, 25 July 2014, fl., R.C. Forzza 8113 (RB); *Ibid.*, mata de igapó com interferência da água branca do rio Branco, 1°23'0.2"S, 61°51'6"W, 35 m, 13 May 2015, fl., B.M. Gomes 648 (SPF); *Ibid.*, em direção à Caracarái, mata de igapó, 1°12'12.7"S, 61°50'37.3"W, 34 m, 13 May 2015, fr., B.M. Gomes 651 (SPF); *Ibid.*, ao encontro dos rio Branco com o Negro, mata de igapó com influência das águas do rio Negro, 1°5'46.5"S, 61°52'53"W, 28 m, 15 May 2015, fl., B.M. Gomes 659 (SPF); *Ibid.*, mata de igapó, 1°14'42.7"S, 61°50'56.2"W, 29 m, 16 May 2015, fl., B.M. Gomes 662 (SPF); Rorainópolis, Rio Negro, mata de igapó, 01°33'14.2"S, 61°30'27.8"W, 13 m, 12 May 2015, fl., M. Beyer 336 (SPF); *Ibid.*, 01°33'14.2"S, 62°30'27.8"W, 13 m, 12 May 2015, fl., M. Beyer 337 (SPF); *Ibid.*, 1°22'5.2"S, 61°45'55.3"W, 18 m, 13 May 2015, fl., B.M. Gomes 639 (SPF); *Ibid.*, Rio Xixuaú, floresta beirando pequenos igarapés, 0°48'22"S, 61°33'32"W, 5 Mar 2010, fl., M.J.G. Hopkins 1961 (INPA); *Ibid.*, Ilha da casa do Chris, 0°48'01"N, 61°33'29"W, 25 m, 3 Feb 2011, fl., T. Marinho 208 (INPA). **COLOMBIA.** Llamos de Cumaral ad vedem Andim bogosensim orinocum versus, 386 m, Jan 1876, fl., L. Aruz 1035 (P). **Amazonas:** Aracuara, rocks along Rio Caqueta, Aracuara, 17 Jan 1989, fr., A.H. Gentry 64809 (MO). **Antioquia:** Chigorodo, Rio Leon 15 km W of Chigorodo, 07°45'N, 76°50'W, 100 m, 19 Mar 1962, fl., C. Feddema 1954 (MICH, MO, US); Necoclí, Reserva Indígena Cainán Nuevo, 76°46'W, 8°36'N, 2 m, Aug 1992, fl., L. Castaño 93a (HUA). **Bolívar:** La Raya, Achi, Inspeccion de la Raya, 8°19'48.0"N, 74°33'36.0"W, 30 m, 5 May 1987, fl., H.V. Cuadros 3601 (MO). **Chocó:** Boca del Togoroma, Bank of Quebrada Togoroma, 13 June 1944, fl., fr., E.P. Killip 39122 (COL, F, MO, US); Las Animas, Jequedo, 42 km W of Las Animas, E of Rio Pato on Pan American (under construction) W of Las Animas, 5°16'48.0"N, 76°36'36.0"W, 250 m, 11 Jan 1979, fl., A.H. Gentry 23990 (MO); Truando, cativo swamps along Rio Truando, 18 Jan 1974, fl., A.H. Gentry 9313 (MO). **FRENCH GUIANA.** Javanés de Mana, 1855, fl., Guslet s.n. (P); s.loc., 15 Dec 1956, fl., fr., A. Lemée 11 (P); s.loc., 1845, fl., fr., M. Melinón 64 (P); s.loc., 1856, fl., s.inf. s.n. (P); s.loc., 8 May 1874, fl., M. Melinón 121 (P); s.loc., Jan 1900, fl., F. Geay 1861 (P). **Cayenne:** Camopi, Camopi River, env. 12 km en amout de Camopi, 16 Dec 1965, fl., R.A.A. Oldeman 1796 (P, MO); Mahury River, Crique Gabrielle, tributary of the Mahury River, across from Stoupan, 4°45'00.0"N, 52°18'36.0"W, 10 m, 18 Oct 1991, fl., S.A. Mori 22137 (MO, NY); Mana River, Awara, village Galibi sur la reiver S de l'estucire de la Mana, env. à 18 km de Mana, 26 Jan 1978, fl., A. Raynal-Roques 19920 (MO, P); Maroni River, 1861, fl., M. Melinón 201 (P); *Ibid.*, 1982, fl., M. Melinón 205 (K, P); Montagne de Kaw, Montagnes de Kaw, Auberge de Brousse des Cascades, savanna and forest edges at end of road, 4°34'48.0"N, 52°16'48.0"W, 140 m, 12 Sept

1987, fl., A. Weitzman 287 (MO); Rives de l'Oyapock, entre St George at Maripa, Mar 1968, fr., R.A.A. Oldeman B-1449 (MO); Rivière Counana, affluent de l'Orapu, Dégrad Counana, 23 Dec 1966, fr., R.A.A. Oldeman B-778 (P); pont sur la crique Kourouaie, RN2, Régina, 04°06'53"N, 52°03'37"W, 4 m, 21 Mar 2009, fl., O. Tostain 2664 (P, NY, US). **GUYANA.** Pomeroon river, Mora Island, Wakapoa, 27 Dec 1958, fl., V. Graham P232 (K); s.loc., s.d., fl., Senudeas s.n. (P); Madoony Creek, Jan 1889, fl., G.S. Jenman 20968 (K). **Cuyuni-Mazaruni:** Mazaruni Station, 28 Aug 1937, fl., N.Y. Sandwith 1226 (K); *Ibid.*, 29 Oct 1943, fl., Fanshawe 4155 (K). **Upper Demerara-Berbice:** Moraballi Creek near Bartica, Essequibo River, 15 Nov 1929, fl., N.Y. Sandwith 617 (K, MO). **Venezuela:** Beryen de L'orenoque, 1864, fl., R. Grosourdy 13 (P). **PERU. Amazonas:** Condorcanqui, Monte virgin, 1 km atras de la comunidad de Caterpiza, trocha de metayar, banda este de la Quebrada Caterpiza, Rio Santiago, 3°54'36.0"S, 77°42'00.0"W, 180 m, 30 Oct 1979, fl., V. Huashikat 1145 (MO). **Huánuco:** Pachitea, region of Pucallpa, western part of the Sira mountains and adjacent lowland, c 26 km of Puerto Inca, next to the junction of the Rio Pachitea and Rio Yuyapichis, biological field station Panguana, primary lowland rain forest with some xer, 9°36'36.0"S, 74°55'48.0"W, 260 m, 21 Sept 1988, fl., fr., W. Morawetz 11-21988 (MO). **Loreto:** Boca del Rio Itaya, above Iquitos, 110 m, 17 Sept 1929, fl., E.P. Killip 29401 (F); Indiana, trail from Indiana on Rio Amazonas to Rio Napo, well drained upland forest on clay, 3°27'36.0"S, 73°00'00.0"W, 200 m, s.d., fl., A.H. Gentry 22205 (MO); Iquitos, Carretera de Picuruyacu, en terreno arenoso, 3°44'24.0"S, 73°14'24.0"W, 160 m, 23 Sept 1981, fl., Y.M. Rimachi 5716 (MO); Maynas, explorer's inn tourist camp near Indiana on Rio Amazonas, seasonally inundated tahuampa forest, 3°30'S, 73°00'W, 120 m, 21 Feb 1988, fl., A.H. Gentry 61828 (MO); *Ibid.*, Mishana, (Rio Nanay), bosque secundario de mas de 20 años, 03°55'S, 73°35'W, 130 m, 25 July 1984, fl., R. Vásquez 5404 (MO); *Ibid.*, Pto. Almendras (Rio Nanay), bosque inundable estacional (tahuampa), 3°48'00.0"S, 73°24'36.0"W, 122 m, 7 Sept 1984, fl., R. Vásquez 5540 (MO); Requena, Sanangal, bosque secundario inundable (Tahuampa), 04°10'S, 73°20'W, 120 m, 8 Aug 1980, fl., R. Vásquez 347 (MO). **Madre de Dios:** Laguna Cocacocha, edge of Laguna Cocacocha 39 km SW of Pto Moldanado near confl of Rios La Torre & Tambopata, 17 Oct 1968, fl., fr., S.F. Smith 408 (MO, US); Manu, Puerto Maldonado, Los Amigos Biological Station, ca. 7km upriver from mouth of Rio Los Amigos, between Cocha Llena and Cocha Lobo, 12°34'12.0"S, 70°06'00.0"W, 270 m, 4 Nov 2001, fr., J.P. Janovec 2606 (SPF); Tambopata, Cusco Amazonico, 15 km ENE of Puerto Maldonado, 12°24'48.0"S, 69°04'48.0"W, 200 m, 17 Dec 1989, fr., A.H. Gentry 68887 (MO); *Ibid.*, explorer's inn tourist camp at junction of Rios La Torre and Tambopata, swampy forest, 12°48'36.0"S, 69°42'36.0"W, 270 m, 28 July 1985, fl., A.H. Gentry 51536 (MO). **SURINAME.** Île Portal, 1888, fl., P. Sagot s.n. (P); Sipiwalini, Voltzberg Nature Reserve, Coppename River, 1-2 Km north of Foengoe Island, 4°44'N, 56°11'W, 40 m, 21 Feb 1999, fl., B. Hoffman 5362 (MO). **VENEZUELA.** Des bords de l'Orinoque, 27 Sept 1886, fl., M. Chaffanjon 336 (P). **Amazonas:** Boca Casiquiare, selvas pluviales en y los alrededores de la orilla del Rio Casiquiare, entre la boca y Isla de la Paloma, 18 Feb 1986, fl., B. Stergios 9001

(MO); Carinagua, Dept Atures, alrededores de Puerto Ayacucho (ca. 9 Km al S), bosque de galería del Caño Carinagua, alrededor del puente de la carretera Pto. Ayacucho-Samariapo, 10 Jan 1978, fl., O. Huber 1406 (MO); Dept. Átures, Puerto Ayacucho, end of road from airport to Rio Orinoco, gallery forest along river, 4 Apr 1984, fl., T. Plowman 13473 (F); Puerto Ayacucho, seasonally inundated forest at edge of Raudales del Orinoco, behind Pto. Ayacucho airport, sandy beach and adjacent laja, 5°39'36.0"N, 67°39'36.0"W, 100 m, 3 Apr 1984, fl., A.H. Gentry 46267 (MO); Rio Casiquiare, entre Piedra Guachapita y Curimacare, 2°00'00.0"N, 66°19'48.0"W, 150 m, 16 Jan 1987, fl., B. Stergios 9778 (MO); Rio Orinoco, caño Morocoto below San Fernando de Atabapo, 03°40'41"N, 67°14'15"W, 26 Mar 1974, fl., A.H. Gentry 10943 (MO). **Apure:** La Ceiba, between Rio Borgue and El Jordan, 7 km E de la Ceiba, 16 km E del Jordan, 350 m, 6 Apr 1968, fl., J.A. Steyermark 101948 (K); locally frequent along Rio Cinaruco for 20 km above las Galeras de Cinaruco, 24 Jan 1956, fl., J.J. Wurdack s.n. (JBRJ, RB); San Fernando, mouth of Rio Arauca at Rio Orinoco, 7°24'N, 66°36'W, 35 m, 14 May 1977, fl., G. Davidse 13198 (MO). **Bolívar:** Dpto. de Atures, Territorio Federal Amazonas, bosque humedo del rio Cataniapo, cercano a la desembocadura con el rio Orinoco, 6°24'36.0"N, 67°24'36.0"W, 37 m, 15 Feb 1983, fl., A. Castillo 1604 (MO); Moitaco, Distrito Sucre, rebalse del Orinoco, Hato Curumutopo, 11 Sept 1963, fl., fr., G. Martino 18 (MO, NY); Rio Orinoco, frequent on rocky outcrops on Isla Sta. Elena, opposite mouth of Rio Pargueni, 80 m, 13 Dec 1955, fl., J.J. Wurdack 39860 (K); Rio Parhueña, near Rio Pargueña, 38–40 km N of Puerto Ayacucho, 6°21'00.0"N, 67°09'36.0"W, 100 m, 30 June 1975, fr., A.H. Gentry 14686 (US, MO). **Delta Amacuro:** Depto. Antonio Diaz, Cano Atoiba, 9°15'N, 60°57'W, 50 m, 19 Oct 1977, fl., J.A. Steyermark 114985 (MO); Depto. Antonio Diaz, Cano Joba-Suburu, 8°59'N, 61°00'W, 50 m, 21 Oct 1977, fl., fr., J.A. Steyermark 115147 (MO); Rio Amacuro, between Amacuro and mouth of Deadwater Creak Moat, 8°31'12.0"N, 60°28'12.0"W, 65 m, 7 Nov 1960, fr., J.A. Steyermark 87341 (MO); *Ibid.*, between Amacuro and mouth of Deadwater Creek Moat, 8°31'12.0"N, 60°28'12.0"W, 65 m, 7 Nov 1960, fl., J.A. Steyermark 87347 (MO).

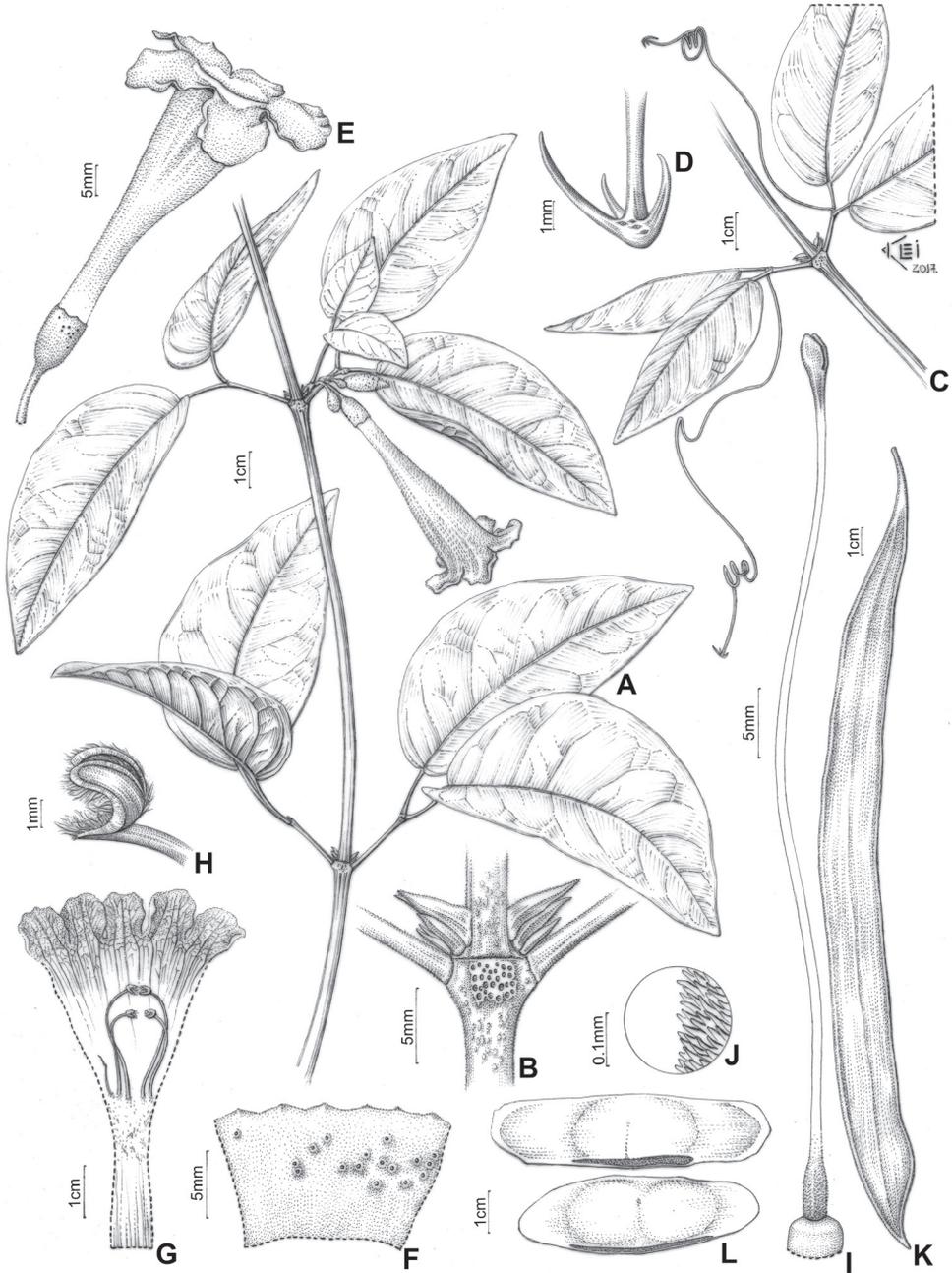
### 5. *Pachyptera linearis* Francisco & L.G.Lohmann, sp. nov.

urn:lsid:ipni.org:names:60475860-2

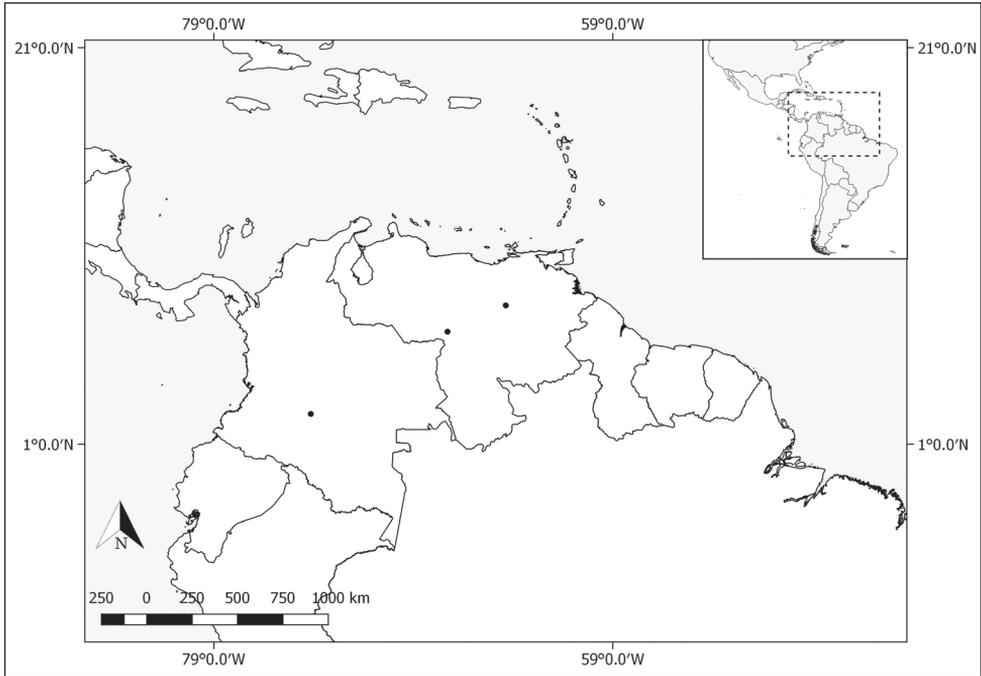
Fig. 13

**Type.** Colombia. Meta: Parque Nacional Natural Tinigua, Serrania Chamusa Centro de Investigación Primatológicas La Macarena, 120 m, Apr 1992, fr., P. Stevenson 403 (holotype: MO088944!; isotypes, COL000349706!, COAH21210, not seen).

**Diagnosis.** *Pachyptera linearis* is similar to *Pachyptera kerere*, but can be distinguished by the linear and flattened capsule (vs. the fusiform and inflated capsule of *P. kerere*), inconspicuous longitudinal midline on each valve (vs. conspicuous and raised longitudinal midline on each valve of *P. kerere*) and thin, oblong and wingless seeds (vs. corky, irregularly circular, obcordate and wingless seeds of *P. kerere*).



**Figure 13.** *Pachyptera linearis*. **A** Flowering branch **B** Interpetiolar region with ENFs and prophylls of axillary buds 3-seriated, flattened and ensiform **C** Branchlets with terminal leaflet replaced by trifid tendrils (leaflet falls) **D** Trifid tendril **E** Flower **F** Calyx external view **G** Open flower showing the androecium with anthers united **H** Stamen with villous and curved thecae **I** Gynoecium **J** Ovary surface pubescent (J.J. Wurdack 41357, K) **K** Fruit flattened, with an inconspicuous longitudinal midline **L** Seeds wingless (P. Stevenson 403, MO).



**Figure 14.** Distribution of *Pachyterra linearis*.

**Description.** *Liana*; stems solid, tetragonal (cylindrical in younger portions), with greyish striations, lenticellate; prophylls of axillary buds 3-seriated, flattened and ensiform. *Leaves* with blades discolorous or concolor, membranaceous to chartaceous, elliptic, obovate-lanceolate, asymmetric, apex acute, acuminate, base cordate, lateral blades 6.0–12.4 × 3.0–4.9 cm, apical blades 8.0–14.7 × 3.4–6.0 cm; petiole semi-cylindrical, 1.0–4.2 cm long, petiolules not puvinated, lateral petiolules 0.5–1.6 cm long, apical petiolules 1.5–3.5 cm long. *Inflorescence* a congested raceme, 0.6–1.2 cm long; pedicel ca. 0.8 cm long; bracts ca. 0.7 mm long; bracteoles cymbiform, ca. 0.7 mm. *Calyx* green, tubular, minutely 5-lobed, 0.9 × 0.8 cm. *Corolla* white, infundibuliform, ca. 6.7 cm long, ca. 1.4 cm of diameter at the tube mouth; lobes rounded, 0.8 × 0.9 cm. *Androecium* with the longer stamens ca. 32.0 mm long, the shorter stamens ca. 10.9 mm long, glabrous; anthers villous, included, thecae curved forward, 2.5 × 0.9 mm; pollen 3-colpate, microreticulate. *Gynoecium* 5.0–5.2 cm long; ovary 2.9–4.0 × 1.2 mm, cylindrical, not-sulcate, smooth, sparsely to moderately pubescent, with simple trichomes, sparsely lepidote, with glandular peltate trichomes, without patelliform glandular trichomes; stigma capitate or ovate, 1.7–2.8 × 1.7–2.8 mm; nectar disc 1.8 × 2.0 mm. *Capsule* linear, flattened, 19.0–35.0 × 2.2–2.4 cm, each valve with an inconspicuous longitudinal midline; seeds oblong, 4.0–7.0 × 1.5–1.8 cm, thin, not-corky, coriaceous to woody, striated, secondary sculpture regularly interrupted by lateral rays, wingless, with short membranaceous or chartaceous and hyaline wings.

**Distribution.** *Pachyptera linearis* is only known from wet forests of Venezuela (Apure, Bolívar) and Colombia (Meta). Fig. 14.

**Phenology.** *Pachyptera linearis* flowers in January and fruits in April.

**Etymology.** The epithet *linearis* makes reference to the linear fruit.

**Nomenclatural note.** *Pachyptera linearis* is a new species described here based on new morphological and molecular phylogenetic data (Fig. 1; Francisco and Lohmann submitted). The best quality material was selected as the holotype.

**Taxonomic comments.** *Pachyptera linearis* is characterised by white and infundibuliform corollas, with a sparsely pubescent and sparsely lepidote ovary. Furthermore, the capsule is linear, flattened, coriaceous to woody, with an inconspicuous longitudinal midline on the valves. The seeds are oblong, thin, coriaceous to woody, winged, with short membranaceous or coriaceous and hyaline wings. *Pachyptera linearis* shares the white infundibuliform flowers with its sister species *P. kerere* (Fig.1). Nevertheless, *P. linearis* is easily distinguishable from *P. kerere* by the fruit morphology.

**Paratypes. VENEZUELA. Apure:** galeras del Cinaruco, Rio Cinaruco, 29 km above Las Galeras de Cinaruco, 80 m, 24 Jan 1956, fl., J.J. Wurdack 41357 (K, MO, RB, S, VEN). **Bolívar:** Moitaco, rebalse del Orinoco, Hato Curumutopo, 8°00'00.0"N, 64°21'36.0"W, 24 Apr 1991, fr., G. Martino 22 (MO).

#### Doubtful and excluded names

*Bignonia incarnata* var. *caribaea* DC., Prodr. 9: 154. 1845. Type: Guadeloupe. s.loc., s.d., fl., F.L. L'Herminier s.n. (holotype, G-DC [G00133268]!) = *Bignonia aequinoctialis* L.

*Pachyptera alliacea* (Lam.) A.H. Gentry Brittonia 25(1): 236. 1973. Type: French Guiana. s.loc., s.d., fl., J.B.C.F. Aublet s.n. (holotype, P-AD [P00307351]!) = *Mansoa alliacea* (Lam.) A.H. Gentry

*Pachyptera dasyantha* DC. Prodr. 9: 176. 1845. Type: Brazil. Bahia: Rio São Francisco, s.d., fl., J.S. Blanchet 2903 (holotype, G-DC [G00133367]!, K not seen) = *Tanaecium pyramidatum* (Rich.) L.G. Lohmann

*Pachyptera hymenaea* (DC.) A.H. Gentry Brittonia 25(3): 236. 1973. Type: Brazil. Bahia, s.d., fl., J.S. Blanchet 1434 (holotype, G-DC [G00133196]!; isotype, P00481498!) = *Mansoa hymenaea* (DC.) A.H. Gentry

*Pachyptera parvifolia* A.H. Gentry Phytologia 26(6):447–450. 1973. Type: Colombia, Sur de Santander, vicinity of Puerto BerRío between carare and Magdalena Rivers, raizudo, large liana, flowers light purple, forest at about 200m, 22 Apr 1937, fl., O. Haught 2179 (holotype, MO100091!) = *Mansoa parvifolia* (A.H.Gentry) A.H. Gentry

*Pachyptera perrottetii* DC. Prodr. 9: 176. 1845. Type: French Guiana, s.loc., s.d., fl., G.S. Perrottet 2851 (holotype, G-DC [G00133301]!) = *Tanaecium pyramidatum* (Rich.) L.G. Lohmann

- Pachyptera puberula* DC. Prodr. 9: 175. 1845. Type: Brazil: Mato Grosso: close to Cuiabá, s.d., fr., S. Manso 105a (holotype, G-DC [G00133299]!) = *Dolichandra uncata* (Adrews) L.G. Lohmann
- Pachyptera standleyi* (Steayerm.) A.H. Gentry Brittonia 25(3): 236.1973. Type: Guatemala, Quetzaltenango, between Finca Pirineos and Finca Soledad, lower southern slopes of Volcán de Santa María, between Santa María de Jesús and Calahuaché, 1300–1400 m, 5 Jan 1940, J.A. Steyermark 33533 (holotype, F1054546!; isotype, F1054531!, F-1054543!, US00125753!) = *Mansoa standleyi* (Steayerm.) A.H. Gentry
- Pachyptera striata* DC. Prodr. 9: 176. 1845. Type: Brazil, São Paulo, s.d., P.W. Lund 783 (holotype, G-DC [G00133363]!) = *Tanaecium pyramidatum* (Rich.) L.G. Lohmann
- Pachyptera umbelliformis* DC. Prodr. 9: 175. 1845. Type: Brazil, São Paulo, s.d., fl., C.F.P. von Martius (syntype, M not seen; isosyntype, G-DC [G00133346]!), Brazil, Rio da Paraíba, Neuwied (syntype, M not seen) = *Tanaecium pyramidatum* (Rich.) L.G. Lohmann
- Pachyptera ventricosa* (A.H. Gentry) L.G. Lohmann Ann. Missouri Bot. Gard. 99(3): 456. 2014. *Mansoa ventricosa* A.H. Gentry Ann. Missouri Bot. Gard. 66 (4): 783. 1979 [1980]. Type: Brazil, Pará: along Belém-Brasília hwy., Km 345, 9 Aug 1963, fl., B. Maguire et al. 56083 (holotype, MO2232816!; isotypes, COL000004276!, MG136673!, NY00328882!, US00289053!) = *Mansoa ventricosa* A.H. Gentry

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## References

- Aublet JBCF (1775) Histoire des plantes de la Guiane Française. Pierre-François Didot. (Paris) 2: 1–4563.
- Baillon HE (1891) Histoire des Plantes. Librairie Hachette & Co, 112 pp.
- Barbosa Rodrigues J (1891) Eclogae plantarum novarum. Vellozia, Rio de Janeiro 1: 1–133.

- Barthlott W (1981) Epidermal and seed surface characters of plants: systematic applicability and some evolutionary aspects. *Nordic Journal of Botany* 1: 345–355. <https://doi.org/10.1111/j.1756-1051.1981.tb00704.x>
- Bureau E, Schumann KM (1896) Bignoniaceae. In: von Martius CFP, Eichler AG, Urban I (Eds) *Flora Brasiliensis*. Lipsiae apud Frid. Fleischer in Comm. Monachii (Leipzig) 8(2) [1897]: 1–452.
- Candolle AP (1845) Bignoniaceae. In: de Candolle AP (Eds) *Prodromus systematis naturalis regni vegetabilis*. Fortin, Masson. (Paris) 9: 142–248.
- Cracraft J (1983) Species concepts and speciation analysis. *Current Ornithology* 1: 159–187. [https://doi.org/10.1007/978-1-4615-6781-3\\_6](https://doi.org/10.1007/978-1-4615-6781-3_6)
- De Queiroz K (2007) Species concepts and species delimitation. *Systematic Biology* 56: 879–886. <https://doi.org/10.1080/10635150701701083>
- Dugand A (1955) Bignoniaceas nuevas o notables de Colombia. *Caldasia* 7: 7–32.
- Francisco JNC, Lohmann LG (2017) Reestablishment of *Mansoa ventricosa* (Bignoniaceae, Bignoniaceae) based on molecular and morphological data. *Phytotaxa* 327: 141–156. <https://doi.org/10.11646/phytotaxa.327.2.3>
- Funk DJ, Omland KE (2003) Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics* 34: 397–423. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132421>
- Gentry AH (1973) Generic delimitations of Central American Bignoniaceae. *Brittonia* 25: 226–242. <https://doi.org/10.2307/2805585>
- Gentry AH (1974) Coevolutionary patterns in Central American Bignoniaceae. *Annals of the Missouri Botanical Garden* 61: 728–759. <https://doi.org/10.2307/2395026>
- Gentry AH (1976) Bignoniaceae of southern Central America: distribution and ecological specificity. *Biotropica* 8: 117–131. <https://doi.org/10.2307/2989632>
- Gentry AH (1977) Studies in Bignoniaceae: New taxa and combinations in northwestern South American Bignoniaceae. *Phytologia* 35: 183–198. <https://doi.org/10.5962/bhl.part.2611>
- Gentry AH (1979) Additional generic mergers in Bignoniaceae. *Annals of the Missouri Botanical Garden* 66: 778–787. <https://doi.org/10.2307/2398918>
- Gentry AH (1980) Bignoniaceae. Part I (tribes Crescentieae and Tourretieae). *Flora Neotropical. Monografy* 25: 1–131.
- Gentry AH (1983) Dispersal and distribution in Bignoniaceae. *Sonderbaende des Naturwissenschaftlichen Vereins in Hamburg* 7: 187–199.
- Gentry AH (1990) Evolutionary patterns in neotropical Bignoniaceae. *Memoirs of the New York Botanical Garden* 55: 118–129.
- Gentry AH, Tomb AS (1979) Taxonomic implications of Bignoniaceae palynology. *Annals of the Missouri Botanical Garden* 66: 756–855. <https://doi.org/10.2307/2398917>
- Hesse M, Halbritter H, Zetter R, Weber M, Buchner R, Frosch-Radivo A, Ulrich S (2009) *Pollen terminology: An illustrated handbook*. Springer, Wien, 264 pp.
- Hickey LJ (1973) Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* 60: 17–33. <https://doi.org/10.2307/2441319>

- Lohmann LG (2004) Phylogeny, classification, morphological diversification and biogeography of Bignoniaceae (Bignoniaceae). PhD Dissertation, University of Missouri-St. Louis.
- Lohmann LG (2006) Untangling the phylogeny of Neotropical lianas (Bignoniaceae, Bignoniaceae). *American Journal of Botany* 93: 304–318. <https://doi.org/10.3732/ajb.93.2.304>
- Lohmann LG, Taylor CM (2014) A new generic classification of Tribe Bignoniaceae (Bignoniaceae). *Annals of the Missouri Botanical Garden* 99: 348–489. <https://doi.org/10.3417/2003187>
- McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Prud'homme Van Reine WF (2012) International Code of Nomenclature for algae, fungi and plants. *Regnum vegetabile*, 154 pp.
- Mori SA, Ferreira FC (1987) A distinguished Brazilian botanist, João Barbosa Rodrigues (1842–1909). *Brittonia* 39: 73–85. <https://doi.org/10.2307/2806978>
- Nogueira A, El-Отtra JHL, Guimarães E, Machado SR, Lohmann LG (2013) Trichome structure and evolution in Neotropical lianas. *Annals of Botany* 112: 1331–1350. <https://doi.org/10.1093/aob/mct201>
- Nogueira A, Rey PJ, Alcántara JM, Feitosa RM, Lohmann LG (2015) Geographic mosaic of plant evolution: extrafloral nectary variation mediated by ant and herbivore assemblages. *PloS One* 10: e0123806. <https://doi.org/10.1371/journal.pone.0123806>
- QGIS Development Team (2016) QGIS Geographic Information System. Open Source Geospatial Foundation Project.
- Radford AE, Dickson WC, Massey JR, Bell CR (1974) *Vascular plant systematics*. Harper Collins, 891 pp.
- Reginato M (2016) MonographaR: An R package to facilitate the production of plant taxonomic monographs. *Brittonia* 68: 212–216. <https://doi.org/10.1007/s12228-015-9407-z>
- Sandwith NY (1937) Notes on tropical American Bignoniaceae. *Mededelingen van het Botanisch Museum en Herbarium van de Rijksuniversiteit te Utrecht* 40: 205–232.
- Seibert RJ (1948) The use of glands in a taxonomic consideration of the family Bignoniaceae. *Annals of the Missouri Botanical Garden* 35: 123–137. <https://doi.org/10.2307/2394389>
- Sprague TA, Sandwith NY (1932) Contributions to the flora of tropical America: X. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)* 2: 81–93.
- Weberling F (1992) *Morphology of flowers and inflorescences*. Cambridge University Press, 1–344.

## Appendix I

Vouchers used in analysis on scanning electron microscopy micrographs study.

*Pachyptera aromatica* (Barb. Rodr.) L.G. Lohmann: **BRAZIL. Amazonas:** 2–5 km N of Manaus-Itacoatiara, road at km 79 near R o Preto da Eva, 24 Nov 1974, fl., A.H. Gentry 12832 (MO); Iranduba, estrada entre Novo Air o e Manacapur , 2 54'46.6"S, 60 57'58.8"W, fl., L.H. Fonseca 327 (SPF); Manaus, outskirts of Manaus, road to INPA, boat landing, behind airport, 26 Nov 1974, fr., A.H. Gentry 12862 (MG).

*Pachyptera erythraea* (Dugand) A.H. Gentry: **COLOMBIA. Antioquia:** Caucasia, along road to Nechi 24 km from Caucasia-Planeta Rica road, hacienda Costarica, margin of primary forest and trees remaining in cleared pasture, 8°03'36.0"N, 75°04'48.0"W, 60 m, 21 Mar 1987, fl., J.L. Zarucchi 4887 (K).

*Pachyptera incarnata* (Aubl.) Francisco & L.G. Lohmann: **BRAZIL. Amazonas:** Presidente Figueiredo, Balbina, Rebio Uatumã, grade do PPBio, 6 Oct 2006, fr., J.R. Carvalho-Sobrinho 1078 (INPA). **Pará:** Belterra, Floresta Nacional do Tapajós, estrada para comunidade de Jamaraguá, km 72, 02°55'15.9"S, 55°01'39.4"W, 114 m, 16 Sept 2015, fl., J.N.C. Francisco 89 (SPF); Óbidos, lago Maria Teresa, floresta de várzea, 01°52'38.2"S, 55°35'27.4"W, 14 m, 23 Sept 2015, fr., J.N.C. Francisco 122 (SPF); Santarém, ramal próximo à Usina Hidrelétrica Curuá-Uma, solo areno argiloso, floresta de terra firme, 02°48'45.2"S, 54°18'08.8"W, 47 m, 19 Sept 2015, fl., J.N.C. Francisco 105 (SPF).

*Pachyptera kerere* (Aubl.) Sandwith: **BRAZIL. Roraima:** Caracaraí, Parque Nacional do Viruá, margem do Rio Branco, igapó, 01°40'29.0"N, 61°11'24.6"W, 42 m, 26 Sept 2014, fl., J.N.C. Francisco 41 (SPF); Caracaraí, Parque Nacional do Viruá, próximo da sede do Parque, floresta de terra firme, 01°29'23.3"N, 61°00'09.1"W, 68 m, 24 Sept 2014, fl., J.N.C. Francisco 40 (SPF); Rorainópolis, Rio Branco, Ponto 11, 0°56'24.0"S, 61°50'24.0"W, 22 m, 14 May 2015, fl., fr., A. Frazão 136 (SPF).

*Pachyptera linearis* J.N.C. Francisco & L.G. Lohmann *new sp.*: **VENEZUELA. Apure:** galeras del Cinaruco, Rio Cinaruco, 29 km above Las Galeras de Cinaruco, 80 m, 24 Jan 1956, fl., J.J. Wurdack 41357 (K). **Bolivar:** Moitaco, rebalse del Orinoco, Hato Curumutopo, 8°00'00.0"N, 64°21'36.0"W, 24 Apr 1991, fr., G. Martino 22 (MO).

## Appendix 2

### Index to numbered collections

Specimens are listed by collector in alphabetical order, followed by collector's number. Collections by anonymous collectors without date or other identifying features are not listed here. Type specimens are shown in bold.

Aguilar, R. 818, 4824 (kerere). Almeida, J.C. INPA137, INPA1540, INPA1687, INPA5722 (aromatica); INPA606, INPA6383 (kerere). Amaral, I.L. 1248 (incarnata). Andrade, A.G. 855 (kerere). Árbocz, G.F. 4256 (incarnata). Aruz, L. 1035 (kerere). **Aublet, J.B.C.F. s.n. (BM00092379) (kerere)**. Beck, H.T. 178 (kerere). Beyer, M. 324, 332, 336, 337 (kerere). Black, G.A. 47-1861, 54-16283 (kerere); 48-3355 (incarnata); 52-14674 (aromatica). Braga, M.A. 77 (kerere). Brant, A.E. 2917 (kerere). Campbell, D.G. P22008 (incarnata). Campbell, E.J.F. 95 (kerere). Carvalho-Sobrinho, J.R. 1078 (incarnata). Castaño, L. 93a (kerere). Castillo, A. 1604 (kerere). Chafanjon, M. 336 (kerere). Chagas, J.C. 606 (kerere); INPA1701 (aromatica). Coêlho,

L.F. INPA1731 (aromatica); s.n.(kerere). Conceição, P.N. 5 (kerere). Croat, T.B. 5406, 11085 (kerere). Cuadros, H.V. 3601 (kerere). Daly, D.C. D264 (kerere). Dardano 48-3092 (incarnata). Davidse, G. 13198, 32046 (kerere). Delprete, P.G. 7688 (kerere). Duarte, A.P. 7048 (aromatica). Ducke, A. 239, 22698a, 22698b, 35624, s.n. (R), s.n. (MO) (aromatica); s.n. (K, MO), MG6821, (kerere); 24091 (incarnata). Dwyer, J.D. 8450, 12737 (kerere). Ehrendorfer, F. 6400-22 (kerere). Evando 542 (incarnata). Fanshawe 4155 (kerere). Feddema, C. 1954 (kerere). Fendler, A. 206 (kerere). Fonseca, L.H. 327 (aromatica). Forzza, R.C. 5994, 8094, 8113 (kerere). Francisco, C.M. s.n. (MG)(aromatica). Francisco, J.N.C. 39, 40, 41 (kerere); 89, 103, 105, 121, 122, 130, 151 (incarnata). Frazão, A. 136, 149, 153 (kerere); 313 (aromatica). Fróes, R.L. 27540 (kerere). Geay, F. 1861 (kerere). Gentry, A.H. 1766, 9313, 10943, 11191, 13075, 13477, 13528, 14686, 22205, 23990, 46267, 51536, 61828, 64809, 68887 (kerere); 13027, 13323 (incarnata); 15369, 15372, 15402, 20050 (erythraea); 11201, 11207, 12778, 12815, 12832, 12862, 12888, 13022, 13056, 69107, 69308 (aromatica). Gerolamo, C.S. 9 (aromatica). Gomes, B.M. 639, 648, 651, 659, 662 (kerere). Gottsberger, G. 16-23186, 115-19186 (kerere). Goulding, M. 66a, 2120 (kerere). Graham, V. P232 (kerere). Grayum, M.H. 4411, 8032 (kerere). Grosourdy, R. 13 (kerere). Guedes, M. s.n. (MO)(kerere). Guslet s.n. (P)(kerere). Herrera, G. 7551 (kerere). Hoffman, B. 5362 (kerere). Honda, M. INPA36004 (kerere). Hopkins, M.J.G. 1570, 1543, 1574 (aromatica); 1961 (kerere). Huashikat, V. 1145 (kerere). Huber, O. 1406 (kerere). Janovec, J.P. 2606 (kerere). Jenman, G.S. 20968 (kerere). Jobert, M. 857 (kerere). Kataoka, E. 349 (aromatica). Killip, E.P. 29401, 39122 (kerere). Knowles, O.H. 1106, 1120 (incarnata). Krukoff, B.A. 1517 (kerere); 6845, 12511 (aromatica). Labroy, M. 1906 (aromatica). Lemée, A. 11 (kerere). Lobato, L.C.B. 2398 (kerere); 3870 (incarnata). Lohmann, L.G. 28, 794 (aromatica); 836 (kerere). Loureiro, A.A. s.n. (INPA), INPA37554 (kerere). Luís, s.n. (MG)(aromatica). Maciel, U.R. 1793, 1823, 1971 (kerere). Maguire, B. s.n. (INPA), 56679 (aromatica). Marinho, T. 208 (kerere). Martinelli, G. 17395 (kerere). Martino, G. 18 (kerere); 22 (linearis). McPherson, G. 20983 (kerere). Melinón, M. 64, 121, 201, 205 (kerere). Mello, F.C. s.n. (INPA)(aromatica). Melo, F.F. 532 (kerere). Miranda, F.E. 362 (incarnata); 576 (kerere). Moraes, M. 550 (kerere). Morawetz, W. 11-21988 (kerere). Mori, S.A. 15783 (incarnata); 22137, 22470 (kerere). Mota, C.D.A. 18, 26, INPA60703 (aromatica). Nadruz, M. 2647 (kerere). Nee, M.H. s.n. (INPA) (aromatica); 8948 (kerere). Neill, D.A. 4030 (kerere). Nogueira, A. 190 (aromatica). Oldeman, R.A.A. B-778, B-1449, 1796 (kerere). Oliveira, E. 1243 (kerere); 2790 (aromatica). Pereira-Silva, G. 8765 (incarnata). Perrottet, G.S. s.n. (P03578200)(kerere). Pires, J.M. 12075 (incarnata). Plowman, T. 13473, INPA126243 (kerere). Poiteau, M. s.n. (G00014105)(kerere). Prance, G.T. 1736, 4012, 6759, 14036, 15178 (kerere); 17773 (aromatica). Pyramo, R.V. PSACF\_EX06147 (incarnata). Rabele, B. 1003 (aromatica). Ramiro Fon-negra, G. 2580 (erythraea). Ramos, J. 1011 (incarnata). Raynal-Roques, A. 19920 (kerere). Revilla, J. 8326, 8397 (incarnata); 8681 (kerere). Ribeiro, R.S. 78 (incarnata). Rimachi, Y.M. 5716 (kerere). Robles, R. 1121, 1391 (kerere). Rocha, J.B.P. 701 (incarnata). Rodrigues, W.A. 4578, 4693, 5476 (aromatica). **Romero-Castañeda, R.**

**4727, 4979 (erythraea)**. Rusby, H.H. s.n. (NY00313053), 1143 (kerere). Rosario, C.S. s.n. (MBM)(kerere). Rueda, R. 3216, 16901 (kerere). Sales, J. 1539 (incarnata). Sandwith, N.Y. 617; 1226 (kerere). Santos, C.A. 31 (kerere). Santos, G. 183, 226, 287 (kerere); 282 (incarnata). Sagot, P. (P)(kerere). Saunders, J.G. 397, 453 (kerere). Senudeas, s.n. (P)(kerere). Silva, B.R. PSACF\_EX06201 (incarnata). Silva, M. 1024 (aromatica); 1604 (incarnata). Silva, M.F. 1092 (kerere). Silva, N.T. 1654 (kerere). Smith, S.F. 408 (kerere). Soares, C.R.A. 3594 (kerere). Solomon, J.C. 6349 (kerere). Souza, J.A. s.n. (INPA), INPA61048, INPA61920, INPA71827, INPA71828, INPA71829, INPA71832, INPA71839 (aromatica). Souza, V.C. 18583 (incarnata). Sucre, A. s.n. (R, RB), (RB)(aromatica). Standley, P.C. 73082 (kerere). Stergios, B. 9001, 9778 (kerere). **Stevenson, P. 403 (linearis)**. Steyermark, J.A. 39022, 87341, 87347, 101948, 114985, 115147 (kerere). Thode, V. 17, 424 (kerere). Tostain, O. 2664 (kerere). Tsugaru, S. B-690 (aromatica). Udulutsch, R.G. 2708 (kerere). Ule, U. 4217, 5217 (aromatica). Vásquez, R. 347, 5404, 5540 (kerere). Verônica 17 (kerere). Vieira, C.M. 72 (kerere). Wedel, H. von 1754 (kerere). Weir, M. 72 (erythraea). Weitzman, A. 287 (kerere). Williams, L. 18222 (incarnata). Woodworth, R.H. 363 (kerere). Wurdack, J.J. s.n. (JBRJ, RB), 39860 (kerere); 41357 (linearis). Zartman, C.E. 6333, 6349 (kerere). Zarucchi, J.L. 4862A, 4887 (erythraea).

