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Reestablishment of *Mansoa ventricosa* (Bignonieae, Bignoniaceae) based on molecular and morphological data

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Abstract

Pachyptera ventricosa is a rare and poorly known species of liana that occurs in wet forests from the state of Pará, in Brazil. This species is characterized by features that are diagnostic of four genera within tribe Bignonieae: *Mansoa, Martinella, Pachyptera*, and *Tanaecium*. The currently recognized *P. ventricosa* was originally described in *Mansoa*, but subsequently transferred to *Pachyptera* based on morphological similarities. In this study, we use a combination of molecular and morphological data to evaluate the current placement of *P. ventricosa*. We conduct a broad scale molecular phylogenetic study based on 114 sequences of *ndh*F and *PepC* representing 112 taxa and members of all genera recognized in Bignonieae. In addition, we also conduct detailed morphological studies of selected characters. Our molecular phylogenetic study indicates that the currently recognized *Pachyptera ventricosa* is more closely related to members of *Mansoa* than to *Pachyptera*. New morphological data corroborates the molecular phylogenetic placement indicating that this species is indeed best placed within *Mansoa*. We here propose the reestablishment of *Mansoa ventricosa*, and show the detailed description for this species, along with new distribution information, and the first illustration for this taxon.

Key words: Amazonian biota, Brazilian flora, generic circumscription

Introduction

Bignonieae is the largest tribe in the plant family Bignoniaceae. It is composed mostly by neotropical lianas, except from *Bignonia capreolata* L. (1753: 624) that occurs in southeastern United States (Gentry 1979). The broad morphological diversity of members of the tribe, coupled with a lack of phylogenetic information has led to a problematic generic delimitation within the tribe in the past (Gentry 1973). The first phylogeny of Bignonieae recovered 21 generic-level clades (Lohmann 2006), that were subsequently recognized as genera in the first comprehensive generic-level classification for the whole tribe (Lohmann & Taylor 2014). While current generic limits (Lohmann & Taylor 2014) are quite stable, there are still a few genera whose delimitation may need adjustments. For instance, the circumscription of *Mansoa* de Candolle (1838: 128) and *Pachyptera* de Candolle (1840: 299) has been problematic historically and may still need some refinement. These genera have several overlapping morphological features (Figure 1) that has led to multiple nomenclatural changes during the last Century (Table 1).

When *Mansoa* was first described, it included two species, *M. hirsuta* de Candolle (1845: 182) and *M. laevis* de Candolle (1845: 182) [= *M. difficilis* (Chamisso 1832: 714) Bureau & Schumann (1896 [1897]: 201)]. The genus was then characterized by a bilabiate calyx with five subulate denticles, an infundibuliform corolla, inserted stamens, thick nectariferous disc, and an oval-oblong ovary. Under the most recent treatment of the tribe (Lohmann & Taylor 2014), *Mansoa* includes 12 species. Five additional species were subsequently described (Silva-Castro & Queiroz 2016), expanding the genus to 17 species. Species of *Mansoa* are characterized by angular stems, prophylls of the axillary buds minute and triangular or bromeliad-like, garlic smell in the foliage, leaflets with basal actinodromous venation and nectaries at the base, trifid tendrils, pink to purple corollas that are pubescent outside, and linear fruits. The genus is strongly supported as monophyletic by molecular characters and is positioned within the "multiples-of four" clade (Lohmann 2006).

On the other hand, when *Pachyptera* was first described it included six species characterized by seeds with coriaceous wings (de Candolle 1845): *P. umbelliformis* de Candolle (1845: 175), *P. striata* de Candolle (1845: 176), *P.*

dasyantha de Candolle (1845: 176), *P. perrottetii* de Candolle (1845: 176) [all synonyms of *Tanaecium pyramidatum* (Richard 1792: 110) L.G. Lohmann (2008: 274)], *P. puberula* de Candolle (1845: 175) [= *Dolichandra uncata* (Andrews 1808: tab. 530) L.G. Lohmann (2008: 273)], and *P. foveolata* de Candolle (1845: 175) [= *Pachyptera kerere* (Aublet 1775: 644) Sandwith (1937: 219)]. Currently, *Pachyptera* includes only four species: *P. aromatica* (Barbosa Rodrigues 1891: 47) L.G. Lohmann (2014: 456), *P. erythraea* (Dugand 1955: 16) A.H. Gentry (1977: 186), *P. kerere* (Aublet 1775: 644) Sandwith (1937: 219), and *P. ventricosa* (A.H.Gentry 1979 [1980]: 783) L.G. Lohmann (2014: 456). In its current circumscription, species in the genus are characterized by stems with four phloem wedges, bark papery that peels off as the branchlets age, interpetiolar glands, trifid tendrils, prophylls of the axillary buds flattened and ensiform or minute and triangular, tubular truncate calyces, white tubular corollas with glands arranged in lines in the upper portion, and linear fruits with glands scattered throughout the surface (Lohmann & Taylor 2014). Circumscription of *Pachyptera* has also been supported by information from a broad molecular phylogeny of the whole tribe Bignonieae that sampled half of the species currently recognized in *Pachyptera*. More specifically, Lohmann (2006) sampled *P. kerere* and *P. aromatica*, but did not include *P. erythraea* and *P. ventricosa*.

The generic placement of *P. ventricosa* is particularly complicated as this species possess morphological features that are shared among multiple genera. For instance, this species was originally described within *Mansoa* due to the trifid tendrils, interpetiolar gland fields, striate branchlets, and corolla densely pubescent on lobes (Gentry 1979 [1980]). However, these traits are also found in *Pachyptera*, with which *P. ventricosa* also shares tricolpate pollen. Furthermore, *P. ventricosa* shares subulate prophylls of the axillary buds with *Tanaecium* Swartz (1788: 91) emend L.G. Lohmann in L.G. Lohmann & Taylor (2014: 463), and a campanulate corolla and tricolpate coarse reticulate pollen with *Martinella* Baillon (1891 [1888]: 30). This broad morphological diversity has led to an unclear position for this taxon since its description. Indeed, when this species was first described, Gentry (1979 [1980]: 783) noted that: "the species has a combination of features of so many genera making it difficult to establish its clear position, especially because the fruit is unknown."

Author	Taxonomic changes	Shared morphological features
Baillon (1891)	Pachyptera was synonymized with Adenocalymma	Broad and thick capsule
Bureau & Schumann (1896)	Species of <i>Pachyptera</i> and <i>Mansoa</i> were transferred to <i>Adenocalymma</i> section <i>Hanburyophyton</i>	Large and pubescent capsules; terminal leaflets larger than lateral leaflets; inflorescences in racemes or panicles
Sprague & Sandwith (1932)	<i>Pachyptera</i> was restored to generic rank as a monotypic genus	Pollen tricolpate
Sampaio & Kuhlmann (1933)	<i>Pseudocalymma</i> [= <i>Mansoa</i>] was described a monospecific genus	Ovary with 2-series of ovules per locule; pollen tricolpate; nectars on calyx lacking
Gentry (1973)	Pseudocalymma was synonymized with Pachyptera	Trifid tendrils, interpetiolar gland-fields; white to red or purple corollas; 3-colpate pollen
Gentry (1979) and Gentry & Tomb (1979)	Pachyptera and Hanburyphython were merged into Mansoa	Various pollen characters
Lohmann & Taylor (2014)	<i>Pachyptera</i> was restored to generic rank including the monotypic <i>Leucocalantha</i>	Older branchlets with papery peeling epidermis or bark; calyx with glands arranged in a line
Lohmann & Taylor (2014)	Circumscription of <i>Mansoa</i> similar to that adopted by Gentry (1979, 1997) except from the transfer of <i>M. erythraea</i> , <i>M. kerere</i> and <i>M.</i> <i>ventricosa</i> to <i>Pachyptera</i>	Angular stems, garlic smell; leaflets with basal actinodromous venation and nectaries at the base; pink to purple corollas

TABLE 1. Summary of main taxonomic changes between *Mansoa*, *Pachyptera*, and related genera followed by a comparison of morphological features among these taxa.



FIGURE 1. Morphological comparison among leaves, the interpetiolar region, flowers and anthers among species of *Pachyptera* and *Mansoa*. A–D. *Pachyptera kerere (J.N.C. Francisco 41*, SPF); E–H. *Mansoa ventricosa (J.N.C. Francisco 102*, SPF); and I–L. *Pachyptera aromatica (L.H. Fonseca 327*, SPF). Illustrations by Klei Souza.

In this study, we use molecular phylogenetic data and new morphological information to investigate the generic placement of *Pachyptera ventricosa*. We paid particular attention to pollen characters, which are known to aid generic or specific delimitations within Bignoniaceae (e.g., Gentry & Tomb 1979, Zuntini *et al.* 2015). We propose moving *P. ventricosa* to the genus *Mansoa* and the reestablishment of *Mansoa ventricosa*, as well as a detailed description for this species, along with new information on its distribution, and the first illustration for this taxon.

Material and methods

Sampling, DNA extraction, PCR amplification and sequencing:—We extracted total genomic DNA from herbarium and silica-dried leaflets of the four species of *Pachyptera* recognized by Lohmann & Taylor (2014): *P. aromatica, P. erythraea, P. kerere*, and *P. ventricosa*. Extractions were conducted using the Invisorb Plant Mini Kit (Invitek, Berlin, Germany), following the manufacturer's protocol. We amplified the chloroplast marker *ndh*F (NADH dehydrogenase) following Zuntini *et al.* (2013) and the nuclear marker *Pep*C (Phosphoenolpyruvate carboxylase) using a nested PCR approach with the external primers (4F and 5R) from Lohmann (2006) for the first round, and internal primers (IV-119F and V-25R) from Zuntini *et al.* (2013) for the second round. The first-round PCR contained 8.5 μ L of H₂O, 1 μ L dimethyl sulfoxide (DMSO), 12.5 μ L GoTaq Promega Master Mix, 1 μ L 10mM each primer and 1 μ L 10 ng of template DNA. Cycling conditions were as follows: 94°C for 3 min, 20 cycles of denaturation at 94°C for 30 s, annealing at 48°C for 30 s, 72°C for 1 min, and a final extension step at 72°C for 5 min. Whenever PCR amplifications were unsuccessful, we added 5 μ L 5 M of betaine and adjusted the volume of water to a reaction of 25 μ L. We used 1 μ L of the first round PCR from 9:1 dilution in water as template for the second PCR, which followed the same conditions as the first PCR. We then loaded 2 μ L of the second round PCR product onto a 1% agarose gel to verify the amplification and size of the amplified product. Products were purified and sequenced by Macrogen (Seoul, South Korea). Sequences were deposited on GenBank under the accessions KY983570 to KY983578.

Molecular datasets and phylogenetic analyses:—We combined the five ndhF and PepC newly generated sequences of *Pachyptera* with the combined molecular dataset of Lohmann (2006) that consists of *ndh*F and *PepC* sequences for 104 taxa. In addition, we included two additional ndhF sequences of Mansoa (i.e., Mansoa alliacea and Mansoa parvifolia) and one of Perianthomega vellozoi from Lohmann (2006), plus ndhF and PepC sequences of Mansoa ononhualcoides from Fonseca & Lohmann (2015). Following Lohmann (2006) we used Tecoma capensis Lindley (1827 [1828]: 13) as outgroup. The final dataset included 114 sequences of ndhF and 110 sequences of PepC representing 111 species (Appendix 1). Individuals not sampled for PepC were coded as missing data in the final matrix. Sequences were aligned with MAFFT (Katoh et al. 2002) using default parameters (Auto algorithm, Scoring matrix: 200PAM/k=2, Gap open penalty: 1.53, Offset value 0.123) in Geneious 9.0.2 (Kearse et al. 2012). Alignments were subsequently analyzed visually and adjusted manually. We used jModelTest 2.0 (Guindon & Gascuel 2003, Darriba et al. 2012) and the Akaike information criterion (AIC) to select the best-fit model of nucleotide substitution for each dataset. The TVM+I+G was selected as the best model for the *ndh*F dataset whereas the TVM+G was selected as the best model for PepC. Bayesian Inference (BI) analyses were conducted using MrBayes 3.1 (Ronquist & Huelsenbeck 2003) with four Markov Chain Monte Carlo (MCMC) runs using a random starting tree, and 10 million generations, with a sampling frequency of one every 1000 generations. We used Tracer 1.5 (Rambaut & Drummond 2014) to check for convergence of the MCMC chain and to check for stationarity. We discarded 25% of the trees as burn-in.

Morphological studies:—We prepared a detailed description for *P. ventricosa* based on voucher specimens deposited at COL, MG, MO, SPF, NY, US, and UB (acronyms following Thiers 2017) and fresh material collected during field expeditions to the Brazilian state of Pará. Morphological descriptions follow the terminology of Lohmann & Taylor (2014), with additional terms from Radford *et al.* (1974) and Hickey (1973) for leaf morphology and venation, Nogueira *et al.* (2013) for trichomes, and Weberling (1992) for inflorescences.

We further analyzed calyx, corolla, stamen, and pollen morphology using a Zeiss DSM 970 Scanning Electron Microscope (SEM). We studied selected morphological structures from a representative specimen of *P. ventricosa* (*J.N.C. Francisco 84*, SPF). These structures were mounted on stubs and sputter-coated with gold. Pollen terminology follows Hesse *et al.* (2009) and Gentry & Tomb (1979).

We compared the new morphological data obtained for *P. ventricosa* in this study to the descriptions of *Pachyptera* and *Mansoa* available in the most recent generic treatment of the tribe (Lohmann & Taylor 2014).



FIGURE 2. Phylogenetic placement of *Pachyptera ventricosa* and other species of *Pachyptera* recognized by Lohmann & Taylor (2014) within Tribe Bignonieae. Majority-rule consensus tree derived from the Bayesian analyses of the combined *ndh*F and *PepC* dataset. Posterior probabilities are shown above nodes. The outgroup is shown in grey. New sequences generated in this study are shown in bold and marked with asterisks (*).

Results

Phylogenetic placement of Pachyptera ventricosa

We obtained high quality *ndh*F and *Pep*C sequences from five accessions of *Pachyptera* (Appendix 1). The new *ndh*F sequences of *P. ventricosa* were 2066 bp long, which is the same length as other *Pachyptera* sequences in our data set. The length of *Pep*C sequences of *P. ventricosa* ranged from 315 to 441 bp, while the other sequences of *Pachyptera* in our data set ranged from 341 to 402 bp. The final combined Bignonieae dataset contains 2977 bp and included 114 terminals, one of which was the outgroup belonging to tribe Tecomeae. The *ndhF* alignment was 2108 bp long, whereas the *Pep*C alignment was 869 bp long. In the final alignment we found an insertion of 3 bp in the *ndh*F dataset supporting a clade with five species of *Mansoa* (i.e., *M. verrucifera*, *M. hirsuta*, *M. laceolata*, *M. difficilis* and *M. alliacea*). Multiple indels were recovered in the *Pep*C dataset. Among those indels there was a 7 bp insertion (GACGTAT) unique to *M. standleyi*.

Both accessions of *P. ventricosa* formed a clade that was distantly related to the other three species of *Pachyptera* sampled. The *P. ventricosa* clade was nested within *Mansoa* and strongly supported (PP=0.97) as sister to a clade containing *M. alliacea*, *M. difficilis*, *M. hirsuta*, *M. lanceolata*, and *M. verrucifera*. This whole clade is sister to a smaller clade composed by *M. onohualcoides* and *M. standleyi*. *Mansoa parvifolia* emerges as sister to the remaining species sampled. On the other hand, *Pachyptera* (excluding *P. ventricosa*) is poorly supported as monophyletic (PP=0.54). The genus as a whole includes a *P. aromatica* clade that is sister to a strongly supported clade (PP=1.0) that included *P. erythraea* and *P. kerere* (Figure 2). Overall, other relationships recovered in the BI analyses were identical to those recovered by Lohmann (2006).

Morphological studies of Pachyptera ventricosa

Pachyptera ventricosa has a number of vegetative and reproductive characters in common with species of *Mansoa*. For instance, extra-floral nectaries (EFN) grouped on the abaxial leaflet surface and actinodromous venation are found exclusively in *P. ventricosa* and *Mansoa*. In addition, *P. ventricosa* and *Mansoa* share uniseriate prophylls of the axillary buds, unlike other *Pachyptera* species, all of which have 3-seriated prophylls (Figures 1B, F). The thyrsoid inflorescence and light purple flower color are also shared between *P. ventricosa* and *Mansoa*, whereas remaining species of *Pachypera* have a racemose inflorescence with flowers that can be white, light pink or red (Table 2).

Our SEM studies showed that *P. ventricosa* has a densely puberulous calyx that bears well-developed peltate and patelliform glands. This same type of glands is also found on the corolla lobes, which includes a pair of clustered glands arranged in lines similar to those found in *Pachyptera*. The anther connective bears short simple trichomes similar to some species of *Mansoa*. The pollen is tricolpate and coarse reticulate showing many bacula into the lumen (Figure 3) that are more similar to those found in members of *Mansoa* than members of *Pachyptera* (Table 2).

Character	Pachyptera s.s.	Mansoa	Pachyptera ventricosa
EFN grouped on the abaxial surface of leaflets	absent	present (except from some <i>M. alliacea</i>)	present
Prophylls of the axillary buds	triangular and minute or flattened and ensiform, 3-seriate	triangular and minute or bromeliad-like	subulate, paired
Primary venation	pinnate	actinodromous	basal actinodromous
Inflorescence	raceme	thyrse or fascicle	thyrse
Flower color	white, light pink or red	pink to purple	light purple
Connective indumentum	glabrous	puberulous or glabrous	puberulous
Pollen aperture	3-4-colpate	3-colpate, pantocolpate or pantossincolpate	3-colpate
Pollen ornamentation	psilate foveolate or micro- reticulate	reticulate, heterobrocade or areolate	coarse reticulate with bacula into the lumen

TABLE 2. Morphologica	l comparison between	Pachyptera s.s., Mansoa	and Pachyptera ventricosa.
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Discussion

Our phylogenetic and morphological study has demonstrated that *P. ventricosa* is more closely related to species in the genus *Mansoa* than any other species of *Pachyptera*. Moreover, this phylogeny also recovers a monophyletic *Pachyptera*, excluding *P. ventricosa*. However, *Pachyptera* is only poorly supported as monophyletic, indicating the need for additional studies (Francisco & Lohmann in prep.). In addition, the placement of *P. erythraea* within *Pachyptera* corroborates the recent inclusion of this species into *Pachyptera* by Lohmann & Taylor (2014) based on morphology.

Our study highlights the importance of combining molecular phylogenetic data with morphological studies while assessing the placement of taxonomically complicated species (see Pace *et al.* 2016). More specifically, our morphological study indicates that *P. ventricosa* shares thyrsoid inflorescences with purple flowers, glandular stipitate trichomes on the upper portions of the corolla tube, pubescent anther connective, extra-floral nectaries grouped on the abaxial surface of leaflets, and actinodromous venation with members of *Mansoa* (Figures 3, 4). However, *P. ventricosa* also shares a number of other features with *Pachyptera*, namely the trifid tendrils, glands near the calyx margin and upper portion of the corolla tube, and glands at the interpetiolar region, all of which led Lohmann & Taylor (2014) to place this species in *Pachyptera*. Nevertheless, *P. ventricosa* lacks the supra-numerary prophylls of the axillary buds and the white tubular corollas, that are so typical of *Pachyptera*, only lacking in *P. erythraea* (red corolla) and a couple populations of *P. kerere* that have pink corollas.



FIGURE 3. Morphological features of *Mansoa ventricosa*. A. Inflorescence; B. Corolla lobes puberulous, with patelliform glands; C. Glandular stipitate trichomes on the corolla; D. Detail of patelliform glands on the corolla lobes; E. Anther connective; F. Calyx puberulous, with peltate and patelliform glandular trichomes; G. Tricolpate and coarse reticulate pollen grain; H. Pollen detail showing the bacula into the lumen (*J.N.C. Francisco 84*, SPF). Photo A by Annelise F. Nunez.

Pollen morphology also supports the inclusion of *P. ventricosa* within *Mansoa*. More specifically, while species of *Pachyptera* have tetracolpate pollen, that is psilate, foveolate (*P. aromatica*) or tricolpate, microrreticulate (*P. kerere* and *P. erythraea;* Francisco and Lohmann in prep.), species of *Mansoa* have pollen that is tricolpate and reticulate (Gentry & Tomb 1979). The combination of tricolpate pollen and reticulate ornamentation is exclusive of *Mansoa* (Silva-Castro 2010), and has never been found within *Pachyptera*. The pollen type of *P. ventricosa* (Figures 5G, H) is tricolpate and coarse reticulate, similar to that of other *Mansoa* (i.e., tricolpate and reticulate), further supporting the placement of *P. ventricosa* within *Mansoa*. The tricolpate and reticulate pollen is also found in *M. parvifolia* (A.H. Gentry 1973: 447) A.H. Gentry (1979 [1980]: 783), and *M. standleyi* (Steyermark 1947: 235) A.H. Gentry (1979 [1980]: 783), corroborating our molecular phylogenetic findings, and indicating that *P. ventricosa* is best placed within *Mansoa*.



FIGURE 4. Morphological features of *Mansoa ventricosa*. A. Flowering branch; B. Interpetiolar region with extra-floral nectaries and subulate prophylls of the axillary buds; C. Abaxial leaflet surface showing the extra-floral nectaries; D. Trifid tentril; E. Calyx; F. Opened flower showing the androecium; G. Stamen with straight thecae; H. Gynoecium; I. Detail of ovary surface with simple and glandular patelliform trichomes (*J.N.C. Francisco 102*, SPF). Illustration by Klei Souza.

In light of the novel molecular phylogenetic and morphological data gathered here, we propose the reestablishment of *Mansoa ventricosa*, bringing the number of species of *Mansoa* to 18.

Taxonomy treatment

Mansoa ventricosa A.H. Gentry (1979 [1980]: 783). *Pachyptera ventricosa* (A.H. Gentry) L.G. Lohmann (2014: 456)

Type:—BRAZIL. Pará: Along the Belém-Brasilia highway, km 345, 9 August 1956, *B. Maguire et al. 56083* (holotype, MO-2232816!; isotypes, COL-110166 not seen, MG-136673, NY-328882!, US-3189002 image!).

Liana; branchlets cylindrical, striated, swollen at nodes, without lenticels, sparsely to moderately puberulous, with simple and glandular peltate trichomes, without onion smell, with "V" shaped interpetiolar glands fields, with a continuous interpetiolar ridge; pith solid, with four phloem wedges in cross-section; prophylls of the axillary buds persistent, subulate, paired, $3.94-4.85 \times 1.98-2.07$ mm, sparsely to densely puberulous, with simple and glandular peltate trichomes. Leaves 2–3-foliolated, with the terminal leaflet often replaced by a trifid tendril; petiole cylindrical, 0.8–3.2 cm, sparsely to densely puberulous, with simple and glandular peltate trichomes; petiolule cylindrical, 0.5–1.6 cm, sparsely to densely puberulous, with simple and glandular peltate trichomes; blade concolor, chartaceous, elliptic, apex caudate, sometimes mucronulate, base cuneate, obtuse or rounded, margin entire, flat or sub-revolute; lateral leaflets with $8.0-14.5 \times 3.0-7.9$ cm, abaxial surface glabrous or very sparsely puberulous, with simple trichomes distributed only on veins, glandular peltate trichomes distributed throughout the surface, with patelliform glandular trichomes grouped at base, adaxial surface sparsely puberulous, with simple trichomes distributed on veins, and with peltate glandular trichomes distributed over the lamina; venation basal, actinodromous, secondary venation festoonedbrochidromous, tertiary venation random-reticulate. Inflorescence terminal, thyrse, congested, 6-9 cm long, densely puberulous, with simple and glandular peltate trichomes, many-flowered, ca. 15–34 flowers; pedicel with 1.0–1.9 cm long, moderately to densely puberulous, with simple and glandular peltate trichomes; bracts caducous; bracteole triangular or rhombic 0.04–1.68 mm, densely puberulous, with simple and glandular peltate trichomes. Calyx green with apex light purple, cupular, minutely 5-denticulate, coriaceous, smooth, $0.4-0.6 \times 0.4-0.6$ cm, densely puberulous, with simple and glandular peltate trichomes externally, often with clustered patelliform glands near the margin, glabrous inside. Corolla cream or greenish at base, tube and lobes light purple, with vellowish mouth, campanulate, rounded, membranous, 4.2–5.1 cm long, 1.9–2.0 cm of diameter at the distal end (mouth), 0.4–0.5 cm diameter at the base, tube densely puberulous externally, with simple, dendritic, and glandular peltate trichomes, glabrous at base and internally, except from the point of staminode insertion, which is villose with stipitate glandular trichomes; lobes oblong, 1.3–1.5 \times 0.7–1.2 cm, imbricate, densely puberulous outside, with simple and peltate glandular trichomes and patelliform glands arranged at the base of lobes, glabrous inside. Androecium didynamous; stamens glabrous, subexseted, longer 2.85–3.09 mm long, shorter 2.69–2.78 mm long; anthers yellow, glabrous, basifixed, connective thick, acute, round; thecae straight, $5.85-6.43 \times 0.51-0.87$ mm, with longitudinal slits; pollen tricolpate and coarse reticulate. *Gynoecium* 4.4–4.9 cm long, exserted, sparsely puberulous, with simple and glandular peltate trichomes; stigma ovate, 1.69×3.52 mm, with irregularly toothed margin, glabrescent, with simple trichomes; ovary greenish, linear-oblong, $4.74-4.78 \times$ 1.29–1.62 mm, smooth, densely puberulous, with simple, glandular, peltate and patelliform trichomes; ovules arranged in two series per locule, placentation axillar; nectary disc well-developed, $2.70-3.14 \times 3.34-4.78$ mm, pubescent, with glandular peltate trichomes. Fruit unknown.

Phenology:-Flowers from August to October; fruiting season is unknown.

Pollination:—The corolla morphology is classified as a variant of the *Martinella* type (Gentry 1974), and is likely associated with bat pollination (Alcantara & Lohmann 2010, Machado & Vogel 2004). This species shares tricolpate coarse reticulate pollen grains with *Martinella obovata* (Gentry & Tomb 1979) suggesting convergent evolution of pollen type. Such convergence has also been observed in other floral traits such as the purple colored flower, thick corolla texture, open mouth, and subexserted anthers.

Distribution and habitat:—*Mansoa ventricosa* is endemic to Northeastern Brazil (Maranhão, Pará), where it occurs in wet evergreen forests (Figure 5). Prior to this work, this species was only known from the holotype collected in the Brazilian state of Pará, a paratype collected in the Brazilian state of Maranhão (*G.T. Prance 58978*; UB and NY), and one collection from 1980 (*D.C. Daly 774*; MG, MO, and NY). Two additional specimens were collected during our fieldwork in Pará, (Brazil), expanding the distribution of this species to Santarém and Belterra.

Conservation status:—The species is only known from one locality of Maranhão and four localities from the state of Pará (i.e., Belterra, Itinga do Pará, Paragominas, and Santarém), and is categorized as Data Deficient (DD) according to IUCN Standards and Petitions Committee (2014). Further field studies are needed to evaluate its conservation status more accurately.

Additional specimens examined:—BRAZIL. Maranhão: 15 Km S of Para-Maranhão border on Belém-Brasília highway, in forest, 31 August 1963, *G.T. Prance* 58978 (UB, NY). Pará: Belterra, Floresta Nacional do Tapajós. Beira da estrada para Jamaraquá, km 74, 194 m, 02°55'50.2"S, 55°00'44.6"W, 164 m, 16 September 2015, *J.N.C. Francisco et al.* 84 (SPF). Itinga do Pará, Fazenda Santa Rosa, W of Belém-Brasilia Hwy, 26 October 1980, *D.C. Daly* 774 (MG, MO). Santarém, Beira da PA-370, 164 m, 02°46'10.1"S, 54°25'42.6"W, 164m, 19 September 2015, *J.N.C. Francisco et al.* 102 (SPF).

Taxonomic notes:—*Mansoa ventricosa* is easily recognized by a combination of cylindrical and striated branchlets with "V" shaped interpetiolar clusters of glands, subulate prophylls of the axillary buds, and leaflets with nectaries grouped at the base of the abaxial surface. Reproductive characters that can help in its identification are the thyrsoid inflorescences, calyx with patelliform glands clustered next to the margin, corolla campanulate, with tube light purple, densely puberulous outside, with patelliform glands at the upper portion of the apex tube, androecium subexserted with yellow anthers, and exserted gynoecium.



FIGURE 5. Distribution of Mansoa ventricosa in Northeastern Brazil (Pará).

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APPENDIX 1. Species, locality, vouchers and GenBank accession numbers used in this study. Sequences obtained in this study are marked with an asterisk (*).'-' indicates sequence was not available/generated.

Species, locality, voucher (herbarium): *ndh*F, *Pep*C Genbank accession numbers.

Adenocalymma adenophorum (Sandwith) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Lohmann 30, (INPA, K, MG, MO, NY, RB, SP): DQ222608, DQ222766. Adenocalymma bracteatum (Cham.) DC., BRAZIL, São Paulo, Santa Cruz da Conceição, Lohmann 719, (MO, SPF): DQ222527, DQ222649. Adenocalymma bracteosum (DC.) L.G.Lohmann, BRAZIL, Amazonas, Rio Negro, Lohmann 290, (MO, NY, SPF, UNIP): DQ222609, DQ222767. Adenocalymma campicola (Pilg.) L.G.Lohmann, BRAZIL, Minas Gerais, Uberlândia, Lohmann 266, (MO, SPF, U): DQ222610, DQ222770. Adenocalymma cymbalum (Cham.) Bureau & K.Schum., BRAZIL, Minas Gerais, PE do Rio Doce, Lombardi 2495, (BHCB, MO): DQ222528, DQ222650. Adenocalymma impressum (Rusby) Sandwith, BRAZIL, Amazonas, Reserva Ducke, Vicentini 1155, (INPA, K, MG, MO, NY, SP, U): DQ222529, DQ222652. Adenocalymma magnificum Mart. ex DC., BRAZIL, Pará, PE Moju, Silva 30, (IAN, MO): DQ222612, DQ222771. Adenocalymma moringifolium (DC.) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Lohmann 19, (INPA, K, MG, MO, NY, R, SP, SPF, U): DQ222613, DQ222773. Adenocalymma salmoneum J.C.Gomes, BRAZIL, Espírito Santo, Linhares, Lohmann 658, (CVRD, MO): DQ222530, DQ222653. Adenocalymma subincanum Huber, BRAZIL, Amazonas, Reserva Ducke, Lohmann 12, (INPA, MO): DQ222531, DQ222654. Adenocalymma trichocladum (DC.) L.G.Lohmann, BRAZIL, Bahia, Santa Maria da Vitória, Hatschbach 50496, (MO): DQ222635, DQ222807. Amphilophium aschersonii Ule, BRAZIL, Acre, Rio Juruá, Lohmann 390, (MO, NY, SPF, UFAC): DQ222532, DQ222655. Amphilophium bauhinioides (Bureau ex Baill.) L.G.Lohmann, BRAZIL, Espírito Santo, Linhares, Lohmann 655, (CVRD, MO): DQ222586, DQ222734. Amphilophium crucigerum (L.) L.G.Lohmann , BRAZIL, Espírito Santo, Linhares, Lohmann 685, (CVRD, MO): DQ222623, DQ222789. Amphilophium elongatum (Vahl) L.G.Lohmann, BRAZIL, Minas Gerais, PE do Rio Doce, Lombardi 2433, (BHCB, MO): DQ222578, DQ222720. Amphilophium frutescens (DC.) L.G.Lohmann, BRAZIL, Paraíba, Rio Tinto, Lohmann 695, (MO, SPF): DQ222581, DQ222724. Amphilophium granulosum (Klotzsch) L.G.Lohmann, BRAZIL, Acre, Rio Juruá, Lohmann 470, (MO, NY, SPF, UFAC): DQ222582, DQ222726. Amphilophium lohmanniae (A. Pool) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Lohmann 20, (INPA, MO): DQ222580, DQ222723. Amphilophium magnoliifolium (Kunth) L. G.Lohmann, SURINAME, Sipaliwini, Tafelberg Tepui, Lohmann 214, (BBS, MO): DQ222579, DQ222722. Amphilophium nunezii (A.H.Gentry) L.G.Lohmann, PERU, Madre Díos, Manu National Park, Lohmann 606, (MO, MOL): DQ222587, DQ222735. Amphilophium paniculatum (L.) Kunth, PERU, Madre Díos, Manu National Park, Lohmann 609, (MO, MOL): DQ222533, DQ222656. Amphilophium rodriguesii (A.H.Gentry) L.G.Lohmann, BRAZIL, Acre, Rio Arara, Lohmann 475, (MO, NY,SPF, UFAC): DQ222588, DQ222737. Anemopaegma floridum Mart. ex DC., BRAZIL, Amazonas, Reserva Ducke, Lohmann 121, (INPA, MO, SPF): DQ222534, DQ222658. Anemopaegma foetidum Bureau & K.Schum., BRAZIL, Amazonas, Reserva Ducke, Lohmann 35, (INPA, MO, SPF): DQ222535, DQ222659. Anemopaegma laeve DC., BRAZIL, Bahia, Chapada Diamantina, Lohmann 253, (MO, SPF): DQ222536, DQ222661. Anemopaegma robustum Bureau & K.Schum., BRAZIL, Amazonas, Reserva Ducke, Apostolo 126, (INPA, MO): DQ222538, DQ222663. Bignonia aequinoctialis L., BRAZIL, Amazonas, Rio Negro, Lohmann 320, (MO, NY, SPF, UNIP): DQ222577, DQ222719. Bignonia bracteomana (K.Schum. ex Sprague) L.G.Lohmann, PERU, Madre Díos, Manu National Park, Lohmann 614, (MO, MOL): DQ222634, DQ222806. Bignonia callistegioides Cham., U.S.A., Missouri, MOBOT, Lohmann 352, (MO): DQ222569, DQ222708. Bignonia capreolata Kunth , U.S.A., Illinois, Johnson County, Lohmann 356, (MO): DQ222566, DQ222706. Bignonia corymbosa (Vent.) L.G.Lohmann, BRAZIL, Espírito Santo, Linhares, Lohmann 654, (MO): DQ222621, DQ222785. Bignonia hyacinthina (Standl.) L.G.Lohmann, PERU, Madre Díos, Manu National Park, Lohmann 642, (MO, MOL): DQ222614, DQ222775. Bignonia microcalyx G.Mey., SURINAME, Sipaliwini, Road between Blanche Marie and Paramaribo, Evans 3198, (BBS, MO): DQ222629, DQ222797. Bignonia nocturna (Barb.Rodr.) L.G.Lohmann, BRAZIL, Acre, Rio Juruá, Lohmann 451, (MO, NY, SPF, UFAC): DQ222641, DQ222813. Bignonia prieurii DC., BRAZIL, Espírito Santo, Linhares, Lohmann 651, (INPA, MO): DQ222615, DQ222776. Bignonia uleana (Kraenzl.) L.G.Lohmann, PERU, Madre Díos, Manu National Park, Lohmann 617, (MO, MOL): DQ222572, DQ222709. Cuspidaria cinerea (Bureau ex K.Schum.) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Lohmann 34, (INPA, K, MG, MO, NY, SP, SPF, U, UB): DQ222631, DQ222801. Cuspidaria convoluta (Vell.) A.H.Gentry, BRAZIL, São Paulo, Instituto Plantarum, Lohmann 713, (MO, SPF): DQ222573, DQ222711. Cuspidaria floribunda (DC.) A.H.Gentry, BRAZIL, Acre, Rio Juruá, Lohmann 418, (MO, NY, SPF, UFAC): DQ222574, DQ222713. Cuspidaria inaequalis (DC. ex Splitg.) L.G.Lohmann, SURINAME, Sipaliwini, Tafelberg Tepui, Lohmann 127, (BBS, MO):

DQ222548, DQ222679. Cuspidaria lateriflora (Mart.) DC., PERU, Madre Díos, Manu National Park, Lohmann 628, (MO, MOL): DQ222575, DQ222716. Cuspidaria sceptrum (Cham.) L.G.Lohmann, BRAZIL, São Paulo, Santa Cruz da Conceição, Lohmann 717, (MO, SPF): DQ222557, DQ222698. Cuspidaria subincana A.H.Gentry, BRAZIL, Amazonas, Reserva Ducke, Lohmann s.n. (Tree # 2638-24), (INPA, MO): DQ222576, DQ222717. Dolichandra cynanchoides Cham., ARGENTINA, Buenos Aires, , Galleto 1019, (MO): DQ222583, DQ222728. Dolichandra quadrivalvis (Jacq.) L.G.Lohmann, U.S.A., Missouri, MOBOT, Lohmann 353, (MO): DQ222607, DQ222764. Dolichandra steyermarkii (Sandwith) L.G.Lohmann, BRAZIL, Acre, Rio Arara, Lohmann 477, (MO, NY, SPF, UFAC): DQ222617, DQ222780. Dolichandra unguis-cati (L.) L.G.Lohmann, BRAZIL, Minas Gerais, PE do Rio Doce, Lombardi 2432, (BHCB, MO): DQ222595, DQ222749. Fridericia chica (Bonpl.) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Lohmann s.n. (Tree # 2618-24), (INPA): DQ222542, DQ222671. Fridericia cinerea (Bureau ex K.Schum.) L.G.Lohmann, BRAZIL, Bahia, Chapada Diamantina, Lohmann 358, (MO, SPF): DQ222543, DQ222673. Fridericia cinnamomea (DC.) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Vicentini 809, (INPA, MO): DQ222544, DQ222674. Fridericia conjugata (Vell.) L.G.Lohmann, BRAZIL, Espírito Santo, Linhares, Lohmann 650, (CVRD, MO): DQ222545, DQ222675. Fridericia dispar (Bureau ex K.Schum.) L.G.Lohmann, BRAZIL, Paraíba, Santa Rita, Lohmann 694, (MO, SPF): DQ222546, DQ222676. Fridericia erubescens (DC.) L.G.Lohmann, BRAZIL, Bahia, Chapada Diamantina, Lohmann 359, (MO, SPF): DQ222622, DQ222787. Fridericia leucopogon (Cham.) L.G.Lohmann, BRAZIL, São Paulo, Santa Cruz da Conceição, Lohmann 714, (MO, SPF): DQ222549, DQ222681. Fridericia nigrescens (Sandwith) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Lohmann 78, (G, INPA, K, MG, MO, NY, RB, SP, U, UB): DQ222550, DQ222683. Fridericia oligantha (Bureau & K.Schum.) L.G.Lohmann, BRAZIL, Acre, Rio Juruá, Lohmann 483, (MO, NY, SPF, UFAC): DQ222551, DQ222685. Fridericia patellifera (Schltdl.) L.G.Lohmann, BRAZIL, Acre, Rio Juruá, Lohmann 412, (MO, NY, SPF, UFAC): DQ222552, DQ222687. Fridericia platyphylla (Cham.) L.G.Lohmann, PERU, Madre Díos, Manu National Park, Lohmann 639, (MO, MOL): DQ222554, -. Fridericia prancei (A.H.Gentry) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Sothers 460, (INPA, K, MBM, MG, MO, NY, RB, SPF, U, UFMT): DQ222555, DQ222689. Fridericia pubescens (L.) L.G.Lohmann, BRAZIL, Minas Gerais, PE do Rio Doce, Lombardi 2529, (BHCB, MO): DQ222556, DQ222690. Fridericia rego (Vell.) L.G.Lohmann, BRAZIL, Espírito Santo, Linhares, Lohmann 660, (CVRD, MO): DQ222558, DQ222692. Fridericia speciosa Mart., BRAZIL, Minas Gerais, PE do Rio Doce, Lombardi 2521, (BHCB, MO): DQ222584, DQ222730. Fridericia spicata (Bureau & K.Schum.) L.G.Lohmann, PERU, Madre Díos, Manu National Park, Lohmann 607, (MO, MOL): DQ222561, DQ222699. Fridericia subincana (Mart.) L.G.Lohmann, BRAZIL, Espírito Santo, Linhares, Lohmann 659, (CVRD, MO): DO222562, DO222701. Fridericia trailii (Sprague) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Lohmann 29, (INPA, K, MG, MO, NY, SPF): DQ222563, DQ222703. Fridericia triplinervia (Mart. ex DC.) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Lohmann 18, (GH, IAN, INPA, K, MO, PEUFR, S, SPF, UEC): DQ222564, DQ222705. Lundia cordata (Vell.) DC., BRAZIL, Espírito Santo, Linhares, Lohmann 652, (CVRD, MO): DQ222590, DQ222741. Lundia densiflora DC., BRAZIL, Amazonas, Reserva Ducke, Lohmann 82, (INPA, MO): DQ222592, DQ222743. Lundia laevis Kaehler, BRAZIL, Acre, Rio Abuna, Lohmann 497, (MO,NY, SPF, UFAC): DQ222591, DQ222742. Lundia spruceana Bureau, PERU, Madre Díos, Manu National Park, Lohmann 610, (MO, MOL): DQ222593, DQ222745. Lundia virginalis DC., BRAZIL, Minas Gerais, PE do Rio Doce, Lombardi 2530, (BHCB, MO): DQ222594, DQ222747. Manaosella cordifolia (DC.) A.H.Gentry, BRAZIL, Minas Gerais, PE do Rio Doce, Lombardi 2546, (BHCB, MO): DQ222596, DQ222750. Mansoa alliacea (Lam.) A.H.Gentry, BRAZIL, Amazonas, Reserva Ducke, Vicentini 672, (INPA, K, MG, MO, NY, RB, SPF): DQ222597, -. Mansoa difficilis (Cham.) Bureau & K.Schum., BRAZIL, Espírito Santo, Linhares, Lohmann 662, (CVRD, MO): DQ222598, DQ222752. Mansoa hirsuta DC., BRAZIL, Bahia, Chapada Diamantina, Lohmann 364, (MO, SPF): DQ222599, DQ222753. Mansoa lanceolata (DC.) A.H.Gentry, BRAZIL, Espírito Santo, Linhares, Lohmann 661, (CVRD, MO): DQ222601, DQ222755. Mansoa onohualcoides A.H. Gentry, BRAZIL, Espírito Santo, Linhares, Zuntini 276, (SPF): KP691455, KP697961. Mansoa parvifolia (A.H.Gentry) A.H.Gentry, PERU, Madre Díos, Manu National Park, Lohmann 605, (MO, MOL): DQ222602, -. Mansoa standleyi (Steyerm.) A.H.Gentry, PERU, Madre Díos, Manu National Park, Lohmann 638, (MO, MOL): DO222603, DO222757. Mansoa ventricosa A.H. Gentry, BRAZIL, Pará, Belém, Francisco 102, (SPF): KY983570*, KY983574*; Belterra, Francisco 84, (SPF): KY983573*, KY983578*. Mansoa verrucifera (Schltdl.) A.H.Gentry, PERU, Madre Díos, Manu National Park, Lohmann 612, (MO, MOL): DQ222604, DQ222759. Martinella iquitoensis A.Samp., PERU, Madre Díos, Manu National Park, Lohmann 616, (MO, MOL): DQ222605, DQ222760. Martinella obovata (Kunth) Bureau & K.Schum., SURINAME, Sipaliwini, Tafelberg Tepui, Lohmann 126, (BBS, MO): DQ222606, DQ222762. Neojobertia candolleana (Mart. ex DC.) Bureau & K.Schum., BRAZIL, Bahia, Chapada Diamantina, Lohmann 363, (MO, SPF): DQ222616, DQ222778. Neojobertia mirabilis (Sandwith) L.G.Lohmann, BRAZIL, Espírito Santo, Linhares, Lohmann

681, (CVRD, MO): DQ222585, DQ222732. Pachyptera aromatica (Barb.Rodr.) L.G.Lohmann, BRAZIL, Amazonas, Novo Airão, Lohmann 794, (SPF): KY983572*, KY983575*; Reserva Ducke, Lohmann 28, (INPA, MO, SPF): DQ222589, DQ222739. Pachyptera erythraea (Dugand) A.H. Gentry, COLOMBIA, Santander, Gentry 15372, (MO): KY983571*, KY983577*. Pachyptera kerere (Aubl.) Sandwith, BRAZIL, Amazonas, Rio Negro, Lohmann 336, (MO, NY, SPF, UNIP): DQ222600, KY983576*. Perianthomega vellozoi Bureau, BOLIVIA, Santa Cruz, Close to the Santa Cruz Botanical Garden, Nee 35808, (LPB, MO): DQ222619, -. Pleonotoma jasminifolia (Kunth) Miers, BRAZIL, Amazonas, Reserva Ducke, Lohmann 122, (INPA): DQ222625, DQ222793. Pleonotoma longiflora B.M. Gomes & Proença, BRAZIL, Amazonas, Reserva Ducke, Forzza 290, (G, INPA, K, MG, MO, NY, RB, SP, U, UB): DQ222624, DQ222791. Pleonotoma stichadenia K.Schum. , BRAZIL, Espírito Santo, Linhares, Lohmann 656, (CVRD, MO): DQ222627, DQ222795. Pyrostegia venusta (Ker Gawl.) Miers, BRAZIL, Acre, Plácido do Castro, Lohmann 534, (MO, NY, SPF, UFAC): DQ222632, DQ222803; São Paulo, Santa Cruz da Conceição, Lohmann 718, (MO, SPF): DQ222633, DQ222804. Stizophyllum inaequilaterum Bureau & K.Schum., BRAZIL, Acre, Rio Juruá, Lohmann 454, (MO, NY, SPF, UFAC): DQ222638, DQ222808. Stizophyllum perforatum (Cham.) Miers, BRAZIL, Minas Gerais, PE do Rio Doce, Lombardi 2431, (BHCB, MO): DQ222639, DQ222809. Tanaecium affine (A. H.Gentry) L.G.Lohmann, PERU, Madre Díos, Manu National Park, Lohmann 633, (MO, MOL): DQ222539, DQ222665. Tanaecium bilabiatum (Sprague) L.G.Lohmann, BRAZIL, Amazonas, Rio Solimões, Lohmann 92, (MO, NY, SPF, UNIP): DQ222540, DQ222667. Tanaecium caudiculatum (Standl.) L.G.Lohmann, BELIZE, Cayo, Grano de Oro Camp, Whitefoord 9231, (BRH, MO): DQ222630, DQ222800. Tanaecium crucigerum Seem., U.S.A., Missouri, MOBOT, Lohmann 355, (MO): DQ222640, DQ222811. Tanaecium pyramidatum (Rich.) L.G.Lohmann, BRAZIL, Amazonas, Rio Solimões, Lohmann 274, (MO, NY, SPF, UNIP): DQ222618, DQ222781. Tanaecium revillae (A.H.Gentry) L.G.Lohmann, BRAZIL, Amazonas, Rio Solimões, Lohmann 265a, (MO, NY, SPF, UNIP): DQ222559, DQ222694. Tanaecium selloi (Spreng.) L.G.Lohmann, BRAZIL, Paraíba, Guarabira, Lohmann 702, (MO, SPF): DQ222560, DQ222696. Tanaecium tetragonolobum (Jacq.) L.G.Lohmann, PERU, Madre Díos, Manu National Park, Lohmann 619, (MO, MOL): DQ222568, DQ222707. Tanaecium truncatum (A.Samp.) L.G.Lohmann, BRAZIL, Amazonas, Reserva Ducke, Lohmann 33, (INPA, K, MG, MO, NY, SPF): DQ222620, DQ222783. Tecoma capensis (Thunb.) Lindl., SURINAME, Paramaribo, , Lohmann 125, (BBS, MO): DQ222642. Tynanthus elegans Miers, BRAZIL, Espírito Santo, Linhares, Lohmann 663, (CVRD, MO): DQ222643, DQ222815. Tynanthus panurensis (Bureau ex Baill.) Sandwith, BRAZIL, Amazonas, Reserva Ducke, Procopio 14, (G, INPA, K, MG, MO, NY, RB, SP, U, UB): DQ222644, DQ222817. Tynanthus polyanthus (Bureau ex Baill.) Sandwith, BRAZIL, Acre, Cruzeiro do Sul, Lohmann 370, (MO, NY, SPF, UFAC): DQ222645, DQ222819. Tynanthus villosus A.H.Gentry, BRAZIL, Acre, Rio Juruá, Lohmann 413, (MO, NY, SPF, UFAC): DQ222647, DQ222820. Xylophragma harleyi (A.H.Gentry ex M.M.Silva & L.P.Queiroz) L.G.Lohmann, BRAZIL, Bahia, Chapada Diamantina, Lohmann 362, (MO, SPF): DQ222547, DQ222678. Xylophragma myrianthum (Cham.) Sprague, BRAZIL, Espírito Santo, Linhares, Lohmann 649, (CVRD, MO): DQ222648, DQ222822.