



TYNNANTHUS fasciculatus s.

REVISÃO TAXONÔMICA, FILOGENIA E
EVOLUÇÃO DO NICHU ECOLÓGICO DE
***TYNNANTHUS* MIERS**
(BIGNONIEAE, BIGNONIACEAE)

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Revisão taxonômica, filogenia e evolução do nicho ecológico de *Tynanthus* Miers (Bignonieae, Bignoniaceae)

Taxonomic revision, phylogeny and evolution of the ecological niche of *Tynanthus* Miers (Bignonieae, Bignoniaceae)

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Orientadora: Lúcia G. Lohmann

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Ao Rafael, com amor.

“The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during each former year may represent the long succession of extinct species. At each period of growth all the growing twigs have tried to branch out on all sides, and to overtop and kill the surrounding twigs and branches, in the same manner as species and groups of species have tried to overmaster other species in the great battle for life.”

Charles Darwin

(On the origin of species, Chapter IV)

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Resumo

Tynanthus Miers inclui 14 espécies distribuídas desde o sul do México até o sul do Brasil, que ocorrem predominantemente em áreas de florestas úmidas. Todas as espécies de *Tynanthus* são lianas, com flores pequenas e corola fortemente bilabiada, frutos com margens proeminentes e cheiro semelhante ao de cravo-da-índia em órgãos vegetativos. Esta tese compreende um estudo detalhado do gênero, abrangendo aspectos taxonômicos, evolutivos, biogeográficos e ecológicos. No primeiro capítulo, é apresentada a filogenia de *Tynanthus*, reconstruída com base em três marcadores moleculares (*ndhF*, *rpl32-trnL* e *pepC*). A filogenia de *Tynanthus* corroborou o monofiletismo do gênero e contribuiu com informações importantes para a circunscrição de espécies de delimitação confusa. Além disso, a filogenia também permitiu um melhor entendimento dos padrões de evolução morfológica no grupo, além de ter constituído a base para um estudo da história biogeográfica do gênero. No segundo capítulo, são apresentadas as descrições de duas espécies novas de *Tynanthus*, reconhecidas com base em caracteres morfológicos e corroboradas pelas análises filogenéticas moleculares. No terceiro capítulo, é apresentada uma monografia do gênero, incluindo descrições morfológicas detalhadas para todas as espécies reconhecidas, dados de fenologia, distribuição geográfica, comentários taxonômicos, ilustrações e uma chave para a identificação de todas as espécies. No quarto capítulo, é apresentado um estudo da evolução do nicho ecológico de *Tynanthus*, contribuindo com informações importantes para um melhor entendimento dos padrões biogeográficos observados.

Abstract

Tynanthus Miers includes 14 species distributed from southern Mexico to southern Brazil, that occur predominantly in rainforests. All species of *Tynanthus* are lianas with small flowers and a strongly bilabiate corolla, fruits with raised margins and a smell of cloves in vegetative portions. This thesis comprises a detailed study of the genus, including taxonomic, evolutionary, biogeographical and ecological aspects. The first chapter presents the phylogeny of *Tynanthus*, reconstructed based on three molecular markers (*ndhF*, *rpl32-trnL* and *pepC*). The phylogeny of *Tynanthus* corroborated the monophyly of the genus and contributed important information for the circumscription of species with confusing delimitation. In addition, this phylogeny also led to an improved understanding of morphological evolution in the group, as well as provided the basis for a study on the biogeographical history of the genus. The second chapter presents the description of two new species of *Tynanthus* recognized based on morphological features and corroborated by the molecular phylogenetic analyses. The third chapter presents a monograph of the genus, including detailed morphological descriptions for all species recognized, as well as information on phenology, geographical distribution, taxonomy, illustrations and a key for the identification of all species. The fourth chapter presents a study on the evolution of the ecological niche of *Tynanthus*, contributing important information for a better understanding of the observed biogeographic patterns.

Introdução Geral

Bignoniaceae abrange cerca de 827 espécies, distribuídas em 82 gêneros (Lohmann & Ulloa 2006 em diante). A família é Pantropical, com cerca de 78% das espécies na região Neotropical e centro de diversidade no Brasil (Gentry 1980). Espécies de Bignoniaceae ocorrem em uma ampla gama de habitats, incluindo ambientes secos e florestas úmidas (Olmstead *et al.* 2009). Representantes de Bignoniaceae são frequentemente utilizados na horticultura e paisagismo, bem como representam uma importante fontes de madeira e produtos farmacológicos (Gentry 1980, 1992).

A família inclui árvores, arbustos e lianas, raramente ervas. Os ramos são cilíndricos ou angulosos, geralmente lenticelados, podendo apresentar campos de glândulas interpeciolares e perfis da gema axilar bem desenvolvidos. As folhas são compostas e opostas, com morfologia bastante variável em relação à forma do limbo, divisões e indumento, podendo apresentar domácias e gavinhas. As inflorescências são geralmente panículas, tirso, fascículos ou racemos, axilares, terminais ou caulifloras, às vezes reduzidas. As flores são bissexuais, diclamídeas, simpétalas e zigomorfas, geralmente grandes e vistosas. O cálice pode ser tubuloso, campanulado ou urceolado, com ápice truncado ou subdividido, pentâmero. A corola é 5-lobada, usualmente com a porção basal estreitada e apical ampla, apresentando morfologia variada, relacionada a diferentes síndromes de polinização. O androceu é formado por quatro estames férteis, com anteras com tecas divaricadas, e um estaminódio, geralmente curto. O gineceu é bicarpelar, com ovário súpero e bilocular, estilete terminal e estigma bífido. Na maioria dos representantes há um disco nectarífero ao redor do ovário. Os frutos são cápsulas, com deiscência septífraga ou loculicida, ou bacáceos, indeiscentes. As sementes são geralmente achatadas, aladas ou pubescentes, dispersas pelo vento ou água (Gentry 1980; Fischer *et al.* 2004; Judd *et al.* 2009; Lohmann 2004).

A tradicional subdivisão de Bignoniaceae em tribos foi reavaliada com base em estudos filogenéticos (Spangler & Olmstead 1999; Olmstead *et al.* 2009) (Fig. 1), que levaram ao atual reconhecimento de oito clados: Bignonieae, Catalpeae, “*Tabebuia Alliance*” (incluindo Crescentieae), “Paleotropical clade” (incluindo Coleeae), Oroxyleae, Tecomeae, Turretieae, e Jacarandae. Cerca de metade das espécies descritas em Bignoniaceae compõem a tribo Bignonieae, a qual constitui o principal grupo de lianas nas florestas do Novo Mundo (Lohmann & Taylor 2014). As sinapomorfias morfológicas de

Bignonieae incluem folíolos modificados em gavinhas e anatomia da madeira marcada por crescimento anômalo de feixes de floema (Lohmann 2006; Lohmann & Taylor 2014). A tribo compreende 393 espécies e 21 gêneros monofiléticos (Lohmann & Taylor 2014), caracterizados por sinapomorfias morfológicas e bem sustentados por dados provenientes de uma filogenia molecular que amostrou cerca de 1/3 das espécies de Bignonieae (Lohmann 2006) (Fig. 2).

Dos gêneros atualmente reconhecidos em Bignonieae, *Tynanthus* é um dos poucos que manteve sua circunscrição inalterada ao longo da história taxonômica da tribo (Lohmann 2006). O gênero é caracterizado pelas flores pequenas (em comparação às demais flores de Bignoniaceae), o que inspirou o nome genérico adotado por Miers (1863) (do grego: *τύννος* = pequeno; *άνθος* = flor). O gênero é caracterizado por uma corola profundamente bilabiada, frutos com margens proeminentes e órgãos vegetativos que exala um odor semelhante ao de cravo-da-índia (Lohmann 2006; Lohmann & Taylor 2014). Outros caracteres diagnósticos de *Tynanthus* são as tecas das anteras curvadas, o ovário densamente pubescente e o disco nectarífero inconspícuo (Gentry 1980; Lohmann & Taylor 2014).

Apesar de *Tynanthus* apresentar uma circunscrição clara, a delimitação de suas espécies permaneceu confusa. Isso se deve ao fato de muitas espécies serem raras, tendo sido coletadas apenas poucas vezes (Lohmann & Taylor 2014), e pelo fato dos estudos taxonômicos disponíveis para o gênero serem muito antigos (p.ex. Bureau 1868; Bureau & Schumann 1896). Essas observações foram os principais motivadores da realização do presente estudo, o qual visou sintetizar e atualizar o conhecimento taxonômico sobre o gênero, tendo como base dados morfológicos e moleculares (Capítulos 1, 2 e 3).

Espécies de *Tynanthus* apresentam distribuições geográficas geralmente restritas, com muitas espécies endêmicas de regiões biogeográficas particulares (Fig. 3). Como a distribuição geográfica de espécies resulta da atuação de fatores históricos (p.ex. dispersão, vicariância) (Morrone & Crisci 1995) e ecológicos (p.ex., distribuição de habitats, interações biológicas) (Soberón & Peterson 2005), o entendimento de padrões biogeográficos depende da integração de dados de ambas naturezas.

O nicho ecológico compreende as condições e recursos que uma espécie necessita para sobreviver (Hutchinson 1957) representando uma excelente maneira para caracterizar a ecologia e distribuição espacial das espécies. Nos últimos anos, as análises de características relacionadas ao nicho ecológico das espécies têm sido realizadas num contexto evolutivo, com a incorporação de informações sobre a história filogenética dos

organismos de interesse. Alguns estudos desta natureza indicaram que algumas linhagens evolutivas apresentam características ecológicas conservadas, o que se tornou conhecido como conservantismo de nicho (ver Wiens & Graham 2005; Wiens *et al.* 2010). Entretanto, outras linhagens incluem espécies com características do nicho bastante variáveis (Losos 2008; Pearman *et al.* 2008). Essa ambiguidade encontrada na literatura revela que estudos de caso sobre a evolução do nicho ecológico são extremamente necessários para que um melhor entendimento dos padrões e processos associados à evolução do nicho possa ser obtido (Losos 2008).

O conservantismo de nicho apresenta, como importante consequência, a restrição da distribuição geográfica das espécies (Wiens & Graham 2005). Neste contexto, *Tynanthus*, um gênero com alto número de espécies com distribuição restrita, representa um excelente modelo para estudos sobre a evolução de conservantismo de nicho em plantas. Para que pudéssemos obter um melhor entendimento dos padrões de diversificação e papel de fatores históricos e ecológicos na distribuição espacial das espécies de *Tynanthus*, reconstruímos a história biogeográfica do grupo (Capítulo 1) e testamos hipóteses relacionadas à evolução de características ecológicas no gênero (Capítulo 4). Ambas as abordagens utilizaram a filogenia molecular reconstruída no Capítulo 1 como base.

Esta tese está inserida num projeto mais amplo que visa elucidar e compreender aspectos taxonômicos, filogenéticos e evolutivos da tribo Bignonieae. Desta forma, além de ampliar o conhecimento acerca de *Tynanthus*, especificamente, os resultados desta tese também contribuirão diretamente para o entendimento da história biogeográfica e evolutiva da tribo Bignonieae como um todo.

Objetivos

Esta tese tem como objetivos: (1) Reconstruir a filogenia de *Tynanthus* a partir de marcadores moleculares visando elucidar as relações de parentesco infragenéricas e um melhor entendimento do padrão de evolução de caracteres morfológicos (Capítulo 1); (2) Reconstruir a história biogeográfica de *Tynanthus* (Capítulo 1); (3) Elaborar uma revisão taxonômica do gênero, visando solucionar problemas taxonômicos e melhorar a delimitação das espécies e sua identificação (Capítulos 2 e 3); e (4) Estudar a evolução de características ecológicas do grupo, como base para o entendimento de padrões de distribuição das espécies (Capítulo 4).

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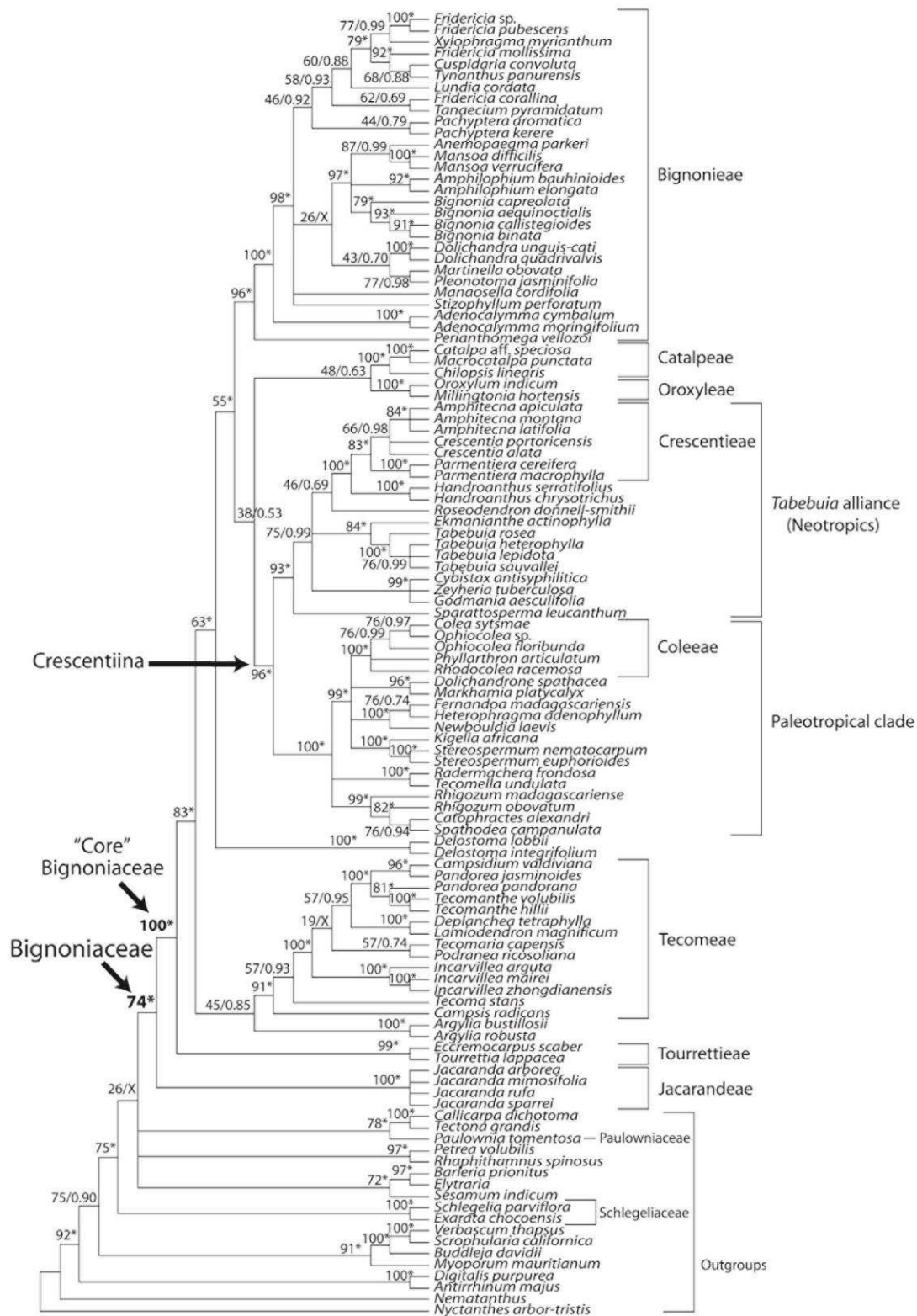


Figura 1. Árvore de consenso estrito oriunda da análise de parcimônia dos dados combinados de *ndhF*, *trnL-F* e *rbcL*, indicando os clados atualmente reconhecidos em Bignoniaceae (extraído de Olmstead *et al.* 2009).

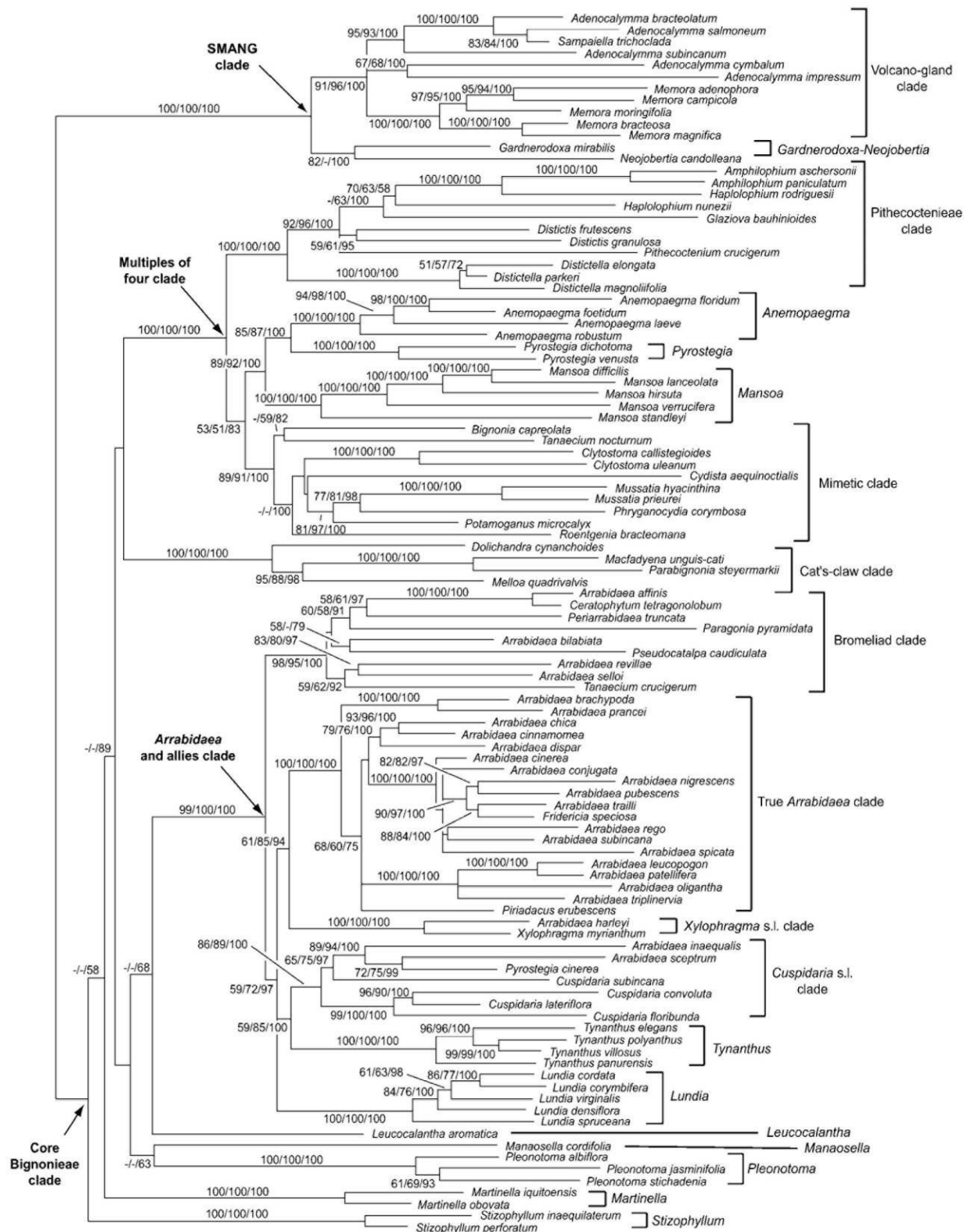


Figura 2. Árvore oriunda da análise de máxima verossimilhança dos dados combinados de *ndhF* e *pepC*, utilizada como base para a classificação genérica atual de Bignoniaceae (extraído de Lohmann 2006).

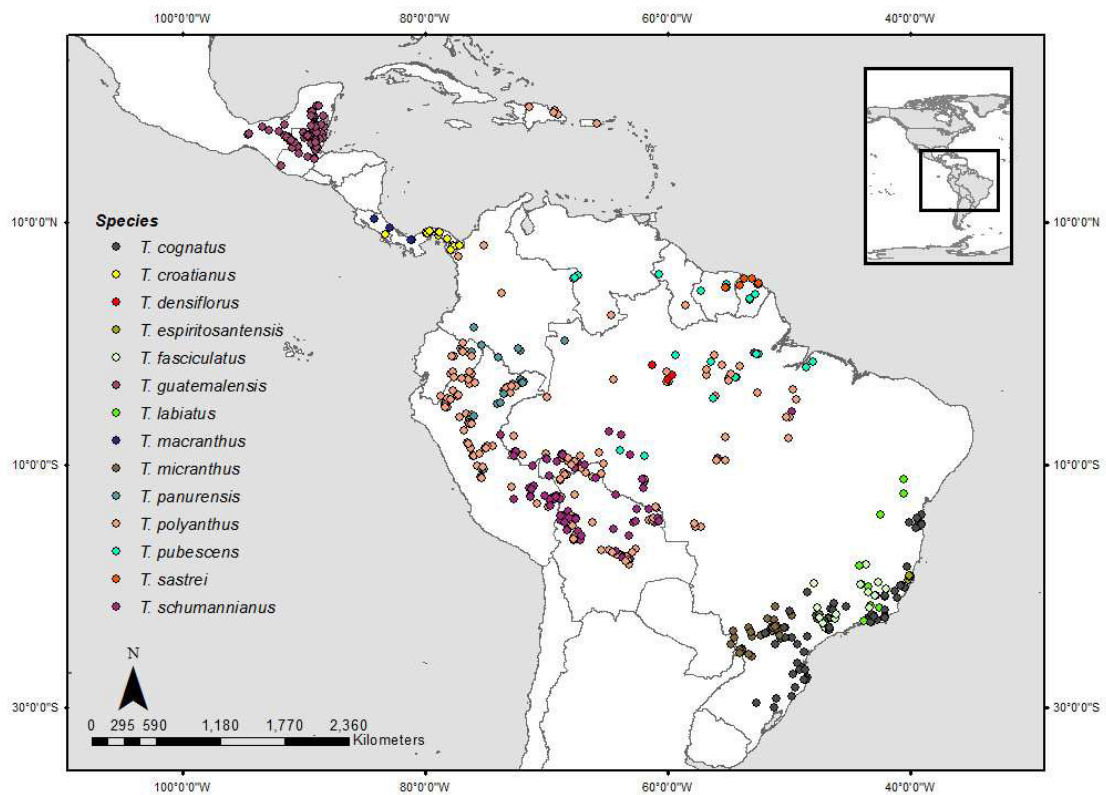


Figura 3. Mapa de distribuição de *Tynanthus*, indicando as localidades de ocorrência conhecida para cada uma das 14 espécies reconhecidas neste trabalho.

Capítulo 1

Phylogeny and Biogeography of *Tynanthus* Miers (Bignoniaceae, Bignoniaceae)

Phylogeny and Biogeography of *Tynanthus* Miers (Bignoniaceae, Bignoniaceae)

Abstract

The origin of Neotropical biodiversity represents a key question in evolutionary biology. Despite the attempts to decipher the role of ecological and historical factors to present-day distribution patterns, robust phylogenetic studies of Neotropical clades are still needed before a comprehensive picture of the origin of Neotropical biodiversity can be achieved. *Tynanthus* Miers (Bignoniaceae, Bignoniaceae) is a well-circumscribed genus of Neotropical lianas that includes 15 species in a recent synopsis of the tribe Bignoniaceae, most of which are narrowly distributed. The genus is characterized by a clove odor, small bilabiate flowers with the two upper lobes almost fused, and fruits with raised margins, all of which represent good morphological synapomorphies for this clade. Other distinctive characters are the thecae reflexed forward, the densely pubescent ovaries and the poorly-developed nectariferous disk. The circumscription of the genus has remained constant over the years, despite the problematic limits of most genera of tribe Bignoniaceae. In this study, we reconstruct the phylogeny of *Tynanthus* based on two plastid (*ndhF* and *rpl32-trnL*) and one nuclear marker (*pepC*) and use this phylogenetic framework to investigate the biogeographical history of the genus. Our phylogenetic hypothesis provides further support for the monophyly of *Tynanthus*, and strongly supports a series of infra-generic clades. Most species are reconstructed as monophyletic while *T. cognatus* and *T. polyanthus* are paraphyletic. Biogeographic reconstructions suggest that *Tynanthus* originated between 9.4-21.5 Mya, most likely at approximately 15.3 Mya. The MRCA of the genus was likely broadly distributed through Lowland Amazonia and Central America and diversified in the Neotropics during the Miocene. Closely related species are generally distributed within the same biogeographic area, suggesting that niche conservatism has played an important role in the diversification history of the group.

Keywords. Ancestral area reconstructions, Bignoniaceae, Bignoniaceae, biogeography, Lamiales, lianas, neotropical flora, niche conservatism, phylogeny

Introduction

The Neotropical region includes ca. 100.000 species of plants (Hughes *et al.* 2013), representing one of the most species-rich areas on Earth (Myers *et al.* 2000). The origin of such high diversity has fascinated naturalists and biogeographers for a long time (Hughes *et al.* 2013). It is now widely accepted that the present-day distribution of taxa has resulted from both historical (e.g., dispersal and vicariance) (Morrone & Crisci 1995) and ecological factors (e.g., environmental tolerances and species interactions) (Soberón & Peterson 2005). Yet, the exact role of history and ecology to current distribution patterns remains to be understood (Wiens & Donoghue 2004; Ricklefs 2007). Over the past decade, several studies have been conducted to elucidate the history of different lineages of Neotropical plants and understand the processes driving current distribution patterns (see Hughes *et al.* 2013). Nevertheless, a much higher number of phylogeny-based analyses focused on Neotropical clades are still needed so that a comprehensive picture of the origin and maintenance of Neotropical biodiversity can be achieved.

Tynanthus Miers. (Bignoniaceae, Bignoniaceae) includes 15 species of neotropical lianas (Lohmann & Taylor 2014). Most of its species are narrowly distributed, occurring in Western South America, Central America, Amazonia or Mata Atlantica exclusively (Lohmann & Taylor 2014). The narrow distribution of most species of *Tynanthus* provides an excellent model within which to test specific biogeographical hypotheses within the neotropics. Species of *Tynanthus* are locally known as “cipó-cravo” (Brazil) or “clavohuasca” (e.g., Peru, Ecuador and Colombia), in allusion to the clove odor that vegetative organs present after cracking (Lohmann & Taylor 2014; Medeiros & Lohmann in prep.).

The genus was described by Miers (1863), who included nine species in its original circumscription. Since the publication of *Tynanthus*, several species were described, while new combinations and synonymizations were proposed (e.g., Bureau 1868; Gentry 1974, 1980a). Despite these taxonomic novelties, the circumscription of the genus has remained constant over the years, with its monophyly receiving strong support from molecular characters (Lohmann 2006).

Miers (1863) mainly characterized the new genus by the relatively small bilabiate flowers. Since then, other morphological features have been used to diagnose *Tynanthus*, namely: absence of interpetiolar gland fields, trifid tendrils, thecae reflexed forward, densely pubescent ovaries and poorly-developed nectariferous disk (e.g., Bentham & Hooker 1876; Bureau & Schumann 1896; Gentry 1980b). In a recent synopsis of the whole tribe Bignoniaceae (Lohmann & Taylor 2014), species of *Tynanthus* are characterized by a

clove odor, small bilabiate flowers with two upper lobes almost fused, and fruits with raised margins.

To date, the only phylogenetic study to sample species of *Tynanthus* aimed at testing generic limits within Bignoniaceae and only included one third (5/15) of the species currently recognized (Lohmann 2006). A more comprehensive phylogeny of the genus is still needed so that further taxonomic, morphological, evolutionary and biogeographical studies can be conducted. In particular, a detailed biogeographical analysis of *Tynanthus* would provide important insights as to how the genus occupied different regions in South and Central America, which would, in turn, provide key insights to a better understanding of the origin and maintenance of Neotropical biodiversity as a whole.

In this study, we reconstruct phylogenetic relationships among species of *Tynanthus* and use the resulting phylogenetic framework to investigate the biogeographic history of the genus.

Material and methods

Taxon sampling. We sampled 14 from the 15 species currently recognized in *Tynanthus* (Lohmann & Taylor 2014) and two new species (Medeiros & Lohmann submitted); only *T. goudotianus*, a poorly known species from Western South America was not sampled. When species were widely distributed, morphologically polymorphic or presented complicated circumscriptions, multiple individuals were included in the analyses. A total of 28 specimens of *Tynanthus* were sampled overall (Appendix 1). In addition, 11 species, representing five genera of Bignoniaceae were selected as outgroups, following Lohmann (2006).

DNA extraction, amplification, and sequencing. Total DNA was extracted from silica-dried or herbarium leaf tissue using a Spin Plant Mini Kit (Invisorb) according to the manufacturer's protocol, except for the utilization of 600 µl of Lysis Buffer P and 50-200 µl of Elution Buffer D, depending on the conditions of the material. Three molecular markers were selected for this study: the plastid *ndhF* and *rpl32-trnL* and the nuclear *pepC*. Amplification primers and procedures followed Zuntini *et al.* (2013). Amplification of all markers were conducted in 25 µl reactions containing 13.8 µl of water, 5 µl of 10X GoTaq buffer, 2.5 µl of 25 mM MgCl₂, 1 µl of dNTP (10 µM), 0.5 µl of BSA, 0.5 µl of each primer (10 µM), 0.2 µl of Taq (Hot start, Promega) and 1 µl of template DNA. PCR reaction conditions were as follows: 94°C for 1 min, followed by 40 cycles of 94°C for 1 min, 48-56°C for 1 min, 72°C for 45 sec-2 min, with a final extension at 72°C for 10 min. Products were purified

using ExoSAP or the Illustra GFX PCR DNA and Gel Band Purification Kit (GE Healthcare), following the manufacturer's protocol, except for the addition of 20 μ l of Elution Buffer in the final step in order to obtain a more concentrated DNA. Cloning of *pepC* amplification products was performed with a pGEM-T Easy Vector (Promega), following the manufacturer's protocol. Whenever possible, up to four colonies per species were collected and used in PCR reactions that used M13 primers (Promega). Sequencing was performed at Macrogen Inc. (Korea).

Phylogenetic analyses. Sequences were edited and assembled in Geneious 6.0 (Drummond *et al.* 2012a) and aligned using Muscle (Edgar 2004), with subsequent manual adjustments. Regions with ambiguous or doubtful alignments were excluded. Gaps were coded using the simple indel coding method (Simmons & Ochoterena 2000) in Seqstate 1.4 (Müller 2005) and added to the final matrix as a binary data partition. A four nucleotide reverted portion was identified in *ndhF*; this region was manually coded and excluded.

Maximum likelihood (ML) analyses were run in RaxMLGUI 1.3 (Silvestro & Michalak 2012), followed by 1000 replicates of thorough Bootstrap (BS). Bayesian inferences (BI) were performed with MrBayes 3.2 (Ronquist and Huelsenbeck 2003). Two independent MCMC runs were conducted, each composed of four linked chains that ran for 10,000,000 generations with sampling every 100 generations. Likelihood values were monitored graphically to detect stationarity with Tracer 1.6 (Rambaut *et al.* 2013). Posterior probabilities (PP) were used to assess clade support. The best-fit models of nucleotide substitution for the individual data partitions were determined with jModeltest 2.1.3 (Darriba *et al.* 2012) using the Akaike Information Criterion. TVM + G was identified as the most appropriate model for the *ndhF* and *pepC* data sets while TPM3uf + I + G was identified as the most appropriate model for the *rpl32-trnL* data set. Those models were replaced by the GTR option in both RaxMLGUI and MrBayes given that the selected models were not available for analyses in both of these softwares. Clades with BS higher than 75% or PP higher than 0.95 were considered strongly supported (Cummings *et al.* 2003; Simmons *et al.* 2004).

Incongruence among data partitions was tested using the KH (Kishino & Hasegawa 1989) statistical test of trees implemented in Phylip 3.695 (Felsenstein 1989). Topologies resulting from ML analyses containing branches with BS \geq 75% were tested against a rival tree. Polytomies in rival trees were resolved according to the test tree, in order to avoid inflating the rival tree length. The test was firstly conducted to compare the two plastid data sets and then to compare the combined plastid and *pepC* data set. Reciprocal tests were

conducted in both cases. *Tynanthus sastrei* and one of the accessions of *T. villosus* were excluded from the comparisons because sequences were only available for the *ndhF* data set.

Ancestral area reconstructions. Species distribution data were compiled from herbarium specimens. Occurrences were categorized according to the four biogeographic areas adopted by Lohmann *et al.* (2013), which reflect patterns of endemism in Neotropical Bignoniaceae as a whole, namely: (1) Eastern South America, (2) South American dry areas, (3) Lowland Amazonia and (4) Western South America and Central America.

Ancestral areas of *Tynanthus* were estimated using a maximum likelihood analysis of geographic range evolution using the package BioGeoBEARS 0.2.1 (Matzke 2013) implemented in R 3.0.2 (R Core Team; available at <http://www.rproject.org/>). Estimates were conducted using the dispersal-extinction-cladogenesis (DEC) (Ree & Smith 2008) and the DEC+j models. In this test, apart from the parameters ‘dispersal’ (d) and ‘extinction’ (e), a third free parameter (j) is added to the framework under the DEC+j model. This additional parameter simulates the process of founder-event speciation, allowing for long-distance dispersal events. The two analyses were compared by a Likelihood Ratio Test and Akaike Information Criterion weights (AICwt), which gives a sense of the relative probability of the two models. The test is also implemented in BioGeoBEARS.

Estimates were conducted based on a simplified ultrametric bayesian combined tree generated with BEAST 1.7.5 (Drummond *et al.* 2012b). This analysis used a relaxed uncorrelated lognormal clock and Yule process speciation prior to infer trees. A secondary calibration was applied, based on previous estimates derived from a comprehensive study of the whole tribe Bignonieae (Lohmann *et al.* 2013). We used a normal prior with mean 13.4 and standard deviation of 2.0. Two separate and convergent runs were conducted, with 10,000,000 generations, sampling each 1,000 steps and 25% burn-in. Trees were combined using LogCombiner and tree topology was assessed using TreeAnnotator and FigTree 1.4.0 (available at <http://tree.bio.ed.ac.uk/software/figtree/>). We excluded all outgroups and selected a single accession per species of *Tynanthus* to generate the tree. Results based on poorly supported relationships were not interpreted.

Results

Molecular data sets. We obtained 24 new sequences of *ndhF*, 38 of *rpl32-trnL* and 23 of *pepC*. These sequences were combined with 15 *ndhF* and 14 *pepC* sequences available from a previous study (Lohmann 2006). Complete sequences were generated for

all taxa, except from *T. pubescens*, *T. sastrei* and one of the accessions of *T. panurensis*, for which we were only able to generate partial *ndhF* sequences. Variation in all *pepC* sequences generated from each species did not transcend species boundaries and a single sequence per species was included in the final *pepC* analyses.

The original aligned *ndhF*, *rpl32-trnL* and *pepC* data sets presented 2,069 bp, 871 bp and 536 bp in length, respectively. In the case of the *rpl32-trnL* data set, ca. 90 bp were removed from the initial matrix due to the presence of ambiguous or doubtful alignment portions (e.g., single or multiple nucleotide repeats). The total length of the final matrices after gap-coding was 2072 bp, 900 bp and 552 bp, in that same order.

Phylogenetic analyses. KH tests did not indicate significant topological incongruence between the plastid data sets nor between the combined plastid and *pepC* data sets in all reciprocal comparisons (Table 1). Visual inspection of the compared trees corroborates the results derived from those tests. Most of the well-supported clades in the *ndhF* topology were also recovered in the *rpl32-trnL* topology. Nevertheless, some relationships recovered in the *rpl32-trnL* tree were less well supported than those from the *ndhF* tree. Similarly, the tree derived from the analysis of the combined plastid data set was generally more resolved than the tree derived from the analysis of the *pepC* data set. Bayesian trees derived from the analyses of each marker separately and from the combined plastid data set are given in Supplementary material (Figs. S1-S4).

Statistical and visual comparisons of all topologies indicate that the BI tree that resulted from the analysis of the total evidence data set represent the best phylogenetic hypothesis of *Tynanthus* (Fig. 1). This topology recovers a monophyletic *Tynanthus* (BS=100, PP=1) within a polytomy that includes species of *Cuspidaria*, *Fridericia*, *Lundia*, *Tanaecium* and *Xylophragma*. *Tynanthus macranthus* is the first species to diverge within the genus and is sister to a large clade that includes all other members of *Tynanthus* (BS=100, PP=1). This large clade includes two major clades: (i) the cognatus clade, including *T. cognatus* and *T. polyanthus* (BS=94, PP=1) and (ii) a larger clade (BS=100, PP=1) that includes the panurensis clade (BS=79, PP=1) and the labiatus clade (BS=100, PP=1). While the panurensis clade is formed by a polytomy composed of *Tynanthus* sp.1, the sub-clade *T. croatianus* + *T. guatemalensis* (BS=100, PP=1), and the sub-clade *T. panurensis* + *T. pubescens* (BS=97, PP=1), the labiatus clade is formed by a polytomy composed of *Tynanthus* sp.2, *T. schumannianus*, and the sub-clade (*T. micranthus* (*T. fasciculatus* + *T. labiatus*)) (BS=91, PP=0.99).

All species whose sampling included multiple individuals were strongly supported as monophyletic (BS=100, PP=1), except from *T. cognatus* and *T. polyanthus*. While the former includes *T. elegans* nested within a broader *T. cognatus*, the latter includes *T. villosus* nested within a broader *T. polyanthus*. These findings are corroborated by morphological traits, suggesting that these taxa need to be re-circumscribed; the necessary taxonomic adjustments are proposed elsewhere (Medeiros & Lohmann in prep.).

The topology recovered from the ML analysis of the total evidence data set recovered a very similar topology, with similar support values for the various nodes. The only difference between the topologies derived from the ML and BI analyses is the strongly supported sister-group relationship between two samples of *T. polyanthus* encountered in the BI tree (PP=0.98), which is only poorly supported by the ML analysis (BS=73).

Biogeographic history. Divergence time estimates suggest a Miocene origin for *Tynanthus*, with a mean crown age of 15.3 Mya (CI 9.4-21.5 Mya). The timing of divergence of all well-supported internal nodes is provided in Table 2.

The DEC+j model was selected as the most appropriate model for the *Tynanthus* data ($p=0.0098$, AICwt=0.91), with ancestral area reconstructions under this model recovering a lnL value of -22.9.

The analysis of the free parameters revealed that long-distance dispersal predominated during the history of *Tynanthus* ($d=0.009$, $e=0$, $j=0.08$). This analysis further suggested that the MRCA (i.e., Most Recent Common Ancestor) of *Tynanthus* was most likely broadly distributed through lowland Amazonia and Central America (37%) (Fig. 2; Table 2). *Tynanthus macranthus* was the first lineage to diverge from this MRCA and to establish in Central America. The large clade containing the remaining species of *Tynanthus* had a MRCA that was most likely broadly distributed through lowland Amazonia, Central America and Eastern South America (38%). Similarly, the MRCA of the cognatus clade also seem to have been broadly distributed through those three areas (52%), with *T. cognatus* subsequently establishing in Eastern South America and *T. polyanthus* subsequently establishing in Amazonia and Central America. The MRCA of the lineage that is sister to the cognatus clade was most likely (44%) restricted to Amazonia. A major split within this clade leads to two main sub-clades. The first sub-clade (panurensis clade) includes an Amazonian lineage (composed of *T. pubescens*, *T. panurensis*, and *Tynanthus* sp. 1) that is sister to a Central American clade (composed of *T. croatianus* + *T. guatemalensis*). The second sub-clade (labiatus clade) includes an Amazonian lineage (*Tynanthus schumannianus*) that is sister to a clade that is predominantly distributed

through Eastern South America, with only a few representatives in the South American Dry Areas; this clade includes *T. micranthus*, *T. fasciculatus*, *T. labiatus*, and *Tynanthus* sp.2.

Discussion

In this study, we present a comprehensive molecular phylogeny of *Tynanthus* based on plastid and nuclear markers and all species currently recognized, except from *Tynanthus goudotianus*, a poorly known species from Colombia. Our results recovered a monophyletic *Tynanthus*, providing further support to earlier findings (Lohmann 2006). Within *Tynanthus*, *T. macranthus* is sister to a large clade that includes all other species of the genus. This large clade includes the cognatus clade, which is sister to a larger clade that contains the labiatus and panurensis sub-clades. While this study identified several strongly supported clades and identified major relationships among species, relationships within the labiatus and panurensis clades remain poorly resolved. This phylogenetic framework also helped elucidate patterns of morphological evolution and outstanding taxonomic problems as well as provided the basis for a biogeographical study.

Morphological evolution. Perhaps the most outstanding character of *Tynanthus* is the small bilabiate flowers with the upper lobes almost fused (Lohmann & Taylor 2014). Interestingly, the first species to diverge, *T. macranthus* has the largest flowers in the genus (resembling other Bignoniaceae), but also the most strongly bilabiated. Such a strongly bilabiate corolla is due to a very short corolla tube that measures only up to 1/3 of the corolla total length, in contrast to the remaining *Tynanthus* species in which the tube usually includes half of the corolla length (Medeiros & Lohmann in prep.). Other remarkable reproductive characters in *Tynanthus* are the thecae reflexed forward, the densely pubescent ovaries, the poorly-developed nectariferous disk, and the fruits with raised margins (Medeiros & Lohmann in prep.), all of which represent good morphological synapomorphies for this clade.

The most striking vegetative characters of *Tynanthus* are the clove odor found on stems, the trifold tendrils, and lack of interpetiolar glands. While all species present the clove odor, this character can vary with development, reaching its peak in young branchelets. While clove odor represents a good diagnostic feature for the genus, the trifold tendrils, and lack of interpetiolar glands vary across taxa. More specifically, while most species of *Tynanthus* have trifold tendrils, simple tendrils are found in *T. macranthus*, *T. guatemalensis* and *T. polyanthus* (Medeiros & Lohmann in prep.), having evolved at least twice in the genus. Similar tendril shifts are common in other Bignoniaceae genera and seem

to be associated with changes in the expression of PISTILATTA instead of environmental plasticity (Sousa-Baena *et al.* 2014a; Sousa-Baena *et al.* 2014b). Similarly, while most species of *Tynanthus* lack interpetiolar gland fields, these glands are present in *T. macranthus*, *T. pubescens*, and *Tynanthus* sp. 1, also having evolved at least twice in the genus. Various Bignoniaceae genera include species with or without glandular fields (Gentry 1980b). Furthermore, the density of nectaries can vary within a single species, leading to various degrees of protection among populations (Nogueira *et al.* 2013).

Overall, none of the morphological features described above, nor other morphological characters investigated (e.g., inflorescence type, prophyll morphology, indument) seem to represent good morphological synapomorphies of sub-clades within *Tynanthus*. Instead, a complex pattern of morphological evolution has marked the evolutionary history of the genus.

Taxonomic implications. While most species sampled are monophyletic, *T. cognatus* and *T. polyanthus* are polyphyletic as currently circumscribed. The patterns recovered in the molecular phylogeny corroborate the overlapping patterns of morphological variation encountered in those two species (Medeiros & Lohmann in prep.). More specifically, indument of vegetative organs, the character traditionally used to separate *T. cognatus* and *T. elegans*, varies continuously within these taxa, while prophyll persistence and number of flowers in the inflorescences overlap between *T. polyanthus* and *T. villosus*. Such confusing patterns of morphological and molecular variation indicate the confusing delimitation of those species and the need for the recognition of more broadly circumscribed taxa.

The molecular phylogeny of *Tynanthus* provided additional support for earlier morphological observations that suggested that *Tynanthus* sp.1 and *Tynanthus* sp.2 represented undescribed new species. More specifically, detailed analyses of herbarium specimens and field observations indicated that *Tynanthus* sp.1 could be easily separated from the close relatives *T. panurensis* and *T. pubescens* by the densely arranged inflorescences (Medeiros & Lohmann submitted). Similarly, detailed morphological studies of *Tynanthus* sp.2 indicated that this species differed from the closely related *T. schumannianus* by calyx dimensions and the type of the trichome that covers the vegetative organs (Medeiros & Lohmann submitted). Apart from the morphological and molecular characters supporting the distinction of these taxa, *Tynanthus* sp. 2 and *T. schumannianus* are also geographically isolated, with the former occurring in the Atlantic Forest of Brazil and the latter in Amazonia. *Tynanthus* sp. 1, *T. panurensis* and *T.*

pubescens, on the other hand, occur sympatrically in Amazonia. Further population genetic and phylogeographic studies would provide great insights into the diversification of these interesting Amazonian species.

Biogeography. Our divergence time estimates suggest that *Tynanthus* diverged during the Miocene, at approximately 15.3 Mya (9.4-21.5 Mya), from an ancestral that was broadly distributed through Amazonia, Western South America and Central America. At that time, Central America was still separated from South America, but only by a narrow strait (Kirby *et al.* 2008; Montes *et al.* 2012; Coates & Stallard 2013). The climate throughout that region was already tropical and wet, similar to the current climate, although a few degrees warmer (Scotese 2014). Furthermore, a semi-evergreen or evergreen forest predominated (Pound *et al.* 2012).

Apart from occurring in Amazonia, Western South America and Central America, the MRCA of the large clade that contains the remaining species of *Tynanthus* also occupied Eastern South America. At that time, ca. 12.4 Mya (8.3-16.4 Mya), wet forests in South America were probably contiguous and extensive (Morley 2000), which may have facilitated the occupation of new biogeographic areas. The next divergence events, at approximately 10 Mya, led to the cognatus clade and to a larger clade that subsequently divided into the panurensis and labiatus clades.

Within the cognatus clade, *T. cognatus* represents the first occupation of Eastern Brazilian Forests. At around that same time, ca. 10 Mya (6.2-14 Mya), *T. polyanthus* established in Amazonia, at a moment in which important geological changes were taking place in that region. More specifically, the complex lacustrine system that covered the western portions of South America due to the Andean uplift, the Pebas system, gave place to a fluvial or fluviotidal system, the Acre system (Hoorn *et al.* 2010). The resulting changes in the terrestrial conditions in Western Amazonia seem to have played a key role in the evolution of the Amazonian biota (Antonelli *et al.* 2009; Hoorn *et al.* 2010).

Changes in the Amazonian environment seem to have played key roles during the diversification of the labiatus + panurensis lineages, given that the diversification of lineages within these sub-clades coincides with the time of replacement of the Pebas system and formation of the Amazon river basin at approximately 9.7 Mya (CI 6.2-13.2 Mya). More specifically, the crown group of the Amazonian sub-clade formed by *T. panurensis* and *T. pubescens* has been dated to 8.2 Mya (CI 5.0-11.4 Mya), which coincides with the time of divergence of the Amazonas river, ca. 7 Mya (Hoorn *et al.* 2010). At around that same time (ca. 5.8 Mya, CI 3.1-8.6 Mya), a new occupation of Central America occurred by *T.*

croatianus and *T. guatemalensis*, ca. 2.8 Mya before the complete closure of the Isthmus of Panama, estimated to have occurred at around 3 Mya (Coates & Stallard 2013).

As far as the *labiatus* clade is concerned, the divergence of its MRCA occurred at around 5.9 Mya (3.6-8.6 Mya), possibly with the establishment of *T. schumannianus* in Amazonia. Uncertainties in tree topology do not allow a complete interpretation of diversification patterns within this clade. However, our results indicate an occupation and diversification of a lineage throughout the forests of Eastern South America. This radiation probably occurred after the global cooling that led to the expansion of dry areas in South America, which resulted in the formation of the “diagonal of open formations” that separated the Brazilian Atlantic Forest from Amazonia at around 5 Mya (Morrone 2006; DaSilva & Pinto-da-Rocha 2011).

It is interesting to note that *Tynanthus labiatus* and *T. fasciculatus*, two of the four species of *Tynanthus* that occur in the Atlantic Forest, also have a few populations growing within the Brazilian dry areas. Even though the dry area records of *T. labiatus* and *T. fasciculatus* are adjacent to the Atlantic Forest, the expansions into a drier environment indicate that these species present broader tolerances than the other species of *Tynanthus*. The predominant distribution of species of *Tynanthus* through wet forests, associated to the fact that many species have restricted geographic distribution patterns suggests that niche conservatism (Wiens & Graham 2005; Losos 2008; Wiens *et al.* 2010) may have played an important role in the history of the group. This hypothesis is corroborated by the fact that sub-clades from the *panurensis* and *labiatus* clades are restricted to a single biogeographical area. A more detailed investigation of niche conservatism in *Tynanthus* is being conducted elsewhere (Medeiros *et al.* in prep.).

Concluding remarks. The phylogeny of *Tynanthus* presented here represents the first comprehensive phylogenetic reconstruction of the genus. This study provided a basis for a detailed understanding of morphological evolution and biogeographic history within Bignoniaceae. This phylogenetic framework further provides important information for a monograph of *Tynanthus* (Medeiros & Lohmann in prep.), as well as for a detailed study of the evolution of the ecological niche of *Tynanthus* (Medeiros *et al.* in prep.). The analysis of ecological niches allow us to assess whether and how individual ecological factors might have helped shape current distribution patterns, thus representing a valuable complementary approach to the biogeographic analyses presented here. Results presented here provide new information from a neotropical plant clade for which no phylogenetic, biogeographical or ecological data were previously available. These results provide new

insights for a better understanding of the origin and evolution of the neotropical biota as a whole.

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Table 1. KH tests results for reciprocal comparisons between *ndhF* x *rpl32-trnL* data sets and combined plastid x *pepC* datasets. Diff. logL = Log-likelihood difference between trees; s.d. = standard deviation of Diff. logL.

Test data and tree	Rival tree	Diff. logL	s.d.
<i>ndhF</i>	<i>rpl32-trnL</i>	-37.8	19.9
<i>rpl32-trnL</i>	<i>ndhF</i>	-3.5	4.0
Plastid combined	<i>pepC</i>	-3.0	14.2
<i>pepC</i>	Plastid combined	-37.5	23.8

Table 2. Divergence time estimates and ancestral areas for nodes indicated in Fig. 2. CI = Confidence Interval; A = Eastern South America; B = South American dry areas; C = Lowland Amazonia; D = Western South America and Central America.

Node	Ages (Mya)		Ancestral areas	
	Mean	95% CI	Area	Probability
1	15.3	9.4-21.5	CD	0.37
2	12.4	8.3-16.4	ACD	0.38
3	10.0	6.2-14.0	ACD	0.52
4	9.7	6.2-13.2	C	0.44
5	8.2	5.0-11.4	D	0.34
6	5.8	3.1-8.6	D	1
7	4.6	2.4-7.0	C	1
8	5.9	3.6-8.6	C	0.34
9	4.4	2.5-6.6	A	0.64
10	3.2	1.6-5.0	AB	0.68

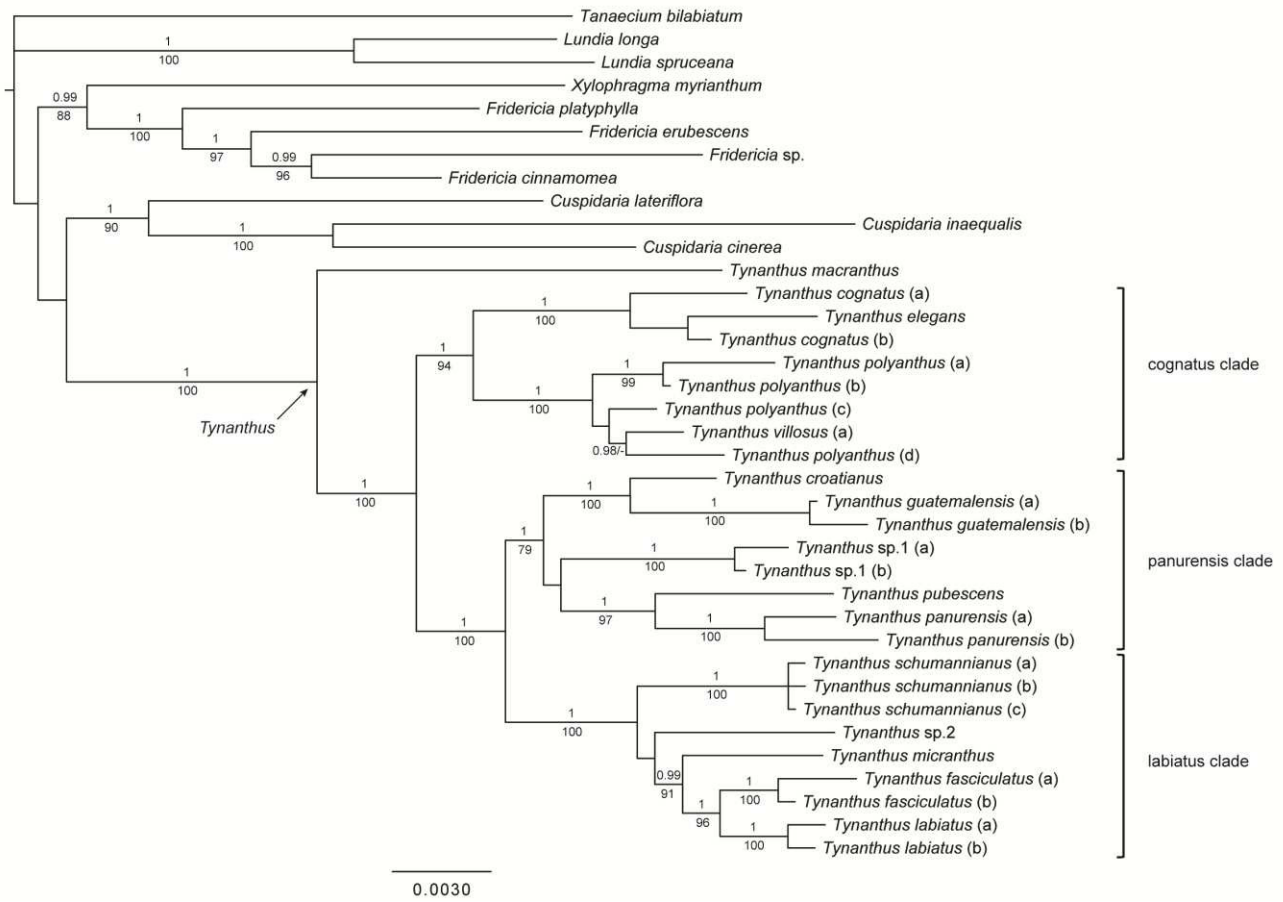


Figure 1. Majority-rule consensus tree derived from the Bayesian total evidence analysis (*ndhF*, *rpl32-trnL* and *pepC*). Posterior probabilities (≥ 0.95) are indicated above branches and maximum likelihood bootstrap values ($\geq 75\%$) are indicated below branches.

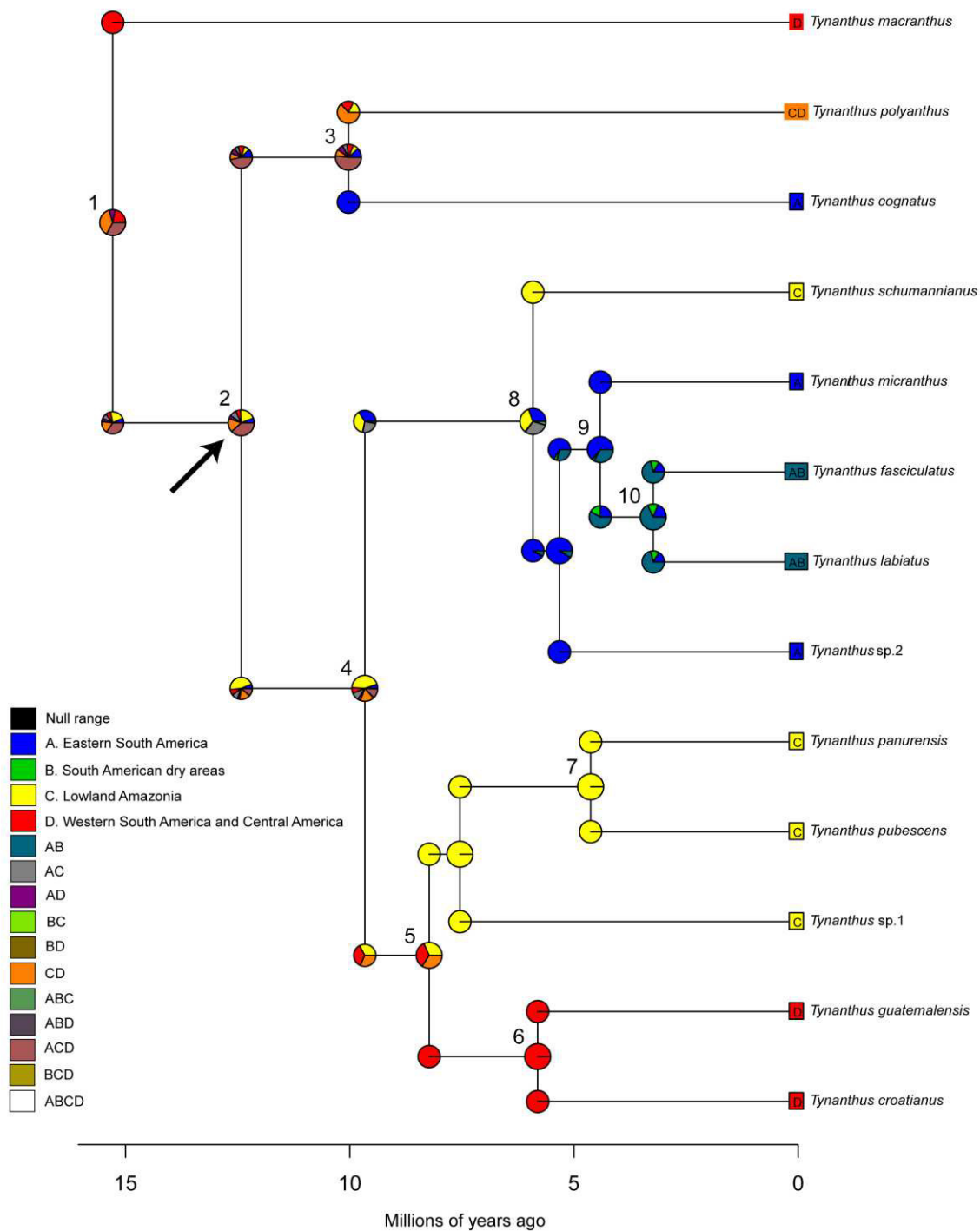


Figure 2. Chronogram with ancestral area estimates based on DEC+j model. Numbers correspond to well-supported nodes. Black arrow indicates the calibration point. Distributions assigned to each species are indicated before tip names. Pie charts reflect relative probabilities of each area being ancestral.

Appendix 1. Taxa, vouchers, localities and GenBank accession numbers for sampled taxa. Asterisk (*) indicates sequences derived from an earlier study (Lohmann 2006). Taxa are listed alphabetically. Data are presented in the following order: taxon, voucher, locality, accession number: *ndhF*, *rpl32-trnL*, *pepC*. (“na” = sequence not available).

***Cuspidaria cinerea* (Bureau ex K. Schum.) L.G. Lohmann**, Lohmann 34 (INPA, K, MG, MO, NY, SP, SPF, U, UB), Brasil, Amazonas, Reserva Ducke, DQ222631*, __, DQ222801*.

***Cuspidaria inaequalis* (DC. ex Splitg.) L.G.Lohmann**, Lohmann 127 (BBS, MO), Surinam, Sipaliwini, Tafelberg Tepui, DQ222548*, __, DQ222679*. ***Cuspidaria lateriflora* (Mart.) DC.**, Lohmann 628 (MO, MOL), Peru, Madre de Dios, Manu National Park, DQ222575*, __, DQ222716*.

***Fridericia cinnamomea* (DC.) L.G.Lohmann**, Vicentini 809 (INPA, MO), Brasil, Amazonas, Reserva Ducke, DQ222544*, __, DQ222674*. ***Fridericia erubescens* (DC.) L.G.Lohmann**, Lohmann 359 (MO, SPF), Brasil, Bahia, Chapada Diamantina, DQ222622*, __, DQ222787*.

***Fridericia platyphylla* (Cham.) L.G.Lohmann**, Lohmann 709 (MO, SPF), Brasil, São Paulo, Instituto Plantarum, DQ222541*, __, DQ222669*. ***Fridericia* sp.**, Nogueira 350 (SPF), Brasil, Minas Gerais, Delfinópolis, __, __, __.

***Lundia longa* (Vell.) DC.**, Lohmann 652 (CVRD, MO), Brasil, Espírito Santo, Reserva Vale do Rio Doce, DQ222590*, __, DQ222741*. ***Lundia spruceana* Bureau**, Lohmann 610 (MO, MOL), Peru, Madre de Dios, Manu National Park, DQ222593*, __, DQ222745*.

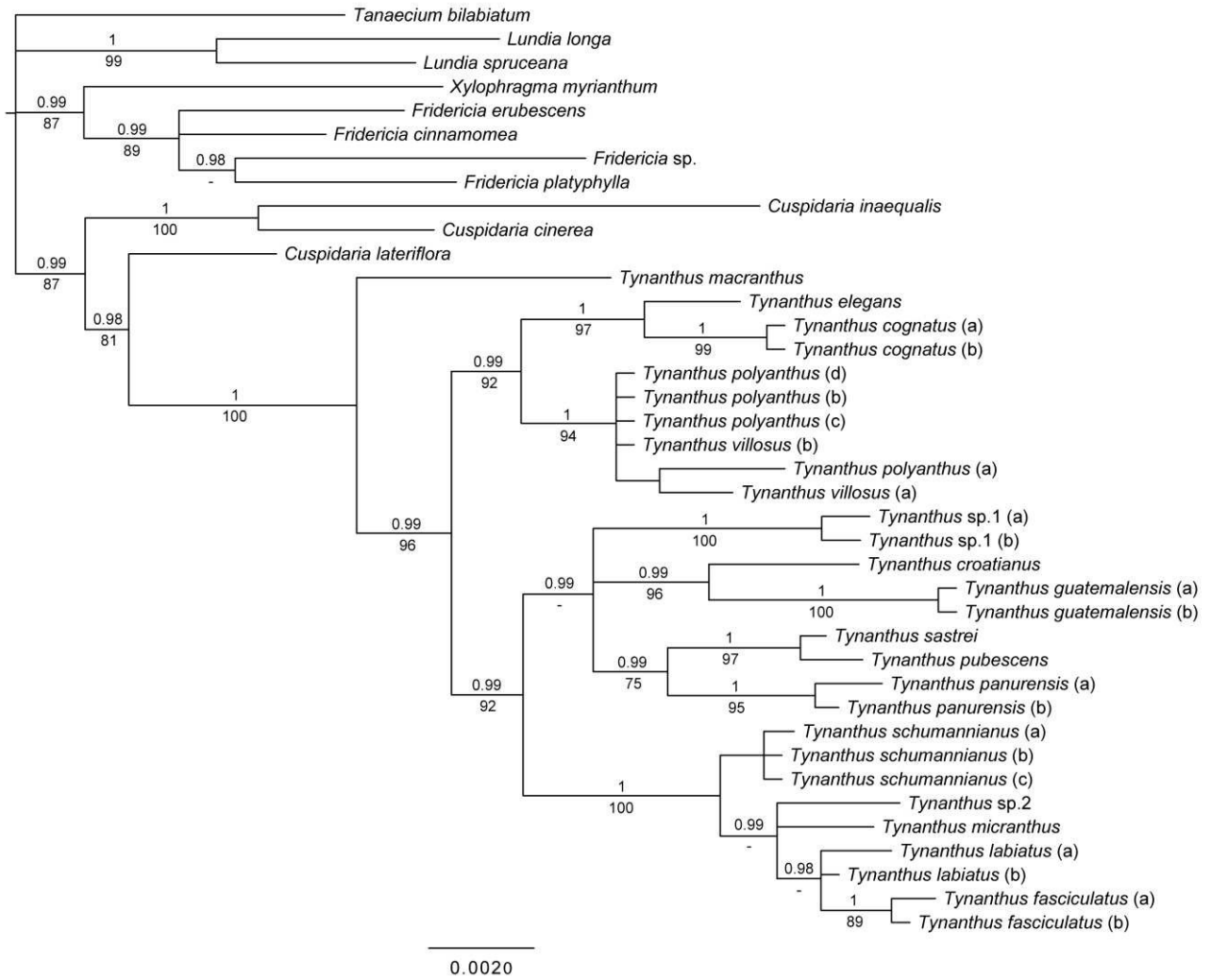
***Tanaecium bilabiatum* (Sprague) L.G.Lohmann**, Lohmann 92 (MO, NY, SPF, UNIP), Brasil, Amazonas, Rio Solimões, DQ222540*, __, DQ222667*.

***Tynanthus cognatus* (Cham.) Miers (a)**, Medeiros 28 (SPF), Brasil, Rio de Janeiro, Parque Nacional da Serra dos Órgãos, __, __, __. ***Tynanthus cognatus* (Cham.) Miers (b)**, Medeiros 33 (SPF), Brasil, Paraná, Londrina, __, __, __. ***Tynanthus croatianus* A.H. Gentry**, Croat 13975 (MO), Panama, Barro Colorado Island, __, __, __. ***Tynanthus elegans* Miers**, Lohmann 663 (CVRD, MO), Brasil, Espírito Santo, Reserva Vale do Rio Doce, DQ222643*, __, DQ222815*. ***Tynanthus fasciculatus* (Vell.) Miers (a)**, Medeiros 19 (SPF), Brasil, Minas Gerais, Campus UFV, __, __, __. ***Tynanthus fasciculatus* (Vell.) Miers (b)**, Santos s.n. (F 2170556), Brasil, Minas Gerais, Estação Ecológica UFMG, __, __, __. ***Tynanthus guatemalensis* Donn. Sm. (a)**, Aguilar 1399 (MO), Mexico, Chiapas, Ocosingo, __, __, __. ***Tynanthus guatemalensis* Donn. Sm. (b)**, Álvarez 9517 (MO), Mexico, Quintana Roo, Adolfo de la Huerta, __, __, __. ***Tynanthus labiatus* (Cham.) Miers (a)**, Medeiros 30 (SPF), Brasil, Minas Gerais, Estrada Corinto-Conselheiro Mata, __, __, __. ***Tynanthus labiatus* (Cham.) Miers (b)**, Queiroz 10661 (SPF), Brasil, Bahia, Rui Barbosa, __, __, __. ***Tynanthus macranthus* L.O. Williams**, Barringer 2671 (F), Costa Rica, Talamanca, Southern Limon, __, __, __. ***Tynanthus micranthus* Corr. Méllo ex K. Schum.**, Medeiros 34 (SPF), Brasil, Paraná, Londrina, __, __, __. ***Tynanthus panurensis* (Bureau ex Baill.) Sandwith (a)**, Gentry 52280 (F), Peru, San

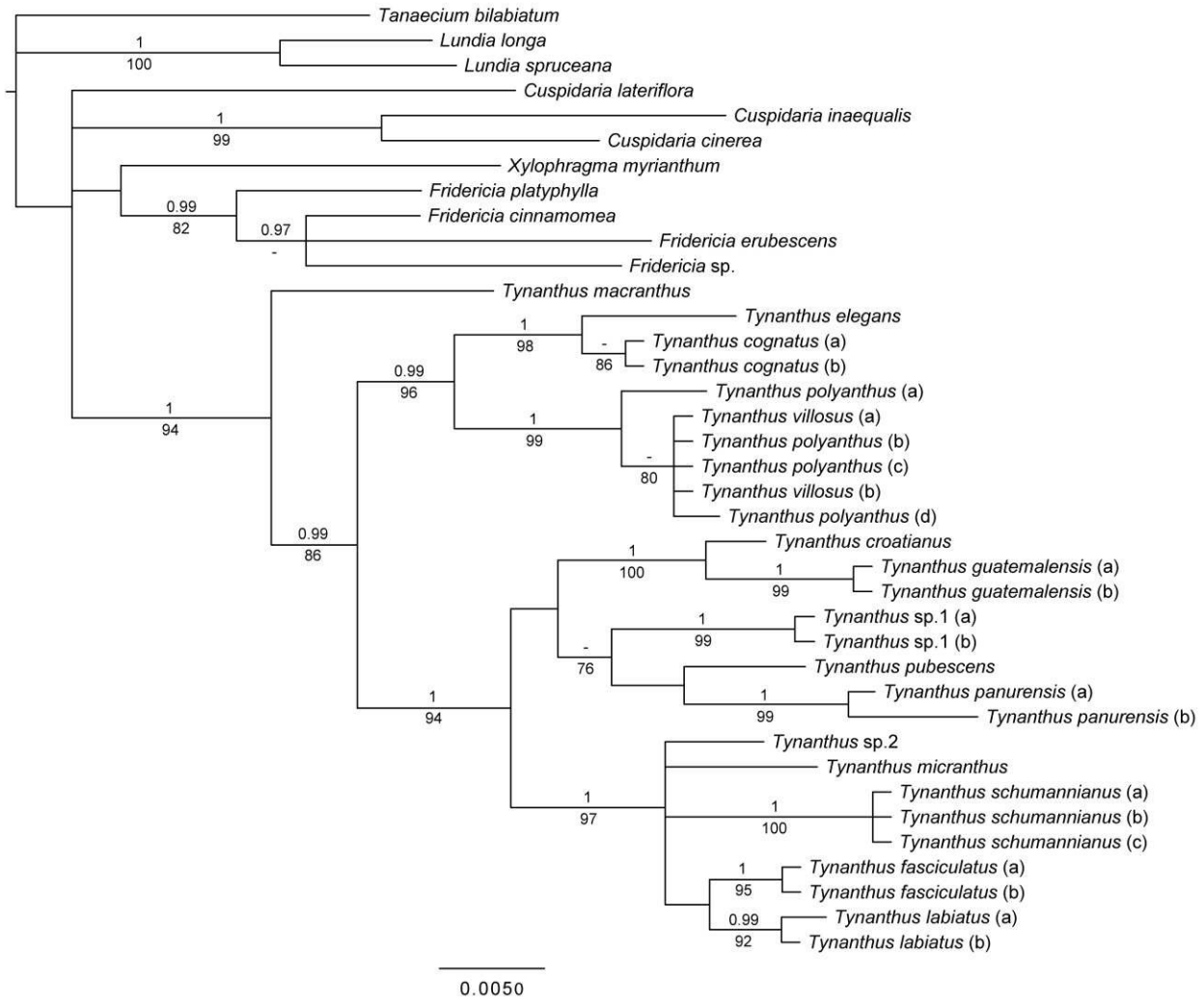
Martin, Yurimaguas-Tarapoto road, __, __, __. ***Tynanthus panurensis* (Bureau ex Baill.) Sandwith (b)**, Burnham 2307 (MO), Ecuador, Tiputini Biodiversity Station, __, __, __. ***Tynanthus polyanthus* (Bureau ex Baill.) Sandwith (a)**, Lohmann 370 (MO, NY, SPF, UFAC), Brasil, Acre, Cruzeiro do Sul, DQ222645*, __, DQ222819*. ***Tynanthus polyanthus* (Bureau ex Baill.) Sandwith (b)**, Medeiros 40 (SPF), Brasil, Acre, Xapuri, __, __, __. ***Tynanthus polyanthus* (Bureau ex Baill.) Sandwith (c)**, Nogueira 363 (SPF), Brasil, PA, Santarém, __, __, __. ***Tynanthus polyanthus* (Bureau ex Baill.) Sandwith (d)**, Schunke-Vigo 12280 (MO), Peru, San Martin, Tocache Nuevo, __, __, __. ***Tynanthus pubescens* A.H. Gentry**, Hoffmann 5282 (MO), Suriname, Brokopondo, __, __, __. ***Tynanthus sastrei* A.H. Gentry**, Hoffman 5302 (MO), Suriname, Brokopondo, Road to Brownsberg Nature Reserve, __, na. ***Tynanthus schumannianus* (Kuntze) A.H. Gentry (a)**, Lohmann 545 (MO, NY, SPF, UFAC), Brasil, Acre, Xapuri, __, __, __. ***Tynanthus schumannianus* (Kuntze) A.H. Gentry (b)**, Lohmann 452 (NY), Brasil, Acre, Rio Juruá, DQ222646*, __, __. ***Tynanthus schumannianus* (Kuntze) A.H. Gentry (c)**, Araújo 4222 (MO), Bolivia, La Paz, Parque Nacional Madidi, __, __, __. ***Tynanthus sp.1***, Procópio 14 (G, INPA, K, MG, MO, NY, RB, SP, U, UB), Brasil, Amazonas, Reserva Ducke, DQ222644*, __, DQ222817*. ***Tynanthus sp.1***, Medeiros 21 (SPF), Brasil, Amazonas, Reserva Ducke, __, __, __. ***Tynanthus sp.2***, Folli 5931 (SPF), Brasil, Espírito Santo, Reserva Vale do Rio Doce, __, __, __. ***Tynanthus villosus* A.H. Gentry (a)**, Lohmann 413 (MO, NY, SPF, UFAC), Brasil, Acre, Rio Juruá, DQ222647*, __, DQ222820*. ***Tynanthus villosus* A.H. Gentry (b)**, Biset 370 (SPF), Peru, San Martín, Chazuta, __, __, na.

***Xylophragma myrianthum* (Cham.) Sprague**, Lohmann 649 (CVRD, MO), Brasil, Espírito Santo, Reserva Vale do Rio Doce, DQ222648*, __, DQ222822*.

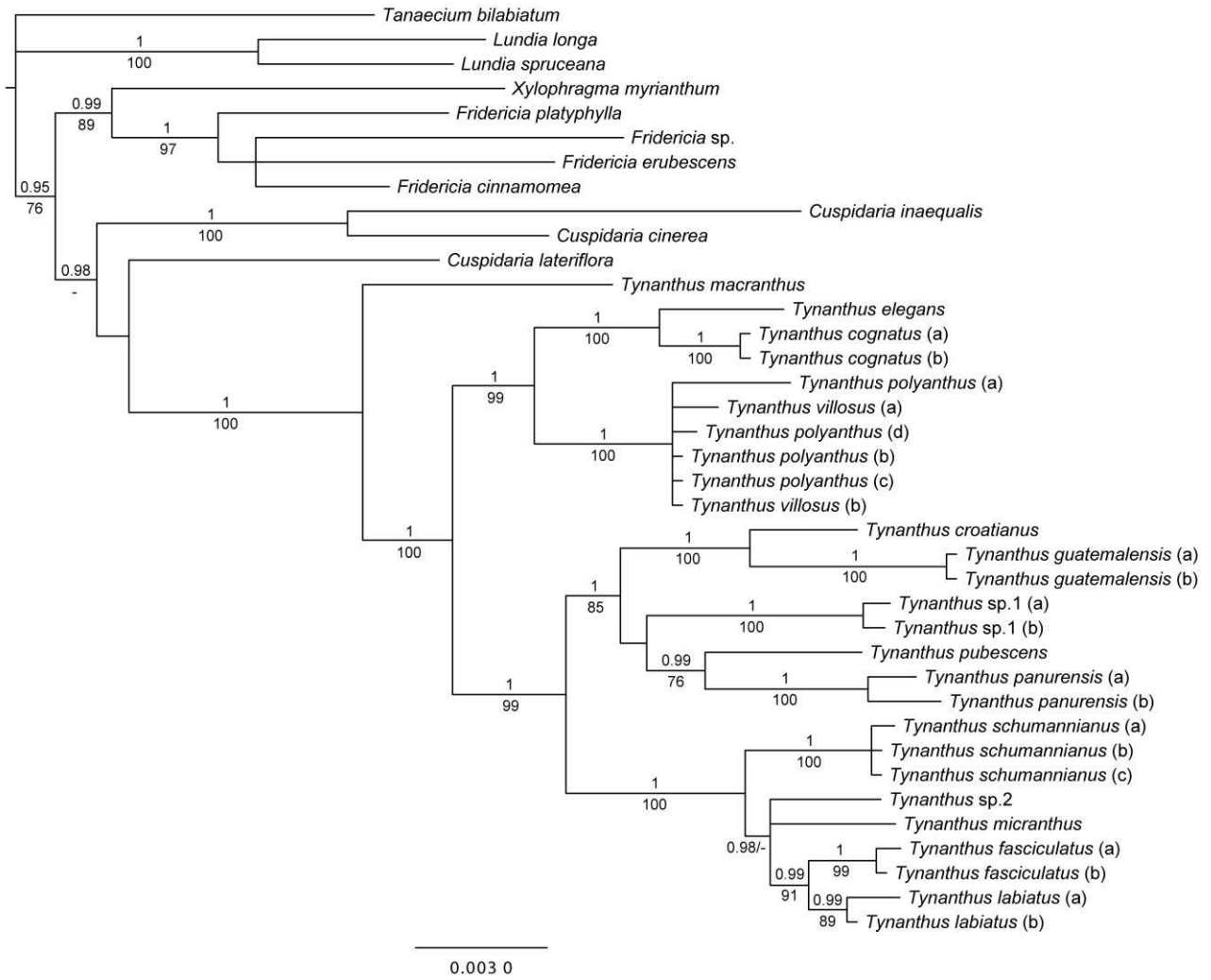
Supplementary material



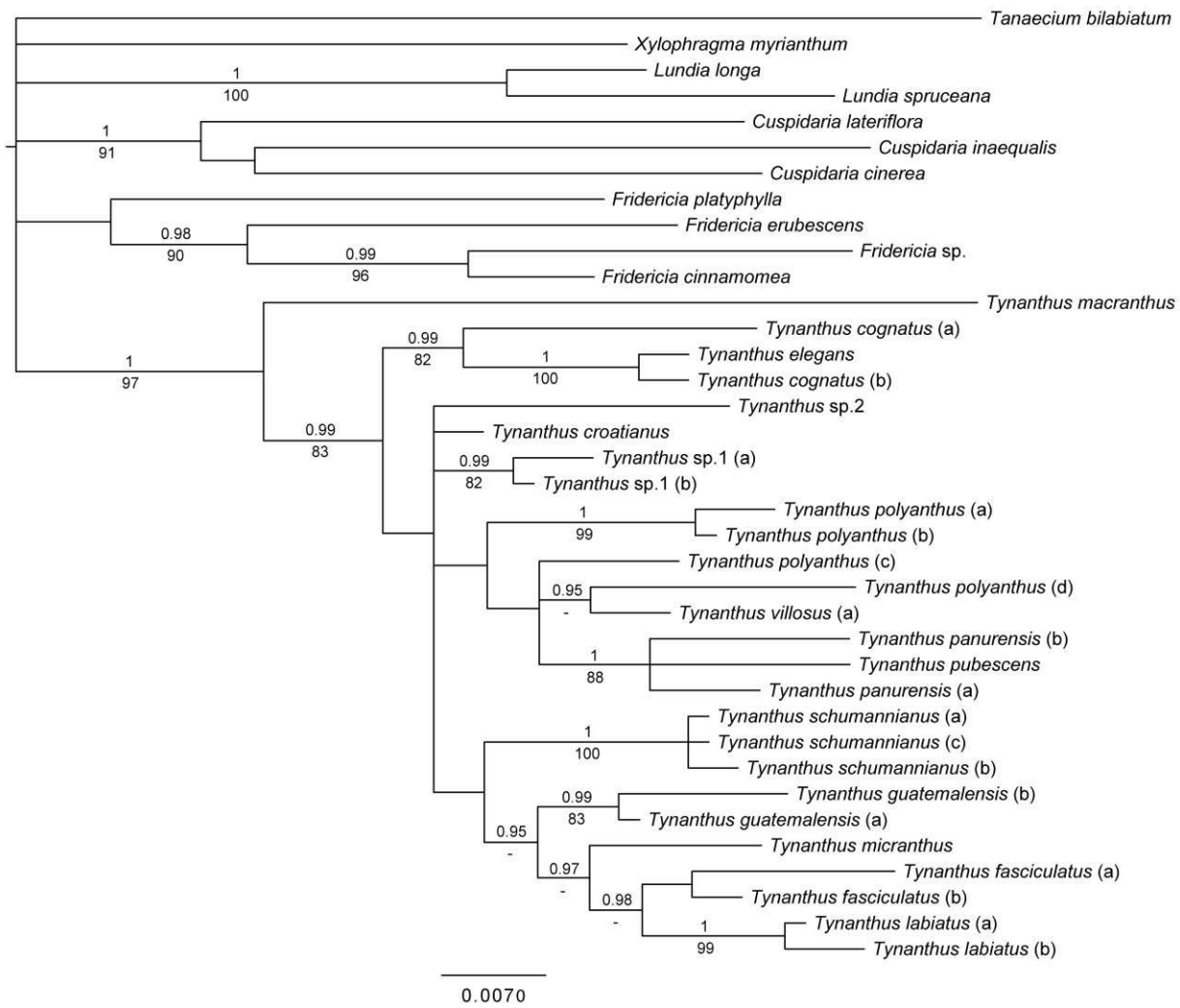
(S1)



(S2)



(S3)



(S4)

Figures S1-S4. Majority-rule consensus trees derived from Bayesian analyses of (S1) *ndhF*, (S2) *rpl32-trnL*, (S3) combined plastid (*ndhF* and *rpl32-trnL*) and (S4) *pepC*. Posterior probabilities (≥ 0.95) are indicated above branches and maximum likelihood bootstrap values ($\geq 75\%$) are indicated below branches.

Capítulo 2

**Two new species of *Tynanthus* Miers (Bignoniaceae, Bignoniaceae)
from Brazil**

Two new species of *Tynanthus* Miers (Bignoniaceae, Bignoniaceae) from Brazil*

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Abstract

Tynanthus is a genus of lianas that is broadly distributed through the Neotropics. Two new species of *Tynanthus* from Brazil are here described and illustrated: *T. densiflorus*, from Amazonas, and *T. espiritosantensis*, from Espírito Santo. *T. densiflorus* is recognized by the conspicuous interpetiolar glandular fields, a feature rarely found in *Tynanthus*, and the dense thyrses. *Tynanthus espiritosantensis*, on the other hand, is recognized by the bromeliad-like prophylls of the axillary buds and the lax thyrses. Information on the distribution, conservation status and morphologically similar species are provided.

Keywords. Amazonia, Atlantic forest, “cipó-cravo,” lianas, neotropical flora

Introduction

Tynanthus Miers (Bignoniaceae, Bignoniaceae) is a monophyletic genus of lianas that is easily recognized by small bilabiate flowers, fruits with raised margins and smell of cloves in vegetative organs (Lohmann 2006). These features, associated to the flowers arranged in thyrses, corolla densely pubescent externally, thecae curved forward, ovary densely pubescent and poorly developed nectar disk characterize the genus (Medeiros & Lohmann in prep.). Species of *Tynanthus* are distributed throughout the Neotropics, occurring predominantly in wet forests (Lohmann and Taylor 2014). Brazil includes the highest diversity of *Tynanthus*, with most species occurring in Amazonia and the Atlantic Forest.

During the preparation of a taxonomic revision of *Tynanthus* (Medeiros & Lohmann in prep.), multiple collections with morphological features that did not match any of the

described species were found. Additional fieldwork and molecular phylogenetic studies provided further support for the recognition of two new species in the genus, one from the Amazon region and another from the Atlantic Forest of Brazil.

Material and methods

Morphological analyses and compilation of phenology and distribution data were based on specimens deposited at CVRD, G, INPA, K, MBM, MG, MO, NY, RB, SP, SPF and US (Thiers, continuously updated). Descriptions were elaborated following terminology presented in Radford (1986), Weberling (1989), the Leaf Architecture Working Group (1999), Gomes-Silva (2009), Nogueira *et al.* (2013) and Lohmann & Taylor (2014).

1. *Tynanthus densiflorus* M.C. Medeiros & L.G. Lohmann, sp. nov.

Type. Brazil. Amazonas: Reserva Florestal Adolpho Ducke, Manaus-Itacoatiara, km 26, 16 aug 1996, L.C. Procópio *et al.* 14 (holotype: INPA!; isotypes: G!, K!, MO!, NY!, RB!, SP!) Fig. 1 A-I.

Diagnosis. *Tynanthus densiflorus* differs from *Tynanthus panurensis* (Bureau) Sandwith by the interpetiolar gland fields (lacking in *T. panurensis*), minute triangular prophylls of the axillary buds (versus foliaceous in *T. panurensis*) and dense thyrses (versus lax in *T. panurensis*). It further differs from *Tynanthus pubescens* A.H. Gentry in the leaflets with a caudate-mucronate apex (versus acuminate or obtuse-mucronate apices in *T. pubescens*) and the dense inflorescences (versus lax inflorescences in *T. pubescens*).

Description. *Liana*. *Branchelets* subtetragonal to terete, finely striated, with lenticels, pubescent to puberulent, with simple and peltate trichomes; interpetiolar ridge absent or present; interpetiolar glands present; prophylls of the axillary buds 0.5–0.8 mm long, 1–2.5 mm wide, minute, shallowly triangular, puberulent throughout, with simple and peltate trichomes. *Leaves* 2–3 foliolated; terminal leaflets modified into a trifid tendril; petioles and petiolules with a more or less conspicuous canalicule on the upper side, puberulent to glabrescent throughout, with simple and peltate trichomes; petioles 1.8–5.6 cm long; petiolules (0.6–)1.4–3.8 cm long, lateral ones with equal lengths and the terminal one longer, when present; leaflets (3.2–)5–16.1 cm long, (1.3–)2–9.5 cm wide, membranous to chartaceous (sometimes subcoriaceous), discolor or concolor, ovate; apex caudate, mucronate; base cuneate to truncate or subcordate, symmetrical or asymmetrical; margin entire; the abaxial surface pubescent to puberulent throughout (sometimes only on and

near the veins), with simple, peltate and patelliform trichomes; the adaxial surface pubescent to glabrescent throughout (sometimes only on and near the veins), with simple, peltate and patelliform trichomes; glandular trichomes evenly distributed throughout both surfaces; first venation pinnate; second venation weak brochidodromous; third venation alternate percurrent (sometimes random reticulate); pocket domatia with (sometimes without) trichomes. *Inflorescence* 3–9.5 cm long, a thyrse, axilar, dense, with corymbose to conical aspect; floral pedicels 1–7 mm long; axis densely pubescent to puberulent, with simple and peltate trichomes; inflorescence bracts 0.5–2.5 mm long, predominantly caducous, triangular to linear triangular, densely pubescent to pubescent throughout; floral bracts 0.4–0.6 mm long, triangular. *Calyx* green to grayish, 1.5–2.2 mm long, 1.4–1.9 mm wide, without patelliform glands, membranous to chartaceous, with transversal aperture, truncate or minutely 5-denticulate, densely pubescent to pubescent outside, glabrous inside; lobes 0.1–0.2 mm long. *Corolla* cream or pale yellow, 0.8–1.5 cm long, 3–5 mm wide at the tube opening, bilabiate, with two (almost totally fused) upper lobes and three lower lobes, densely pubescent throughout outside, with simple and peltate trichomes; tube 3–5 mm long, internally glabrous at the top, tomentose at the base, with simple and long and short stipitate trichomes; nectar guides present, yellow; lobes entire, densely pubescent to pubescent throughout lower ones and at margins of or throughout upper ones; upper ones 0.4–1.4(–2.9) mm long, 0.7–1.5(–2.4) mm wide, acute to obtuse; lower ones 2.1–4 mm long, 2–3.6 mm wide, obtuse to rounded. *Androecium* with four fertile stamens, inserted, 1.5–2.5 mm from the base of the corolla; shorter ones 3.5–5.5 mm long; longer ones 4.5–7 mm long; filaments with long and short stipitate trichomes at the base; anther thecae cream, 1.1–1.4 mm long, obovate to elliptic, divergent and reflexed forward, glabrous, subexserted; connective extending 0.2–0.3 mm beyond anther attachment; staminode covered with long and short stipitate trichomes, 1.5–2.7 mm long. *Gynoecium* with pistil 7–9 mm long; ovary 1.3–1.5 mm long, 0.7–0.8 mm wide, conical, velutinous, with simple trichomes, with two to four series of ovules per locule, and a ring of longer trichomes at the base; nectar disc reduced, not evident; style 5–7 mm long, tomentose at the base, with simple trichomes; stigma with lamellae lanceolate, glabrous. *Fruit* not seen. *Seeds* not seen.

Distribution and habitat. Known from wet forests from Manaus and proximity (Amazonas, Brazil).

Etymology. The species epithet refers to the thyrses with flowers densely arranged.

Phenology. Flowers in August. Fruiting period is unknown.

Conservation status. According to IUCN (2001) criteria, this species is considered Vulnerable (VU B2a; B2biii). The type collection is from a protected area (Reserva Florestal Adolpho Ducke), where a reasonable number of individuals are found (pers. obs.). Additional studies on its distribution and abundance are still necessary in order to confirm its conservation status.

Discussion. *Tynanthus densiflorus* is characterized by dense thyrses, with corymbose to conical aspect, as well as the presence of interpetiolar glands and ovate leaflets. The type collection of *T. densiflorus* was treated as *T. panurensis* (Bureau) Sandwith for the Guide of the Ducke Reserve (Lohmann & Hopkins 1999). Indeed, the two species are similar in the occurrence of ovate leaflets and corolla tube that is internally tomentose at base. However, the presence of interpetiolar glands in *T. densiflorus* (versus absent in *T. panurensis*), the minute prophylls (versus foliaceous in *T. panurensis*) and dense inflorescences (versus lax in *T. panurensis*) allow the distinction of these taxa. *Tynanthus pubescens* A.H. Gentry is another congeneric species that is morphologically similar to *T. densiflorus*. Both taxa have similar corolla lengths (around 1-1.6 cm in *T. pubescens*) and show interpetiolar gland fields; however, the caudate-mucronate leaflet apex (versus acuminate or obtuse-mucronate in *T. pubescens*) and the dense inflorescences (versus lax in *T. pubescens*) differentiate both taxa.

Additional specimens examined. BRAZIL. Amazonas: 2-5 km N of Manaus-Itacoatiara Road at km 79 near Rio Preto da Eva, 100-200 m, 24 November 1974, A. Gentry 12849 (INPA photo, MG, MO). Rio Camanau, 28 June 1987, P. Grenand et al. 2787 (INPA). Manaus, Campus of INPA, Estrada do Aleixo, 22 November 1974, A. Gentry 12792 (INPA photo); 30 November 1974, A. Gentry 13018 (INPA, MO); *Ibid.*, Transect vouchers, Line 1, 11 December 1974, A. Gentry 13181 (INPA, MO); Estrada do Aleixo near Manaus, km 6-7 past INPA, 2 December 1974, A. Gentry 13040 (INPA photo, MO); Reserva Florestal Adolpho Ducke, Parcela PPBio (Lo3 1000 m), 100 m, 02°56'03"S, 59°57'32"W, 14 December 2010, M.C. Medeiros et al. 21 (SPF); *Ibid.*, próximo à estação meteorológica, 120 m, 02°55'37"S, 59°58'33"W, 15 December 2010, M.C. Medeiros et al. 22 (SPF); *Ibid.*, proximidades do refeitório da base da reserva, na beira da estrada, 110 m, 02°55'59"S, 59°57'56"W, 16 December 2010, M.C. Medeiros et al. 25 (SPF).

2. *Tynanthus espiritosantensis* M.C. Medeiros & L.G. Lohmann, sp. nov.

Type. Brazil. Espírito Santo: Linhares, Reserva Natural da CVRD, Estrada Oiticica, km 2.3, 6 Feb 2008, D.A. Folli 5931 (holotype CVRD!; isotype SPF!) Fig. 2 A-I.

Diagnosis. *Tynanthus espiritosantensis* differs from *Tynanthus schumannianus* (Kuntze) A.H. Gentry by the presence of trichomes in the leaflet domatia (versus absence of trichomes in *T. schumannianus*), lack of patelliform glands on petioles, petiolules and inflorescence axis (versus present in *T. schumannianus*) and larger calyx, 2.3–2.7 mm long x 1.8–2.5 mm wide (versus 1–2 mm long x 1.1–1.9 mm wide in *T. schumannianus*).

Description. *Liana*. *Branchelets* tetragonal to terete, finely striated, with lenticels, glabrescent (sometimes pubescent at the nodes), with peltate and patelliform trichomes (sometimes simple trichomes also present); interpetiolar ridge absent; interpetiolar glands absent; prophylls of the axillary buds 1.2–2.5 mm long, 0.7–1.1 mm wide, bromeliad-like, glabrescent (rarely puberulent), with peltate trichomes (rarely with simple trichomes as well). *Leaves* (2–)3 foliolated; terminal leaflets modified into a trifid tendril; petioles and petiolules with a more or less conspicuous canalicule on the upper side, puberulent throughout, with simple and peltate trichomes; petioles 1–6 cm long; petiolules 0.5–3.5 cm long, lateral ones with equal lengths and the terminal one longer, when present; leaflets (4–)5–11.9 cm long, (1.5–)1.9–5.4 cm wide, membranous to chartaceous, discolor, elliptic; apex acuminate or caudate, mucronate; base cuneate, symmetrical; margin entire; the abaxial surface glabrescent (sometimes pubescent) on and near the veins, with peltate and patelliform trichomes (sometimes also simple); the adaxial surface glabrescent on and near the veins, with peltate and patelliform trichomes; glandular trichomes distributed especially on the abaxial surface; first venation pinnate; second venation weak brochidodromous; third venation alternate percurrent (sometimes random reticulate); pocket domatia with trichomes. *Inflorescence* 3.6–7 cm long, a thyrse, axilar, lax, with conical aspect; floral pedicels 3.5–9 mm long; axis pubescent, with simple and peltate trichomes; inflorescence bracts 0.7–3.9(–9) mm long, predominantly caducous, triangular to linear triangular, pubescent throughout or only at margins; floral bracts 0.5–0.7 mm long, triangular. *Calyx* green, 2.3–2.7 mm long, 1.8–2.5 mm wide, with patelliform glands, membranous to chartaceous, with transversal (sometimes oblique) aperture, minutely 5-denticulate, glabrescent (sometimes pubescent at teeth) outside, glabrous inside; lobes 0.1–0.4 mm long. *Corolla* white, 0.7–0.8 cm long, 2.5–3.4 mm wide at the tube opening, bilabiate, with two (almost totally fused) upper lobes and three lower lobes, densely pubescent throughout outside, with simple and peltate trichomes; tube 2.5–4 mm long, internally glabrous at the top, tomentose to pubescent at the base or glabrescent, with simple and long and short

stipitate trichomes; nectar guides absent, but with a path of long and short stipitate trichomes; lobes entire, densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.4–1.1 mm long, 1–1.5 mm wide, acute to obtuse; lower ones 1.8–3.2 mm long, 2.1–2.5 mm wide, obtuse to rounded (sometimes acute). *Androecium* with four fertile stamens inserted 1–1.5 mm from the base of the corolla; shorter ones 2.5–3.5 mm long; longer ones 4.5–5 mm long; filaments with long and short stipitate trichomes at the base; anthers thecae cream, 0.8–1.1 mm long, obovate to elliptic, divergent and reflexed forward, glabrous, subexserted; connective extending 0.2–0.3 mm beyond anther attachment; staminode glabrescent, with long and short stipitate trichomes, 2.4 mm long. *Gynoecium* with pistil 4.5–6 mm long; ovary 0.8–1 mm long, 0.7–0.9 mm wide, conical, velutinous, with simple trichomes, with two to four series of ovules per locule, and a ring of longer trichomes at the base; nectar disc reduced, not evident; style 3.3–5 mm long, tomentose at the base, with simple trichomes; stigma with lamellae lanceolate, glabrous. *Fruits* not seen. *Seeds* not seen.

Distribution and habitat. Known exclusively from wet forests from Linhares and proximity (Espírito Santo, Brazil).

Etymology. The species epithet refers to the type locality.

Phenology. Flowers from December to February. Fruiting period if unknown.

Conservation status. According to the IUCN (2001) criteria, this species is considered Data Deficient (DD), given the small number of known collections. Further detailed investigation on the distribution of *T. espiritosantensis* is necessary in order to properly assess its conservation status. The two localities in which this species has been collected fall within a single municipality (Linhares), suggesting that this might represent another narrowly distributed species of *Tynanthus*. Fortunately, the type collection was obtained inside an officially protected area (Reserva Natural da CVRD).

Discussion. *Tynanthus espiritosantensis* is characterized by the bromeliad-like prophylls of the axillary buds and lax thyrses. This species is morphologically similar to the Amazonian *T. schumannianus* (Kuntze) A.H. Gentry. However, these taxa can be easily separated by the pubescent leaflet domatia (versus glabrous leaflet domatia in *T. schumannianus*), absence of patelliform glands on petioles, petiolules and inflorescence axis (versus present in *T. schumannianus*) and the larger calyx, 2.3–2.7 mm long, 1.8–2.5 mm wide (versus 1–2 mm long x 1.1–1.9 mm wide in *T. schumannianus*).

Additional specimens examined. BRAZIL. Espírito Santo: Linhares, Rancho Alto, 7 December 1984, G. Hatschbach & J.M. Silva 48693 (MBM, MO, US); Reserva

Natural da CVRD, Estrada Oiticica, próximo à porteira, antes do cruzamento com a estrada municipal, 53 m, 19°07'59"S, 40°00'07"W, 27 January 2014, *M.C. Medeiros & R.B. Louzada 41* (CVRD, SPF).

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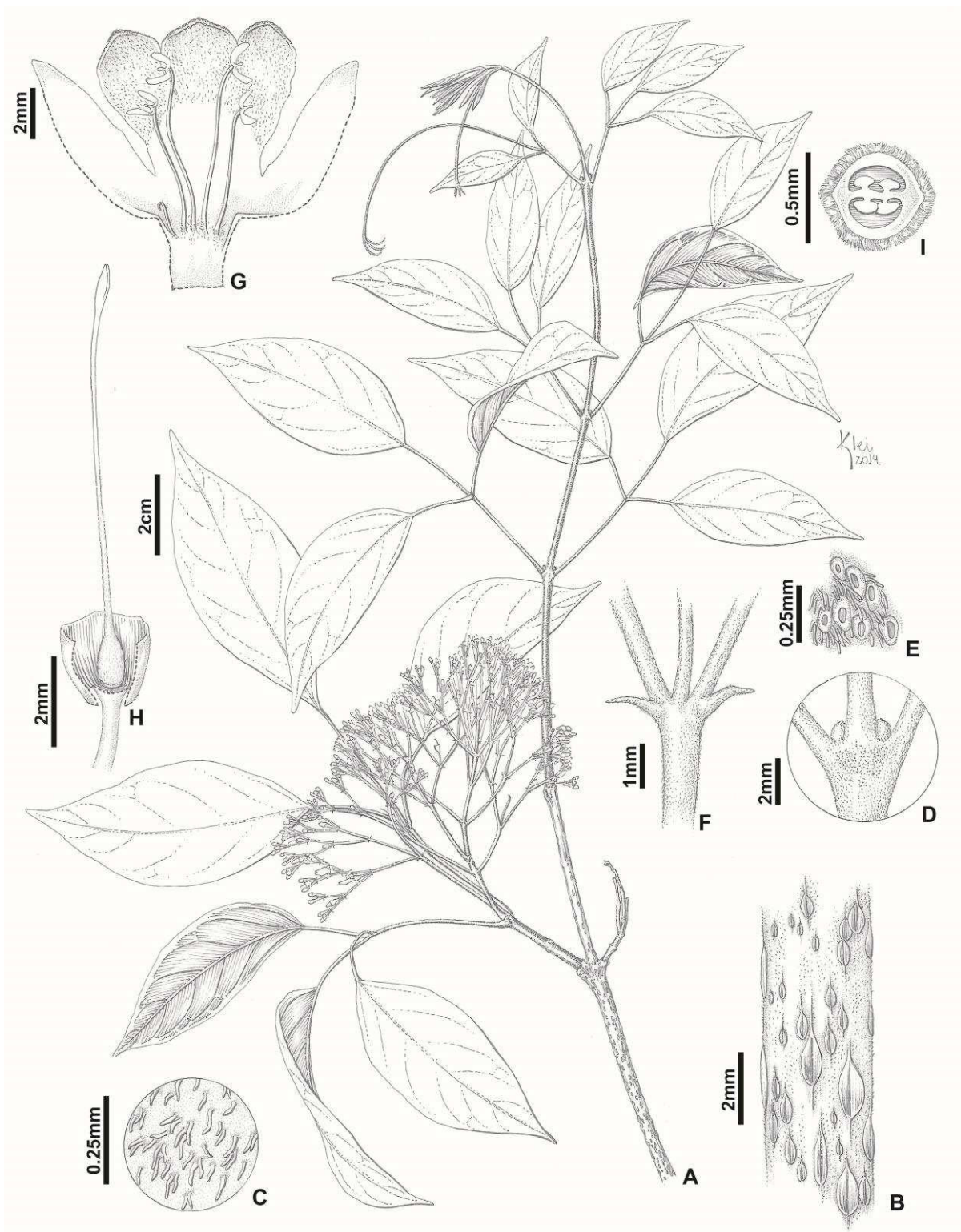


Figure 1. A-I. *Tynanthus densiflorus*: A. Habit; B. Detail of lenticels in the oldest portion of branchelet; C. Detail of pubescent indument in the youngest portion of branchelet; D-E. Interpetiolar glands; F. Detail of inflorescence axis with bracts; G. Open corolla showing the androecium; H. Open calyx showing the gynoecium; I. Ovary cross section showing ovules.

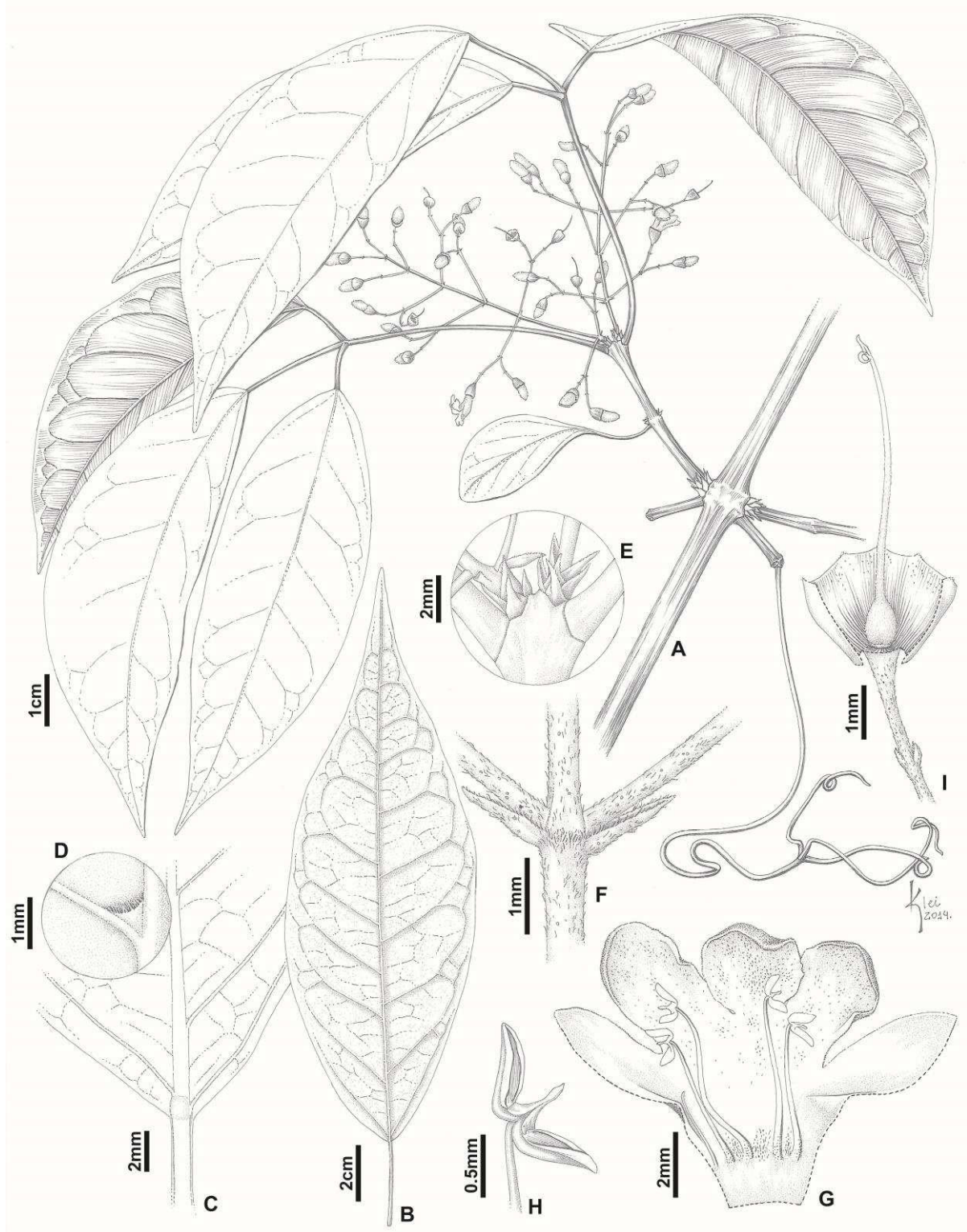


Figure 2. A-I. *Tynanthus espiritosantensis*: A. Habit; B-D. Leaflet with pubescent domatia in the abaxial surface; E. Interpetiolar region, with bromeliad-like prophylls of the axillary buds; F. Detail of inflorescence axis, with bracts, simple and peltate trichomes; G. Open corolla, showing the androecium; H. Anther; I. Open calyx showing the gynoecium.

Capítulo 3

Taxonomic Revision of *Tynanthus* Miers (Bignoniaceae, Bignoniaceae)

Taxonomic Revision of *Tynanthus* Miers (Bignoniaceae, Bignoniaceae)

Abstract

Tynanthus Miers is a genus of Neotropical lianas that are distributed from southern Mexico to southern Brazil. Extensive herbarium work, field studies and new molecular phylogenetic data were used as basis to recognize 14 species in the genus. Here, we provide a detailed treatment of the group, including an identification key to all species recognized, as well as morphological descriptions, a complete list of synonymy, nomenclatural information, taxonomic notes, phenological data, information on habitat and distribution, and illustrations. Two species are circumscribed differently from earlier classifications, in particular *Tynanthus elegans* Miers is synonymized with *Tynanthus cognatus* (Cham.) Miers, while *Tynanthus villosus* A.H. Gentry is synonymized with *Tynanthus polyanthus* (Bureau) Sandwith. In addition, *Tynanthus goudotianus* (Bureau) Bureau is excluded and treated as a doubtful name, while two recently described species are recognized, *Tynanthus densiflorus* M.C. Medeiros & L.G. Lohmann and *Tynanthus espiritosantensis* M.C. Medeiros & L.G. Lohmann. One species name is neotypified, *Tynanthus caryophylleus* (Bello) Alain, and nine species names are lectotypified, namely *Cuspidaria ovalis* Rusby, *Tynanthus cognatus* (Cham.) Miers, *Tynanthus elegans* Miers, *Tynanthus guatemalensis* Donn. Sm., *Tynanthus lindmanii* K. Schum., *Tynanthus myrianthus* Bureau & K. Schum., *Tynanthus panurensis* (Bureau) Sandwith, *Schizopsis chimonantha* Bureau, and *Schizopsis regnelliana* Bureau. A complete list of doubtful and excluded names is presented.

Keywords. Bignoniaceae, Bignoniaceae, “cipó-cravo”, “clavo-huasca”, Neotropical flora

Introduction

Tynanthus Miers includes 14 species, representing a small genus of Neotropical lianas. The genus is distributed from southern Mexico to southern Brazil, where it predominates in humid forests, although few representatives are also found in dry areas. Species of *Tynanthus* generally present restricted distribution patterns occurring in Western South America, Central America, Amazonia or Mata Atlantica exclusively (Lohmann & Taylor 2014).

The genus was described ca. 150 years ago by Miers (1863), who originally included nine species in the genus. From those, only four names were validly published, *T. cognatus* (Cham.) Miers, *T. elegans* Miers, *T. fasciculatus* (Vell.) Miers, and *T. labiatus* (Cham.) Miers. Two years later Bureau (1865), without noticing the publication of *Tynanthus*, described the new genus *Schizopsis* in which he included seven species. Three years later, Bureau (1868) had already noticed the overlap between *Tynanthus* and *Schizopsis* and published a taxonomic revision of *Tynanthus* in which he proposed the appropriate synonymizations and combinations [i.e., *T. goudotianus* (Bureau) Bureau, *T. laxiflorus* Miers, *T. petiolatus* Miers]. Three new species were included in *Tynanthus* within the next years, *T. igneus* (Vell.) Barb. Rodr., *T. guatemalensis* Donn. Sm. and *T. micranthus* Corr. Mello ex K. Schum., until the genus was treated in the Flora Brasiliensis of Bureau & Schumann (1896[1897]). In this treatment, two new species were described, *T. lindmanii* K. Schum. and *T. myrianthus* Bureau & K. Schum., totalizing eight species recognized for Brazil in this treatment (Bureau & Schumann 1896[1897]). Since then, the genus has never been treated in a comprehensive fashion. Instead, three new combinations were made by various authors, i.e., *T. caryophylleus* (Bello) Alain, *T. panurensis* (Bureau) Sandwith, and *T. polyanthus* (Bureau) Sandwith, while three others were newly described, i.e., *T. hyacinthinus* Standl., *T. macranthus* L.O. Williams, and *T. weberbaueri* Sprague. Furthermore, Alwyn Gentry described four new species (i.e., *T. croatianus* A.H. Gentry, *T. pubescens* A.H. Gentry, *T. sastrei* A.H. Gentry and *T. villosus* A.H. Gentry) and transferred *T. schumannianus* (Kuntze) A.H. Gentry into the genus. More recently, a synopsis of tribe Bignonieae recognized 15 species in *Tynanthus* (Lohmann & Taylor 2014).

Tynanthus is clearly circumscribed and characterized by three morphological synapomorphies: a smell of cloves on the vegetative organs, small flowers with bilabiate corollas, and fruits with raised margins (Lohmann 2006; Lohmann & Taylor 2014). The strong smell of cloves on the vegetative portions has led to the popular name “cipó-cravo” (Brazil) or “clavo huasca” (e.g., Colombia, Peru and Ecuador). Other morphological features

such as the inflorescences in thyrses or compound thyrses, the densely pubescent corolla, thecae curved forward, densely pubescent or velutinous ovary, and nectar disk poorly developed are also useful features to recognize the genus, although none of these features are exclusive of *Tynanthus*, being also found in other genera of Bignoniaceae (Lohmann & Taylor 2014). In addition, the presence of trifid tendrils and lack of interpetiolar gland fields are also useful to identify species, although these traits present variation in some species of the genus.

Although *Tynanthus* is strongly supported as monophyletic (Lohmann 2006; Medeiros & Lohmann in prep.) and well characterized morphologically, the delimitation of species and patterns of morphological variation within the genus have remained unclear (Lohmann & Taylor 2014). This is in part because several of its species are only known from few herbarium collections and also because a detailed account for the species of *Tynanthus* has not been conducted since the Flora Brasiliensis of Bureau and Schumann (1896[1897]). Extensive herbarium studies in association with fieldwork and new molecular phylogenetic data (Medeiros & Lohmann in prep.) provide new morphological, ecological, evolutionary and biogeographical information about *Tynanthus*, and an excellent foundation for a new comprehensive taxonomic treatment of all species in the genus.

Material and methods

The taxonomic treatment of *Tynanthus* is based on new morphological observations, and novel molecular phylogenetic data (Medeiros & Lohmann in prep.). Protologues and type collections of all species names, including the recognized taxa and respective synonyms were examined. All accepted names are listed alphabetically, with nomenclatural discussions and citations following McNeill *et al.* (2012).

Morphological characters, phenological and distributional data were collected from collections obtained during fieldwork and specimens deposited in the following herbaria: BHCB, BM, BR, CVRD, ESA, F, FUEL, G (incl. G-DC), HRCB, IAC, IAN, INPA, K, LE, M, MBM, MG, MO, NY, P, R, RB, SP, SPF, SPSF, UEC, UFACPZ, UPCB, US, VIC (acronyms follow Thiers, continuously updated). Morphological descriptions follow the terminology of Radford (1986), as well as Weberling (1989) for inflorescence morphology, the Leaf Architecture Working Group (1999) for leaf venation, Gomes-Silva (2009) for mite-domatia, Nogueira *et al.* (2013) for trichomes, and Lohmann & Taylor (2014) for prophyll morphology.

A large dataset with ca. 650 geo-referenced localities was compiled for all species in *Tynanthus*. This data was then inserted into ArcGIS 10.2.1 (ESRI) for the preparation of distribution maps for all species recognized. Examined specimens are ordered alphabetically, and by date within localities; question marks indicate dubious or ambiguous information.

Results

Taxonomic treatment

Tynanthus Miers (1863: 193). *Tynnanthus*, *orth. var.* Lectotype (designated by Sandwith 1962: 454): *Tynanthus fasciculatus* (Vell.) Miers.

Schizopsis Bureau (1864: 44). Type: *Schizopsis labiata* (Cham.) Bureau [= *Tynanthus labiatus* (Cham.) Miers]

Lianas. *Branchelets* with four phloem wedges in cross section, strong clove odor, conspicuously tetragonal to terete (in general, somewhat flattened when young), with or without ritidome, finely striated or not, few to densely lenticled (sometimes without lenticels), villous, tomentose, pubescent, puberulent or glabrescent, with simple, peltate or patelliform trichomes; interpetiolar ridge absent or present; interpetiolar patelliform glands absent or present; prophylls of the axillary buds minute, foliaceous or bromeliad-like, triangular, elliptic, ovate or obovate, villous, tomentose, pubescent, puberulent or glabrescent throughout, with simple, peltate or patelliform trichomes. *Leaves* 2–3 foliolate; terminal leaflets modified into simple or trifid tendrils (rarely bifid, when very young), with or without adhesive-disks on tips; petioles and petiolules with a more or less conspicuous canalicule on the upper side, villous, tomentose, pubescent, puberulent or glabrescent throughout surface or only at the upper canalicule, with simple, peltate or patelliform trichomes; lateral petiolules with equal lengths and the terminal one longer, when present; leaflets membranous to coriaceous, discolor or concolor, elliptic, ovate or obovate; apex acuminate, caudate, mucronate or obtuse; base cuneate, obtuse, truncate or subcordate, symmetrical or asymmetrical; margin entire (rarely dentate); the abaxial surface villous, tomentose, pubescent, puberulent or glabrescent throughout or only on and near the veins, with simple, peltate or patelliform trichomes; the adaxial surface villous, tomentose, pubescent, puberulent, or glabrescent throughout or only on and near the veins, with simple, peltate or patelliform trichomes; glandular trichomes evenly distributed throughout both surfaces or especially on one surface; first venation pinnate; second venation weak

brochidodromous or brochidodromous; third venation alternate percurrent (sometimes random reticulate); pocket domatia, with or without trichomes. *Inflorescence* axilar or terminal, a thyrse or a compound thyrse, lax, with conical aspect, or dense, with corymbose, subcorymbose or conical aspect; axis villous, tomentose or pubescent, with simple, peltate or patelliform trichomes; bracts of the inflorescence caducous or persistent, triangular to linear triangular, villous to pubescent or glabrescent throughout or only at margins; floral bracts triangular. *Calyx* green to yellowish, grayish or reddish, campanulate, with or without patelliform glands, membranous to chartaceous, with transversal or oblique aperture, truncate, denticulate or laciniate, tomentose, pubescent, puberulent or glabrescent throughout outside, with simple and peltate trichomes, glabrous inside. *Corolla* white, cream or pale yellow (sometimes pale lilac, pale green, pale pink, pale red or pale blue), bilabiate, with 2 (almost totally fused) upper lobes and 3 lower lobes, densely pubescent throughout outside, with simple and peltate trichomes, internally glabrous at the top of the tube, tomentose to pubescent or glabrescent at the base, with simple and/or long and short stipitate trichomes; nectar guides present or absent, with long and short stipitate trichomes; lobes entire, densely pubescent to pubescent throughout or only at margins, with simple and peltate trichomes, acute, obtuse or rounded. *Androecium* with fertile stamens inserted at the same position; filaments with long and short stipitate trichomes at the base; anthers thecae cream, obovate to elliptic, divergents and reflexed forward, glabrous, inserted or subexserted; staminode glabrous, glabrescent or with long and short stipitate trichomes. *Gynoecium* with ovary conical to oblong, densely pubescent or velutinous, with simple trichomes, with two to four series of ovules per locule, with a ring of longer trichomes at the base; nectar disc not evident; style tomentose to pubescent at the base, with simple trichomes; stigma with lamellae lanceolate, glabrous. *Fruit* a linear flattened to subtetragonal capsule, with extremities acuminate, acute or obtuse, coriaceous to woody, smooth or granular throughout, without lenticels to densely lenticelled, villous, tomentose, pubescent, puberulent or glabrescent, with simple, peltate or patelliform trichomes; central ridge double or single, prominent or not; margins slightly or prominently raised. *Seeds* thin, bialatae, more or less oblong, finely striated; body brown; wings hyaline-membranaceous, sharply demarcated from the body.

Key to species of *Tynanthus*

- 1** Lax thyrse, with conical aspect**2**
 - Dense thyrse, with corymbose or subcorymbose aspect (or conical in *T. densiflorus*)**11**

2 Tendrils simple.....	3
- Tendrils trifid (rarely bifid, in young individuals of <i>T. cognatus</i>)	4
3 Leaflets with apex caudate-mucronate; calyx with patelliform glands; fruits winged, with margins prominently raised	<i>T. guatemalensis</i>
- Leaflets with apex acuminate-mucronate; calyx without patelliform glands; fruits unwinged, with margins slightly raised	<i>T. polyanthus</i>
4 Prophylls foliaceous	5
- Prophylls minute, triangular to shallowly triangular, or bromeliad-like	6
5 Leaflets discolor; corolla 1.2-1.7 cm.....	<i>T. panurensis</i>
- Leaflets concolor; corolla 0.6-0.8 cm.....	<i>T. sastrei</i>
6 Prophylls bromeliad-like	7
- Prophylls minute, triangular to shallowly triangular	8
7 Domatia pubescent; inflorescence axis without patelliform trichomes; Atlantic forest, Brazil	<i>T. espiritosantensis</i>
- Domatia glabrous; inflorescence axis with patelliform trichomes; Amazon forests, Bolivia, Brazil and Peru	<i>T. schumannianus</i>
8 Interpetiolar patelliform glands present; fruits with double central ridge ..	<i>T. pubescens</i>
- Interpetiolar patelliform glands absent; fruits with single central ridge	9
9 Branchelets tomentose to pubescent throughout; calyx without patelliform glands; fruits unwinged, with margins slightly raised	<i>T. cognatus</i>
- Branchelets glabrescent (if pubescent, only at nodes); calyx with patelliform glands; fruits winged, with margins prominently raised	10
10 Petioles and petiolules with patelliform trichomes; corolla 1-1.4 cm, with nectar guides... ..	<i>T. labiatus</i>
- Petioles and petiolules without patelliform trichomes; corolla 0.5-0.9 cm, without nectar guides	<i>T. micranthus</i>
11 Interpetiolar patelliform glands present	12
- Interpetiolar patelliform glands absent	13
12 Tendrils trifid; corolla 0.8-1.5 cm.....	<i>T. densiflorus</i>
- Tendrils simple; corolla 2-3.8 cm	<i>T. macranthus</i>
13 Young brancheletes pubescent; calyx minutely denticulate (sometimes truncate); fruits unwinged, with margins slightly raised	<i>T. croatianus</i>
- Young brancheletes tomentose; calyx laciniate; fruits winged, with margins prominently raised	<i>T. fasciculatus</i>

1. *Tynanthus cognatus* (Cham.) Miers (1863: 193). *Bignonia cognata* Cham. (1832 [1833]: 703). Lectotype (designated here):—BRAZIL. "Brasil aequinoct.", s.d., *F. Sellow s.n.* (US! (barcode 125821)).

Tynanthus elegans Miers (1863: 193). *Bignonia elegans* Cham. (1832 [1833]: 702), *nom. illeg., non Bignonia elegans* Vell. 1825 [1829]. Lectotype (designated here):—BRAZIL. Sin loc., s. d., *F. Sellow s.n.* (US! (barcode 125825)). *syn. nov.*

Schizopsis chimonantha Bureau (1865: 375). Lectotype (designated here):—BRAZIL. Bahia: "Prope Ilheos", 1838, *B. Luschnath s.n.* (BR!; isoelectotype BR!). Syntype: BRAZIL. Rio de Janeiro: "Bords de la rivière d'Hytu, près la fazenda de Bemfica", 1816-1821, *A. St.-Hilaire Catal. D, N° 25* (P!, K!).

Schizopsis regnelliana Bureau (1865: 376). Lectotype (designated here):—BRAZIL. Minas Gerais: "Caldas", 28 December 1859, *A. F. Regnel III-52* (S (14-19845) photo!; isoelectotype K!). Syntypes:—BRAZIL. São Paulo: "Prés de la Paranapitany", 1816-1821, *A. St.-Hilaire Catal. C2, N° 1342* (P!).—Minas Gerais: Sin. loc., 1845, *Widgren 743* (BR!).

Fig. 1: A-E

Lianas. Branchelets tetragonal to terete, with or without ritidome, finely striated, lenticled to densely lenticled, tomentose to pubescent, with simple and peltate trichomes; interpetiolar ridge present (sometimes absent); interpetiolar patelliform glands absent; prophylls of the axillary buds 0.7–1.7 mm long, 0.6–1.5 mm wide, minute, shallowly triangular to triangular, tomentose to pubescent or glabrescent throughout, with simple and peltate trichomes. *Leaves* 2–3 foliolate; terminal leaflets modified into trifid tendrils (rarely bifid, when very young), sometimes with adhesive-disks on tips; petioles and petiolules tomentose to puberulent throughout the surface, with simple and peltate trichomes; petioles (0.2–)0.5–3.6 cm long; petiolules (0.3–)0.5–2.3 cm long; leaflets (1.6–)4–10.6 cm long, (0.6–)1.8–6.2 cm wide, chartaceous to coriaceous, discolor, obovate to elliptic; apex acuminate or obtuse, mucronate; base cuneate or obtuse, symmetrical; margin entire; the abaxial surface tomentose to pubescent throughout (sometimes only on and near the veins), with simple, peltate and patelliform trichomes; the adaxial surface pubescent to glabrescent throughout or only on and near the veins, with simple, peltate and patelliform trichomes; glandular trichomes evenly distributed throughout both surfaces; second venation weak brochidodromous or brochidodromous; pocket domatia, with (sometimes without) trichomes. *Inflorescence* axilar or terminal, a thyse or a compound thyse, lax, with conical

aspect, first order (2.5–)3–13 cm long, second order 2.5–5.5 cm long; floral pedicels 1–7.5 mm long; axis tomentose to densely puberulent, with simple and peltate trichomes; bracts of the inflorescence predominantly caducous, tomentose to pubescent throughout, 0.5–1.9 mm long; floral bracts 0.3–0.7 mm long. *Calyx* green, 1.3–2.7 mm long, 1.3–2.3 mm wide, without patelliform glands, with transversal (sometimes oblique) aperture, truncate or minutely 5-denticulate, tomentose to puberulent throughout outside; lobes 0.1–0.4 mm long. *Corolla* white, cream or pale yellow (sometimes pale lilac), 0.5–1.1 cm long, 2.3–3.7 mm wide at the tube opening; tube 3–4.9 mm long, internally pubescent to glabrescent at the base, with simple and long and short stipitate trichomes; nectar guides absent, but with a path of long and short stipitate trichomes; lobes densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.3–1.7 mm long, 0.6–1.9 mm wide, acute to obtuse; lower ones 1.6–3.6 mm long, 1.2–3.1 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 1–1.5 mm from the base of the corolla; shorter ones 2.5–3.5 mm long; longer ones 3.5–4.5 mm long; anthers thecae 0.7–0.8 mm long, obovate to elliptic, subexserted; connective extending 0.1–0.2 mm beyond anther attachment; staminode 1.3–1.7 mm long, glabrous. *Gynoecium* with pistil 4.5–8.9 mm long; ovary 1–1.3 mm long, 0.7–0.9 mm wide, conical, velutinous; style 3.5–7.5 mm long, tomentose at the base. *Fruit* a linear flattened capsule, (6.5–)10–25 cm long, 0.5–1.1 cm wide, coriaceous, smooth to granular near the midvein and granular near the margins, without lenticels to densely lenticled, tomentose to pubescent, with simple and peltate trichomes; central ridge single, slightly or not prominent; margins slightly raised (unwinged), 0.1–0.2 cm wide. *Seeds* body (0.7–)0.9–1.7 cm long, (0.3–)0.5–0.7 cm wide; wings (0.3–)0.5–1 cm long.

Phenology. Flowers from October to March and produces fruits from February to September.

Distribution and habitat. Occurs in moist broadleaf forests of Brazil (Bahia, Espírito Santo, Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul, Santa Catarina and São Paulo) (Fig. 2).

Additional specimens examined. BRAZIL. Sin loc., s.d., *A. Glaziou s.n.* (F 539388). Sin loc., s.d., *J.C. Mello 8yt* (P 3606711). Sin loc., s.d., *A.F. Regnell s.n.* (K). Sin loc., s.d., *L. Riedel s.n.* (NY). Sin loc., s.d., *Sellow 1074* (BM). Sin loc., 1814–1817, *J. Bowie & A. Cunningham s.n.* (BM). Sin

loc., 1823, *L. Riedel?* s.n. (LE). **Bahia:** Rio Gongogi Basin, 100-500 m, 1 October-30 November 1915, *H.M. Curran 213* (US); Rodovia Itabuna-Camacan, 12 km L de Itabuna, 8 April 1965, *R.P. Belém & M. Magalhães 719* (IAN, K, NY). Rodovia Banco Central a Gongogi, 17 March 1971, *Raimundo S.P. 1163* (RB). Ilhéus, Área do CEPEC (Centro de Pesquisas do Cacau), km 22 da Rodovia Ilhéus-Itabuna (BR-415)?, 50 m, 17 February 1982, *J.L. Hage 1641* (K, MO); CEPLAC, Quadra “D”, Matinha das Preguiças, 1 August 2007, *R.O. Perdiz et al. 84* (SPF). Jussari, RPPN Serra Teimoso, entrada 7.5 km da Rodovia Jussari-Palmira, Fazenda Teimoso, 1.7 km da entrada, 26 January 2006, *J.L. Paixão et al. 684* (SPF). Maraú, 13 January 1967, *R.P. Belém & R.S. Pinheiro 3129* (K, MO, NY). Una, Rodovia São José-Una, ca. 9 km da rodovia BR-101, 18 March 1999, *J.G. Jardim et al. 2063* (SPF). **Espírito Santo:** Conceição do Castelo, Alto Bananal, 6 November 1986, *G. Hatschbach & J.M. Silva 50691* (MBM, MO). Itapemerim, Fazenda do Ouvidor, Usina Paineiras, acesso pela Rodovia ES-490, entrada à esquerda, 2.5 km após o trevo da SAFRA, em direção a Marataízes, 29 December 2007, *A.M. Assis et al. 1292* (SPF). Linhares, Reserva Natural da Companhia Vale do Rio Doce, Estrada 243, 31 January 1985, *A. Peixoto et al. 3037* (MO); *Ibid.*, 2 February 1985, *A. Peixoto et al. 3404* (MO, NY); *Ibid.*, 2 February 1985, *A. Peixoto et al. 3406* (F photo, K, MO, NY); *Ibid.*, 20 m, 14 September 1987, *A. Gentry et al. 59208* (MO); *Ibid.*, Aceiro com a LASA, próximo à estrada Gonçalo Alves, 18 January 1993, *D.A. Folli 1795* (CVRD, SPF, US); *Ibid.*, Próximo ao aceiro com a Lasa, 14 June 1993, *D.A. Folli 1898* (CVRD, SPF); *Ibid.*, 150 m, 15 July 2001, *L.G. Lohmann & B. Whitney 663* (CVRD, MO); *Ibid.*, at the end of the road “Peroba Amarela”, 150 m, 17 July 2001, *L.G. Lohmann et al. 680* (CVRD, MO); *Ibid.*, Aceiro com Catelã Jueirana, Estrada Orelha de Macaco, km 2.4, 17 December 2001, *D.A. Folli 4148* (CVRD, SPF); *Ibid.*, Estrada Municipal do Canto Grande, próximo à entrada da cabana Martinelli, 32 m, 2 May 2008, *A.R. Zuntini et al. 241* (CVRD, MO, RB); *Ibid.*, Estrada Municipal Canto Grande, 36 m, 6 January 2009, *D.A. Folli 6274* (CVRD); *Ibid.*, Estrada Flamengo, após o cruzamento com a Gonçalo Alves, 40 m, 28 January 2014, *M.C. Medeiros & R.B. Louzada 42* (CVRD, SPF); próximo à Reserva Natural da Companhia Vale do Rio Doce, Projeto1, córrego da Jacutinga, APP da Aracruz, 37 m, 2 May 2008, *A.R. Zuntini et al. 240* (MO, RB). Pinheiros, Reserva Biológica Córrego do Veado, 9 May 2008, *D.A. Folli 6021* (CVRD). Santa Leopoldina, Distrito de Mangaraí, Cachoeira do Retiro, 2 October 2005, *M.O.S. Crepaldi 54* (RB). Santa Teresa, Vale do Canaã, 800-850 m, 1 February 1969, *D. Sucre & P.I.S. Braga 4576* (MO, RB); Várzea Alegre, Cachoeira do Magdalon, 26 October 2000, *V. Demuner et al. 1510* (SPF). Sooretama, Estrada Municipal Canto Grande, próximo à Reserva Natural da Companhia Vale do Rio Doce (“Reserva de Linhares”), 34 m, 13 December 2007, *A.R. Zuntini et al. 147* (CVRD, SPF). **Minas Gerais:** Sin loc., 1845, *Widgren s.n.* (BR, P 3606716). Sin loc., Campos da Mantiqueira, perto do vale do Rio Verde, January 1885, *J. Saldanha s.n.* (R 128076). Caldas, 1868, *S.E. Henschen s.n.* (US 201385). Coronel Pacheco, 3 March 1943, *E.P. Heringer 1176* (RB); Água Limpa, 10 December 1946, *E.P. Heringer 2519* (SP). Faria Lemos, Fazenda Santa Rita, 600 m, 6 February 2000, *L.S. Leoni & A.E. Silva 4366* (MO). Monte Belo, Fazenda Lagoa, 800 m, 6

September 1987, *A. Gentry et al. 59095* (MO, UEC); *Ibid.*, 6 September 1987, *A. Gentry et al. 59101* (MO, UEC); *Ibid.*, 6 September 1987, *M.C.W. Vieira 1235* (RB). Poços de Caldas, Fazenda Chiqueirão, 3 December 1981, *H.F. Leitão Filho et al. 1583* (BHCB, FUEL, UEC). Tombos, Fazenda da Cachoeira, 12 July 1935, *M. Barreto 1563* (MO, R). **Paraná:** Antonina, Sapitanduva, 18 January 1974, *G. Hatschbach 33671* (M, MO, SPF, UEC, US). Apucarana, Parque da Raposa, 22 February 2005, *J.S. Carneiro et al. 297* (FUEL). Arapongas, Fazenda do Bule, 22 June 1999, *D.A. Estevan et al. 89* (FUEL, VIC). Cerro Azul, Cabeceira do Ribeirão do Tigre, 8 December 1983, *G. Hatschbach 48829* (MO, US). Fênix, Parque Estadual Vila Rica do Espírito Santo, 11 December 1998, *M. Borgo & S.M. Silva 349* (NY, UPGB). Iporã, Chácara Alcides Pelisson, Água Tucano, 28 May 1989, *A. Pelisson & F.M.E. Longhi s.n.* (FUEL 7382); Fazenda Doralice, 1 December 1995, *M.C. Dias et al. 21* (FUEL). Jaguariaíva, 740 m, 13 January 1915, *P. Dusén 16341* (F, K, NY). Jundiá do Sul, Fazenda Monte Verde, 16 December 1999, *J. Carneiro 848* (SPF); *Ibid.*, Mata do Cruzeiro, 14 January 2000, *G. Hatschbach et al. 69944* (SPF); Mata do Cruzeiro, 3 March 2003, *J. Carneiro 1393* (MBM). Londrina, Parque Municipal Arthur Thomas, 19 December 1984, *M.I.O.J. Neves et al. s.n.* (FUEL 523); *Ibid.*, 13 March 1986, *A.C. Amorin s.n.* (MO 3386506); *Ibid.*, Trilha da Capivara, 520 m, 13 October 2011, *M.C. Medeiros & E.F. Rossetto 33* (SPF); Floresta dos Irmãos Godoy, 21 August 1985, *L.A.C. Rodas et al. 8* (FUEL); *Ibid.*, 28 November 1985, *F.C. Silva et al. 950* (FUEL); *Ibid.*, 20 March 1986, *L.N. Pizzaia et al. 45* (FUEL, MO); *Ibid.*, 14 January 1989, *L.H.S. Silva & F.C. Silva 170* (FUEL, K, MBM, UPGB); *Ibid.*, 9 July 1997, *R. Iríó & L. Lima 194* (UFACPZ); *Ibid.*, 16 July 1997, *V.F. Kinupp et al. 1630* (FUEL); Mata do IAPAR, 30 June 1988, *L.A. Volpato s.n.* (FUEL 6375, HRCB 34681); Paiquerê, 6 February 1997, *V.F. Kinupp et al. 230* (FUEL); Fazenda Figueira-Paiquerê, Fragmento 16, 19 February 2003, *M.C. Lovato et al. 388* (FUEL, R); *Ibid.*, Fragmento 16, 19 February 2003, *M.C. Lovato et al. 400* (ESA, FUEL, MBM); *Ibid.*, 19 February 2003, *D.A. Estevan s.n.* (HRCB 44200, 44201); *Ibid.*, 2004, *J.S. Carneiro et al. 164* (FUEL, HRCB); *Ibid.*, Fragmento 2, 2 April 2004, *J.S. Carneiro et al. 162* (FUEL); *Ibid.*, Fragmento 2, 13 April 2004, *J.S. Carneiro 163* (FUEL, R); *Ibid.*, Fragmento 19, 15 June 2004, *J.S. Carneiro et al. 161* (FUEL); *Ibid.*, Fragmento 2, 22 June 2004, *J.S. Carneiro et al. 173* (FUEL); *Ibid.*, Fragmento 1, 1 July 2004, *J.S. Carneiro et al. 167* (FUEL). Ortigueira, Futuro eixo da Barragem, margem esquerda do Rio Tibagi, 30 October 2008, *M. Kaehler 338* (MBM, UPGB). Ribeirão do Pinhal, Fazenda São Pedro, 11 February 2001, *J. Carneiro 1068* (SPF). Rolândia, December-1936, *G. Tessmann 6001* (MBM, SP). São Jerônimo da Serra, 22 December 1999, *C. Medri et al. 305?* (FUEL 29356). São Pedro do Ivaí, 23 January 1991, *F. Barros 2112* (SP); Fazenda Santa Bárbara?, 18 December 2003, *O.S. Ribas et al. 5668* (G, K, MBM, MO, RB, SPF). Telêmaco Borba, Rio Tibagi, próximo à ponte, 12 December 1996, *V.F. Kinupp et al. 75* (FUEL, HRCB, SPF); Margem da estrada de acesso ao eixo da Barragem, 680 m, 22 September 2008, *M. Kaehler 276* (MBM). Tereza Cristina (“Theresina”), 27 November 1911, *P. Dusén 11172* (BM, K, US). Ventania, Fazenda Santo Expedito, 4 May 2004, *D.A. Estevan et al. 498* (FUEL). **Rio de Janeiro:** Serra Tingua, 1780, *Schott 5971* (F). Sin loc., 1830, *L. Riedel s.n.*

(BM, G, K, P 3606732). Sin loc., 1831-1833, *Gaudichaud 559?* (P 3606674). Sin loc., 1832, *L. Riedel 231* (LE). Fazenda do Sobral, 8 September 1881, *A. Glaziou et al. 12973* (LE, P). Pr. Sumidouro, na Rodovia BR-3, entre Itaipava e Pedro do Rio, 600 m, 10 December 1956, *G.F.J. Pabst 10319* (RB). E of Rio Bonito, between Niteroi and Silva Jardim, 100 m, 19 January 1985, *A. Gentry & E. Zardini 49709* (MO); *Ibid.*, *A. Gentry & E. Zardini 49727* (MO). Cabo Frio, Parque Ecológico Municipal do Mico-Leão-Dourado, 13 June 2003, *G.S.Z. Rezende et al. 162* (RB); Casemiro de Abreu, Monte São João, 3 February 1970, *S.P.S. s.n.* (RB 146284). Guapimirim, Parque Nacional da Serra dos Órgãos, trilha do Poço da Preguiça, 410 m, 6 January 2011, *M.C. Medeiros et al. 28* (SPF). Nova Iguaçu (“Iguassú”), s.d., *Sin col. 8061* (P 3606667). Petrópolis, Mandioca, 1821-1824, *L. Riedel s.n.* (MO 4618844, NY 483757, NY 1032824); February-March 1823, *L. Riedel s.n.* (LE). Rio de Janeiro, Floresta da Tijuca, Gávea, Caminho do Macaco, 1865?, *A. Glaziou 2638* (BR, C photo in F, K, P); 8 March 1871, *A. Glaziou 4719* (P, US); *Ibid.*, Corcovado, 22 May 1870, *A. Glaziou 4124* (P); 22 May 1870, *A. Glaziou 4683* (P, US); *Ibid.*, Grande cascade, 24 June 1870, *A. Glaziou 4692* (P); *Ibid.*, 21 January 1871, *A. Glaziou 4709* (BM, K, NY, P, US); *Ibid.*, Estrada de Sumare, km 5, 300 m, 19 January 1975, *W. Benson 45* (MO); Prope hort. bot., 29 November 1888, *Schwacke s.n.* (K, R 23784); Mundo Novo, Botafogo, May 1921, *J.G. Kuhlmann s.n.* (R 23803, RB 16258); Gávea, Mesa do Imperador, 10 March 1950, *Kuhlmann s.n.* (RB 69023, RB 69114, NY 483758); Jardim Botânico do Rio de Janeiro, orla do parque, 13 September 1991, *A.F. Vaz et al. 949* (RB). Santa Maria Madalena, Mata do Laureano Vicente, 7 March 1934, *S. Lima & Brade 13194* (R, RB). Teresópolis, Próximo à Fazenda Boa Vista, 12 January 1943, *H.P. Velloso s.n.* (MO 2286403). **Rio Grande do Sul:** Vila Manresa p. Porto Alegre, 25 July 1949, *B. Rambo 42705* (MO). Caxias do Sul, Santa Lucia do Piaí, 780 m, 27 January 1999, *A. Kegler 158* (M, MBM, US). Vale do Sol, Linha XV de Novembro, 23 January 1993, *J.A. Jarenkow & D.B. Falkenberg 2281* (MBM). **Santa Catarina:** Sin loc., June 1868, *F. Müller 166* (K). Blumenau, Bom Retiro, Mata da Companhia Hering, 350 m, 17 September 1959, *P.R. Reitz & R.M. Klein 9102* (K, US). Florianópolis, Morro Costa da Lagoa, 300 m, 15 February 1967, *R.M. Klein 7238* (K, R); Morro da Cutia, Tapera, Ribeirão, 150 m, 20 January 1970, *R.M. Klein & Bresolin 8542* (K, R). Itajaí, s.d., *F. Müller 298* (R). Jacinto Machado, Sanga da Areia, 200 m, 13 July 1959, *P.R. Reitz & R.M. Klein 8936* (K, US); *Ibid.*, 250 m, 27 January 1960, *P.R. Reitz & R.M. Klein 9424* (BR, F photo, G, K, M, NY, UPGB, US). Lauro Müller, Novo Horizonte, 450 m, 15 January 1959, *P.R. Reitz & R.M. Klein 8245* (BR, F, G, K, M, NY, SP, US). Luis Alves, Braço Joaquim, 250 m, 13 January 1955, *R.M. Klein 1054* (K, NY, US). Palhoça, Morro do Cambirela, 300 m, 18 January 1972, *R.M. Klein & Bresolin 10008* (K). Rio do Sul, 350 m, 31 December 1958, *P.R. Reitz 6147* (BR, K, NY, US); Serra do Matador, 550 m, 12 March 1959, *P.R. Reitz & R.M. Klein 8537* (K, US). São Bento do Sul, Braço esquerdo, 417 m, 21 November 2009, *T.J. Cadorin et al. 799* (SPF). **São Paulo:** Sin loc., 27 November 1871, *J.C. Mello 51* (US). Sin loc., 25 December 1873, *H. Mosén 1488* (P). Barretos, Margem do Rio Pardo, November 1917, *A. Sampaio s.n.* (R 23545, RB 23359). Campinas, Barão Geraldo, Santa Genebra Forest Reserve, Transect 3, 550 m, 27 August 1987, *A.*

Gentry & A. Silva 58727 (MO, UEC); *Ibid.*, Transect 4, 550 m, 27 August 1987, *A. Gentry 58752* (MO, UEC). Ipeúna, Ribeirão Passa-Cinco, 26 January 1984, *A. Furlan 175* (HRCB). Marília, Estação Experimental, 14 January 1993, *G. Durigan 30691* (UEC). Rio Claro, Fazenda São José, 15 November 2000, *R. Ubulutsch & M.A. Assis 101* (HRCB); *Ibid.*, trilha que atravessa o fragmento, 20 December 2000, *R. Ubulutsch & M.A. Assis 134* (HRCB). São Paulo, Bosque da Avenida, 17 December 1933, *J.G. Kuhlmann s.n.* (RB 48111); Jardim Botânico, 15 January 1938, *O. Handro s.n.* (SP 43041); *Ibid.*, Trilha Fontes do Ipiranga, 24 October 2006, *B.L.P. Villagra 225* (SP); Cidade Jardim, 4 January 1944, *W. Hoehne 1184* (MO, SPF); Serra da Cantareira, Picada Dom Bento, Pedra Grande, 1000 m, 6 January 1953, *F. Markgraf s.n.* (SPSF 4061).

Taxonomic notes. The morphological similarity between *Tynanthus cognatus* and *T. elegans* has long been noted. Indeed, Chamisso (1832) commented on their overall similarity when those taxa were originally described as *Bignonia cognata* and *B. elegans*, respectively. On the other hand, Chamisso (1832) also noted differences in the type and density of the indument encountered in the vegetative and reproductive organs of these taxa, which he considered sufficient to maintain the taxa as separate. However, a detailed analysis of the indument of these species along the entire range of distribution of these taxa showed that indument density varies geographically. More specifically, the collections from the northern portion of the range (states of Bahia and Espírito Santo) were shown to have glabrescent branches and leaves, while the specimens from the southern portion (states of Paraná and Rio Grande do Sul) are generally densely pubescent to pubescent. Therefore, indument variation is not a diagnostic trait and not sufficient to keep those taxa as separate. Furthermore, molecular phylogenetic data (Medeiros & Lohmann in prep.) indicated that *T. elegans* is nested within *T. cognatus*, corroborating the synonymization of *T. elegans* in *T. cognatus*.

Tynanthus cognatus can be easily recognized by its obovate to elliptic leaflets. *Tynanthus pubescens* is the only other species of *Tynanthus* to present this feature; however, these species can be separated by the winged fruits of *T. pubescens* (versus unwinged in *T. cognatus*) and Amazonian distribution (versus Atlantic Forest in *T. cognatus*). *Tynanthus cognatus* shares lax inflorescences and unwinged fruits with its sister species *T. polyanthus*, (Medeiros & Lohmann in prep.). Nevertheless, *T. cognatus* is easily distinguished from *T. polyanthus* by the minute prophylls (versus foliaceous prophylls in *T. polyanthus*) and the inconspicuously tetragonal young branchelets (versus conspicuously tetragonal in *T. polyanthus*).

Nomenclatural notes. Chamisso (1832) described *T. cognatus* and *T. elegans* based on Sellow collections. Chamisso's types are deposited at LE (Stafleu & Cowan 1976: 482), but we were not able to locate those materials during two visits to the LE herbarium. The types of *T. cognatus* and *T. elegans* deposited at B were destroyed during the World War II (Hiepko 1987) and are no longer available. Despite that, we were able to access photos of the B types from the F website. The photographed collection of *T. cognatus* was labeled as *Sellow 166* while the photographed collection of *T. elegans* was labeled *Sellow 5596*. Unfortunately, we were unable to locate any duplicates of the *Sellow 166* and *5596* collections in any of the herbaria visited. Instead, we were able to locate Sellow unnumbered collection at K that match the identifications of *T. cognatus* (barcode 449541). In addition, we were also able to locate Sellow unnumbered collections at US that had been correctly identified as *Bignonia cognata* (US barcode 125821) and *B. elegans* (US barcode 125825), which we selected as lectotypes. In US barcode 125821, the calligraphy of identification matches with Chamisso's. In US barcode 125825, the identification was made by Schumann, who worked at B and accessed Chamisso's types kept in that herbarium.

Two syntypes were cited by Bureau (1865) in the protologue of *Schizopsis chimonantha* (*Luschnath s.n.* and *St. Hilaire Catal. D N° 25*) and four syntypes in the protologue of *S. regnelliana* (*Regnel III-52*, *St. Hilaire Catal. D N° 25*, *Widgren 743*, and *Martius s.n.*). For *S. chimonantha*, four sheets of the collection *Luschnath s.n.* were located at BR. The duplicate that has a hand-written label with calligraphy that matches Bureau's hand writing, with the identification of *Tynanthus cognatus* is here selected as a lectotype, since it is also the best quality material from the four duplicates. For *S. regnelliana*, three duplicates of the *Regnell III-52* were located in the S herbarium (cited in the protologue), one dated from 1859 (S 14-19845), one from 1867 (S 14-19860) and one from 1868 (S 14-19863). The only material whose date predates the publication of the protologue of *S. regnelliana* (S 14-19845) is here selected as a lectotype. Additional duplicates of the *Regnell III-52* collection were located in other herbaria (i.e., K!, LE!, MO!, P!, R!, US!); however, Regnell's collection numbering system often reflect individual species and not collections from a single individual (Mia Ehn, S curator, pers. comm.) and thus, do not represent duplicates of the holotype. We chose one of the Regnell's collections as lectotype because of the good conditions of the material and also because of the epithet "regnelliana" which directly refers to collections of A.F. Regnell. It is also important to note that a Martius collection, presumably kept at M, was also cited in the protologue of *S. regnelliana*. Unfortunately, we were unable to locate this collection. Furthermore, this collection is also

cited in the protologue of *Arrabidaea fasciculata* [= *T. fasciculatus* (Vell.) Miers], complicating its identity. This material was thus excluded from the list of syntypes of *T. regnelliana*.

2. *Tynanthus croatianus* A.H. Gentry (1971: 93) (as "*Tynnanthus*"). Type:—PANAMA.

Panama: Shoreline of broad-mouthed cove NE of Drayton House on Barro Colorado Island, 28 August 1970, *T.B. Croat 11927* (holotype MO!; isotypes F!, GH! photo, K!, MO!, NY!, SCZ! photo, STRI! photo, US!).

Fig. 1: F-N

Lianas. Branchelets tetragonal to terete, without ritidome, finely striated, lenticled to densely lenticled, pubescent to glabrescent, with simple and peltate trichomes; interpetiolar ridge absent (sometimes present); interpetiolar patelliform glands absent; prophylls of the axillary buds 1.3–2.5 mm long, 1–2.5 mm wide, minute, shallowly triangular, pubescent or puberulent to glabrescent throughout, with simple and peltate trichomes. *Leaves* 2–3 foliolate (more commonly 2); terminal leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules pubescent throughout surface or only at the upper canalicule, with simple, peltate and patelliform trichomes; petioles (1.4–)1.8–7.5 cm long; petiolules (0.5–)1.1–3.8 cm long; leaflets (3.5–)5–11.4 cm long, (1.4–)3–9 cm wide, membranous to chartaceous (sometimes subcoriaceous), discolor, ovate to elliptic; apex acuminate or caudate, mucronate; base cuneate, obtuse, truncate or subcordate, symmetrical or asymmetrical; margin entire (rarely dentate); the abaxial surface pubescent to glabrescent on and near the veins (sometimes throughout), with simple, peltate and patelliform trichomes; the adaxial surface pubescent to glabrescent throughout or only on and near the veins, with simple, peltate and patelliform trichomes; glandular trichomes evenly distributed throughout both surfaces; second venation weak brochidodromous; pocket domatia, without trichomes. *Inflorescence* axilar or terminal, a thyse, dense, with corymbose or subcorymbose aspect, (2.3–)3.3–6.5 cm long; floral pedicels 1–5 mm long; axis densely pubescent to pubescent, with simple, peltate and patelliform trichomes; bracts of the inflorescence predominantly caducous, densely pubescent to pubescent throughout, 0.5–1.5 mm long; floral bracts 0.4–0.6 mm long. *Calyx* green, 3–4 mm long, 3–4 mm wide, with patelliform glands, with transversal aperture, minutely 5-denticulate (sometimes truncate), densely pubescent to puberulent throughout outside; lobes 0.1–0.3 mm long. *Corolla* white, 1.2–2 cm long, 4–7 mm wide at the tube

opening; tube 5–9 mm long, internally tomentose at the base, with simple and long and short stipitate trichomes; nectar guides present, yellow; lobes densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 1–3 mm long, 1–4 mm wide, acute to obtuse; lower ones 3–7 mm long, 3–5.5 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 2 mm from the base of the corolla; shorter ones 7–9(–10) mm long; longer ones 8–10(–12) mm long; anthers thecae 1.4–1.9 mm long, obovate to elliptic, subexserted; connective extending 0.2–0.3 mm beyond anther attachment; staminode 4–5 mm long, glabrous. *Gynoecium* with pistil 13–15(–17) mm long; ovary 1.5–2 mm long, 0.8–1.1 mm wide, conical, densely pubescent; style 11–13 mm long, tomentose to pubescent at the base. *Fruit* a linear flattened capsule, 16–37 cm long, 0.7–1.2 cm wide, coriaceous to woody, smooth to granular near the midvein and granular near the margins, without lenticels to densely lenticelled, densely pubescent to pubescent, with simple and peltate trichomes; central ridge single, slightly or not prominent; margins slightly raised (unwinged), 0.1–0.3 cm wide. *Seeds* body 1.1–1.9 cm long, 0.4–0.8 cm wide; wings 0.6–1.1 cm long.

Phenology. Flowers from July to September and fruits from October to March.

Distribution and habitat. Occurs in moist broadleaf forests from Colombia (Choco), Costa Rica (Puntarenas) and Panama (Colón, Darién and Panamá) (Fig. 3).

Additional specimens examined. COLOMBIA. **Choco:** Trail from Unguia along Rio Tigre toward base of Serrania del Darién, 200–300 m, 16 July 1975, A. Gentry & L.E. Aguirre 15209 (MO). COSTA RICA. **Puntarenas:** Buenos Aires, Rey Curré, Camino a Sabana Mamey, 200–400 m, 16 October 1992, S. Rojas & L.M. Rojas 102 (F, MO). PANAMA. **Colón:** Ca. 2–3 miles on Pipeline road, north of Gamboa, 0–10 m, 1 September 1981, S. Knapp 1053 (NY, MO). **Darién:** Rio Balsa, between Manene and Tusijuanda, 26 July 1967, J.A. Ducke 13544 (3) (MO); 26 July 1967, J.A. Ducke 13579 (3) (MO). El Real, 3 March 1972, A. Gentry 4538 (BM, MO). Rio Tuirá between Boca de Cupe and mouth of Rio Pucro, 12 January 1975, A. Gentry & S. Mori 13527 (F, MO). Santa Fe, s.d., J.A. Ducke 8396 (1) (MO). **Panamá:** Barro Colorado Island, Gigant Bay, 2 August 1934, O. Shattuck 1108 (F, MO, US); Shore, east side of Barrunga Peninsula, 27 July 1969, R. Foster 1178 (F, MO); Drayton House Clearing, 23 November 1970, T.B. Croat 12681 (F photo, MO, NY); North shore of Gigant Bay, 8 March 1971, T.B. Croat 13975 (F, MO, NY); Gigant Bay, 5 April 1971, A. Gentry 708 (MO); Vicinity of Laboratory Clearing, fairchild ridge above boatman's house, 19 October 1973, G. Montgomery 195 (MO); *Ibid.*, near butterfly cage on east bank of Allee Stream in

treefall, 24 October 1973, *G. Montgomery 199* (MO). Alhajuella, July 1961, *J.D. Dwyer 1144* (MO). Madden Forest Road at entrance to Boy Scout Road Vine, 27 December 1970, *T.B. Croat 12904* (MO). Boy Scout Camp Road near Madden Lake, 13 October 1971, *A. Gentry 2058* (F, MO); 12 July 1972, *A. Gentry 5502* (F photo, MO); 100 m, 19 December 1972, *A. Gentry 6696* (MO, NY). Mouth of Rio Pasiga near coast in cutover forest, 26 October 1971, *A. Gentry 2203* (F, MO). Rio Pasiga to above waterfall on second main fork, 29 October 1971, *A. Gentry 2271* (F, MO). First bend of Rio Pasiga, edges of clearing around Indian's house, 1 November 1971, *A. Gentry 2365* (MO, NY). 0 to 4 km from Río Bayano crossing on road to Santa Fé, 26 January 1972, *A. Gentry 3875* (MO). Near archeological site at edge of Madden Lake, 9 April 1972, *A. Gentry 5024* (MO). Along stream ca. 3 miles E of Transisthmian highway on road to Salamanca, 100 m, 19 December 1972, *A. Gentry 6723* (MO). Bordeando el Majé, campamento del G.M.I. isla Bayano, 22 August 1976, *C. Garibaldi 225* (MO).

Taxonomic notes. *Tynanthus croatianus* can be recognized by its ovate to elliptic leaflets and dense inflorescences. These features are also found in *T. densiflorus*, but the occurrence of interpetiolar patelliform glands (versus absent in *T. croatianus*) differentiate these species. *T. croatianus* is morphologically very distinct from its sister species, *T. guatemalensis*, another species from Central America (Medeiros & Lohmann in prep.). Both species share pubescent to glabrescent leaflets but *T. croatianus* can be easily separated by the trifid tendril (versus simple in *T. guatemalensis*), minute prophylls of the axillary buds (versus foliaceous in *T. guatemalensis*), 1.2–2 cm long, 4–7 mm wide corolla (versus 0.5–0.9 cm long, 1.9–3.5 mm wide in *T. guatemalensis*), and unwinged fruit margins (versus winged in *T. guatemalensis*).

3. *Tynanthus densiflorus* M.C. Medeiros & L.G. Lohmann, *sp. ined.* (submitted)

Type:—BRAZIL. Amazonas: Reserva Florestal Adolpho Ducke, Manaus-Itacoatiara, km 26, 16 August 1996, *L.C. Procópio et al. 14* (holotype INPA!; isotypes G!, K!, MO!, NY!, RB!, SP!).

Fig. 4: A-I

Lianas. *Branchelets* subtetragonal to terete, without ritidome, finely striated, lenticled to densely lenticled, pubescent to puberulent, with simple and peltate trichomes; interpetiolar ridge absent or present; interpetiolar patelliform glands present; prophylls of the axillary buds 0.5–0.8 mm long, 1–2.5 mm wide, minute, shallowly triangular, puberulent throughout, with simple and peltate trichomes. *Leaves* 2–3 foliolate; terminal

leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules puberulent to glabrescent throughout surface, with simple and peltate trichomes; petioles 1.8–5.6 cm long; petiolules (0.6–)1.4–3.8 cm long; leaflets (3.2–)5–16.1 cm long, (1.3–)2–9.5 cm wide, membranous to chartaceous (sometimes subcoriaceous), discolor or concolor, ovate; apex caudate, mucronate; base cuneate to truncate or subcordate, symmetrical or asymmetrical; margin entire; the abaxial surface pubescent to puberulent throughout (sometimes only on and near the veins), with simple, peltate and patelliform trichomes; the adaxial surface pubescent to glabrescent throughout (sometimes only on and near the veins), with simple, peltate and patelliform trichomes; glandular trichomes evenly distributed throughout both surfaces; second venation weak brochidodromous; pocket domatia, with (sometimes without) trichomes. *Inflorescence* axilar, a thyrse, dense, with corymbose, subcorymbose or conical aspect, 3–9.5 cm long; floral pedicels 1–7 mm long; axis densely pubescent to puberulent, with simple and peltate trichomes; bracts of the inflorescence predominantly caducous, densely pubescent to pubescent throughout, 0.5–2.5 mm long; floral bracts 0.4–0.6 mm long. *Calyx* green to grayish, 1.5–2.2 mm long, 1.4–1.9 mm wide, without patelliform glands, with transversal aperture, truncate or minutely 5-denticulate, densely pubescent to pubescent throughout outside; lobes 0.1–0.2 mm long. *Corolla* cream or pale yellow, 0.8–1.5 cm long, 3–5 mm wide at the tube opening; tube 3–5 mm long, internally tomentose at the base, with simple and long and short stipitate trichomes; nectar guides present, yellow; lobes densely pubescent to pubescent throughout lower ones and at margins of or throughout upper ones; upper ones 0.4–1.4(–2.9) mm long, 0.7–1.5(–2.4) mm wide, acute to obtuse; lower ones 2.1–4 mm long, 2–3.6 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 1.5–2.5 mm from the base of the corolla; shorter ones 3.5–5.5 mm long; longer ones 4.5–7 mm long; anthers thecae 1.1–1.4 mm long, obovate to elliptic, subexserted; connective extending 0.2–0.3 mm beyond anther attachment; staminode 1.5–2.7 mm long, with long and short stipitate trichomes. *Gynoecium* with pistil 7–9 mm long; ovary 1.3–1.5 mm long, 0.7–0.8 mm wide, conical, velutinous; style 5–7 mm long, tomentose at the base. *Fruit* not seen. *Seeds* not seen.

Phenology. Flowers in August; the fruiting season is unknown.

Distribution and habitat. Occurs in moist broadleaf forests from Brazil (Amazonas) (Fig. 5).

Additional specimens examined. BRAZIL. Amazonas: 2-5 km N of Manaus-Itacoatiara Road at km 79 near Rio Preto da Eva, 100-200 m, 24 November 1974, A. Gentry 12849 (INPA photo, MG, MO). Rio Camanau, 28 June 1987, P. Grenand et al. 2787 (INPA). Manaus, Campus of INPA, Estrada do Aleixo, 22 November 1974, A. Gentry 12792 (INPA photo); 30 November 1974, A. Gentry 13018 (INPA, MO); *Ibid.*, Transect vouchers, Line 1, 11 December 1974, A. Gentry 13181 (INPA, MO); Estrada do Aleixo near Manaus, km 6-7 past INPA, 2 December 1974, A. Gentry 13040 (INPA photo, MO); Reserva Florestal Ducke, Parcela PPBio (LO3 1000 m), 100 m, 14 December 2010, M.C. Medeiros et al. 21 (SPF); *Ibid.*, próximo à estação meteorológica, 120 m, 15 December 2010, M.C. Medeiros et al. 22 (SPF); *Ibid.*, proximidades do refeitório da base da reserva, na beira da estrada, 110 m, 16 December 2010, M.C. Medeiros et al. 25 (SPF).

Taxonomic notes. *Tynanthus densiflorus* is characterized by interpetiolar patelliform glands, ovate leaflets and dense inflorescences, with corymbose, subcorymbose or conical aspect (Medeiros & Lohmann, submitted). *T. densiflorus* is closely related to *T. panurensis* and *T. pubescens* (Medeiros & Lohmann in prep.). It shares ovate leaflets and a tomentose corolla tube at base with *T. panurensis*; however, *T. densiflorus* is easily identified by the presence of interpetiolar glands (versus absent in *T. panurensis*), minute prophylls of the axillary buds (versus foliaceous in *T. panurensis*) and dense inflorescences (versus lax in *T. panurensis*). On the other hand, *T. densiflorus* shares patelliform glands and a similar corolla length with *T. pubescens* (i.e., 1-1.6 cm in *T. pubescens* versus 0.8-1.5 cm in *T. densiflorus*), but differs by the caudate-mucronate leaflet apices (versus acuminate or obtuse-mucronate in *T. pubescens*), pubescent to glabrescent inflorescence axis (versus densely pubescent in *T. pubescens*), and dense inflorescences (versus lax in *T. pubescens*) (Medeiros & Lohmann, submitted).

4. *Tynanthus espiritosantensis* M.C. Medeiros & L.G. Lohmann, *sp. ined.* (Medeiros & Lohmann, submitted) Type:—BRAZIL. Espírito Santo: Linhares, Reserva Natural da CVRD, Estrada Oiticica, km 2.3, 6 February 2008, D.A. Folli 5931 (holotype CVRD!; isotype SPF!).

Fig. 6: A-I

Lianas. *Branchelets* tetragonal to terete, with or without ritidome, finely striated, lenticled to densely lenticled, glabrescent (sometimes pubescent at the nodes), with peltate and patelliform trichomes (sometimes also with simple); interpetiolar ridge absent; interpetiolar patelliform glands absent; prophylls of the axillary buds 1.2–2.5 mm long, 0.7–

1.1 mm wide, bromeliad-like, glabrescent (rarely puberulent) throughout, with peltate trichomes (rarely also with simple). *Leaves* 2–3 foliolate (more commonly 3); terminal leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules puberulent throughout surface, with simple and peltate trichomes; petioles 1–6 cm long; petiolules 0.5–3.5 cm long; leaflets (4–)5–11.9 cm long, (1.5–)1.9–5.4 cm wide, membranous to chartaceous, discolor, elliptic; apex acuminate or caudate, mucronate; base cuneate, symmetrical; margin entire; the abaxial surface glabrescent (sometimes pubescent) on and near the veins, with peltate and patelliform trichomes (sometimes also simple); the adaxial surface glabrescent on and near the veins, with peltate and patelliform trichomes; glandular trichomes distributed especially on the abaxial surface; second venation weak brochidodromous; pocket domatia, with trichomes. *Inflorescence* axilar, a thyrse, lax, with conical aspect, 3.6–7 cm long; floral pedicels 3.5–9 mm long; axis pubescent, with simple and peltate trichomes; bracts of the inflorescence predominantly caducous, pubescent throughout or only at margins, 0.7–3.9(–9) mm long; floral bracts 0.5–0.7 mm long. *Calyx* green, 2.3–2.7 mm long, 1.8–2.5 mm wide, with patelliform glands, with transversal (sometimes oblique) aperture, minutely 5-denticulate, glabrescent (sometimes pubescent at teeth) outside; lobes 0.1–0.4 mm long. *Corolla* white, 0.7–0.8 cm long, 2.5–3.4 mm wide at the tube opening; tube 2.5–4 mm long, internally tomentose to pubescent at the base or glabrescent, with simple and long and short stipitate trichomes; nectar guides absent, but with a path of long and short stipitate trichomes; lobes densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.4–1.1 mm long, 1–1.5 mm wide, acute to obtuse; lower ones 1.8–3.2 mm long, 2.1–2.5 mm wide, obtuse to rounded (sometimes acute). *Androecium* with fertile stamens inserted 1–1.5 mm from the base of the corolla; shorter ones 2.5–3.5 mm long; longer ones 4.5–5 mm long; anthers thecae 0.8–1.1 mm long, obovate to elliptic, subexserted; connective extending 0.2–0.3 mm beyond anther attachment; staminode 2.4 mm long, glabrescent, with long and short stipitate trichomes. *Gynoecium* with pistil 4.5–6 mm long; ovary 0.8–1 mm long, 0.7–0.9 mm wide, conical, velutinous; style 3.3–5 mm long, tomentose at the base. *Fruit* not seen. *Seeds* not seen.

Phenology. Flowers from December to February; the fruiting season is unknown.

Distribution and habitat. Occurs in moist broadleaf forests from Brazil (Espírito Santo) (Fig. 7).

Additional specimens examined. BRAZIL. **Espírito Santo:** Linhares, Rancho Alto, 7 December 1984, *G. Hatschbach & J.M. Silva 48693* (MBM, MO, US); Reserva Natural da CVRD, Estrada Oiticica, próximo à porteira, antes do cruzamento com a estrada municipal, 53 m, 27 January 2014, *M.C. Medeiros & R.B. Louzada 41* (CVRD, SPF).

Taxonomic notes. *Tynanthus espiritosantensis* shares bromeliad-like prophylls of the axillary buds, glabrescent elliptic leaflets, corolla tube tomentose at base and lax inflorescences with *T. schumannianus*. Nevertheless, *T. espiritosantensis* is easily separated by the pubescent domatia (versus glabrous domatia in *T. schumannianus*), lack of patelliform glands in the petioles, petiolules and inflorescence axis (versus presence of patelliform glands in *T. schumannianus*) and larger calyx, with ca. 2.3-2.7 x 1.8-2.5 mm (versus smaller calyx, with 1-2 x 1.1-1.9 mm in *T. schumannianus*) (Medeiros & Lohmann, submitted). Additionally, *T. espiritosantensis* occurs in the Atlantic Forest of Espírito Santo, while *T. schumannianus* is an Amazonian species. Apart from being morphologically similar, *T. espiritosantensis* and *T. schumannianus* are also closely related, belonging to a clade that also contains *T. fasciculatus*, *T. labiatus* and *T. micranthus*, all distributed through the Atlantic Forest (Medeiros & Lohmann in prep.).

5. *Tynanthus fasciculatus* (Vell.) Miers (1863: 193). *Bignonia fasciculata* Vell. (1825 [1829]: 247; 1827 [1831]: tab. 25). *Arrabidaea fasciculata* (Vell.) DC. (1845: 185). *Cuspidaria fasciculata* (Vell.) Sond. (1849: 560). *Schizopsis fasciculata* (Vell.) Bureau (1865: 379). Lectotype (designated by Lohmann, in Lohmann & Taylor 2014: 468):—Fl. Flumin. Icones 6: tab. 25. 1827 [1831].

Fig. 8: A-F

Lianas. *Branchelets* tetragonal to terete, with or without ritidome, finely striated, densely lenticled, tomentose to pubescent, with simple and peltate trichomes; interpetiolar ridge absent or present; interpetiolar patelliform glands absent; prophylls of the axillary buds 0.7–1.5(–2.2) mm long, 0.5–1.2(–1.5) mm wide, minute, shallowly triangular to triangular, tomentose to pubescent throughout, with simple and peltate trichomes. *Leaves* 2–3 foliolate (more commonly 3); terminal leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules tomentose to pubescent throughout surface, with simple and peltate trichomes; petioles (0.5–)1.2–5.5 cm long; petiolules (0.4–)0.6–3.4

cm long; leaflets (3.3–)4.3–11.7 cm long, (1.2–)2–7.5 cm wide, membranous to chartaceous (sometimes subcoriaceous), discolor or concolor, elliptic; apex acuminate, mucronate; base cuneate or obtuse, symmetrical; margin entire; the abaxial surface tomentose to pubescent throughout or only on and near the veins, with simple and peltate trichomes; the adaxial surface tomentose to pubescent throughout or only on and near the veins, with simple and peltate trichomes; glandular trichomes evenly distributed throughout both surfaces; second venation weak brochidodromous; pocket domatia, with trichomes. *Inflorescence* axilar or terminal, a thyse, dense, with corymbose or subcorymbose aspect, (2–)3.1–4.5 cm long; floral pedicels 1.5–6 mm long; axis tomentose, with simple and peltate trichomes; bracts of the inflorescence predominantly caducous, tomentose throughout, 1–3.5 mm long; floral bracts 0.6–1.4 mm long. *Calyx* green to reddish, 2.5–4 mm long, 2–3.5 mm wide, with patelliform glands, with transversal (sometimes oblique) aperture, 5-laciniate, tomentose or densely pubescent throughout outside; lobes 0.6–3 mm long. *Corolla* white, cream or pale yellow, 1.2–2.2 cm long, 4–7 mm wide at the tube opening; tube 5–11 mm long, internally tomentose to pubescent at the base, with simple and long and short stipitate trichomes; nectar guides present, yellow; lobes densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.7–2.8 mm long, 1–3.3 mm wide, acute to obtuse; lower ones 4–5.2 mm long, 2.5–5.2 mm wide, acute, obtuse or rounded. *Androecium* with fertile stamens inserted 2.5–3 mm from the base of the corolla; shorter ones 7.5–8.5 mm long; longer ones 9–10 mm long; anthers thecae 1.4–1.7 mm long, obovate to elliptic, subexserted; connective extending 0.4–0.6 mm beyond anther attachment; staminode 2.3–2.8 mm long, glabrescent, with long and short stipitate trichomes. *Gynoecium* with pistil 12–13 mm long; ovary 1.5–2 mm long, 0.9–1.3 mm wide, conical, velutinous; style 10–12 mm long, tomentose at the base. *Fruit* a linear flattened to subtetragonal capsule, 11–39.5 cm long, (0.5–)0.8–2 cm wide, woody, smooth to granular near the midvein and granular near the margins, without lenticels to densely lenticelled, tomentose to pubescent, with simple, peltate and patelliform trichomes; central ridge single, prominent (sometimes not); margins prominently raised (winged), 0.2–0.7 cm wide. *Seeds* body (0.7–)1–2 cm long, (0.4–)0.6–1 cm wide; wings (0.3–)0.5–1.2 cm long.

Phenology. Flowers from September to December and produces fruits from February to October.

Distribution and habitat. Occurs mainly in moist broadleaf forests, although a few populations are known to occur in savanna areas from Eastern Brazil (Minas Gerais and São Paulo) (Fig. 9).

Additional specimens examined. BRAZIL. Sin loc., s.d., *Araujo?* 11364 (P 3606710). Sin loc., s.d., *Blanchet* s.n. (BM). Sin loc., s.d., *J.C. Mello* s.n. (NY 483766, US 2515368). Sin loc., s.d., *Widgren* 243 (BM). Sin loc., 1 September 1866, *J.C. Mello* 8a (K, P 3606703). Sin loc., 18 October 1866, *J.C. Mello* 8 β (P 3606704). Sin loc., 1 October 1867, *J.C. Mello* 8 γ (K, MO 3395613, P 3606705, US 2515615). **Minas Gerais:** Sin loc., s.d., *A.F. Regnell II-198* (MO 3395612). Sin loc., 1845, *Widgren* s.n. (BR, MO 2698894, MO 3395608, P 3606700). Jardim, 20 November 1845, *Widgren* 49 (BR). Sin loc., 1845, *Widgren* 94 (BR). Sin loc., 18 October 1847, *A.F. Regnell II-198* (K, LE). Sin loc., 19 October 1861, *A.F. Regnell II-198* (R 23787, US 201375). Rio Pardo, 7 July 1866, *A.F. Regnell II-198* (K). Sin loc., 9 September 1866, *A.F. Regnell II-198* (P 3606695). Serra da Concha, 21 September 1867, *A.F. Regnell II-198* (P 3606699); 29 September 1867, *A.F. Regnell II-198* (P 3606698). Campos da Bocaina, 8 September 1879, *A. Glaziou* 4692a (P, US). Perpetua, pres Diamantina, 11 April 1892, *A. Glaziou* 19664 (P). Mineração da Itaú, Rodovia Belo Horizonte a Paraopeba, 13 September 1957, *E.P. Heringer* s.n. (RB 105653, RB 134270, MO 2609963). Belo Horizonte, Estação Ecológica UFMG, Trilha J, 6 June 1990, *E.M. Santos et al.* s.n. (F 2170556); 6 June 1990, *E.M. Santos et al.* 76 (BHCB); *Ibid.*, 2a. Estação de coleta, trilha J, 10 October 1990, *E. Tameirão Neto* 215 (BHCB, F). Caldas, s.d., *A.F. Regnell II-198* (K, MO 2305639, P 3606697, R 23786, US 2515367); 8 September 1845, *A.F. Regnell II-198* (P 3606701); 19 October 1861, *A.F. Regnell II-198* (P 3606694); 21 September 1867, *A.F. Regnell II-198* (BR, M); 1869, *A.F. Regnell II-198* (BR). Camanducaia, Mata dos Mota, 1000 m, 12 October 1999, *R.B. Torres et al.* 756 (IAC). Coronel Pacheco, s.d., *E.P. Heringer* s.n. (RB 77360); Estação Experimental, 28 October 1940, *E.P. Heringer* 352 (RB, SP, VIC). Juiz de Fora, Serra do 12^o RI, 11 November 1964, *S.V. Monteiro* 2627 (VIC). Marliérea, Parque Estadual do Rio Doce, Salão Dourado, junto à saída, 15 June 1995, *J.A. Lombardi & L.G. Temponi* 793 (BHCB). Mercês, 1840?, *Gardner* 5030 (BM, K, G, P). Ouro Preto, Parque Estadual do Itacolomi, Trilha da Mata do sibrão, 11 December 2006, *R.S. Araújo et al.* 44 (VIC). Reduto, Reduto E.F.L., 12 October 1950, *E.P. Heringer* 2656 (NY, RB). Tombos, Fazenda da Cachoeira, 9 August 1935, *M. Barreto* 1824 (F, MO, R). Uberaba, 7 July 1860, *A.F. Regnell II-198* (US 1322404). Viçosa, Direction of São Miguel, km 8, Fazenda A. Cocerro, 900 m, 26 June 1930, *Y. Mexia* 4802 (BM, F, G, K, MO, NY, P, US); Mata do Paraíso, 5 December 1935, *J.G. Kuhlmann* s.n. (RB 77457, VIC 2672); *Ibid.*, aceiro, em baixada ca. de 100 m depois da segunda cerca, subindo à esquerda da cancela, 23 October 2002, *M.M.M. Lopes* 158 (VIC); 17 February 2003, *M.M.M. Lopes* 174 (VIC); UFV, 23 February 1959, *H.S. Irwin* 2714 (F photo, K, US); *Ibid.*, Jardim Botânico, 7 October 1962, *M.R.R. Vidal* 199 (VIC); 15 October 1979, *A.J. Filho* s.n. (VIC 6393); 15 October 1979, *R.S. Ramalho* 1621 (RB); 11 November 2010, *M.C. Medeiros & R.B. Louzada* 19 (SPF). **São Paulo:**

Sin loc., September 1868, *S. Henschen s.n.* (US 201374). Estrada de Pirapora a Cabreúva, 4 December 1924, *A. Gehrt s.n.* (NY 483765, SP 12903, US 1543120). Caieiras, Terrenos da Cia. Melhoramentos de São Paulo, 27 October 1936, *M. Kuhlmann s.n.* (SP 36635). Campinas, Souzas, s.d., *H.M. Souza s.n.* (IAC 20158); 4 May 1866, *J.C. Mello 8* (K, P 3606702); 20 July 1875, *H. Mosén 3960* (MO, P); Barão Geraldo, Santa Genebra Forest Reserve, Betel, Transect 1, 600 m, 4 January 1985, *A. Gentry & E. Zardini 49163* (MO); 4 January 1985, *A. Gentry & E. Zardini 49173* (MO); *Ibid.*, Transect 2, 550 m, 26 August 1987, *A. Gentry & A. Silva 58692* (MO, UEC); *Ibid.*, 550 m, 27 August 1987, *A. Gentry & A. Silva 58713* (MO, UEC); *Ibid.*, Transect 5, 550 m, 31 August 1987, *A. Gentry 58780* (MO, UEC); *Ibid.*, 550 m, 5 September 1987, *A. Gentry 59067* (K, MO, NY, UEC); *Ibid.*, 550 m, 5 September 1987, *A. Gentry 59077* (UEC); Sítio São Francisco, 31 January 2000, *T. Spinelli et al. 219* (UEC). Helvetia, 3 November 1943, *D.B.J. Pickel s.n.* (SPF 200750, SPSF 948, US 1564384); *Ibid.*, 10 November 1943, *D.I. Stehle s.n.* (SPSF 1012). Jundiá, E.E. Jundiá, 12 April 1994, *L.C. Bernacci et al. 1* (HRCB, SPF). Limeira, Orla da mata da S.A.F.B, 10 October 1946, *M. Kuhlmann 1278* (US). Rio Claro, Fazenda São José, 24 August 2000, *M.A. Assis et al. 1367* (HRCB); *Ibid.*, 4 October 2000, *R. Udulutsch & V.T. Rampin 57* (HRCB); *Ibid.*, 15 November 2000, *R. Udulutsch & M.A. Assis 112* (HRCB); *Ibid.*, 11 January 2001, *R. Udulutsch & M.A. Assis 169* (HRCB); *Ibid.*, 24 March 2001, *R. Udulutsch et al. 232* (HRCB); *Ibid.*, 24 March 2001, *R. Udulutsch et al. 245* (HRCB); *Ibid.*, 7 October 2001, *M.A. Assis & A.G. Manzatto 1595* (HRCB); *Ibid.*, 30 October 2001, *R. Udulutsch et al. 429* (HRCB); *Ibid.*, 3 October 2003, *M.A. Assis et al. 1666* (HRCB). Santa Rita do Passa Quatro, Parque Estadual de Vassununga, Gleba Maravilha, 17 December 2002, *Y.J.A. Tibiriçá & L.F. Coelho 70* (HRCB). São Paulo, Cidade Jardim, 13 November 1941, *W. Hoehne 804* (G, RB). Serra Negra, October-November 1901, *G. Edwall s.n.* (F 896072, SP 15045).

Taxonomic notes. *Tynanthus fasciculatus* can be easily recognized by the laciniate calyx that contrasts with the denticulate or truncate calyx apices found in the remaining species of the genus. This species is the only Southern Brazilian species to bear dense inflorescences with a corymbose or subcorymbose aspect. *Tynanthus fasciculatus* is sister to *T. labiatus*, another Atlantic Forest species (Medeiros & Lohmann in prep.), with which it shares winged fruits. However, *T. fasciculatus* can be easily separated by the dense inflorescences (versus lax inflorescences in *T. labiatus*) and the dense indument on young branchelets (versus glabrescent branchelets in *T. labiatus*).

6. *Tynanthus guatemalensis* Donn. Sm. (1893: 6). Lectotype (designated here):—GUATEMALA. Quezaltenango: Banks of Rio Ocosito, April 1892, *J. Donnell Smith 1488* (US! (barcode 125785); isolectotypes GH! photo, K!, M!, NY!, P!, US! (barcode 125786)).

Fig. 8: G-J

Lianas. Branchelets tetragonal to terete, with or without ritidome, finely striated, lenticled to densely lenticled, pubescent to glabrescent, with simple and peltate trichomes; interpetiolar ridge present; interpetiolar patelliform glands absent; prophylls of the axillary buds 3.5–20 mm long, 2.1–14 mm wide, foliaceous, ovate to elliptic, pubescent or puberulent to glabrescent throughout, with simple, peltate and patelliform trichomes. *Leaves* 2–3 foliolate (more commonly 3); terminal leaflets modified into simple tendrils, without adhesive-disks on tip; petioles and petiolules pubescent throughout surface, with simple and peltate trichomes; petioles (0.9–)1.5–5.6 cm long; petiolules (0.4–)0.6–3.4 cm long; leaflets (2.5–)3.5–12.2 cm long, (1.2–)1.9–7.9 cm wide, membranous to chartaceous (sometimes subcoriaceous), discolor or concolor, elliptic; apex caudate, mucronate; base cuneate or obtuse, symmetrical; margin entire; the abaxial surface pubescent to glabrescent on and near the veins, with simple, peltate and patelliform trichomes; the adaxial surface pubescent to glabrescent on and near the veins, with simple, peltate and patelliform trichomes; glandular trichomes distributed especially on the abaxial surface; second venation weak brochidodromous; pocket domatia, without (sometimes with) trichomes. *Inflorescence* axilar or terminal, a thyrses or a compound thyrses, lax, with conical aspect, first order (1.5–)2.6–10.5 cm long, second order 0.5–2.1 cm long; floral pedicels 1–4 mm long; axis pubescent, with simple and peltate (sometimes also with patelliform) trichomes; bracts of the inflorescence caducous or persistent, pubescent throughout (sometimes only at margins), 0.4–3.3 mm long; floral bracts 0.3–0.5 mm long. *Calyx* green, 1.5–2.5 mm long, 1.3–2.5 mm wide, with patelliform glands, with transversal aperture, truncate or minutely 5-denticulate, pubescent to puberulent (sometimes glabrescent) throughout outside; lobes 0.1–0.4(–0.5) mm long. *Corolla* white, cream or pale yellow, 0.5–0.9 cm long, 1.9–3.5 mm wide at the tube opening; tube 2–5 mm long, internally pubescent at the base, with simple and long and short stipitate trichomes; nectar guides present, yellow; lobes densely pubescent to pubescent throughout lower ones and at the margin of (sometimes throughout) upper ones; upper ones 0.3–1.8 mm long, 0.6–1.9 mm wide, acute to obtuse; lower ones 1.4–3.1 mm long, 1.6–3.2 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 1 mm from the base of the corolla; shorter ones 2–4 mm long; longer ones 3–5 mm long; anthers thecae 0.6–1 mm long, obovate to elliptic, subexserted; connective extending 0.1–0.3 mm beyond anther attachment; staminode 1.7–2 mm long, glabrous. *Gynoecium* with pistil 4–6.5 mm long; ovary 1–1.4 mm long, 0.6–0.8 mm wide, conical,

densely pubescent; style 3–5 mm long, tomentose to pubescent at the base. *Fruit* a linear flattened capsule, (12.7–)14–38 cm long, 0.8–2.4 cm wide, woody, smooth or granular throughout, without lenticels to densely lenticeled, glabrescent (sometimes pubescent at extremities), with peltate and patelliform trichomes (sometimes also with simple); central ridge single, slightly or not prominent; margins prominently raised (winged), 0.3–0.9 cm wide. *Seeds* body 0.8–2 cm long, 0.5–0.9 cm wide; wings 0.6–1.8 cm long.

Phenology. Flowers from April to July and produces fruits from August to April.

Distribution and habitat. Occurs in moist broadleaf forests from Belize (Belize, Cayo, Orange Walk, Stann Creek and Toledo), Guatemala (Alta Verapaz, El Petén, Izabal and Quetzaltenango) and Mexico (Campeche, Chiapas, Quintana Roo, Tabasco and Veracruz-Llave) (Fig. 10).

Additional specimens examined. BELIZE. **Belize:** Gracy Rock Bank (“Gracie Rock”), Sibun River, 27 May 1935, *P.H. Gentle 1652* (K, MO, NY, P). Maskall, 25 May 1934, *P.H. Gentle 1324* (F, K, MO, NY, US). South of Yalbac Hills, Terra Nova Medicinal Plant Reserve, 40 m, 11 June 1993, *J.B. Walker & L. Romero 138* (NY). **Cayo:** Cayo village, May 1907, *E. Campbell 112* (K). Arenal-Valentin road, June-August 1936, *C.L. Lundell 6168* (F, NY, US). 53 Miles Section, Humming Bird Highway, 18 June 1956, *P.H. Gentle 9132* (F, K, MO). Maccal River, bridge between Augustine and Cuevas, 7 October 1972, *J.D. Dwyer & R. Pippin 10189* (MO). Vicinity of Cuevas south of Millionario, 29-30 May 1973, *T.B. Croat 23599* (F, MO, NY). South of Millionario, 1900 ft, 29 May 1973, *A. Gentry 7661* (F, INPA, MO, NY, US). Vicinity of Millionario, 1800 ft, 30 May 1973, *A. Gentry 7689* (MO, NY); 30 May 1973, *A. Gentry 7730* (F, MO, NY). Between Cuevas & Millionario, 30 May 1973, *Dwyer 10814* (MO, US). Vicinity of Millionario between the McCal River and Cuevas, 1900 ft, 30 May-3 June 1973, *T.B. Croat 23715* (F, K, MO, NY, US). 3 miles S of Grano de Oro, 1700 ft, 2 June 1973, *A. Gentry 7755* (F, MO, NY). Vicinity of Grano de Oro lumber camp south of Millionario, 1700 ft, 2 June 1973, *A. Gentry 7768* (F, MO, NY). 4 miles south of Grano de Oro on road to La Flor, 2 June 1973, *J.D. Dwyer 10923* (MO, US). Vicinity of La Flor at Rio de La Flor, 6 mi. south of Grano de Oro, 1700-2000 ft, 3 June 1973, *T.B. Croat 23812* (F, MO). Western Highway, near Belmopan, 3 June 1981, *C. Whitefoord 3115* (BM, MO). Monkey Tail track, 450 m, 29 May 1995, *C. Whitefoord 9499* (BM, F, MO). Chiquibul Forest Reserve, San Pastor track, c. 1 km from Las Cuevas, 560 m, 10 June 1996, *A.I. Garcia A68* (BM, MO). Augustine, Rio Frio Caves road, Mountain Pine Ridge Forest Reserve, 460 m, 3 July 1989, *J. Meave & A. Howe 1433* (BM, MO). Valentin, June-July 1936, *C.L. Lundell 6354* (F, NY, US). **Orange Walk:** Mile 58 on Northern Highway, ca. 4 miles south of Tower Hill, 23 June 1973, *A. Gentry 8489* (MO). 1.5 km S of Program

for Belize Camp, 13 May 1991, *R. Arvigo et al. 502* (NY). Programme for Belize Rio Bravo Research Station, 150 m, 28 May 1997, *D. Lentz et al. 2744* (NY). **Stann Creek:** Stann Creek Valley, Mountain Cow Ridge, 25 March 1940, *P.H. Gentle 3275* (MO, NY, US). Cockscomb Mountains, tributary of Cocoa Branch of Sittee River, 2 km due north of Victoria Peak, 300-500 ft, 5-6 June 1973, *A. Gentry 8014* (MO). **Toledo:** Temash River, 200 ft, 7 May 1935, *W.A. Schipp 8910* (F photo); 5 June 1944, *P.H. Gentle 4654* (MO, NY). Near Agua Caliente, near San Antonio, 18 April 1945, *P.H. Gentle 5335* (F, K, MO). Beyond Central Camp, Edwards Road beyond Columbia, 21 May 1951, *P.H. Gentle 7339* (F, K, MO, NY). Broken ridge, Joe Taylor creek, 2 October 1952, *P.H. Gentle 7775* (F, K, MO). 1.5 miles from Maya village of San Jose on road to Columbia Forestry Station, 12 June 1973, *A. Gentry 8119* (MO). Mile 13 on road west from Punta Gorda, near junction of Southern Highway and road to San Antonio, 100 ft, 14 June 1973, *A. Gentry 8222* (MO). Southwestern Maya Mountains, Columbia River Forest Reserve, Trail between Gloria Camp and Edwards Camp to the South, 15 April 1992, *B.K. Holst 4468* (MO). GUATEMALA. **Alta Verapaz:** Along Río Icvolay between Río Apia and Río Soctelá, 8-10 miles northwest of Cubilgüitz, 200-210 m, 14 March 1942, *J.A. Steyermark 45058* (F). Panzós, Finca Mercedes, Teleman, 70 m, 3 September 1988, *E. Martínez S. et al. 23472* (MO). **El Petén:** Fallabón-Yaxha Road, 22 March 1933, *C.L. Lundell 2193* (F). Carmelita, 1 m south of village, on trail to Flores, 24 June 1942, *F.E. Egler 42-227* (F). Tikal National Park, Tikal, in ramonal on Remate road, 19 May 1959, *C.L. Lundell 15999* (US); *Ibid.*, in zapotal on Remate road, 3 July 1959, *C.L. Lundell 16142* (F, G, NY, US); *Ibid.*, in ramonal covering the ruins, 27 August 1960, *E. Contreras 1467* (F, K, MO, NY). Remate, on Tikal Road, in zapotal, about 12 km NE of the village, 14 May 1960, *E. Contreras 942* (US). Dos lagunas, Ixcanrio, on Aguas Turbias Road, 12 km E, in zapotal, 11 May 1969, *E. Contreras 8517* (F). Laguna Yaxja, Banks of Laguna Yaxja and dry wooded hills of limestone to north and south, 160-250 m, 28 June 1970, *W.E. Harmon & J.D. Dwyer 2772* (MO). Dolores, Rio Mopan, 21 February 1971, *E. Contreras 10583* (MO, NY). Santa Elena, en la orilla del camino para San Andrés, a km 17, lado noreste, 25 May 1971, *R.T. Ortíz 1782* (F, MO, NY, US). Ca. 5 miles S of Tikal, logging road 0-4 miles W of road to Tikal, 19 June 1973, *A. Gentry 8346* (MO, US). **Izabal:** Trail from Los Amates to Izabal, 31 May 1919, *S.F. Blake 7802* (US). Vicinity of Quiriguá, 75-225 m, 15-31 May 1922, *P.C. Standley 24535* (MO, NY, US). MEXICO. Yucatán, September 1935, *R.S. Flores s.n.* (F 782747). **Campeche:** Calakmul, A 500 m al NW de Dos Naciones, 190 m, 23 October 1997, *E. Martínez S. et al. 29324* (NY); A 5 km al E de La Mancolona, 200 m, 17 November 1997, *E. Martínez S. et al. 29720* (NY); 6.5 km al O de Flores Magón, 153 m, 12 March 2002, *J.C. Soto et al. 22687* (MBM); A 6.7 km al E de La Nueva Vida, 302 m, 13 May 2003, *D. Álvarez 5026* (MO, SPF); A 4.3 km al O del poblado Flores Magón, 182 m, 3 June 2003, *D. Álvarez 5219* (MBM, MO); A 7.6 km al E del poblado "Unión 20 de Junio" (antes la Mancolona), 160 m, 2 August 2003, *D. Álvarez & C. Jiménez J. 6140* (MO). Hopelchén, A 4 km al O del ejido Santa Rosa, sobre el camino al ejido Carlos A. Madrazo, 100 m, 25 September 1996, *P. Alvaro M. 605* (BM, MO); A 2.7 km al S de Chan Chen, 12 June 2004, *D. Álvarez et al. 8957* (MO);

A 6.64 km al S de Xmejia, 164 m, 15 June 2004, *D. Álvarez et al.* 9199 (MBM, MO). **Chiapas:** Ocosingo, Ruins of Bonampak, 14 March 1975, *W.S. Hoover* 244 (MO, US); En el viejo poblado de Jalisco (Selva Lacandona), 350 m, 1 December 1976, *J.I. Calzada et al.* 2907 (MO); South of Santo Domingo on road to Bonampak and Echeverria from Chancala, 455 m, 25 January 1982, *D.E. Breedlove & F. Almeida* 57938 (MO); Siria, a 62 Km al SE de Palenque, 400 m, 12 May 1982, *M. Sousa et al.* 12397 (BM, MO); A 9 km al NW de Boca Lacantum, camino a Crucero Corozal-Palenque, 160 m, 16 October 1984, *E. Martínez S.* 8301 (MO); A 5 km al NO de Crucero Corozal, 170 m, 14 June 1985, *E. Martínez S. & G. Aguilar* 15000bis (MO); Camino a las ruinas de Bonampak, reserva Montes Azules, 10 km NE del poblado de Lacanjá, 200 m, 26 October 1985, *S.S. Colín & G.I. Manriquez* 319 (MO); En Ejido Roberto Bárrrios a 60 km al S de Boca Lacantum, camino a Chajul, 200 m, 18 April 1986, *E. Martínez S.* 18357 (F, MO); A 15 km al NW de Boca Lacantum, camino a Palenque, 220 m, 12 June 1986, *E. Martínez S. & M.A. Soto A.* 18582 (F photo, MO); En Nuevo Chihuahua a 70 km al S de Boca Lacantum, 200 m, 23 June 1986, *E. Martínez S.* 18966 (F, MO); Borde del río Lacantún, Estación Biológica de Chajul, 150 m, 2 August 1996, *G.I. Marínquez et al.* 4035 (MO); Nuevo Guerrero, 200 m, 11 April 2002, *G. Aguilar M.* 472 (MBM, MO); A 0.2 km de Nuevo Jerusalem camino a Nuevo Francisco León, 12 m, 4 May 2002, *G. Aguilar M. et al.* 630 (MBM, MO); 4 May 2002, *G. Aguilar M. et al.* 685 (MO); A 6.5 km al S de Nuevo Guerrero sobre el camino a Santo Domingo, 400 m, 6 May 2002, *D. Álvarez et al.* 961 (M, RB); 0.5 km al S de Nuevo Francisco León (Restaurante El Paraíso), 177 m, 10 May 2002, *J.C. Soto et al.* 23490 (M, MO); A 1 km al S de El Paraíso, 325 m, 22 May 2002, *G. Aguilar M.* 992 (MO); A 600 m al SO de Nuevo Jerusalém, 340 m, 31 May 2002, *G. Aguilar M. et al.* 1286 (MO); A 200 m de Nuevo Francisco León, restaurante El Paraíso, 174 m, 16 June 2002, *G. Aguilar M. et al.* 1399 (M, MBM, MO); A 2 km al N de Nuevo Guerrero, 190 m, 22 June 2002, *G. Aguilar M. et al.* 1561 (M, MO, NY); A 1 km de Nuevo México, al Norte del Poblado, 176 m, 9 July 2002, *G. Aguilar M. & F. Aguilar* 1805 (M, MO); A 3.8 km al SE del paraíso, 385 m, 14 October 2002, *G. Aguilar M. & D. Álvarez* 3449 (MBM, MO, NY); A 4 km al S de San Javier, 350 m, 26 January 2003, *G. Aguilar M. et al.* 5206 (MBM, MO, NY, SPF); A 2.1 km al SE de la comunidad Lacanjá Chansayab, 320 m, 17 June 2003, *D. Álvarez* 5378 (MO); A 1 km de al NO del poblado "El limonar", 521 m, 30 August 2003, *D. Álvarez & A. Chambor* 6297 (MO); A 0.57 km al SO del crucero de Bonampak, 340 m, 15 October 2003, *G. Aguilar M. et al.* 8178 (MO); A 0.64 km al O del crucero de Bonampak, 313 m, 13 December 2003, *G. Aguilar M. et al.* 8908 (MBM). Palenque, Ruinas de Palenque, 160 m, 11 May 1982, *M. Sousa et al.* 12382 (BM, MBM, MO). **Quintana Roo:** A 15 km al Sur de Ejido Laguna OM, 8 June 1980, *O. Téllez & E. Cabrera* 2423 (BM, MO, NY). A 8 km al Norte de La Unión, 9 June 1980, *O. Téllez & E. Cabrera* 2456 (MO, NY). A 12 km al Sur del Ejido Laguna OM, sobre el camino a Tomas Garrido, 7 August 1980, *O. Téllez & E. Cabrera* 3054 (MO, NY). A 7 km al norte de Bacalar, 21 December 1982, *E. Cabrera & H. de Cabrera* 4139 (MO). 4 km al NO de Estero Franco, sobre el camino en construccion a Tomas Garrido, lugar llamado El Danto, 17 May 1985, *E. Cabrera et al.* 8349 (BM, MO). Adolfo de

la Huerta, A 4.2 km al ESE de San Carlos, camino a Pozo Pirata, 102 m, 20 June 2004, *D. Álvarez et al.* 9517 (MBM, MO). Othón P. Blanco, A 1.5 km al N de Dos Aguadas, 66 m, 21 June 2004, *D. Álvarez et al.* 9560 (MO). A 1.8 km al O de El Martirio, camino a Pozo Pirata, 97 m, 9 September 2004, *D. Álvarez et al.* 10585 (BM). **Tabasco:** Balancán, La Palma, 1-6 June 1939, *E. Matuda* 3277 (F, K, MO, NY). Huimanguillo, El 32 rumbo a Díaz Ordaz, 150 m, 15 May 1985, *F. Ventura* A. 21496 (MO, NY). Tacotalpa, Disperso a la orilla de la selva Milpa em el cerro cerca del Ejido Lázaro Cárdenas al este del ejido, 50 m, 7 June 1979, *A. Orozco et al.* 2208 (MO). **Veracruz-Llave:** Hidalgotitlán, Hermanos Cedillo, La escuadra por el Rio Soloxuchil, 150 m, 17 August 1974, *M. Vasquez* 927 (M). Minatitlán, 2.5 km al N de Poblado 10 por el camino a Pob. 9, 180 m, 9 May 1986, *T. Wendt et al.* 5280 (MO).

Taxonomic notes. *Tynanthus guatemalensis* is morphologically similar to the Atlantic Forest species *T. micranthus*, with which it shares elliptic leaflets with caudate-mucronate apices, lax and conical inflorescences, a similar corolla length (0.5-0.9 mm in both species), and winged fruits. However, *T. guatemalensis* presents simple tendrils (versus trifold in *T. micranthus*), foliaceous prophylls of the axillary buds (versus minute in *T. micranthus*) and a pubescent inflorescence axis (versus glabrescent in *T. micranthus*). Despite the morphological similarities between those two species, *T. guatemalensis* is more closely related to *T. croatianus*, another Central American species but morphologically very distinct from *T. guatemalensis* (see notes under *T. croatianus*).

Nomenclatural notes. In the protologue of *T. guatemalensis*, Donnell Smith did not clearly indicate which of the materials examined was the holotype. Two duplicates of the *J. Donnell Smith 1488* collection were located at US, where Donnell Smith worked (Stafleu & Cowan 1985: 698), the best quality material is here selected as the lectotype.

7. ***Tynanthus labiatus*** (Cham.) Miers (1863: 193). *Bignonia labiata* Cham. (1832 [1833]: 701). *Schizopsis labiata* (Cham.) Bureau (1865: 373). Type:—BRAZIL. "Brasil aequinoct.," s.d., *F. Sellow* s.n. (holotype LE!; isotypes B destroyed, G-DC!, HAL! photo, K!, K! as photocopy at MO, NY!, US!).

Fig. 11: A-E

Lianas. *Branchelets* tetragonal to terete, with ritidome (conspicuous when old), finely striated, lenticled to densely lenticled, glabrescent (sometimes pubescent at the nodes), with peltate and patelliform trichomes (sometimes also with simple); interpetiolar

ridge absent or present; interpetiolar patelliform glands absent; prophylls of the axillary buds 0.8–2.2 mm long, 0.8–1.9 mm wide, minute, shallowly triangular to triangular, pubescent or puberulent to glabrescent throughout, with simple, peltate and patelliform trichomes. *Leaves* 2–3 foliolate (more commonly 3); terminal leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules glabrescent (sometimes pubescent) throughout surface, with peltate and patelliform trichomes (sometimes also simple); petioles (0.7–)1.3–6.5 cm long; petiolules 0.6–3.8 cm long; leaflets (3.1–)5.3–13.5 cm long, (1.3–)2.5–7.4 cm wide, membranous to chartaceous, discolor, elliptic; apex acuminate, mucronate; base cuneate or obtuse, symmetrical; margin entire; the abaxial surface glabrescent (sometimes pubescent) on and near the veins, with peltate and patelliform trichomes (sometimes also simple); the adaxial surface glabrescent (sometimes pubescent) on and near the veins, with peltate and patelliform trichomes (sometimes also simple); glandular trichomes distributed especially on the abaxial surface; second venation weak brochidodromous; pocket domatia, with or without trichomes. *Inflorescence* axilar or terminal, a thyrses or a compound thyrses, lax, with conical aspect, first order 5.5–14 cm long, second order 1.5–4 cm long; floral pedicels 1–3 mm long; axis pubescent (at some axis nodes), with simple, peltate and patelliform trichomes; bracts of the inflorescence predominantly caducous, tomentose to pubescent only at margins, 0.5–2 mm long; floral bracts 0.4–1.1 mm long. *Calyx* green to yellowish, 1.6–2.4 mm long, 1.7–2.5 mm wide, with patelliform glands, with transversal aperture, minutely 5-denticulate (sometimes truncate), pubescent at teeth to glabrescent outside; lobes 0.1–0.3 mm long. *Corolla* white, cream or pale yellow (sometimes pale pink), 1–1.4 cm long, 3.5–6 mm wide at the tube opening; tube 4–7 mm long, internally tomentose at the base, with simple and long and short stipitate trichomes; nectar guides present, yellow; lobes densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.4–1.4 mm long, 0.9–2.4 mm wide, acute to obtuse; lower ones 1.5–4 mm long, 2.4–4 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 1.1–2.5 mm from the base of the corolla; shorter ones 2.5–7 mm long; longer ones 3.5–9 mm long; anthers thecae 1–1.4 mm long, obovate to elliptic, subexserted; connective extending 0.2–0.3 mm beyond anther attachment; staminode 1.1–2.5 mm long, glabrescent, with long and short stipitate trichomes. *Gynoecium* with pistil 4–12 mm long; ovary 1–1.2 mm long, 0.7–0.8 mm wide, conical, velutinous; style 3–10 mm long, tomentose to pubescent at the base. *Fruit* a linear flattened capsule, 10–27 cm long, 2.4–3.1 cm wide, woody, smooth to granular near the midvein and granular near the margins, without lenticels, glabrescent, with peltate and patelliform

trichomes; central ridge single, slightly or not prominent; margins prominently raised (winged), 0.6–1.2 cm wide. *Seeds* body 0.9–1 cm long, 0.7–0.8 cm wide; wings not seen.

Phenology. Flowers and produces fruits from January to May.

Distribution and habitat. Occurs mainly in moist broadleaf forests, although some populations also reach dry forests from Brazil (Bahia, Minas Gerais and Rio de Janeiro) (Fig. 12).

Additional specimens examined. BRAZIL. Sin loc., s.d., *A. Glaziou* 16269 (P). **Bahia:** Igreja Velha, 1841, *Blanchet* 3267 (BM, BR, F, G, G-DC, LE, M, NY, P). Caetité, Café Baiano, 9 km E de Caetité em direção a Brumado, 800 m, 7 March 1994, *V.C. Souza et al.* 5334 (SPF 108378, fruit attached to an *Adenocalymma* Mart. ex Meisn. specimen). Rui Barbosa, Serra do Orobó, Fazenda Bom Jardim, 426 m, 26 May 2005, *L.P. de Queiroz et al.* 10661 (SPF). **Minas Gerais:** Sin loc., s.d., *E.P. Heringer s.n.* (RB 77285). Catas Altas?, 1882?, *A. Glaziou* 14108 (BR, F, G, K, LE, MO, P, US). Coronel Pacheco, Fazenda Companhia, 29 February 1944, *E.P. Heringer* 1331 (RB). Monjolos, Estrada Corinto-Conselheiro Mata, margem esquerda do Rio Pardo Pequeno, 540 m, 19 February 2011, *M.C. Medeiros & R.B. Louzada* 31 (SPF). Santo Hipólito, Estrada Corinto-Conselheiro Mata, a 6 km de Santo Hipólito, 550 m, 4 April 1996, *J.R. Pirani et al.* 3775 (SPF); 12 January 1998, *J.R. Pirani et al.* 3900 (SPF); 19 February 2011, *M.C. Medeiros & R.B. Louzada* 30 (SPF); Cerca de 5 km além de Santo Hipólito em direção a Monjolos, no antigo leito da estrada de ferro, afloramento de calcáreo à margem esquerda do Rio Pardo Pequeno, 500 m, 24 March 1997, *R. Mello-Silva et al.* 1317 (SPF). Volta Grande, Foz do rio angu, January 2007, *L.C.S. Viana & G.M. Maciel s.n.* (BHCB 109098). **Rio de Janeiro:** Sin loc., 1832, *L. Riedel* 88 (LE, NY). Vallée du Rio Comprido, 18 February 1871, *A. Glaziou* 4703 (P). Itaguaí, Rio Mazomba, 12 January 1950, *L.E.M. Filho* 1029 (R); 12 January 1950, *Brade & A. Duarte* 20165 (MO, NY, RB). Rio de Janeiro, Parque do Jardim Botânico do Rio de Janeiro, Pedra do Marinheiro, 25 January 1989, *R. Marquete et al.* 202 (RB); *Ibid.*, trecho entre a caixa d'água do Caminho do Boi até Pedra do Marinheiro, 5 March 1991, *M. Madruz et al.* 678 (K).

Taxonomic notes. *Tynanthus labiatus* can be easily recognized in the field by the conspicuous ritidome encountered in old branches and stem. Apart from that, *T. labiatus* is also characterized by the glabrescent elliptic leaflets, conical inflorescences and winged fruits, all of which are shared with the Amazonian *T. schumannianus*, its sister species (Medeiros & Lohmann in prep.). However, *T. labiatus* has glabrous inflorescences axes, pubescent only at nodes (versus densely pubescent to pubescent inflorescences axes

throughout in *T. schumannianus*) and larger corollas, ca. 1-1.4 cm (versus smaller corollas, 0.4-0.9 cm in *T. schumannianus*).

8. *Tynanthus macranthus* L.O. Williams (1967: 250) (as "*Tynnanthus*"). Type:— COSTA RICA. Heredia: Roadside 8 km south of San Miguel, 9 July 1964, *R.W. Lent* 42 (holotype F!; isotypes NY!, OKL! photo, US!).

Fig. 11: F-K

Lianas. Branchelets terete, without ritidome, finely striated, densely lenticled, densely puberulent, with simple and peltate trichomes; interpeltolar ridge absent or present; interpeltolar patelliform glands present; prophylls of the axillary buds 1–3 mm long, 1–2.5 mm wide, minute, shallowly triangular, densely puberulent throughout, with simple and peltate trichomes. *Leaves* 2 foliolate; terminal leaflets modified into simple tendrils, without adhesive-disks on tip; petioles and petiolules densely puberulent throughout surface, with simple, peltate and patelliform trichomes; petioles (0.6–)0.8–2.3 cm long; petiolules (0.3–)0.7–2 cm long; leaflets (2.6–)4.5–14.9 cm long, (1–)2.7–6.4 cm wide, chartaceous to coriaceous, discolor, elliptic; apex acuminate, mucronate; base cuneate or obtuse, symmetrical; margin entire; the abaxial surface densely puberulent to puberulent throughout (sometimes only on and near the veins), with simple, peltate and patelliform trichomes; the adaxial surface puberulent to glabrescent on and near the veins, with simple and peltate trichomes; glandular trichomes distributed especially on the abaxial surface; second venation weak brochidodromous; pocket domatia, with or without trichomes. *Inflorescence* axilar or terminal, a thyrse, dense, with corymbose or subcorymbose aspect, 2.5–3–6 cm long; floral pedicels 2–6 mm long; axis densely puberulent, with simple and peltate trichomes; bracts of the inflorescence predominantly caducous, densely puberulent throughout, 1–2 mm long; floral bracts 0.8–1.2 mm long. *Calyx* green, 5–9(–10) mm long, 4–5 mm wide, without patelliform glands, with transversal aperture, minutely 5-denticulate (sometimes truncate), densely puberulent throughout outside; lobes 0.2–0.5 mm long. *Corolla* white, 2–3.8 cm long, 2.5–4 mm wide at the tube opening; tube 5–11 mm long, internally tomentose at the base, with simple and long and short stipitate trichomes; nectar guides present, yellow; lobes densely pubescent to pubescent throughout lower ones and at the margin of (sometimes throughout) upper ones; upper ones 2–8 mm long, 1.5–4 mm wide, obtuse to rounded (sometimes acute); lower ones 4–8(–10) mm long, 3–7 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 3 mm from the base of the

corolla; shorter ones 7–13 mm long; longer ones 9–18 mm long; anthers thecae 1.7–2.5 mm long, elliptic, inserted; connective extending 0.2–0.4 mm beyond anther attachment; staminode 4–7 mm long, glabrescent, with long and short stipitate trichomes. *Gynoecium* with pistil 14–22 mm long; ovary 1.8–2.5 mm long, 0.9–1.1 mm wide, conical to oblong, densely pubescent; style 12–19 mm long, densely pubescent throughout. *Fruit* not seen. *Seeds* not seen.

Phenology. Flowers from April to November; the fruiting season is unknown.

Distribution and habitat. Occurs in moist broadleaf forests from Costa Rica (Heredia and Limón) and Panama (Veraguas) (Fig. 13).

Additional specimens examined. COSTA RICA. **Heredia:** Entre San Miguel y Cariblanco de Sarapiquí, 725 m, 10 July 1964, A. Jiménez M. 2044 (F photo, NY). **Limón:** Talamanca, Between Cahuita and the oil drilling platforms beyond Suretka, 100–300 m, 23–25 April 1982, K. Barringer et al. 2671 (F, MO). PANAMA. **Veraguas:** Vicinity of Continental Divide, third branch of Rio Santa Maria to drop-off to lowlands, 12–15 km NW of Santa Fe, 650–750 m, 16–17 November 1974, R.L. Dressler 4846 (MO). NW of Santa Fe, 8.8 km from Escuela Agricola Alto de Piedra, 17 May 1975, R. Dressler et al. 6191 (MO, US).

Taxonomic notes. *Tynanthus macranthus* is easily distinguished from the other species of the genus by the large flowers (~2–4 cm), conspicuously bilabiate and short corolla tube (0.5–1.1 cm). Apart from that, *T. macranthus* is also characterized by the densely puberulent branchelets, simple tendrils, interpetiolar patelliform glands and corymbose to subcorymbose inflorescences. *T. macranthus* was the first species to diverge in *Tynanthus* (Medeiros & Lohmann in prep.); this species is sister to the remaining species of the genus.

9. *Tynanthus micranthus* Corr. Mello ex K. Schum. (1894: 221) (as "*Tynnanthus micrantha*"). Lectotype (designated by Lohmann, in Lohmann & Taylor 2014: 469):—BRAZIL. São Paulo: Campinas, 30 September 1867, J.C. de Mello 26 (P!; isolectotypes F!, K!, NY!, P!, P! (barcode 481489) as photocopy at MO, UPS! as photocopy at K, US!).

Fig. 14: A–D

Lianas. Branchelets tetragonal to terete, with or without ritidome, finely striated, lenticled to densely lenticled, glabrescent, with peltate trichomes; interpetiolar ridge absent (sometimes present); interpetiolar patelliform glands absent; prophylls of the axillary buds 0.8–1.6 mm long, 0.5–1.2 mm wide, minute, triangular to shallowly triangular, glabrous. *Leaves* 2–3 foliolate (more commonly 3); terminal leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules glabrescent throughout surface (sometimes pubescent at the junction of petiolules), with peltate trichomes (sometimes also with simple); petioles (0.5–)1.5–5.3 cm long; petiolules (0.3–)0.6–2.7 cm long; leaflets (2.3–)4.1–9.1 cm long, (0.7–)1.3–4.2 cm wide, membranous to chartaceous, discolor or concolor, elliptic; apex caudate, mucronate; base cuneate or obtuse, symmetrical; margin entire; the abaxial surface glabrescent, with peltate and patelliform trichomes; the adaxial surface glabrescent, with peltate trichomes; glandular trichomes distributed especially on the abaxial surface; second venation weak brochidodromous; pocket domatia, with (sometimes without) trichomes. *Inflorescence* axilar or terminal, a thyrse or a compound thyrse, lax, with conical aspect, first order 3.5–5–13.5 cm long, second order 1.5–3 cm long; floral pedicels 1–4 mm long; axis glabrescent, with peltate trichomes; bracts of the inflorescence predominantly caducous, glabrescent (sometimes pubescent only at margins), 0.7–6(–9) mm long; floral bracts 0.5–1 mm long. *Calyx* green, 1.2–2 mm long, 1.5–2.3 mm wide, with patelliform glands, with transversal aperture, minutely 5-denticulate (sometimes truncate), glabrescent (sometimes pubescent at teeth) outside; lobes 0.1–0.6 mm long. *Corolla* white, cream or pale yellow (sometimes pale green), 0.5–0.9 cm long, 2–3.5 mm wide at the tube opening; tube 2.5–3.5 mm long, internally tomentose to pubescent at the base or glabrescent, with simple and long and short stipitate trichomes; nectar guides absent, but with a path of long and short stipitate trichomes; lobes densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.4–1.3 mm long, 0.7–1.4 mm wide, acute to obtuse; lower ones 2–3.1 mm long, 1.5–2.7 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 0.8–1 mm from the base of the corolla; shorter ones 2.1–3.1 mm long; longer ones 2.6–4.5 mm long; anthers thecae 0.6–0.8 mm long, obovate to elliptic, subexserted; connective extending 0.2 mm beyond anther attachment; staminode 1–1.2 mm long, with long and short stipitate trichomes. *Gynoecium* with pistil 4.1–4.6 mm long; ovary 0.9–1 mm long, 0.5–0.6 mm wide, conical, velutinous; style 3–3.7 mm long, tomentose at the base. *Fruit* a linear flattened capsule, 7.2–16.5 cm long, 0.9–1.3 cm wide, coriaceous to woody, smooth to granular near the midvein and granular near the margins, without

lenticels to densely lenticled, glabrescent (sometimes pubescent at extremities), with peltate and patelliform trichomes (sometimes also with simple); central ridge single, not prominent; margins prominently raised (winged), 0.1–0.4 cm wide. *Seeds* body 1.2–1.4 cm long, 0.6–0.8 cm wide; wings 0.4–1 cm long.

Phenology. Flowers from September to December and produces fruits from December to May.

Distribution and habitat. Occurs in moist broadleaf forests from Brazil (Mato Grosso do Sul, Paraná and São Paulo) and Paraguay (Alto Paraná and Canindeyú) (Fig. 15).

Additional specimens examined. BRAZIL. Reserva Florestal II, 21 October 2005, *Adriana et al. s.n.* (HRCB 11876). **Mato Grosso do Sul:** Iguatemi, Arredores, 400 m, 21 October 1987, *G. Hatschbach & J.M. Silva 51518* (BR, MO, US). **Paraná:** Parque Nacional do Iguaçu, N border, 2 1/2 km W of road to Capanema, S of Jardinópolis, 23 November 1966, *J.C. Lindeman & J.H. de Haas 3354* (MO, US); *Ibid.*, by forest road near Aranha, SE of Jardinópolis, 24 November 1966, *J.C. Lindeman & J.H. de Haas 3409* (F photo, K, MO, NY, P, RB, US). Alvorada do Sul, Fazenda Ingá, 19 May 2000, *O.C. Pavão s.n.* (FUEL 29345). Arapongas, Fazenda Solana, 26 April 2004, *J.S. Carneiro et al. 300* (FUEL, HRCB). Califórnia, Sítio Ogido, 9 November 1986, *S.N. Ogido 7* (FUEL); Rio Água do Oito, 19 October 2000, *O.C. Pavão 5* (FUEL). Cambé, Mata da Morada do Sol, 8 October 1999, *C.A. Avanzi et al. s.n.* (FUEL 29323). Campo Mourão, Rio da Várzea, 515 m, 14 October 1965, *G. Hatschbach 13033* (F, K, NY, P, UPCB, US). Céu Azul, Boa Vista, 22 October 1969, *G. Hatschbach 22593* (F, K, MO, NY, UPCB); Parque Nacional do Iguaçu, trilha da Jacutinga, 658 m, 12 October 2011, *J.A. Lombardi et al. 8739* (HRCB). Congonhinhas, Fazenda Planalto, beira da represa, 21 October 1998, *A.L. Cavalleiro et al. s.n.* (FUEL 23840, RB 472273, SPF 197643, SPSF 40442). Dois Vizinhos, Região compreendida entre os municípios de Dois Vizinhos e Pato Branco, proximidades do rio Chopim, 500 m, 8 December 2001, *P.H. Labiak & M. Kaehler 2016* (BHCB). Douradina, Fazenda Santa Rosa?, 2 November 1959, *R. Braga & R. Lange 80* (UPCB, US). Fênix, Fazenda Água Azul, 1 November 1998, *J.M. Silva et al. 2587* (ESA, FUEL, G, INPA, K, R, RB, SP, SPF, UPCB). Goioerê, Parque Municipal Antônio Sestak, 25 September 2007, *E.M. Silva s.n.* (RB 467352). Iporã, Sítio São José, Água das Abóboras, 19 October 1997, *E.M. Nakano & I.M. Medri s.n.* (FUEL 24556). Londrina, Floresta dos Irmãos Godoy, 2 October 1985, *F.C. Silva et al. 901* (FUEL, MO); *Ibid.*, borda do extremo norte do Parque, próximo ao rio, 600 m, 12 October 2011, *M.C. Medeiros & E.F. Rossetto 32* (SPF); Fazenda Santa Ana, 24 October 1985, *A.O.S. Vieira et al. s.n.* (FUEL 1661); *Ibid.*, 24 October 1985, *A.O.S. Vieira et al. 41* (MO); Rio 3 Bocas, Sítio do Gasparino, 22 October 1986, *C. Zampieri et al. 41* (FUEL, HRCB, R); Proximidades do EMAUS, 27

September 1997, *M.C.B. Azevedo et al. s.n.* (FUEL 22931); Estância Cabral, 10 October 1999, *S.F. Andrade et al. s.n.* (HRCB 55991); Fazenda Figueira-Paiquerê, Fragmento 1, December 2002, *M.C. Lovato et al. 381* (FUEL); Fazenda Escola, 3 March 2009, *G.F. Santos 7* (FUEL); Parque Municipal Arthur Thomas, trilha da Capivara, 520 m, 14 October 2011, *M.C. Medeiros & E.F. Rossetto 34* (SPF); *Ibid.*, 14 October 2011, *M.C. Medeiros & E.F. Rossetto 35* (SPF). Lupionópolis, Mata São Pedro, 6 May 2005, *J.S. Carneiro et al. 382* (FUEL). Matelândia, 13 October 1962, *G. Hatschbach 9342* (K). Nova Prata do Iguaçu, Rodovia Nova Prata a Cruzeiro do Iguaçu, Rio Jacaratiá, 15 October 1997, *J.M. Silva et al. 2214* (ESA, G, HRCB, SPF). Rolândia, Sítio Jevy, Contorno Norte, 15 October 1996, *R. Losi et al. s.n.* (FUEL 25345). São Pedro do Ivaí, Fazenda Barbacena, 16 October 2003, *O.S. Ribas et al. 5527* (ESA, FUEL, G, MO, RB). Telêmaco Borba, margem da estrada de acesso ao eixo da barragem, 680 m, 22 September 2008, *M. Kaehler 277* (UPCB); Desmatamento para construção do Eixo da Barragem da UH Mauá, 680 m, 23 September 2008, *M. Kaehler 310* (UPCB). **São Paulo:** Adamantina, Sítio São Paulo estrada 6, 7 September 1995, *E.Y. Sasaki s.n.* (ESA 103223, FUEL 29302, SPF 201517, VIC 31746). Gália, Estação Ecológica dos Caetetus, 12 February 2003, *R. Udulutsch & R. Tsuji 1619* (HRCB). Jundiá, Reserva Biológica Municipal da Serra do Japi, Base-Mirante-estrada para DAE-Base, 850-985 m, 23 October 2007, *J.A. Lombardi & S.M. Hieda 6990* (HRCB). Monte Alegre do Sul, Fazenda Benati, 17 March 1995, *L.C. Bernacci et al. 1366* (HRCB, SPF). Piracicaba, Mata da Pedreira, ESALQ, Beira do Ribeirão Piracicamirim, 2 October 1985, *E.L.M. Catharino 444* (ESA, SP). Rio Claro, Fazenda São José, 30 October 2001, *R. Udulutsch et al. 423* (HRCB); *Ibid.*, 7 October 2002, *M.A. Assis & A.G. Manzatto 1599* (HRCB). **PARAGUAY. Alto Paraná:** Reserva Biológica Limoy, cerca del río Limoy y Embalse de la Represa Itaipú em el río Paraná, 14 October 1996, *A. Schinini et al. 31364* (G, MO). **Canindeyú:** Circa Guadalupe, Canendiyu, 27 October 1978, *L. Bernardi 18227* (BM, F, G, MO, NY).

Taxonomic notes. *Tynanthus micranthus* is characterized by the glabrescent branchlets and leaflets, lax inflorescences, small corollas (0.5-0.9 cm), and winged fruits. This species is morphologically similar to the Central American *T. guatemalensis*, from which it differs on various morphological features (see taxonomic notes under *T. guatemalensis*). *Tynanthus micranthus* is sister to a clade that includes two other Atlantic Forest species, *T. fasciculatus* and *T. labiatus* (Medeiros & Lohmann in prep.). Morphologically, *T. micranthus* is most similar to *T. labiatus*, with which it shares glabrescent branchlets and leaflets; however, these two species can be separated by the smaller flowers of *T. micranthus*, with ca. 0.5–0.9 cm long (versus 1-1.4 cm in *T. labiatus*).

10. *Tynanthus panurensis* (Bureau) Sandwith (1953 [1954]: 465) (as “*Tynnanthus*”).
Schizopsis panurensis Bureau (1865: 373). Lectotype (designated here):—BRAZIL.

Amazonas: “Prope Panuré ad Rio Uaupés”, October 1852-January 1853, *R. Spruce* 2626 (P! (barcode 468600); isolectotypes BM!, BM! as photocopy at MO, BR!, E! photo, G!, G! as photocopy at F, G! as photocopy at MO, G! as photocopy at NY, G! as photocopy at US, K!, LE!, P! (barcodes 3606843, 608100), TCD! photo).

Fig. 14: E-I

Lianas. Branchelets tetragonal to terete, without ritidome, finely striated, lenticled to densely lenticled, puberulent to glabrescent, with simple and peltate trichomes; interpetiolar ridge absent or present; interpetiolar patelliform glands absent; prophylls of the axillary buds 2.5–5 mm long, 1.5–3.5 mm wide, foliaceous, obovate, puberulent throughout, with simple, peltate and patelliform trichomes. *Leaves* 2–3 foliolate (more commonly 3); terminal leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules puberulent to glabrescent throughout surface, with simple and peltate trichomes; petioles 3–12 cm long; petiolules 0.7–7.8 cm long; leaflets (3.7–)6.5–20.4 cm long, (2–)4.1–13.7 cm wide, membranous to chartaceous or coriaceous, discolor, elliptic to ovate; apex acuminate, mucronate; base cuneate or obtuse, symmetrical or asymmetrical; margin entire; the abaxial surface pubescent to glabrescent on and near the veins, with simple, peltate and patelliform trichomes; the adaxial surface pubescent to glabrescent on and near the veins, with simple and peltate trichomes; glandular trichomes distributed especially on the abaxial surface; second venation weak brochidodromous; pocket domatia, without trichomes. *Inflorescence* axilar or terminal, a thyrse, lax, with conical aspect, (3–)5–13 cm long; floral pedicels (0.5–)1–9 mm long; axis pubescent to puberulent, with simple and peltate trichomes; bracts of the inflorescence caducous or persistent, pubescent throughout, 1–2.1 mm long; floral bracts 0.6–0.9 mm long. *Calyx* green, 2.5–4 mm long, 1.9–3 mm wide, without patelliform glands, with transversal aperture, truncate or minutely 5-denticulate, puberulent throughout outside; lobes 0.1–0.3(–0.6) mm long. *Corolla* cream or pale yellow (sometimes pale lilac), 1.2–1.7 cm long, 4–6 mm wide at the tube opening; tube 6–7 mm long, internally tomentose at the base, with simple and long and short stipitate trichomes; nectar guides absent, but with a path of long and short stipitate trichomes; lobes densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.6–1.4 mm long, 0.9–1.9 mm wide, acute to obtuse; lower ones 3.2–5.1 mm long, 3.1–4.2 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 1.5–3 mm from the base of the corolla; shorter ones 3.5–6 mm long; longer ones 4–8 mm long; anthers thecae 1–1.2 mm long, obovate to elliptic,

subexserted; connective extending 0.2–0.4 mm beyond anther attachment; staminode 3–3.3 mm long, glabrous. *Gynoecium* with pistil 7–13 mm long; ovary 1.5–2 mm long, 0.7–0.9 mm wide, conical, densely pubescent; style 5–12 mm long, tomentose to pubescent at the base. *Fruit* a linear flattened capsule, 22–25 cm long, (0.5–)0.9–1.4 cm wide, coriaceous to woody, smooth to granular near the midvein and granular near the margins, densely lenticled, pubescent, with simple, peltate and patelliform trichomes; central ridge single, not prominent; margins slightly raised (unwinged), 0.1–0.2 cm wide. *Seeds* not seen.

Phenology. Flowers from October to April. Two fruiting collections were observed, one made in December and the other in May (fallen fruits).

Distribution and habitat. Occurs in moist broadleaf forests from Brazil (Amazonas), Colombia (Amazonas and Caqueta), Ecuador (Orellana) and Peru (Loreto, Pasco and San Martín) (Fig. 16).

Additional specimens examined. BRAZIL. **Amazonas:** SEPLAC, km 60 on Manaus-Caracarai Road (BR 174), 1 December 1974, A. Gentry 12997 (INPA photo, MG, MO, R). COLOMBIA. **Amazonas:** Araracuara, Villa Azul, Rio Caquetá, margen izquierda frente isla Sumaeta, 12 May 1989, C. Londoño et al. 625 (MO); *Ibid.*, 200–300 m, 22 November 1989, C. Londoño et al. 1449 (MO). **Caqueta:** 10 km S of San Jose de Fragua, 320 m, 11 January 1974, A. Gentry et al. 9144 (MO). Araracuara, 28 January 1989, A. Gentry et al. 65294 (MO). ECUADOR. **Orellana:** Tiputini Biodiversity Station, Río Tiputini, about 20 km (via air) east of confluence with Río Tivacuno, Near Erwin Plot #1 off Sendero Harpia, 250 m, October 1998, R.J. Burnham et al. 2307 (MO). PERU. **Loreto:** Alto Amazonas, Capihuari, 5 km NE of Andoas on Río Capihuari, near Ecuador border, Along oil pipeline, 240 m, 17 November 1979, A. Gentry & C. Díaz 28174 (F, MO, NY); Few km W of Shucushayacu on Río Huallaga above Yurimaguas, 180 m, 11 October 1985, A. Gentry et al. 52229 (SPF). Mariscal Ramón Castilla, Pebas, Bora Native community of Brillo Nuevo, Yaguasyacu River (affluent of Ampiyacu River), ca. 150 km ENE of Iquitos, 106 m, 31 October 1981, J. Treacy & J.B. Alcorn 259 (F); 4 November 1981, J. Treacy & J.B. Alcorn 333 (F). Maynas, Florida, Río Putumayo, at mouth of Río Zubineta, 200 m, March–April 1931, G. Klug 1972 (BM, F, MO, NY, US); Nanay to (ad) Iquitos, 200 m, 10 December 1958, F. Woytkowski 5151 (K, MO); Río Ampiyacu, Pebas and vicinity, Trail north from town, 10 April 1977, T. Plowman et al. 6706 (F photo, MO); Near Brilla Nueva, Borro Indian village on upper Río Yaguasyacu, tributary of Río Ampiyacu, 8 November 1977, A. Gentry & J. Revilla 20476 (F); Mishana, Río Nanay, 130 m, 3 December 1977, A. Gentry et al. 21066 (F, MO, NY); *Ibid.*, Río Nanay halfway between Iquitos and Santa Maria de Nanay, Cerca del campamento No. 1, 140 m, 19 May 1979, C. Diaz et al. 1105 (F, MO); Ecuador

border, 1-2 km from Puerto Peru (military post 8 km from mouth of Río Gueppi, tributary of Río Putumayo), 200 m, 18 May 1978, *A. Gentry et al.* 22055 (MO); Pucaurquillo, Trail behind Bora village towards mounte, 18 August 1981, *R. Hahn & R. Tredwell* 31? (MO 2927651); Río Ampiyacu, Pucuarquillo, Path to Witoto central forest, behind Pucuarquillo, 21 September 1981, *R. Hahn et al.* 145 (MO); Iquitos, Allpahuayo, Estación Experimental del Instituto de Investigaciones de la Amazonia Peruana (IIAP), Muestreo de 1000 m², Transecto No 9, 150-180 m, 26 May 1991, *R. Vásquez & N. Jaramillo* 16543 (MO); *Ibid.*, Línea F de la parcela de 25 ha, subparcela 5, 150 m, 20 March 1992, *R. Vásquez et al.* 17806 (MO); San Francisco de Orellana, Río Napo, trail of Pue San Pedro below caserío of Juancho Playa, 9 November 1978, *M. Rimachi* Y. 4064 (F photo, MO, NY). Requena, Jenaro Herrera, Río Ucayali below Requena, 9 December 1977, *A. Gentry et al.* 21323 (F, MO); *Ibid.*, Río Ucayali, 19 February 1987, *A. Gentry et al.* 56126 (F, MO); Sapuena, Basin of Río Ucayali, Arboretum Jenaro Herrera, 21 April 1987, *D.C. Daly et al.* 5122 (MO, NY). **Pasco:** Oxapampa, Cabeza de Mono, Río Iscozacín, 10 km SW of Iscozacín, Palcazu Valley, 320 m, 9 June 1983, *A. Gentry et al.* 41745 (MO); Shiringamazu, ca 20 km S of Iscozacín, Río Palcazu Valley, 300 m, 6 July 1988, *A. Gentry et al.* 63339A (MO). **San Martín:** San Martín, Near km 50 Yurimaguas-Tarapoto road, 200 m, 12 October 1985, *A. Gentry et al.* 52280 (F, MO).

Taxonomic notes. *Tynanthus panurensis* is characterized by the foliaceous prophylls of the axillary buds, unusually long petioles (up to ca. 12 cm) and petiolules (up to ca. 7.8 cm), lax inflorescences, corollas with 1.2-1.7 cm length and fruits with slightly raised margins. This species is most closely related to *T. pubescens* (Medeiros & Lohmann in prep.), with which it shares lax inflorescences and a similar corolla length (1.2-1.7 cm in *T. panurensis* versus 1-1.6 cm in *T. pubescens*); however, *T. panurensis* can be separated by the foliaceous prophylls of the axillary buds (versus minute prophylls in *T. pubescens*), and only slightly raised fruit margins (versus prominently raised in *T. pubescens*). Despite the phylogenetic proximity between these species, *T. panurensis* is morphologically most similar to *T. densiflorus*, with which it shares a series of morphological features (see taxonomic notes under *T. densiflorus* notes).

Nomenclatural notes. Three duplicates of the collection *Spruce 2626* were located at P, and the best quality flowering material is here selected as the lectotype.

11. *Tynanthus polyanthus* (Bureau) Sandwith (1953 [1954]: 465) (as “*Tynnanthus*”). *Schizopsis polyantha* Bureau (1865: 378). Lectotype (designated by Lohmann, in Lohmann & Taylor 2014: 469):—PERU. San Martín: “Prope Tarapoto”, 1855-1856, *R.*

Spruce 4895 (P!; isolectotypes BM!, BR!, C! photo, C! as photocopy at F, C! as photocopy at MO, E! photo, F! (fragments), F! photo, G!, G! as photocopy at F, G! as photocopy at MO, G! as photocopy at NY, G! as photocopy at US, K!, LE!, MPU! photo, NY!, P!, S! photo, TCD! photo).

Schizopsis polyantha var. *boliviana* Bureau (1865: 379). Type:—BOLIVIA. La Paz: “Environs de Mururata”, 1839, *J.B. Pentland 33* (holotype P!).

Tynanthus myrianthus Bureau & K. Schum. (1896 [1897]: 197) (as “*Tynnanthus*”). Lectotype (designated here):—PERU. Loreto: “Ad Yurimaguas”, April 1831, *E.F. Poeppig 2388* (W, W! as photocopy at F, W! as photocopy at K, W! as photocopy at MO, W! as photocopy at US; isolectotypes F!, LE!).

Tynanthus lindmanii K. Schum. (1896 [1897]: 409) (as “*Tynnanthus*”). Lectotype (designated here):—BRAZIL. Mato Grosso: “Barra do Rio dos Bugres” (Barra do Bugres), 26 February 1894, *C.A.M. Lindman A2967* (S! (09-21559) photo; isolectotypes UPS! photo, S! (09-21560) photo, S! (09-21560) as photocopy at K).

Tynanthus caryophylleus (Bello) Alain (1965: 352) (as “*Tynnanthus*”). *Bignonia? caryophyllea* Bello (1881: 293). Neotype (designated here):—PORTO RICO: “Forest near Humacao”, 28 February 1926, *N.L. Britton 8614* (NY!; isoneotype US!).

Tynanthus villosus A.H. Gentry (1976: 60) (as “*Tynnanthus*”). Type:—PERU. San Martín: Tocache Nuevo, Quebrada de Canuto, 18 August 1973, *J. Schunke Vigo 6852* (holotype MO!; isotypes F!, K!, RB!). *syn nov.*

Fig. 17: A-F

Lianas. Branchelets conspicuously tetragonal (with salient extremities) to terete, with or without ritidome, finely striated (sometimes not evident, when young), few to densely lenticled (sometimes without lenticels), villous to puberulent or glabrescent, with simple and peltate trichomes; interpetiolar ridge absent or present; interpetiolar patelliform glands absent; prophylls of the axillary buds 4–19(–25) mm long, 3–18(–23) mm wide, foliaceous, ovate or obovate to elliptic, villous to puberulent throughout, with simple, peltate and patelliform trichomes. *Leaves* 2–3 foliolate (more commonly 2); terminal leaflets modified into simple tendrils, without adhesive-disks on tip; petioles and petiolules villous to puberulent throughout surface, with simple and peltate trichomes; petioles (0.9–)1.4–5 cm long; petiolules (0.2–)0.6–4.6 cm long; leaflets (2.5–)4–16.5 cm long, (1.6–)2.5–12.6 cm wide, membranous to chartaceous (sometimes subcoriaceous), discolor or concolor, elliptic to ovate; apex acuminate, mucronate; base cuneate, obtuse, truncate or subcordate,

symmetrical or asymmetrical; margin entire (rarely dentate); the abaxial surface villous to puberulent (sometimes glabrescent) throughout (sometimes only on and near the veins), with simple, peltate and patelliform trichomes; the adaxial surface villous to pubescent (sometimes glabrescent) throughout (sometimes only on and near the veins), with simple, peltate and patelliform trichomes; glandular trichomes distributed especially on the adaxial surface (sometimes evenly distributed throughout both surfaces); second venation weak brochidodromous; pocket domatia, with or without trichomes. *Inflorescence* axilar or terminal, a thyrse or a compound thyrse, lax, with conical aspect, first order 3.5–15 cm long, second order 1.5–8 cm long; floral pedicels 0.5–7.3(–10.5) mm long; axis villous to pubescent, with simple and peltate trichomes; bracts of the inflorescence caducous or persistent, villous to pubescent throughout, 0.5–3.3(–6) mm long; floral bracts 0.4–0.7 mm long. *Calyx* green to yellowish, 1–2.7 mm long, 1.2–2.2 mm wide, without patelliform glands, with transversal (sometimes oblique) aperture, minutely 5-denticulate (sometimes truncate), tomentose to puberulent throughout outside; lobes 0.1–0.3(–0.6) mm long. *Corolla* white, cream or pale yellow (sometimes pale lilac, pale red or pale blue), 0.4–0.8 cm long, 1.2–3.5 mm wide at the tube opening; tube 2–4.5 mm long, internally glabrescent, with long and short stipitate trichomes; nectar guides absent, but with a path of long and short stipitate trichomes; lobes densely pubescent to pubescent throughout (sometimes only at margins of) lower ones and at margins of or throughout upper ones; upper ones 0.4–1.6 mm long, 0.5–1.5 mm wide, acute to obtuse; lower ones 1.3–3 mm long, 1.2–2.8 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 0.7–1.3 mm from the base of the corolla; shorter ones 2–3 mm long; longer ones 2.5–4 mm long; anthers thecae 0.6–0.8 mm long, obovate to elliptic, subexserted; connective extending 0.1–0.3 mm beyond anther attachment; staminode 0.9–1.2 mm long, glabrescent, with long and short stipitate trichomes. *Gynoecium* with pistil 3.2–5.1 mm long; ovary 0.7–1.3 mm long, 0.5–1 mm wide, conical, velutinous; style 2–3.9 mm long, tomentose at the base. *Fruit* a linear flattened capsule, 10.5–25 cm long, 0.4–0.9 cm wide, coriaceous to woody, granular throughout (sometimes smooth near the midvein), without lenticels to densely lenticelled, villous to puberulent or glabrescent, with simple and peltate trichomes; central ridge single, slightly or not prominent; margins slightly raised (unwinged), 0.1 cm wide. *Seeds* body 0.7–1.5 cm long, 0.3–0.9 cm wide; wings (0.2–)0.4–1.2 cm long.

Phenology. Flowers throughout the year and produces fruits from March to August.

Distribution and habitat. Occurs in moist broadleaf forests from Bolivia (Beni, Cochabamba, La Paz, Pando and Santa Cruz), Brazil (Acre, Amazonas, Mato Grosso, Pará and Rondônia), Colombia (Antioquia, Choco and Meta), Dominican Republic (El Seybo, Monte Cristi and Samaná), Ecuador (Morona-Santiago, Napo and Zamora-Chinchipe), Guiana (Upper-Essequibo), Peru (Amazonas, Cusco, Huánuco, Junín, Loreto, Madre de Diós, Pasco, Puno, San Martín and Ucayali), Porto Rico and Venezuela (Amazonas) (Fig. 18).

Additional specimens examined. Sin loc.. October 1831, *Poeppig 2651* (LE, P). BOLIVIA. **Beni:** Moxos, 66 km de San Ignacio, San Borja, 200 m, 20 February 1995, *M. Moraes & E. Oviedo 2074* (MO). Vaca Díez, 11-15 km NW of Guayaramerin on road to Cachuela Esperanza, 12 February 1978, *W.R. Anderson 12047* (MO, NY, US); Riberalta, 160 m, 29 June 1992, *A. Gentry et al. 77563* (MO). **Cochabamba:** Carrasco, Entre Ríos, Dist. Tres, Sector Coop. Litoral, 280 m, 12 July 2005, *O. Colque & L. Mendoza 262* (SPF); 6 February 2006, *O. Colque & L. Mendoza 410* (SPF). Cercado, The road from Ivirgarsama, approximately 2 km towards Puerto Villarroel, 200 m, 24 February 1996, *N. Ritter 2996* (MO). Chapare, Villa Tunari, Hotel El Puente, 300 m, 21 January 1996, *J.R.I. Wood 10423* (K). **La Paz:** Sin loc., 1-22 July 1939, *B.A. Krukoff 10456* (K). Abel Iturralde, Tumupasa, 540 m, 10 January 1902, *R.S. Williams 508* (K, NY); Siete Cielos, Río Manupare, 180 m, 4 June 1987, *J.C. Solomon 16919* (MO). Franz Tamayo, Parque Nacional Madidi, río Quendeque, 300 m, 7 February 2002, *A. Fuentes et al. 3753* (MO); *Ibid.*, NW de Apolo, senda Azariamas-San Fermin, Parcela temporal (0.1 ha), 1326 m, 27 May 2006, *I. Loza et al. 73* (SPF); 27 May 2006, *I. Loza et al. 78* (SPF). Nor Yungas, Below San Pedro, Yolosa-Caranavi road, valley of Río Coroico, 760-950 m, 15 January 1984, *A. Gentry et al. 44262* (M, MBM, MO, NY); Corocoro, 12 km NE of Caranavi, 1400-1500 m, 16 January 1984, *A. Gentry et al. 44315* (MO, NY); 16 January 1984, *A. Gentry et al. 44350* (MO); 1 km SW of Yolosa on road to Chuspipata, Ford of Río Cedro, 1400 m, 22 February 1984, *J.C. Solomon & J. Kuijt 11594* (F photo, MO); 5.5 km below Coroico (towards Yolosa) (1.4 km above Yolosa), 1400 m, 16 May 1985, *J.C. Solomon 13733* (MBM, MO, NY); 3.8 km below Coroico and Yolosa, 1500 m, 25 September 1986, *J.C. Solomon 15665* (MO). Sud Yungas, Basin of Río Bopi, Asunta (near Evenay), 690-750 m, 27-31 July 1939, *B.A. Krukoff 10695* (F, G, K, MO, NY, US); Valle del río Unduavi, entre Santa Rosa y Machacamamarca expo. N-o, 1400 m, 4 February 1988, *R. Seidel & E. Richter 1207* (MO). **Pando:** Abuná, Nuevo Mundo, 180 m, 29 June 1992, *A. Gentry et al. 77573* (MO). Nicolás Suárez, Km 15 between Cobija and Porvenir, 300 m, s.d., *M. Cardenas 4167* (US); En la zona de Campoana, junto a la barraca San José, 290 m, 14 January 1983, *F. Casas & Susanna 8264* (G, MO, NY). **Santa Cruz:** Im Gebüsch des Waldes am Westufer des Río Pirai, unweit Santa Cruz, January 1911, *T. Herzog 1460* (G). Andrés Ibáñez, 2 km W of center of La Belgica, 360 m, 24 January 1987, *M. Nee 33781* (G, MO, NY); 4 km S of Pedro Lorenzo

on old road from Santa Cruz to Abapó, 525 m, 21 January 1998, *M. Nee 48058* (MO, NY); Along "old" highway to Cochabamba, vic. Turnoff of highway south to Abapó, 13 km SW of center of Santa Cruz, 450 m, 29 July 2003, *M. Nee 52391a* (NY); 6.4 km (by dirt roads) SE of Pedro Lorenzo on way to Peji, 4.5 km SW of Peji, 530 m, 29 June 2004, *M. Nee 52633* (MO, NY); Camino entre Warnes y La Bélgica, 353 m, 18 February 2006, *D. Villarroel et al. 347* (NY, SPF); Porongo, Localidad del Monumento Natural Espejillos, Precipicio del mirador, 1200 m, 16 January 2008, *I. Linneo & D. Galindo 1326* (SPF). Cercado, Bosques del Piray, 450 m, 4 February 1917, *J. Steinbach 3224* (BM, F photo, K); 20 January 1921, *J. Steinbach 5253* (F, G, MO, NY). Cordillera, 2.5 km (by road) W of railroad and 3.5 km (by road) W of the Santa Cruz-Abapó highway and San Joaquín, along gravel road to "Pozo PCHX1001", the turnoff 5.5 km S of Basilio, 570 m, 24 May 2005, *M. Nee 53129* (MO, NY, SPF). Ichilo, Santa Cruz 130 km NW linea recta, puente Rio Yapacaní 35 kms hacia Puerto Grether, 250 m, 18 March 1981, *S.T. Beck 6557* (M, MO); Vicinity of old buildings for highway construction, ca. 2 km W of Villa San Germán on highway from Buena Vista to Río Ichilo, 275 m, 22 February 1998, *M. Nee 48385* (MBM, MO, NY); 3.5 km SW of turnoff at Villa San Isidro from new highway from Buena Vista to Río Ichilo, 360 m, 1 March 1998, *M. Nee 48546* (MO, NY); Buena Vista, Orillas del camino entre Buena Vista y el Cairo, 320 m, 2 February 1990, *I.G. Vargas C. 377* (MO, NY); Ignacio Warnes, E side of the village of Colonia Okinawa 1, 250 m, 28 January 1987, *M. Nee 33837* (MO, NY). José Miguel de Velasco, Parque Nacional Noel Kempff Mercado, 14 km SE del Estancia Flor de Oro, cerca Rio Itenez, 260 m, 9 March 1992, *A. Perry 686* (MO); *Ibid.*, Comunidad Florida, 200 m, 2 July 1993, *M. Saldias et al. 2928* (MO); *Ibid.*, Lago Caiman, 540 m, 19 January 1997, *M. Garvizu et al. 336* (G, MO); *Ibid.*, Campamento Los Fierros, 200 m, 18 March 1997, *L. Sánchez et al. 402* (G, MO); Carretera al Chore, Entre Arroyo Las Londras y Arroyo El Tigre, 150 m, 24 July 1996, *M. Peña-Chocarro & L. Arroyo 167* (G, MO); 25 km al norte del aseradero Moira yendo al Chore, Bosque de lianas del "Proyecto Bejucal" de USZ, 160 m, 26 July 1996, *A. Jardim et al. 3189* (MO); Camino de Florida hacia las Mechitas, 450 m, 24 January 1997, *J. Guillen et al. 297* (G, MO). Ñuflo de Chávez, Perseverancia, NW of Santa Cruz on Río Negro, Transect 3, 100 m, 11 May 1991, *A. Gentry & M. Peña 73697* (MO); Near San Julian (S), 274 m, 27 February 2003, *L. Rico et al. 1406b* (K, MO). Sara, Área natural de manejo integrado Amboró, camino a San Isidro, pasando el puente del río Moyle, 278 m, 20 February 2006, *D. Villarroel et al. 367* (NY, SPF). BRAZIL. **Acre:** Jordão, Trails and roads 2-3 km SE of Foz de Jordão, 250-275 m, 7 February 2009, *F.A. Michelangeli et al. 1356* (SPF). Acrelândia, BR-364, km 87, Ramal do Projeto 2, 13 February 2000, *I.S. Rivero et al. 309* (SPF). Bujari, Basin of Rio Purus, Riozinho do Andirá (tributary of Rio Acre), Seringal Andirá, 24 March 1995, *D.C. Daly et al. 8457* (MO, NY, UFACPZ); Riozinho do Andirá, Colocação Curitiba, 8 June 1995, *A.R.S. Oliveira et al. 540* (SPF, UFACPZ); Rio Antimari, Floresta Estadual do Antimari, right bank, Colocação Pé da Terra, 11 March 1997, *D.C. Daly et al. 9474* (SPF, UFACPZ). Cruzeiro do Sul, Perto do entroncamento com o ramal Pentecoste, 26 April 2001, *L.G. Lohmann et al. 370* (MO, NY). Marechal Thaumaturgo, Reserva Extrativista do Alto Jurua, Rio

Juruá, S of confluence with Rio Acuriá and N of São João do Breu, Colocação Tapaúna, 31 March 1993, *D.C. Daly et al. 7653* (INPA, NY, UFACPZ); *Ibid.*, Fazenda Paraguay, 3 April 1993, *D.C. Daly et al. 7728* (INPA, NY, UFACPZ); *Ibid.*, Foz do Bajé, Boa Vista da União, 30 April 2001, *L.G. Lohmann et al. 413* (MO, NY); *Ibid.*, Foz do Bajé, Boa Vista da União, Colocação Horizonte, 1 May 2001, *L.G. Lohmann et al. 421* (MO, NY); *Ibid.*, Margem direita do Rio Arara, 6 May 2001, *L.G. Lohmann et al. 476* (MO, NY). Plácido de Castro, Porto Edith, arredores da casa do Sr. João, Margem esquerda do Rio Abunã, 14 May 2001, *L.G. Lohmann & E.C. Oliveira 505* (MO, NY). Porto Acre, Reserva Florestal do Humaita, Beira do Rio Acre, 21 March 1995, *C. Figueiredo et al. 741* (SPF, UFACPZ). Rio Branco, Parque Zoobotânico, Estrada Dias Martins, próximo à entrada do Herbário, s.d., *G. Claros & R. Ehrich 315* (UFACPZ); *Ibid.*, 3 March 1993, *C.S. Figueiredo & H.B.N. Borges 100* (UFACPZ); *Ibid.*, inside main gate, 25 March 2002, *D.C. Daly 11565* (NY); *Ibid.*, estrada de acesso ao herbário, 160 m, 5 March 2012, *M.C. Medeiros et al. 37* (SPF); Km 1 ao km 23 da Rodovia Rio Branco-Porto Velho, 21 February 1978, *J.U. Santos et al. 69* (MG, MO, US); Rio Branco-Porto Velho Highway, between km 22-37, 8 February 1979, *B.W. Albuquerque et al. 1345* (MO, NY, US). Santa Rosa, Rio Purus, left bank, Seringal Refúgio, S of Igarapé Extrema de Baixo, 25 March 1999, *D.C. Daly et al. 10083* (SPF, UFACPZ). Sena Madureira, BR-364, entre km 245-246, Fazenda Liberdade, 140-150 m, 6 February 2002, *M. Alves et al. 2734* (SPF); Basin of Rio Iaco (tributary of Rio Purus), Fazenda São Jorge I, property of Acre Brasil Verde, timber concession of Laminados Triunfo Ltda, 107 km NW of Rio Branco on BR-364, then ca. 22 km E on Toco Preto access road, 200 m, 7 July 2008, *D.C. Daly et al. 13228* (RB). Xapuri, Fazenda Bomfim, 18 March 1995, *D.C. Daly et al. 8365* (MO, NY, UFACPZ); 19 March 1995, *D.C. Daly et al. 8386* (MO, NY, UFACPZ); Margem direita do Rio Xapuri, 18 May 2001, *L.G. Lohmann & E.C. Oliveira 567* (NY); Estrada para Brasília (BR-317) km 243, ramal da Cachoeira, a aproximadamente 8 km da BR, em frente à fazenda Bom Jesus, 200 m, 9 March 2012, *M.C. Medeiros et al. 40* (SPF). **Amazonas:** Along Rio Castanho, tributary of Rio Padauri, upper Rio Negro Basin, 100-140 m, 16-24 February 1946, *F. Cardona 1419* (US). Esperança, Ad ostium fluminis Javary, 11 February? 1942, *A. Ducke 866* (F, IAN, MG, MO, NY, R, RB, US). Lábrea, Rio Curuquetê, Cachoeira Republica, 24 July 1971, *G.T. Prance et al. 14559* (INPA, K, MG, MO, NY, R, US). Manaus, Road to Rio Negro from km 12 of Estrada do Aleixo, vicinity of Manaus, 14 December 1974, *A. Gentry 13303* (INPA, MG). Parintins?, 1 April 1946, *J.M. Pires & G.A. Black 1211* (K, IAN). Presidente Figueiredo, Estrada Manaus-Caracarái, Reserva Biológica do INPA, 1978, *A. Anderson s.n.* (INPA 142420). **Mato Grosso:** Salto do Sepotuba, March 1909, *F.C. Hoehne 1568?* (R); March 1909, *F.C. Hoehne 1582* (R); March 1909, *F.C. Hoehne 1583* (R). Novo Mundo, Reserva Particular do Patrimônio Natural Lote Cristalino, Trilha do Teles Pires, 172 m, 7 May 2007, *D. Sasaki et al. 1625* (K); Parque Estadual Cristalino, Cachoeira do Escondido, entrada pela Fazenda AJJ, 28 January 2008, *D. Zappi et al. 900* (K). Tapirapoan, January 1914, *F.C. Hoehne 5852* (R); January 1914, *F.C. Hoehne 5853* (R). **Pará:** Rio Branco de Óbidos, Castanhal grande, 11 December 1913, *A. Ducke s.n.* (MG 15122); 25 January 1918, *A. Ducke s.n.* (MG 16943).

Roadside on BR 163, Cuiabá-Santarém road, km 879, 310 m, 14 February 1977, *J.H. Kirkbride Jr. & E. Lleras 2787* (F photo, INPA, K, MG, MO, NY, RB, US). Altamira, Xingu River, Assurini Indians, 15 June 1986, *W. Balée 2597* (NY). Faro, 19 August 1907, *A. Ducke s.n.* (K, MG 8392); 30 January 1910, *A. Ducke s.n.* (INPA 11254, K, MG 10565); 11 May 1911, *A. Ducke s.n.* (MG 11647). Itaituba, Rio Tapajós, s.d., *A. Ducke s.n.* (MO 2305625, R 23820, RB 18409). Jacundá, Rio Tocantins, 14 May 1951, *R.L. Fróes 27092* (IAN, K, RB). Marabá, Serra dos Carajás, estrada do estéril sul, às proximidades da Barragem, 6 February 1985, *O.C. Nascimento & R.P. Bahia 1189* (MG). Monte Alegre, Colonia Itauajury, 6 March 1923, *A. Ducke s.n.* (R 23821, RB 18410). Oriximiná, Rio Trombetas ao norte, ao longo do rio próximo à Mineração Rio Norte, 22 July 1980, *C.A. Cid et al. 1710* (F, G, INPA, MG, MO, NY, US); Porto Trombetas, Mineração Rio do Norte, Entrada do Alter do chão, 20 November 1990, *O.H. Knowles 1620* (INPA); *Ibid.*, 1991, *Evandro & Knowles 424* (INPA); Comunidade Pancada, 22 June 2006, *D.R. Oliveira & Augusto 98* (INPA). Parauapebas, Serra dos Carajás, Vila de N-5, final da rua Angelim, 29 March 1989, *J.A.A. Bastos 161* (MG). Pau D'Arco, Marajoara, s.d., *J. Grogan 51* (IAN); 16 February 1997, *J. Grogan 50* (IAN, INPA). Santarém, Serra de Pequiatura, 28 March 1924, *J.G. Kuhlmann 1816* (MO, R, RB); Estrada Santarém-Cuiabá, km 67, Reserva florestal do IBDF, 6 March 1979, *M.R. Cordeiro et al. 1610* (IAN); FLONA Tapajós, BR-163, km 83, estrada de acesso à torre do projeto LBA, 150 m, 21 November 2011, *M.C. Medeiros & T. André 36* (SPF). Tucuruí, BR-423, 15 March 1981, *U.N. Maciel & C.S. Rosário 552* (MG).

Rondônia: Estrada Porto Velho-Cuiabá, BR-364, km 290, margem esquerda da estrada, 13 February 1983, *C.A.A. Freitas et al. 98* (INPA, MO). Porto Velho, Campo da sub-estação, 18 November 1949, *N.T. Silva 358* (IAN, INPA, K); Guajará-Mirim-Abunã, trecho entre o km 12 ao km 36, 1 February 1983, *L. Carreira et al. 414* (IAN, INPA, MG, NY). Presidente Médici, Picadão que confina a 7a. e 8a. linha, margem esquerda da BR 429, 24 March 1986, *N.A. Rosa et al. 4984* (MG, MO).

COLOMBIA. **Antioquia:** Caucasia, Hacienda "La Candelaria", Universidad de Antioquia, 150 m, 5 September 2000, *R. Fonnegra et al. 7157* (MO). **Choco:** Upper Río Truandó, La Teresita (INDERENA Camp.), 100-200 m, 19 January 1974, *A. Gentry 9383* (MO). **Meta:** Villavicencio, 450 m, 1-2 September 1917, *F.W. Pennell 1602* (NY).

DOMINICAN REPUBLIC. **El Seybo:** El Jovero, wooded slope at La Pocilga, 150 m, 27 July 1930, *E.L. Ekman H.15782* (K, NY, US). **Monte Cristi:** Sabaneta, La Cidra, In vicinity of Laguna, 5-600 m, 9 November 1930, *E.J. Valeur 532* (K, MO, NY, US); *Ibid.*, 640 m, 7 April 1955, *J.J. Jimenez et al. 2909* (K, US). **Samaná:** Vicinity of Laguna, Samaná Peninsula, chiefly on the Pilón de Azúcar, 100-500 m, 19 December 1920, *W.L. Abbott 330* (US); Sabana de la Mar, in Loma del Bejuco-clavo, 7 July 1930, *E.L. Ekman H.15590* (US); La Laguna, Península de Samaná, 75 m, 5 August 1930, *E.L. Ekman H.15853* (F, MO).

ECUADOR. **Morona-Santiago:** Basin of Rio Morona, Rio Mangosiza, Mission of Miazal, 45 km ESSE of Sucua (by air), at edge of cultivated field at Chumbee's house, 300 m, 19 February 1990, *C.F. Limbach & M.D. 125* (MO). El Centro Shuar Pampants, Rio Kankaim (Cangaime), 300 m, 13 September 1985, *A. Warush RBAE99* (MO, NY). El Centro Shuar Kankaim (Cangaimine), Rio Kankaim (Cangaime),

20 km WNW del Taisha, 500 m, 15 October 1985, *D. Shiki RBAE216* (NY); 15 October 1985, *D. Shiki RBAE218* (MO, NY). Morona, Cordillera de Cutucú, Centro Shuar Uunsuants/Transkutuku, Bosque intervenido junto al Río Mainpaimi, 600 m, 18 January 2002, *W. Palacios et al. 15532* (MO). **Napo:** Road from Lago Agrio Airport, 250 m, 11 February 1974, *A. Gentry 9836* (MO). 9-11 km S of Coca on road to Auca oil field, 5 November 1974, *A. Gentry 12491* (MO). 43-47 km S of Coca, end of Aucas oil field near Río Tiputini, 300 m, 5 November 1974, *A. Gentry 12512* (MO). 4 km sur de Puerto Napo em el Rio Napo, 500 m, 4 August 1984, *C. Dodson et al. 14934* (MO). Estación Experimental INIAP-Payamino, 5 km NE de Coca, 250 m, 16-26 February 1986, *D. Neill 7151* (MO, NY). Reserva Etnica Huaorani, Carretera y oleoducto de Maxus, km 119-120, Carretera a Plataforma GINTA, 235 m, March 1995, *M. Aulestia et al. 3586* (SPF). Yasuni Forest Reserve, road from PUCE Scientific Station to end of road towards Waoroni Territory, 240-310 m, 29 June 1995, *P. Acevedo-Rdgz. & J.A. Cedeño 7572* (MO, P, US). Tena, Estación Biológica Jatun Sacha, Río Napo, 8 km al este de Misahualli, Parcela Permanente 02, 400 m, 14 December 1989, *W. Palacios 4771* (G, K, MO, NY). **Zamora-Chinchipe:** Nangaritza, Miazi, along Rio Nangaritza, Transect 3, 850 m, 28 July 1993, *A. Gentry 80558* (MO). GUIANA. **Upper Essequibo:** Rewa River, near Camp 2 at foot of Spider Mountains, 200-250 m, 22 September 1999, *M.J. Jansen-Jacobs et al. 6073* (F, K, MO, NY, P, US). PERU. **Amazonas:** Bagua, Quebrada shimpunts alto rio Cenepa, Monte al lado shimpunts, 800-1100 ft, 22 February 1973, *E. Ancuash 41* (F photo, MO, NY); Quebrada Huampami, Rio Cenepa, Monte orilla de Huampami, 600 ft, 29 May 1973, *R. Kayap 829* (F, MO); Marañon valley, between Oracusa and Sta. Maria del Nieva, 240 m, 11 February 1978, *D.C. Wasshausen & F. Encarnación 884* (G, K, MO, US); 2-3 km SW of Chiriaco on road to Bagua Chica, Marañon Valley, valley of Río Chiriaco, 300-330 m, 17 June 1978, *A. Gentry et al. 23123* (MO); Imaza, Comunidad Aguaruna Yamayakat, 240 m, 23 March 1995, *C. Diaz et al. 7597* (F, MO); *Ibid.*, 320 m, 13 March 1996, *N. Jaramillo et al. 1374* (F, MO); *Ibid.*, Quebrada Kusú, transecto 2 x 500 m, 380 m, 1 November 1996, *R. Vásquez et al. 21375* (MO); 5 November 1996, *R. Vásquez et al. 21497* (MO); 9 November 1996, *R. Vásquez et al. 21706* (MO); 9 November 1996, *R. Vásquez et al. 21772* (MO); *Ibid.*, 600 m, 6 June 1997, *R. Vásquez et al. 23937* (F, MO, NY). Condorcanqui, Huambisa, Valle del Rio Santiago, approx. 65 km N de Pinglo, Quebrada Caterpiza, 200 m, 10 March 1980, *V. Huashikat 2218* (MO); El Cenepa, Comunidad Aguaruna Pagki-Suwa, Río Cenepa, 289 m, 21 January 1997, *R. Vásquez et al. 22079* (F, MO). **Cusco:** La Convención, Río Manguriari (Manguyari), Alto Urubamba, upstream to Río Manguriari, 750 m, 2 February 1991, *P. Núñez & G. Ortiz 12758* (MO); 2 February 1991, *P. Núñez & G. Ortiz 12837* (MO); 2 February 1991, *P. Nuñez & G. Ortiz 12845* (MO); Echarate, San Martin-3 Well Site, 400 m, 10 March 1997, *P. Nuñez et al. 19720* (NY, US). Quispicanchi, Hills around Río Araza between Pande Azucar and Quince Mil Airport, 292 km from Cusco, 643 m, 10 August 1991, *P. Nuñez V. 13905* (MO); 10 August 1991, *P. Núñez 14080* (MO); Camanti, 254 km from Cusco road to Maldonado, 15 Quince area, 643 m, 18 February 1991, *P. Núñez 13006* (MO). **Huánuco:** Leoncio Prado, Vicinity of Tingo María, East of Río Huallaga, 670 m, 9 March 1962, *J.*

Schunke-Vigo 5813 (F, K, MO, US); Hills east of Tingo Maria, 5 October 1972, *T.B. Croat 21121* (MO); Across Río Huallaga from Tingo Maria, 650 m, 17 January 1976, *A. Gentry et al. 15894* (F, MO, NY); Rupa Rupa, Tingo María, Limestone hills opposite airport, 700-780 m, 9 December 1981, *T. Plowman et al. 11276* (F, K); Tingo Maria, 670 m, 22 August 1959, *F. Woytkowski 5391* (K, MO). Marañón, Valley of Río Huallaga, 110-140 km N of Tingo Maria, near San Martín border, 550 m, 4 February 1984, *A. Gentry & D.N. Smith 44929* (MBM, MO, NY). Pampahuasi, January 1830, *Poeppig 1617* (G). **Junín:** La Merced, 700 m, 20-4 May-June 1929, *E.P. Killip & A.C. Smith 23670* (US). **Loreto:** Tarapoto, November 1902, *E. Ule 6577* (G, K, MG). Alto Amazonas, Fortaleza, near Yurimaguas, 140 m, December? 1932, *G. Klug 2778* (BM, F, G, K, MO, NY, US); Old Andoas, Río Pastaza, 190 m, 26 December 1985, *W.H. Lewis & M.C. Gnerre 10372* (MO); Washintsa and vicinity, Río Huasaga, Achual Jívaro, 185 m, 16-26 June 1986, *W.H. Lewis et al. 11125* (MO); Puranchim, Río Sinchiyacu, 200 m, 21-27 November 1986, *W.H. Lewis et al. 11849* (MO); Petro Estación Morona, río Morona, 160 m, 22 March 1987, *W.H. Lewis et al. 12934* (MO); Andoas, Río Pastaza near Ecuador border, near airport, 230 m, 16 November 1979, *A. Gentry & C. Díaz S. 28135* (F, MO); *Ibid.*, 210 m, 15 August 1980, *A. Gentry et al. 29814* (F, MO); Balsapuerto, 220 m, January 1933, *G. Klug 2836* (BM, F, G, K, MO, NY, US). Coronel Portillo, IVITA, km 59 from Pucallpa toward Tingo Maria, 250 m, 16 January 1976, *A. Gentry & J. Revilla 15888* (MO). Datem del Marañón, Tierra Blanca, on Río Morona?, s.d., *G. Tessmann 4914* (G, NY). Loreto, Nueva Jerusalem and vicinity, Río Macusari, 220-300 m, 29 December 1985-3 January 1986, *W.H. Lewis et al. 10421* (MO); *Ibid.*, 10-11 June 1986, *W.H. Lewis et al. 10987* (MO); Tigre, Río Corriente, Teniente López, Caserío Jíbaros, Bosque 10, 26 November 1979, *F. Ayala et al. 2428* (MO); Pampa Hermosa and vicinity, Río Corrientes, 1 km al S of junction with Río Macusari, 160 m, 3-20 December 1985, *W.H. Lewis et al. 10184* (MO); Nueva Nazaret, Río Morona, 160 m, 3 December 1986, *W.H. Lewis et al. 12445* (MO). Maynas, Río Zumun, affluent du río Yahuas-Yacu, affluent du río Ampí-Yacu, affluent de l'Amazone à Pebas, commune de Colonia, territoire des Indiens Bora, 14 June 1978, *S. Barrier 1095* (F, G, NY, P); Caseria Alianza, Río Tamshiyacu, trail toward Río Manítí, 140 m, 1 August 1980, *A. Gentry et al. 29319* (MO); 1 August 1980, *A. Gentry et al. 29321* (MO); Yanamono, Explorama Tourist Camp, Río Amazonas halfway between Indiana and mouth of Río Napo, 130 m, 10 July 1983, *A. Gentry et al. 42873* (MO); Alto Nanay, Near Santa María de Nanay, 24 February 1968, *D.R. Simpson & J. Schunke-Vigo 702* (G, NY, US); Iquitos, Manacamiri, Río Nanay, 130 m, 5 March 1995, *F. Ayala 6867* (M); Quistococha, Ca. 10 km of Iquitos, Arboretum of Universidad de Amazonas, 15 November 1974, *A. Gentry & F. Ayala 12689* (F, MO). **Madre de Dios:** Manu, Parque Nacional del Manu, Río Manu, Cocha Cashu Station, 400 m, 3 April 1977, *B. Bell & R.B. Foster 6262* (F photo); *Ibid.*, 380 m, 17 October 1979, *A. Gentry et al. 26862* (F, MO); Pantiacolla, Serranía across Río Alto Madre de Dios from Shintuya, 450-650 m, 28 October 1979, *A. Gentry et al. 27282* (F, MO). Tambopata, Ca. 5 km from Puerto Maldonado near Río Tambopata, 200 m, 24 January 1976, *A. Gentry & J. Revilla 16318* (F, MO); Road from Puerto Maldonado to Tambopata, 0-4 km from Puerto Maldonado, 220

m, 25 January 1976, *A. Gentry & J. Revilla 16354* (F, INPA, MO, NY); Ca. 20 km W of Puerto Maldonado, on road to Quince Mil, 250 m, 23 April 1977, *A. Gentry et al. 19698* (F, MO); Outskirts of Puerto Maldonado, 210 m, 27 February 1981, *A. Gentry & K. Young 31757* (F, G, MO); Cusco Amazónico, Río Madre de Dios below Puerto Maldonado, 200 m, 20 February 1989, *A. Gentry & P. Núñez 66032* (MO); Lago Sandoval, 13 km NE of Puerto Maldonado, lake edge, trails, 200 m, 25 July 1989, *P. Núñez 11199* (MO); Cuzco Amazónico, trail to Lago Sandoval across Río Madre de Dios, ca. 12 km E of Puerto Maldonado, 200 m, 21 February 1990, *A. Gentry & P. Núñez 69375* (MO); Río Heath, Peru/Bolivia border, 200 m, 2 March 1990, *A. Gentry & P. Núñez 69786* (MO, NY); 2 March 1990, *A. Gentry & P. Núñez 69793* (MO, NY); Puerto Maldonado, 650 ft, 21 March 1944, *R.J. Seibert 1899* (MO, US). **Pasco:** Oxapampa, Palcazu valley, near the confluence of Rio Palcazu and Rio Iscosacin, Juan Frantzen property, 300 m, 23 April 1983, *D.N. Smith 3890* (MO). **Puno:** Carabaya, Ridge between Río Candamo and Río Guacamayo, 400-600 m, 22 May 1992, *A. Gentry et al. 76975* (MO, NY). **San Martín:** Yurimaguas a Huallaga, 1924, *G. Tessmann 5513* (G). Tingo Maria, Near 21810, 625-1100 m, 30 October 1949-19 February 1950, *H.A. Allard 21811* (US). Mariscal Cáceres, Juanjui, Alto Rio Huallaga, 400-800 m, December 1935, *G. Klug 4160* (BM, F, K, MO, NY, US); December 1935, *G. Klug 4194* (BM, F, K, MO, NY, US); Tocache Nuevo, Camino al pueblo viejo de Tocache, 18 January 1970, *J. Schunke-Vigo 3732* (F, NY, US); Aeropuerto de Tocache, 400 m, 26 January 1970, *J. Schunke-Vigo 3771* (F, G, NY, US); Al Nor-Oeste del vivero del Instituto Agropecuario de Tocache, 18 April 1970, *J. Schunke-Vigo 3943 A* (F photo); Almendras, camino a pueblo Viejo, 400 m, 5 April 1975, *J. Schunke-Vigo 8216* (MO, NY); Quebrada de Cachiyacu, afluente de la quebrada de Huaquisha, 500-600 m, 17 May 1975, *J. Schunke-Vigo 8481* (MO, NY); Quebrada de Ishichimi, cerca a Tocache, 400 m, 11 March 1978, *J. Schunke-Vigo 10004* (F, MO, NY); Farm of Don Roberto Aguillar, 450 m, 1 July 1978, *T. Plowman & J. Schunke-Vigo 7509* (F, MO); Cerro de Sin Sin, cerca a Bambamarca, 600-630 m, 20 January 1979, *J. Schunke-Vigo 10729* (MO); Trail up Río Huallaga Valley toward Limón, 500 m, 11 March 1979, *A. Gentry et al. 25519* (F, MO, NY); Río de la Plata, cerca a la chacra del Sr. Esteban Arévalo, al borde de la quebrada, 650 m, 14 September 1980, *J. Schunke-Vigo 12280* (F, K, MBM, MO, NY, RB); Río de la Plata, cerca a la Chacra del Sr. Esteban Arévalo, 650 m, 15 September 1980, *J. Schunke-Vigo 12298* (MO). Fundo Jeroglífico, propiedad del Sr. Luis Ludeña, al Sur de Tocache, 400 m, 20 July 1988, *J. Schunke-Vigo 14266* (MO). Rioja, Along road Yorongos-La Florida near Rioja, 1000 m, 31 March 2001, *H. van der Werff et al. 16551* (F, MO, NY). San Martin, Chazuta, Río Huallaga, 260 m, April 1935, *G. Klug 4065* (BM, F, K, MO, NY, US); *Ibid.*, Llucanayacu, 300 m, 3 November 2004, *J.S. Biset 43* (SPF); *Ibid.*, 400 m, 23 May 2005, *J.S. Biset & J.C. de la Cruz 336* (SPF); *Ibid.*, 24 May 2005, *J.S. Biset & J.C. de la Cruz 370* (SPF); *Ibid.*, Llucanayacu, 600 m, 26 May 2005, *J.S. Biset & J.C. de la Cruz 453* (SPF). West side of Río Huallaga, West of Shapaja 2-8 km on trail to Tarapoto in the Cerros de Estoraqui, 1300 ft, 4-7 August 1937, *C.M. Belshaw 3217* (K, MO). **Ucayali:** Coronel Portillo, Bosque Nacional Alexander von Humboldt, km 86 Pucallpa-Tingo Maria road, 300 m, 27

March 1977, A. Gentry et al. 18697 (MO); 27 March 1977, A. Gentry et al. 18739 (MO); *Ibid.*, 270 m, February 1978, C. Froehner 182 (MO, NY); *Ibid.*, 250 m, 8 March 1979, A. Gentry et al. 25475 (INPA, MO, NY); *Ibid.*, 270 m, 9 February 1981, A. Gentry et al. 31133 (G, MO, NY); Aguaytia, Woods to north of house, Don Diogenes del Aguila, 30 June 1960, M.E. Mathias & D. Taylor 5062 (MO, US); Campoverde, Km 36, CF Basadre, 250-270 m, 27 October 1988, F. Chavez 3 (MO). VENEZUELA. **Amazonas:** Alto Orinoco, Raudal de los Guaharibos, 24 July 1951, L. Croizat 335 (F, NY). 22-23 km N of Samariapo on road to Puerto Ayacucho, 100 m, 29 June 1975, A. Gentry & P. Berry 14572 (MO, US).

Taxonomic notes. *Tynanthus villosus* was described as a new species based on the “shaggy indumentum”, “narrow inflorescences” and “persistent prophylls” (Gentry 1976: 60). Nevertheless, analyses of the collections of *T. polyanthus* and *T. villosus* throughout its distribution range indicated a continuum in the patterns of variation in the indumentum and inflorescence morphology, with vegetative portions from both species varying from villous to pubescent or glabrescent, and the inflorescences varying from large, compound and multi-flowered to small, simple or bearing only a few flowers. A careful analysis of specimens collected at different developmental stages (e.g., vegetative, flowering and fruiting) indicated that the prophylls of the axillary buds are generally lost in older specimens. Apart from the morphological similarities between these taxa, *T. villosus* appeared nested within *T. polyanthus* in our molecular phylogenetic studies (Medeiros & Lohmann in prep.). Our morphological and molecular phylogenetic observations thus led us to accept a more broadly circumscribed *T. polyanthus* and to synonymize *T. villosus* in *T. polyanthus*. As circumscribed here, *T. polyanthus* is characterized by the conspicuously tetragonal and angular young brancheletes, simple tendrils, foliaceous prophylls of the axillary buds, lax inflorescences, short corollas (ca. 0.4-0.8 cm length), and unwinged fruits. *T. polyanthus* is sister to *T. cognatus* (Medeiros & Lohmann in prep.), with which it shares a series of morphological features (see taxonomic notes under *T. cognatus*).

Nomenclatural notes. In the protologue of *S. polyantha*, Bureau cited a specimen deposited at G. However, no duplicates of *Spruce 4895* were located at G during a visit in 2006 during which time material were analyzed for the recently published Bignoniaceae synopsis (Lohmann & Taylor 2014). Therefore, Lohmann, in Lohmann & Taylor (2014), designated the specimen *Spruce 4895* deposited at P, where most of Bureau’s types are located, as the lectotype of *T. polyanthus*. In 2013, however, two duplicates of the collection *Spruce 4895* were located at the G herbarium indicating that the G collection cited in the

protologue of *S. polyantha* was not lost or destroyed as previously thought. Despite that, we here follow the lectotypification proposed in Lohmann & Taylor (2014).

As far as *T. myrianthus* is concerned, Bureau & Schuman (1896 [1897]) did not clearly indicate in the protologue which of the duplicates of the collection *Poeppig 2388* was the lectotype. We here select the duplicate deposited at W, which has been broadly photographed and distributed as the holotype of *T. myrianthus* as its lectotype. Similarly, the best quality material of the collection *C.A.M. Lindman A2967* from S is here selected as a lectotype for *T. lindmanii*.

A neotypification of *T. caryophylleus* was necessary given that all Bello's types kept at B (Stafleu & Cowan 1976: 170) were subsequently destroyed during World War II (Hiepko 1987). Since no duplicates of those specimens were distributed to any other collection, a specimen of *T. caryophylleus* from Porto Rico (where the original type was collected), identified by Alain (author of the combination of *T. caryophylleus*) is here selected as the neotype.

12. *Tynanthus pubescens* A.H. Gentry (1978: 275) (as "*Tynnanthus*"). Type:—GUYANA.

"Upper Mazaruni River Basin, Kamarang River, Singh line from Akapai to Eboropu escarpment", 13 October 1960, *S.S. Tillett & C.L. Tillett 45643* (holotype MO!; isotypes K!, NY!, US!, VEN! photo).

Fig. 17: G-K

Lianas. Branchelets tetragonal to terete, without ritidome, finely striated, densely lenticled, densely pubescent to puberulent, with simple and peltate trichomes; interpetiolar ridge absent or present; interpetiolar patelliform glands present; prophylls of the axillary buds 1.4–2.3 mm long, 1.1–2.3 mm wide, minute, shallowly triangular to triangular, densely puberulent throughout, with simple and peltate trichomes. *Leaves* 2–3 foliolate (more commonly 3); terminal leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules densely pubescent to puberulent throughout surface, with simple, peltate and patelliform trichomes; petioles 1.5–7.5 cm long; petiolules 0.4–4 cm long; leaflets 5.9–15.4 cm long, 3.1–11.3 cm wide, chartaceous to coriaceous, discolor, obovate to elliptic; apex acuminate or obtuse, mucronate; base cuneate or obtuse, symmetrical; margin entire; the abaxial surface densely pubescent to puberulent (sometimes glabrescent) throughout, with simple, peltate and patelliform trichomes; the adaxial surface pubescent to glabrescent, throughout (sometimes only on and near the

veins), with simple, peltate and patelliform trichomes; glandular trichomes distributed especially on the abaxial surface; second venation weak brochidodromous or brochidodromous; pocket domatia, with or without trichomes. *Inflorescence* axilar or terminal, a thyse or a compound thyse, lax, with conical aspect, first order (1.8–)3.6–6.3 cm long, second order 1.5–3.5 cm long; floral pedicels 1–10 mm long; axis densely pubescent or densely puberulent, with simple and peltate trichomes; bracts of the inflorescence predominantly caducous, densely pubescent to pubescent throughout, 0.6–1.5 mm long; floral bracts 0.3–1 mm long. *Calyx* green to yellowish, 3–4.5 mm long, 2.5–4 mm wide, without patelliform glands, with transversal aperture, minutely 5-denticulate (sometimes truncate), densely pubescent to puberulent throughout outside; lobes 0.1–0.4 mm long. *Corolla* white, cream or pale yellow (sometimes pale lilac), 1–1.6 cm long, 4–6 mm wide at the tube opening; tube 5–8 mm long, internally tomentose at the base, with simple and long and short stipitate trichomes; nectar guides present, yellow; lobes densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.6–1.4 mm long, 1.2–2.4 mm wide, acute to obtuse; lower ones 3–5.1 mm long, 3–6 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 2–3 mm from the base of the corolla; shorter ones 6–9 mm long; longer ones 7–10 mm long; anthers thecae 0.9–1.2 mm long, obovate to elliptic, subexserted; connective extending 0.1–0.3 mm beyond anther attachment; staminode 2–2.6 mm long, glabrescent, with long and short stipitate trichomes. *Gynoecium* with pistil 11–12 mm long; ovary 1.5–1.7 mm long, 0.9–1.2 mm wide, conical, densely pubescent; style 8–11 mm long, tomentose to pubescent at the base. *Fruit* a linear flattened capsule, 20–55 cm long, (1.2–)2.3–4.2 cm wide, woody, granular throughout (sometimes smooth near the midvein), without lenticels to densely lenticelled, densely pubescent to pubescent, with simple, peltate and patelliform trichomes; central ridge double, prominent to very prominent; margins prominently raised (winged), 0.5–1.4 cm wide. *Seeds* body 1.2–2.8 cm long, 0.9–1.3 cm wide; wings 1–1.8 cm long.

Phenology. Flowers from August to December and produces fruits from February to July.

Distribution and habitat. Occurs in moist broadleaf forests from Brazil (Acre, Amazonas, Pará and Rondônia), French Guiana, Peru (San Martín), Suriname (Brokopondo and Nickerie) and Venezuela (Amazonas) (Fig. 19).

Additional specimens examined. BRAZIL. **Acre:** Sena Madureira, Anjo, 5 September 1997, *I. Miranda et al.* 1657 (INPA). **Amazonas:** Presidente Figueiredo, Rebio Uatumã, grade do PPBio, 9 June 2007, *J.G. Carvalho-Sobrinho & J.R. Mesquita* 1563 (INPA). **Pará:** Região do Rio Jari, Estrada entre Monte Dourado e Munguba, km 4, 15-16 May 1969, *N.T. Silva* 1966 (IAN, MO, NY); *Ibid.*, Estrada do Munguba, km 7, 21 May 1969, *N.T. Silva* 2023 (MO, NY); *Ibid.*, Estrada entre Planalto A e Tinguelim, Km 16, 11 July 1969, *N.T. Silva* 2398 (MO, NY). Entre Acará e Moju, 2 September 1975, *R.R. Santos* 398 (IAN). Belém, Mocambo, Embrapa Forest Reserve, ca. 10 km from Belém, Transect 6, near sea level, 14 November 1984, *A. Gentry* 49049 (IAN, MO). Itaituba, Rio Tapajós, S. Luiz, 4 December 1919, *A. Ducke* s.n. (R 22493, RB 11421). Monte Dourado, Rio Jari, atrás do aviário, 12 June 1968, *E. Oliveira* 4491 (IAN, NY). Oriximiná, Rio Trombetas, margem esquerda ao lado do lago Muçura a 30 km de Porto Trombetas, 23 July 1980, *C.A. Cid et al.* 1748 (INPA, MG, NY). Santarém, Estrada para o Rio Curuá Una, acampamento do Guaraná, 30 November 1966, *P. Cavalcante & M. Silva* 1474 (MG photo, MO, NY); Rio Curuá Una, acima da Cachoeira do Palhão, 8 December 1966, *P. Cavalcante & M. Silva* 1636 (IAN). **Rondônia:** Eixo JP 14, 20 May 1987, *S. Romaniuc Neto et al.* 686 (SP). Porto Velho, Instituto Agrônômico do Norte, 1952, *E. Cordeiro & J.F. da Silva* 162 (MO, RB). FRENCH GUIANA: Station des Nouragues, Bassin de l'Arataye, 7 July 1989, *D. Sabatier & M.F. Prévost* 2616 (P). Saül and vicinity, Route de Bélizon, N of Eaux Claires, 200-400 m, 10 August 1993, *S. Mori et al.* 23213 (NY); *Ibid.*, less than 500 meters S of Eaux Claires, 230-300 m, 19 September 1994, *S. Mori et al.* 23971 (NY, P, US). PERU. **San Martín:** Mariscal Cáceres, Tocache Nuevo, Trail up Río Huallaga Valley toward Limón, 500 m, 11 March 1979, *A. Gentry et al.* 25566 (F photo, MO); 11 March 1979, *A. Gentry et al.* 25579 (F, MO, NY). SURINAME. **Brokopondo:** NW Brokopondo Stuwmeer Lake (E of Brownsberg Nature Reserve), Tonka Island, trail west from main compound, 15 m, 11 February 1998, *M.J. Plotkin et al.* 1293 (MO); *Ibid.*, 15 m, 4 February 1999, *B. Hoffman et al.* 5282 (MO). **Nickerie:** Area of Kabalebo Dam project, ca. 4 km S of road camp, ca. 23 km SW of Avanavero dam site, 18 November 1976, *N.M. Heyde & J.C. Lindeman* 164 (MO). VENEZUELA. **Amazonas:** Forest edge along Puerto Ayacucho-Samariapo highway 16-25 km S of Puerto Ayacucho, 100 m, 28 June 1975, *A. Gentry & P. Berry* 14503 (MO). Parcela de estudio del mamure al E del Raudal Gavilán, 100 m, 1 February 1991, *G.A. Romero et al.* 2289 (MO). Transecta entre Raudal Gavilancito, Río Gavilán, y la parcela de mamure, incluyendo zona al N del caño que bodea la parcela, 80-100 m, 9 February 1992, *G.A. Romero et al.* 2331 (MO).

Taxonomic notes. *Tynanthus pubescens* is morphologically similar to *T. densiflorus* (see taxonomic notes under *T. densiflorus*), as well as shares obovate to elliptic leaflets with *T. cognatus* (see taxonomic notes under *T. cognatus*). *Tynanthus pubescens* is sister to another Amazonian species, *T. panurensis* (Medeiros & Lohmann in prep.), with which it also shares other morphological features (see taxonomic notes under *T.*

panurensis). Despite those morphological similarities, *T. pubescens* can be easily recognized by the densely pubescent to puberulent branchelets and petiolules, interpetiolar patelliform glands, and fruits with double central ridge.

13. *Tynanthus sastrei* A.H. Gentry (1980: 214). Type:—FRENCH GUIANA. Sinnamary: “Route de Ste. Elie, 3 km avant la parcelle, ARBOCEL”, 23 September 1977, *C. Sastre 6015* (holotype MO!; isotypes P!, CAY! photo).

Fig. 20: A-D

Lianas. Branchelets subtetragonal to terete, without ritidome, finely striated or not, lenticled to densely lenticled, pubescent to puberulent (especially at the nodes), with simple and peltate trichomes; interpetiolar ridge absent or present; interpetiolar patelliform glands absent; prophylls of the axillary buds 3.5–6.5 mm long, 1.3–2 mm wide, foliaceous, elliptic to obovate, puberulent throughout, with simple, peltate and patelliform trichomes. *Leaves* 2–3 foliolate (more commonly 3); terminal leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules pubescent to puberulent throughout surface, with simple and peltate trichomes; petioles 2.3–6.6 cm long; petiolules 1.2–3.8 cm long; leaflets (4.8–)6–16.5 cm long, (2.1–)3.6–9.5 cm wide, chartaceous to coriaceous, concolor, elliptic; apex acuminate, mucronate; base cuneate or obtuse, symmetrical; margin entire; the abaxial surface pubescent to puberulent on and near the veins (sometimes throughout), with simple, peltate and patelliform trichomes; the adaxial surface pubescent to glabrescent throughout (sometimes only on and near the veins), with simple, peltate and patelliform trichomes; glandular trichomes distributed especially on the adaxial surface; second venation weak brochidodromous; pocket domatia, with or without trichomes. *Inflorescence* axilar or terminal, a thyrse or a compound thyrse, lax, with conical aspect, first order (4.5–)10–22.5 cm long, second order 6–7 cm long; floral pedicels 2.5–6 mm long; axis densely pubescent to puberulent, with simple and peltate trichomes; bracts of the inflorescence predominantly caducous, densely pubescent to puberulent throughout, (0.3–)0.5–3.2 mm long; floral bracts 0.3–0.6 mm long. *Calyx* green, 1.2–2 mm long, 1.8–2.5 mm wide, without patelliform glands, with transversal (sometimes oblique) aperture, truncate or minutely 5-denticulate, densely pubescent to puberulent throughout outside; lobes 0.1–0.4 mm long. *Corolla* white, cream or pale yellow, 0.6–0.8 cm long, 2.5–4 mm wide at the tube opening; tube 3–4 mm long, internally glabrescent, with long and short stipitate trichomes; nectar guides absent, but with a path of long and short stipitate trichomes; lobes

densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.5–1.1 mm long, 0.8–1.9 mm wide, acute to obtuse; lower ones 1.5–3.3 mm long, 1.9–3.7 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 1–1.3 mm from the base of the corolla; shorter ones 3–4 mm long; longer ones 3.5–4.5 mm long; anthers thecae 0.5–0.6 mm long, obovate to elliptic, subexserted; connective extending 0.1–0.2 mm beyond anther attachment; staminode 1.7–2.3 mm long, glabrescent, with long and short stipitate trichomes. *Gynoecium* with pistil 5–5.5 mm long; ovary 1–1.2 mm long, 0.8–0.9 mm wide, conical, velutinous; style 4–4.3 mm long, tomentose at the base. *Fruit* not seen. *Seeds* not seen.

Phenology. Flowers from February to October; the fruiting season is unknown.

Distribution and habitat. Occurs in moist broadleaf forests from French Guiana and Suriname (Brokopondo) (Fig. 21).

Additional specimens examined. FRENCH GUIANA. Sinnamary, route de St. Elie, 3 km avant la parcelle ARBOCEL, 12 September 1978, *C. Sastre 6103* (MO, NY, P). Bord de la piste de Ste. Elie, km 10.2, 18 April 1979, *M.F. Prévost 529* (MO, P). Région de Paul Isnard, SW de Citron vers le Mont Décou Décou, 8 September 1983, *G. Cremers 8164* (BR, MO, P). Piste de Saut Léodate, Région de Cayenne, 31 March 1986, *C. Feuillet 3683* (MO, P, US). Cayenne region, Along road in Forest Macouria, ca. 20 km in from highway D5 (Tonate-Montsinery), 1–30 m, 25 October 1986, *L. Skog et al. 7043* (MO, NY, US). Piste Forestière de Saut Léodate, Région de Cayenne, 40 m, 19 October 1991, *G. Cremers & C. Feuillet 12399* (K, MO, NY, P, US). Crique Valentin, 50 m, 29 October 1991, *G. Cremers et al. 12506* (NY, P, US). Saül and vicinity: Sentier Botanique, 200–400 m, 8 August 1993, *S. Mori et al. 23171* (NY). Piste de Saint-Elie, Interfluve Sinnamary/Counamama, Piste du km 22, 6 June 1995, *M.F. Prévost 3154* (MO). SURINAME. **Brokopondo:** Road to Brownsberg Nature Reserve, 5 km from Brownsberg village at old railroad grade, 50 m, 5 February 1999, *B. Hoffman et al. 5302* (MO).

Taxonomic notes. *Tynanthus sastrei* shares a series of morphological features with *T. schumannianus*, namely the elliptic, chartaceous to choriaceous and acuminate-mucronate leaflets, similar leaflet dimensions (6–16 x 3.6–9.5 cm in *T. sastrei* and 4.4–14.2 x 2.2–9.1 cm in *T. schumannianus*), lax inflorescences, and a similar corolla length (0.6–0.8 cm in *T. sastrei* and 0.4–0.9 cm in *T. schumannianus*). Nevertheless, *T. sastrei* can be easily separated by the foliaceous prophylls of the axillary buds (versus bromeliad-like prophylls

in *T. schumannianus*), absence of patelliform glands in the branchelets, petiolules and inflorescences (versus presence in *T. schumannianus*), and internally glabrescent corolla tube base (versus tomentose in *T. schumannianus*). *Tynanthus sastrei* was recovered as sister to *T. pubescens* in a recent phylogeny of *Tynanthus* (Medeiros & Lohmann in prep.); however, this relationship was not strongly supported and further molecular phylogenetic studies are still needed in order to confidently establish the phylogenetic position of *T. sastrei*.

- 14. *Tynanthus schumannianus*** (Kuntze) A.H. Gentry (1974: 874) (as “*Tynnanthus*”).
Cuspidaria schumanniana Kuntze (1898: 243). Type:—BOLIVIA. “Rio Yapacani”, June 1892, *C.E.O. Kuntze s.n.* (holotype NY!; isotype US!).
Tynanthus weberbaueri Sprague (1908: 176) (as “*Tynnanthus*”). Type:—PERU. Junín: “Ad La Merced in valle Chanchamayo”, s. d., *A. Weberbauer 1896* (holotype K!; isotype B destroyed).
Cuspidaria ovalis Rusby (1920: 120). Lectotype (designated here):—BOLIVIA. La Paz: Mapiri, July-August 1892, *M. Bang 1485* (NY! (barcode 328763) photo; isolectotypes A! photo, BM!, E! photo, G!, GH! photo, K! photo, LE!, M!, MO!, NY! (barcodes 328764, 328765) photo, US!).

Fig. 20: E-J

Lianas. Branchelets tetragonal to terete, with or without ritidome, finely striated (sometimes not evident, when young), lenticled to densely lenticled, glabrescent (sometimes pubescent at the nodes), with peltate and patelliform trichomes (sometimes also with simple); interpetiolar ridge absent (sometimes present); interpetiolar patelliform glands absent; prophylls of the axillary buds 1.5–3.5(–4.5) mm long, 1–3.5 mm wide, bromeliad-like, glabrescent (rarely puberulent) throughout, with peltate trichomes (rarely also with simple). *Leaves* 2–3 foliolate (more commonly 3); terminal leaflets modified into trifid tendrils, without adhesive-disks on tip; petioles and petiolules glabrescent (sometimes pubescent) throughout surface, with peltate and patelliform trichomes (sometimes also simple); petioles (0.6–)1.1–5.5 cm long; petiolules 0.4–3.8 cm long; leaflets (2.8–)4.4–14.2 cm long, (1.7–)2.2–9.1 cm wide, chartaceous to coriaceous, discolor, elliptic; apex acuminate, mucronate; base cuneate or obtuse, symmetrical; margin entire; the abaxial surface glabrescent on and near the veins, with peltate and patelliform trichomes; the adaxial surface glabrescent on and near the veins, with peltate and patelliform trichomes;

glandular trichomes distributed especially on the abaxial surface; second venation weak brochidodromous; pocket domatia, without trichomes. *Inflorescence* axilar or terminal, a thyse or a compound thyse, lax, with conical aspect, first order 4.1–14.5 cm long, second order 1.2–5 cm long; floral pedicels 0.5–4 mm long; axis densely pubescent to pubescent, with simple, peltate and patelliform trichomes; bracts of the inflorescence predominantly caducous, densely pubescent to pubescent throughout or only at margins, 0.5–3 mm long; floral bracts 0.3–0.6 mm long. *Calyx* green, 1–2 mm long, 1.1–1.9 mm wide, with patelliform glands, with transversal or oblique aperture, truncate or minutely 5-denticulate, pubescent or puberulent throughout or only on teeth outside; lobes 0.1–0.4(–0.5) mm long. *Corolla* white, cream or pale yellow (sometimes pale green), 0.4–0.9 cm long, 1.5–3.5 mm wide at the tube opening; tube 2–4 mm long, internally tomentose to pubescent or glabrescent at the base, with simple and long and short stipitate trichomes; nectar guides absent, but with a path of long and short stipitate trichomes; lobes densely pubescent to pubescent throughout lower ones and at the margin of upper ones; upper ones 0.3–1.7 mm long, 0.7–1.5 mm wide, acute to obtuse; lower ones 1.5–2.9(–3.5) mm long, 1.3–2.6 mm wide, obtuse to rounded. *Androecium* with fertile stamens inserted 0.8–1.3 mm from the base of the corolla; shorter ones 1.5–5 mm long; longer ones 2–6 mm long; anthers thecae 0.5–0.9 mm long, obovate to elliptic, subexserted; connective extending 0.1–0.2 mm beyond anther attachment; staminode 0.8–1.7 mm long, glabrescent, with long and short stipitate trichomes. *Gynoecium* with pistil 3.3–6.3 mm long; ovary 0.8–1 mm long, 0.5–0.7 mm wide, conical, velutinous; style 2.5–5.3 mm long, tomentose at the base. *Fruit* a linear flattened capsule, (5.5–)8–29.5 cm long, (0.5–)1–2.5 cm wide, woody, smooth to granular near the midvein and granular near the margins, without lenticels to densely lenticeled, glabrescent, with peltate and patelliform trichomes; central ridge single, slightly or not prominent; margins prominently raised (winged), (0.2–)0.4–1 cm wide. *Seeds* body 0.7–1.5 cm long, 0.3–0.9 cm wide; wings 0.4–1.4 cm long.

Phenology. Flowers and fruits throughout the year.

Distribution and habitat. Occurs in moist broadleaf forests from Bolivia (Beni, La Paz and Santa Cruz), Brazil (Acre, Amazonas, Mato Grosso, Pará and Rondônia) and Peru (Cusco, Junín, Madre de Dios, Puno and Ucayali) (Fig. 22).

Additional specimens examined. BOLIVIA. **Beni:** Iténez, Cantón Mateguá, Campamento móvil Cerro Azul ubicado a 30 km de la Comunidad de Tiquin, 697 m, 7 November 2006, *N.R. Ledezma et al. 1003* (SPF); 7 November 2006, *N.R. Ledezma et al. 1004* (SPF). José Ballivián, Vic. Rurrenabaque, 1000 ft, 25 November 1921, *M. Cardenas 1180* (NY); Estación Biológica Beni, 45 km E of the Río Maniqui on the road to Trinidad, then 6.5 km N to the Río Curiraba, then 2 hours by trail, passing Estancia Isla de Creta, to Arroyo Aguas Negras, 250 m, 15 November 1985, *J.C. Solomon 14733* (MO). Marbán, Estación Experimental Perotó, 97 km ESE of Trinidad on road to Santa Cruz, 230 m, 28 July 1982, *J. Solomon et al. 8177* (MO). Vaca Diéz, 20.8 km E of Riberalta on road to Guayaramerin, 230 m, 25 September 1981, *J.C. Solomon 6419* (MO); 25 September 1981, *J.C. Solomon 6429* (MO). **La Paz:** Abel Iturralde, Río Satariapo, 300 m, 1 June 1990, *A. Gentry & R. Foster 70824* (G, MO); Comunidad de Buena Vista, Senda a la Parcela Permanente de 1 ha de Estudio Etnobotánico, 3 km al NE de Buena Vista, 180 m, 14 April 1995?, *S. DeWalt et al. 130* (MO). Franz Tamayo, Serranía de Chepite, Campamento Scismico de Texaco, 15 km O del Río Tuichi, 700 m, 3-8 April 1992, *T. Killeen 3808* (MO); Parque Nacional y Area Natural de Manejo Integrado Madidi, NW de Apolo, Parcela temporal de muestreo (0.1 ha), 1175 m, 19 March 2005, *D. Choque et al. 213* (MO, NY); *Ibid.*, Azariamas, Resina, 700 m, 10 June 2005, *A. Araujo-M. et al. 1911* (MO, NY); *Ibid.*, rio Mojós, entre Mojós y Charopampa, Inventario fitosociológico Madidi 56, 1079 m, 4 July 2005, *A. Fuentes et al. 9405* (MO); *Ibid.*, Azariamas, Río San Juan, Bosque seco del sector Azariamas, Parcela Permanente de Muestreo 17, 1150 m, 15 November 2005, *S. Paredes et al. 168* (SPF); *Ibid.*, senda Azariamas-San Fermin, sector Monos PPM-1 (1 ha), 1100 m, 25 May 2006, *E. Ticona et al. 46* (SPF); *Ibid.*, senda Azariamas-San Fermin, Parcela temporal (0.1 ha), 1326 m, 27 May 2006, *I. Loza et al. 43* (SPF); *Ibid.*, 1248 m, 28 May 2006, *I. Loza et al. 85* (SPF); *Ibid.*, 1124 m, 10 June 2006, *I. Loza et al. 449* (SPF); *Ibid.*, Sumpulo, comunidad Virgen del Rosario, 939 m, 9 July 2008, *A. Araujo et al. 4222* (MO, SPF). Larecaja, Copacabana (about 10 km south of Mapiri), 850-950 m, 8 October-15 November 1939, *B.A. Krukoff 11245* (F, MO, NY). Sud Yungas, Basin of Río Bopi, San Bartolome (near Calisaya), 750-900 m, 1-22 July 1939, *B.A. Krukoff 10399* (G, MO, NY, US); Alto Beni, concesión de Sapecho, Yungas, Monte alto (-35 m), 550 m, 3 April 1989, *R. Seidel et al. 2678* (MO). Covendo, 2000 ft, 26 August 1921, *G.S. White 998* (NY, US). **Santa Cruz:** Andrés Ibáñez, Santa Cruz Botanical Garden, 12 km E of Santa Cruz. Transect 5, 375 m, 9 May 1991, *A. Gentry et al. 73634* (MO). Guarayos, 8 km N of Guarayos on road to Urubichá, 190 m, 13 July 1991, *M. Nee 41705* (K, MO, NY). Ichilo, Parque Nacional Amboró, Río Saguayo, 500 m, 19 January 1988, *M. Nee 35987* (MO, NY); *Ibid.*, 0.5 km upstream from last Andean foothills, Study site for native stand of *Bactris gassipaes*, 450 m, 20 December 1988, *M. Nee & M. Saldias P. 37297* (MO, NY); *Ibid.*, 0-2 km upstream from the Quebrada Yapoje, 350 m, 14 December 1989, *M. Nee 38171* (MO, NY); *Ibid.*, 1/2 km NE de El Chontal (Parcela estudiada) sobre el río Saguayo, 13.5 km SW de Huaytú, 450 m, 23 January 1990, *M. Saldias P. 972* (NY); *Ibid.*, Río Yapojé y Saguayo, 8 km SW de la Localidad El Carmen, Terraza antigua 30 m O del Río Saguayo,

Parcela permanente de estudio, 360 m, 15-22 November 1991, *I. Vargas et al. 1143* (MO); 15-22 November 1991, *I. Vargas et al. 1173* (MO); 15 km SSE of Buena Vista, Estancia Rafael de Amboro, 400 m, 19 May 1991, *A. Gentry 74134* (MO). José Miguel de Velasco, El Encanto Camp, near El Encanto waterfall, edge of Huanchaco plateau, Transect 1, 280 m, 4 November 1991, *A. Gentry & B. Mostacedo 75539* (MO); *Ibid.*, Transect 7, 240 m, 5 November 1991, *A. Gentry & B. Mostacedo 75619* (MO); Campamento Los Fierros, camino al aserradero Moira, En el campo de la pista, 200 m, 18 October 1994, *R. Guillén & R. Choré 2401* (F, MO, NY); Alrededores del Parque Nacional "Noel Kempff M.", 131 km al N de Florida, 25 km antes de Bella Vista, 3 November 1994, *B. Mostacedo et al. 2469* (MO); Reserva Ecológica El Refugio, a 180 m al SW de la casa del campamento El Refugio, 750 m, 18 January 1995, *R. Guillén & V. Roca 2854* (K, MO, NY); *Ibid.*, a 2 km sobre la senda ecológica partiendo del campamento, 180 m, 30 January 1995, *R. Guillén & R. Choré 3130* (F, MO, NY); Parque Nacional Noel Kempff Mercado, Campamento Huanchaca I, Parcel Huanchaca I, 600 m, 5 November 1995, *P.F. Foster et al. 626* (MO, NY). Ñuflo de Chávez, Perseverancia, Vicinity of Perseverancia, on the banks of Rio Negro, west bank of the river from the station to the brecha, and following the brecha ca. 2 km North of Santa Cruz 320 km, 250 m, 8 September 1990, *M. Lewis 37532* (MO); NW of Santa Cruz on Río Negro, Transect 10, 100 m, 13 May 1991, *A. Gentry et al. 73772* (MO). BRAZIL. **Acre:** Highway Abunã to Rio Branco, km 242-246, vicinity of Campinas, 18 July 1968, *E. Forero et al. 6336* (INPA, K, MG, MO, NY photo, R, US). 12 km from Rio Branco on Rio Branco-Porto Velho road, 30 September 1980, *S.R. Lowrie et al. 297* (INPA, MG, MO, NY, R, US). Acrelândia, Basin of Rio Madeira, Rio Abunã, Porto Dias, km 130 of BR-364, then 30 km on Ramal do Pelé, then Ramal do Gordo, colocação Bom Jardim, 131 m, 16 May 2005, *D.C. Daly et al. 13705* (RB, UFACPZ). Assis Brasil, Basin of Rio Purus, upper Rio Acre, left bank, Seringal São Francisco, Colocação Duretida, 26 March 1998, *D.C. Daly et al. 9798* (UFACPZ, SPF). Boca do Macauã, Basin of Rio Purus, Near mouth of Rio Macauhan (tributary of Rio Yaco), 11 August 1933, *B.A. Krukoff 5454* (G, K, MO, NY, RB, US). Manoel Urbano, Rio Chandless (tributary of Rio Purus), right bank, "Ananaí", 20 March 2002, *D.C. Daly et al. 11486* (SPF); 20 March 2002, *D.C. Daly et al. 11509* (SPF). Marechal Thaumaturgo, Reserva Extrativista do Alto Juruá, basin of Rio Juruá, Rio Bagé, near mouth of river, 12 March 1992, *D.C. Daly et al. 7363* (NY, UFACPZ); *Ibid.*, proximidades do Igarapé Caipora, Seringal Ceará, Fazenda Paraguaia, Rio Alto Juruá, 20 July 1992, *L.C. Ming & L.A. Ferreira 328* (UFACPZ); *Ibid.*, Colocação Terra Firme, Rio Tejo, 3 May 2001, *L.G. Lohmann & E.C. Oliveira 452* (NY). Plácido de Castro, AC 40, Km 20, no sentido Plácido/Rio Branco, Igarapé Visionário, 5 February 2000, *I.S. Rivero et al. 371* (UFACPZ, SPF). Rio Branco, Parque Municipal Chico Mendes, Rodovia AC-40 km 10, 150 m, 14 November 2006, *J.L.F. Junior et al. 56* (RB). Sena Madureira, Rio Macauã, Seringal Riozinho, Colocação Provenir, 31 March 1994, *L. Lima et al. 544* (MO, NY, UFACPZ); Estrada para Rio Branco (BR-364), km 233, ramal Toco Preto, a aproximadamente 8 km da BR, 170 m, 7 March 2012, *M.C. Medeiros et al. 39* (SPF). Serra do Moa, Vicinity of Serra da Moa village, 26 April 1971, *G.T. Prance et al. 12484* (INPA, K, MG, MO, NY, R,

US). Xapuri, Margem direita do Rio Xapuri, 17 May 2001, *L.G. Lohmann & E.C. Oliveira* 545 (MO, NY). **Amazonas:** Vicinity of Lábrea, 4 July 1971, *G.T. Prance et al.* 13954 (INPA, K, MO, NY, R, US). Estrada Humaitá-Lábrea, km 77, 11 June 1982, *L.O.A. Teixeira et al.* 1088 (MG, K, NY, US). **Mato Grosso:** Novo Mundo, Parque Estadual Cristalino, Serra à sudeste da pousada, à oeste da estrada de terra, 3 June 2007, *D. Sasaki et al.* 1752 (INPA, K). **Pará:** Rio Itacaiuna, mata da cachoeira Grande, 15 June 1949, *R.L. Fróes & G.A. Black* 24530 (K, RB). Almeirim, Pilão, estrada de Castanheiro, 24 January 1969, *N.T. Silva* 1679 (IAN, K, MO, NY). Monte Dourado, Rio Jarí, 1 February 1968, *E. Oliveira* 4064 (IAN, MO, NY); 4 February 1968, *E. Oliveira* 4105 (IAN, NY). Pau D'Arco, Marajoara, 12 February 1997, *J. Grogan* 49 (IAN, INPA). **Rondônia:** Porto Velho to Cuiabá highway, vicinity of Santa Bárbara, 15 km east of km 117, 14 August 1968, *G.T. Prance & J.F. Ramos* 6926 (F photo, INPA, K, MG, NY, P, R). RO-429, km 105, 6 July 1983, *M.G. Silva* 6556 (MG). Ca. 5 km NW of Costa Marques, 150 m, 29 March 1987, *M. Nee* 34568 (INPA, MO, NY). Alta Floresta d'Oeste, Serra dos Parecis, a 27 km de Alta Floresta, na linha 65 da Topografia BASEVI, 3 December 1982, *P. Lisboa et al.* 2748 (MG). PERU. **Cusco:** La Convención, Río Manguriari (Manguyari), Alto Urubamba, upstream to Río Manguriari, 750 m, 2 February 1991, *P. Núñez & G. Ortiz* 12795 (MO). **Junín:** Chanchamayo, Río Colorado, near jct. with Río Chanchamayo, 500-600 m, 7 February 1983, *A. Gentry et al.* 40128 (F, MO). **Madre de Dios:** Manu, Parque Nacional de Manu, Cocha Cashu Station, 380 m, 16 October 1979, *A. Gentry et al.* 26792 (F, MO); *Ibid.*, 350 m, 1 October 1980, *R.B. Foster* 5435 (F, G, MO, NY); *Ibid.*, Calpa guacamayas vicinity, 400 m, 7 September 1986, *P. Nuñez* 5999 (MO, NY); *Ibid.*, 250 m, 24 June 2000, *R.J. Burnham* 2444 (F photo); *Ibid.*, 150 m, 5 June 2001, *L.G. Lohmann et al.* 613 (MO); *Ibid.*, 150 m, 11 June 2001, *L.G. Lohmann & C. Machaca* 631 (MO); Pantiacolla, Serrania across Río Alto Madre de Dios from Shintuya, 480-840 m, 29 October 1979, *A. Gentry et al.* 27352 (MO). Tambopata, Aeropuerto Maldonado, 350 m, 18 January 1967, *C. Vargas C.* 18798 (US); Ca. 5 km from Puerto Maldonado near Río Tambopata, 220 m, 24 January 1976, *A. Gentry* 16291 (F, MO, NY); Road from Puerto Maldonado to Tambopata, 0-4 km from Puerto Maldonado, 220 m, 25 January 1976, *A. Gentry & J. Revilla* 16329 (F, MO, NY); Lago Tres Chimbadas, ca. 65-70 river km SSW Puerto Maldonado, ca. 10-15 air km NW effluence Río La Torre (Río D'Orbigny)/Río Tambopata, 260 m, 16 June 1980, *P.J. Barbour* 5749 (F, G, MO); Tambopata Tourist Camp at junction of Ríos Tambopata and La Torre, 280 m, 22 July 1985, *A. Gentry et al.* 51223 (MO); Trocha a la Colpa de Guacamayos en el riachuelo, Río Manu entre Cumerjali y Cocha Cashu, 350 m, 22 January 1987, *P. Núñez & L. Quiñones* 6912 (MO); Tambopata Nature Reserve, junction of Ríos La Torre and Tambopata, Swamp Tree Plot, 250 m, 1 June 1987, *A. Gentry & N. Jaramillo* 58012 (MO); Comunidad Nativa de Infierno, Hermosa Chica, Study plot 1, 260 m, 4 April 1989, *M. Alexiades & M. Arevalo* 579 (K, MO, NY, US); Cuzco Amazónico, 15 km ENE of Puerto Maldonado, 200 m, 17 December 1989, *A. Gentry et al.* 68930 (MO); *Ibid.*, TREE PLOT 2-U, 200 m, 3 March 1990, *A. Gentry & P. Núñez* 69848 (MO); Cuzco Amazónico, across Río Madre de Dios on road to Lago Sandoval, 200 m, 19 December 1989, *A. Gentry et al.* 68979 (MO); 19 December

1989, A. Gentry et al. 69002 (MO); Pampas de Heath, 200 m, 25 February 1990, A. Gentry & P. Núñez 69560 (MO); Cuzco Amazónico Lodge, Lago Sandobal and Río Madre de Dios, 200 m, 14 April 1990, P. Núñez 12065 (MO); 14 April 1990, P. Núñez 12068 (MO); *Ibid.*, TREEPLOTS, 200 m, 16 April 1990, P. Núñez 12117 (MO); Puerto Maldonado, Los Amigos Biological Station, Madre de Dios River, ca. 7.0 km upriver from mouth of Rio Los Amigos, Trocha Playa 360 m, a 25 m a la derecha, 25 February 2004, A.P. Maceda 1214 (SPF). **Puno:** Carabaya, Río Távora base camp, Non-transect, 400 m, 16 May 1992, A. Gentry et al. 76673 (MO). **Ucayali:** Purús, Purús, Rio Curanja, cerca la comunidad nativa de Colombiana, 250 m, 21 February 2000, J.G. Graham & J.S. Vigo 1054 (INPA, MO, US); 24 February 2000, J.G. Graham & J. Schunke-Vigo 1113 (NY).

Taxonomic notes. *Tynanthus schumannianus* is morphologically similar to *T. sastrei*, as well as shares morphological features with *T. espiritosantensis* and *T. labiatus* (see *T. espiritosantensis*, *T. labiatus* and *T. sastrei* notes). However, this species is easily recognized by the bromeliad-like prophylls of the axillary buds, glabrescent vegetative organs, and winged fruits. *T. schumannianus* is closely related to *T. espiritosantensis*, *T. fasciculatus*, *T. labiatus* and *T. micranthus* (Medeiros & Lohmann in prep.).

Nomenclatural notes. Three duplicates of the collection *M. Bang 1485* were located at NY, where great part of Rusby's collections were kept (Stafleu & Cowan 1976: 114). The best quality flowering material is here selected as lectotype of *Cuspidaria ovalis*.

Doubtful and excluded names

Bignonia laxiflora Poepp. in Fl. Bras. 8(2): 198 (1896), *pro syn.*

Bignonia myriantha Poepp. in Fl. Bras. 8(2): 198 (1896), *pro syn.*

Chasmia ochroleuca Schott, Syst. Veg. 4(2): 409 (1827), *nom. nud.* - Listed as a synonym of *T. elegans* in the Fl. Bras. 8(2): 197 (1896).

Cleosma octandra Urb. & Ekm. in Kew Bull. 15(3): 466 (1962), *pro syn.*

Tynanthus angosturanus K. Schum in Repert. Spec. Nov. Regni Veg. Beih. 43: 636 (1927), *nom. nud.*

Tynanthus confertiflorus Miers, Proc. Roy. Hort. Soc. London 3: 193 (1863), *nom. nud.*

Tynanthus gibbus Miers, Proc Roy. Hort. Soc. London 3: 193 (1863), *nom. nud.*

Tynanthus goudotianus (Bureau) Bureau, Adansonia 8: 274 (1868) (as “*gondotiana*”) - This species is only known from the fragmented type material, deposited at P and F. None of the type fragments provide sufficient information to allow an adequate identification of this taxon. The morphological features described in the protologue of *T. goudotianus* and detailed study of the type suggest that this species is morphologically similar to *T. schumannianus*.

Tynanthus hyacinthinus Standl., Publ. Carnegie Inst. Wash. 461(4): 87 (1935) = *Bignonia hyacinthina* (Standl.) L.G. Lohmann

Tynanthus igneus (Vell.) Barb. Rodr., Vellozia, ed. 2, 1: 50 (1891) = *Pyrostegia venusta* (Ker Gawl.) Miers

Tynanthus laxiflorus Miers, Proc. Roy. Hort. Soc. London 3: 193 (1863), *nom. nud.*

Tynanthus petiolatus Miers, Proc. Roy. Hort. Soc. London 3: 193 (1863), *nom. nud.*

Tynanthus strictus Miers, Proc. Roy. Hort. Soc. London 3: 193 (1863), *nom. nud.*

Vasconcellia chimonantha Mart. in Adansonia 5: 375 (1865), *pro syn.*

Vasconcellia fasciculata (Vell.) Mart. ex DC., Prodr. 9: 185 (1845), *pro syn.*

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Plotkin, M.J. 1293 (12)
Plowman, T. 6706 (10); 7509 (11); 11276 (11)
Poeppig 1617 (11); 2651 (11)
Prance, G.T. 6926 (14); 12484 (14); 13954 (14); 14559 (11)
Prévost, M.F. 529 (13); 3154 (13)
Queiroz, L.P. de 10661 (7)
Raimundo S.P. 1163 (1)
Ramalho, R.S. 1621 (5)
Rambo, B. 42705 (1)
Regnell, A.F. s.n. (1) (K); II-198 (5) (MO 3395612) (K; LE) (R 23787; US 201375) (K) (P 3606695) (P 3606699) (P 3606698) (K; MO 2305639; P 3606697; R 23786; US 2515367) (P 3606701) (P 3606694) (BR; M) (BR) (US 1322404)
Reitz, P.R. 6147 (1); 8245 (1); 8537 (1); 8936 (1); 9102 (1); 9424 (1)
Rezende, G.S.Z. 162 (1)
Ribas, O.S. 5527 (9); 5668 (1)
Rico, L. 1406b (11)
Riedel, L.? s.n. (1) (NY) (LE)
Riedel, L. s.n. (BM; G; K; P 3606732) (MO 4618844; NY 483757; NY 1032824); 88 (7); 231 (1)
Rimachi Y., M. 4064 (10)
Ritter, N. 2996 (11)
Rivero, I.S. 309 (11); 371 (14)
Rodas, L.A.C. 8 (1)
Rojas, S. 102 (2)

Romaniuc Neto, S. 686 (12)
Romero, G.A. 2289 (12); 2331 (12)
Rosa, N.A. 4984 (11)
Sabatier, D. 2616 (12)
Saldanha, J.s.n. (1) (R 128076)
Saldias, M. 972 (14); 2928 (11)
Sampaio, A. s.n. (1) (R 23545; RB 23359)
Sánchez, L. 402 (11)
Santos, E.M. s.n. (5) (F 2170556); 76 (5)
Santos, G.F. 7 (9)
Santos, J.U. 69 (11)
Santos, R.R. 398 (12)
Sasaki, D. 1625 (11); 1752 (14)
Sasaki, E.Y. s.n. (9) (ESA 103223; FUEL 29302; SPF 201517; VIC 31746)
Sastre, C. 6103 (13)
Schinini, A. 31364 (9)
Schipp, W.A. 8910 (6)
Schott 5971 (1)
Schunke V., J. 3732 (11); 3771 (11); 3943 A (11); 5813 (11); 8216 (11); 8481 (11); 10004 (11); 10729
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Schwacke s.n. (1) (K; R 23784)
Seibert, R.J. 1899 (11)
Seidel, R. 1207 (11); 2678 (14)
Sellow 1074 (1)
Shattuck, O. 1108 (2)
Shiki, D. RBAE216 (11); RBAE218 (11)
Silva, E.M. s.n. (9) (RB 467352)
Silva, F.C. 901 (9); 950 (1)
Silva, J.M. 2587 (9); 2214 (9)
Silva, L.H.S. 170 (1)
Silva, M.G. 6556 (14)
Silva, N.T. 358 (11); 1679 (14); 1966 (12); 2023 (12); 2398 (12)
Simpson, D.R. 702 (11)
Skog, L. 7043 (13)
Smith, D.N. 3890 (11)
Solomon, J.C. 6419 (14); 6429 (14); 8177 (14); 11594 (11); 13733 (11); 14733 (14); 15665 (11); 16919
(11)

Soto, J.C. 22687 (6); 23490 (6)
Sousa, M. 12382 (6); 12397 (6)
Souza, H.M. s.n. (5) (IAC 20158)
Souza, V.C. 5334 (7)
Spinelli, T. 219 (5)
Standley, P.C. 24535 (6)
Stehle, D.I. s.n. (5) (SPSF 1012)
Steinbach, J. 3224 (11); 5253 (11)
Steyermark, J.A. 45058 (6)
Sucre, D. 4576 (1)
Tameirão Neto, E. 215 (5)
Teixeira, L.O.A. 1088 (14)
Tellez, O. 2423 (6); 2456 (6); 3054 (6)
Tessmann, G. 4914 (11); 5513 (11); 6001 (1)
Tibiriçá, Y.J.A. 70 (5)
Ticona, E. 46 (14)
Torres, R.B. 756 (5)
Treacy, J. 259 (10); 333 (10)
Udulutsch, R.G. 57 (5); 101 (1); 112 (5); 134 (1); 169 (5); 232 (5); 245 (5); 423 (9); 429 (5); 1619 (9)
Ule, E. 6577 (11)
Valeur, E.J. 532 (11)
Vargas C., C. 18798 (14)
Vargas, I. 377 (11); 1143 (14); 1173 (14)
Vasquez, M. 927 (6)
Vásquez, R. 16543 (10); 17806 (10); 21375 (11); 21497 (11); 21706 (11); 21772 (11); 22079 (11); 23937
(11)
Vaz, A.F. 949 (1)
Velloso, H.P. s.n. (1) (MO 2286403)
Ventura A., F. 21496 (6)
Viana, L.C.S. s.n. (7) (BHCB 109098)
Vidal, M.R.R. 199 (5)
Vieira, A.O.S. s.n. (9) (FUEL 1661); 41 (9)
Vieira, M.C.W. 1235 (1)
Villagra, B.L.P. 225 (1)
Villarroel, D. 347 (11); 367 (11)
Volpato, L.A. s.n. (1) (FUEL 6375; HRCB 34681)
Walker, J.B. 138 (6)

Warush, A. RBAE99 (11)
Wasshausen, D.C. 884 (11)
Wendt, T. 5280 (6)
van der Werff, H. 16551 (11)
White, G.S. 998 (14)
Whitefoord, C. 3115 (6); 9499 (6)
Widgren s.n. (1) (BR; P 3606716); s.n. (5) (BR; MO 2698894; MO 3395608; P 3606700); 49 (5); 94
(5); 243 (5)
Williams, R.S. 508 (11)
Wood, J.R.I. 10423 (11)
Woytkowski, F. 5151 (10); 5391 (11)
Zampieri, C. 41 (9)
Zappi, D. 900 (11)
Zuntini, A.R. 147 (1); 240 (1); 241 (1)

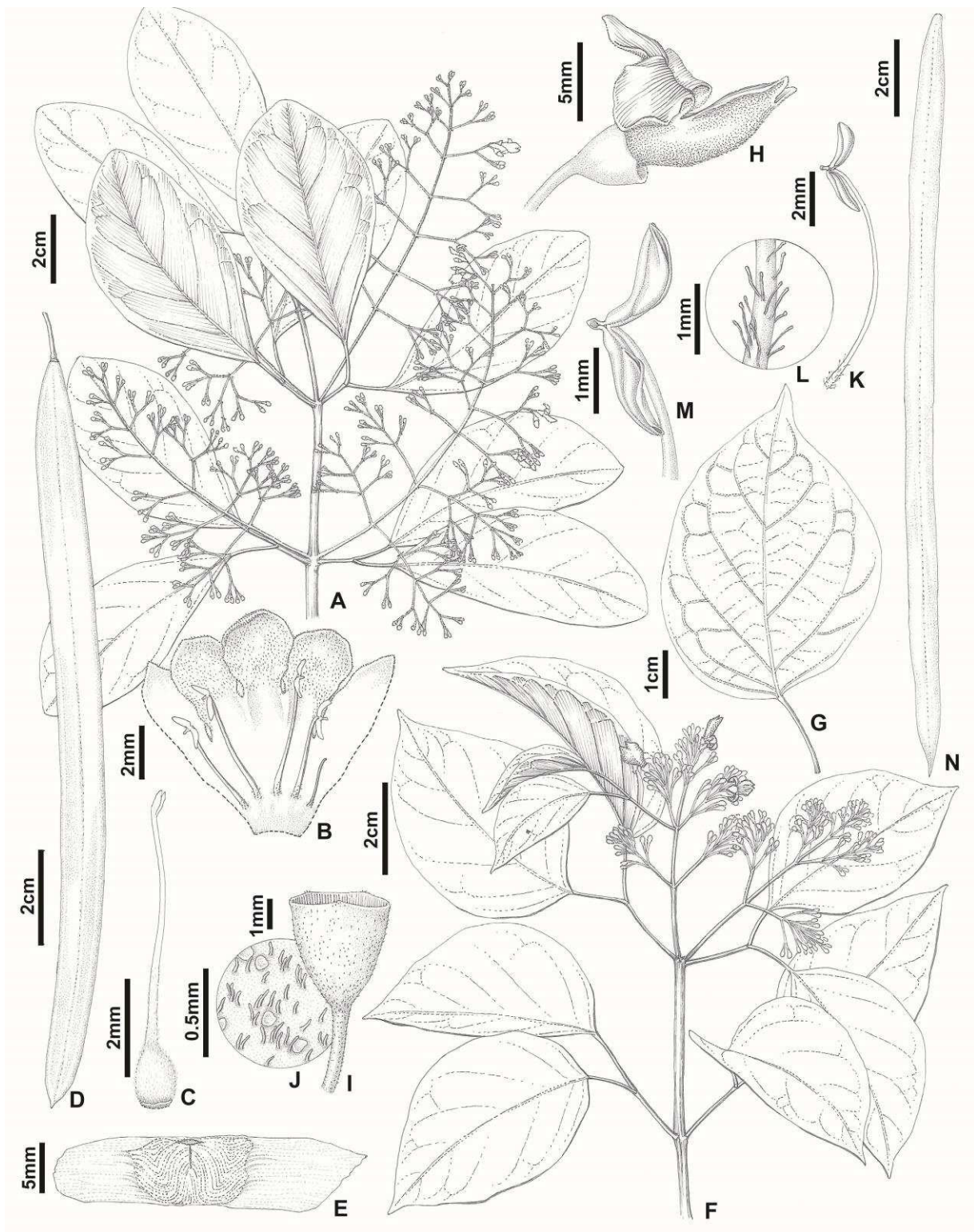


Figure 1. A-E. *Tynanthus cognatus*: A. Habit; B. Open corolla showing the androecium; C. Gynoecium (D.A. Folli 1795, SPF); D. Fruit; E. Seed (J.S. Carneiro 161, FUEL). F-N. *T. croatianus*: F. Habit; G. Leaflet; H. Flower; I-J. Calyx with patelliform glands; K-M. Stamen with stipitate trichomes at the base of filaments and curved thecae (S. Knapp 1053, NY); N. Fruit (A. Gentry 6696, NY).

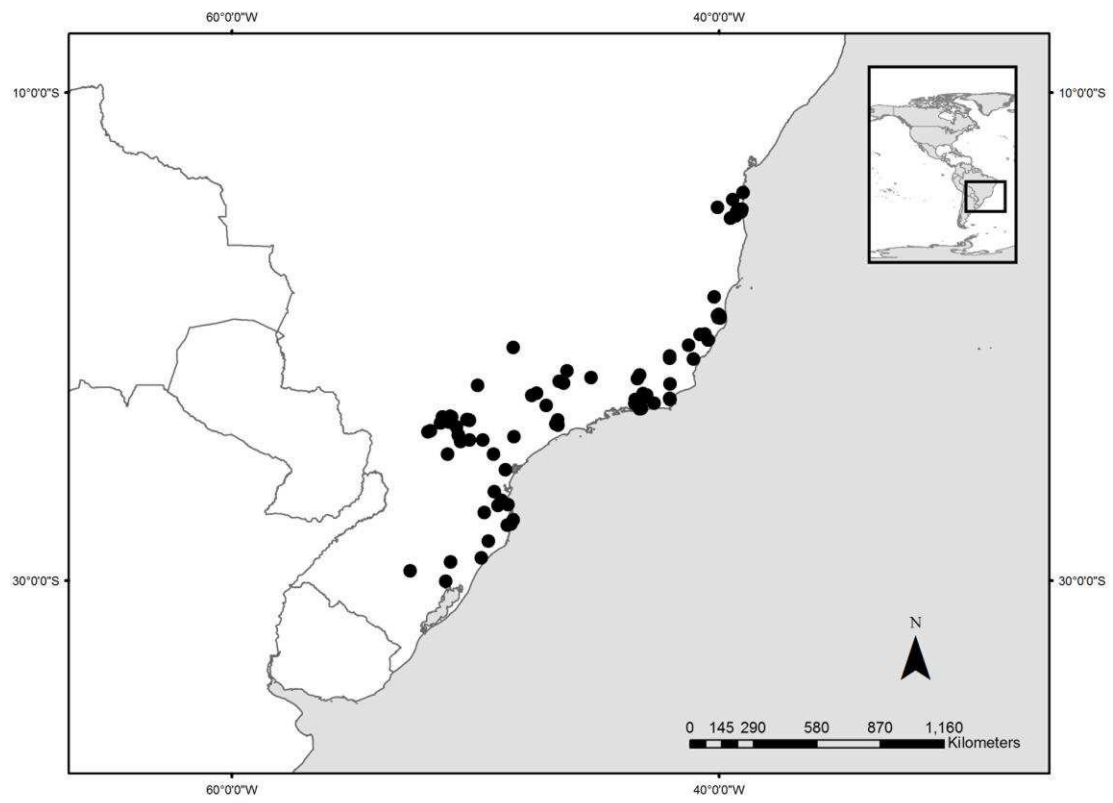


Figure 2. Distribution of *Tynanthus cognatus*.

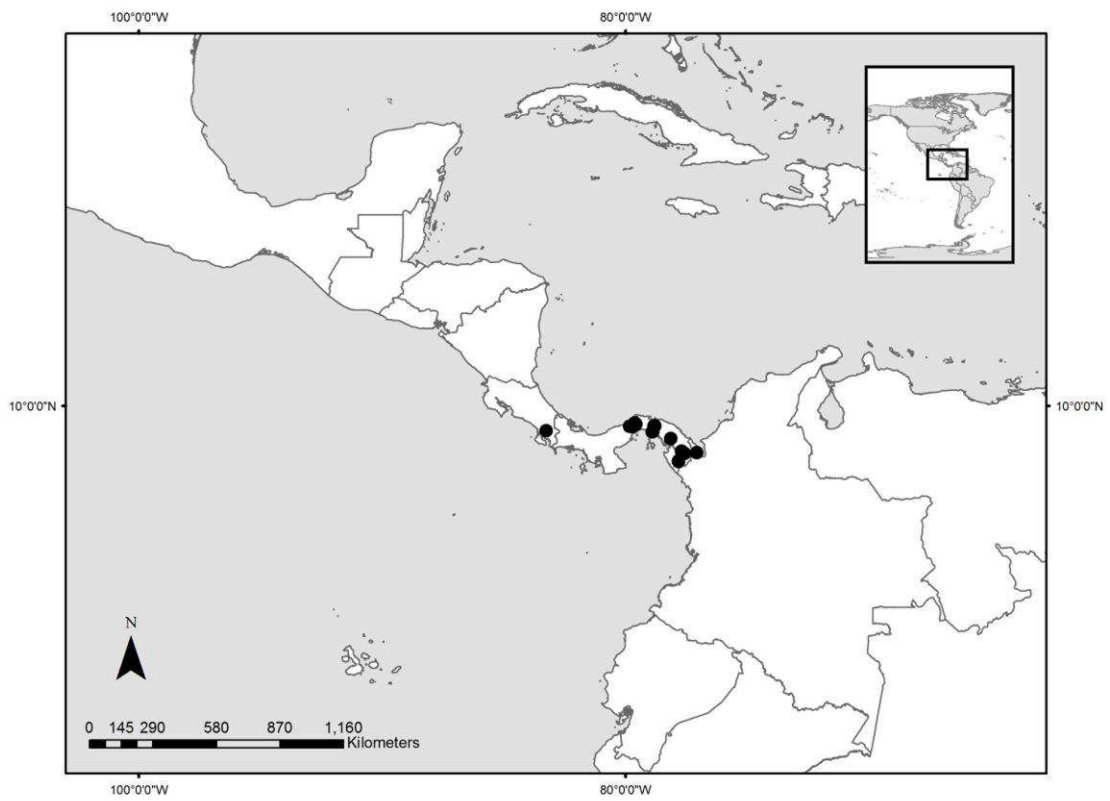


Figure 3. Distribution of *Tynanthus croatianus*.

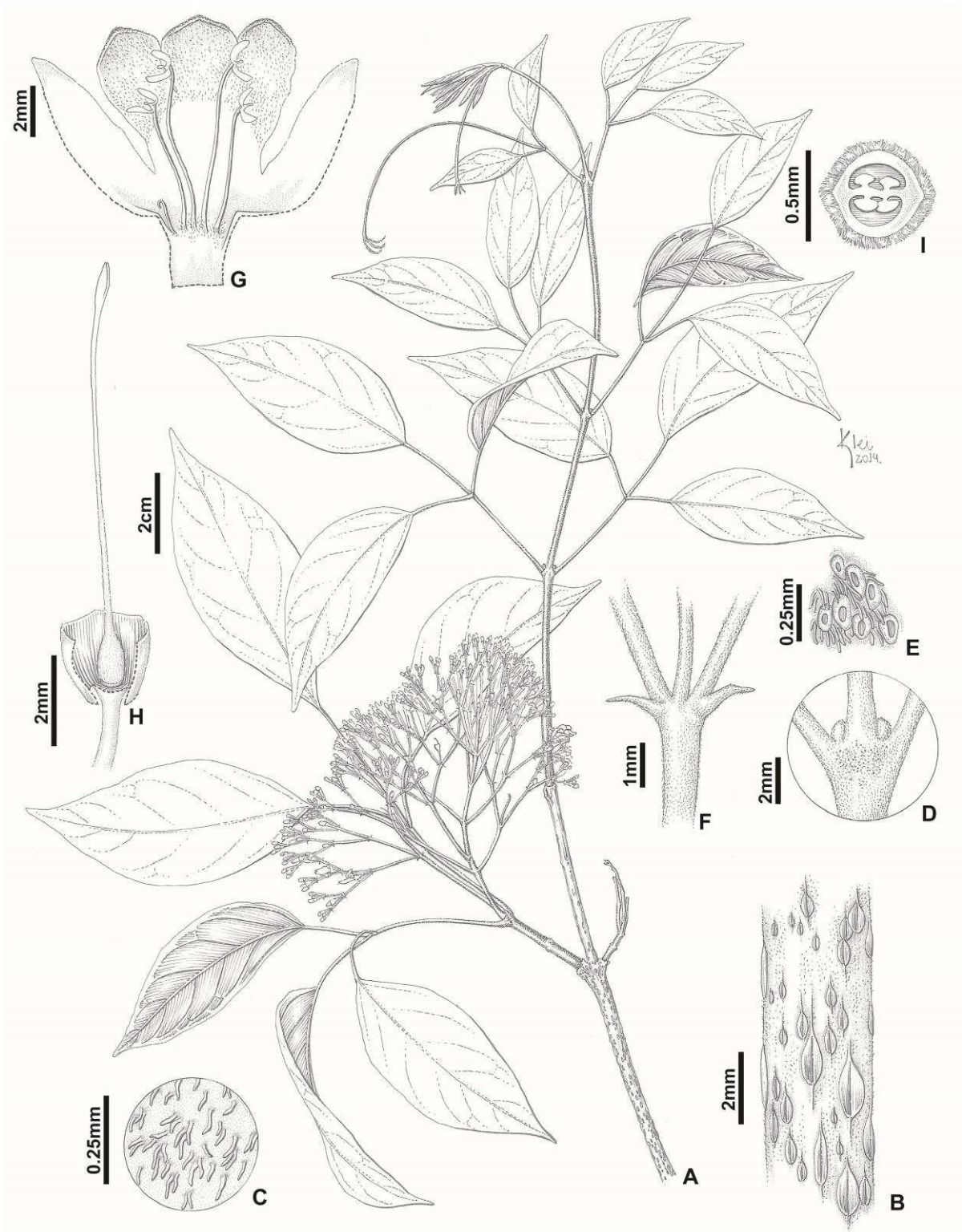


Figure 4. A-I. *Tynanthus densiflorus*: A. Habit; B. Detail of lenticels in the oldest portion of branchelet; C. Detail of pubescent indument in the youngest portion of branchelet; D-E. Interpetiolar region with glands; F. Detail of inflorescence axis showing bracts; G. Open corolla showing the androecium; H. Open calyx showing the gynoecium; I. Cross section of ovary showing ovules (L.C. Procópio 14, NY).

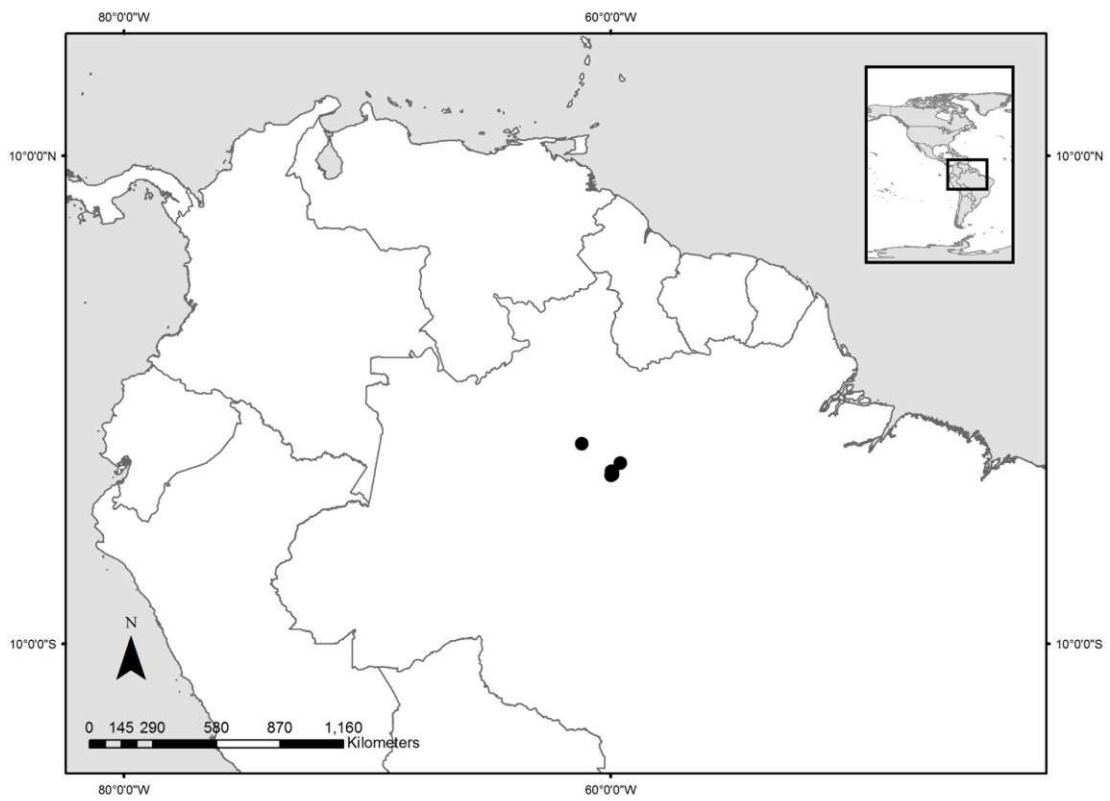


Figure 5. Distribution of *Tynanthus densiflorus*.

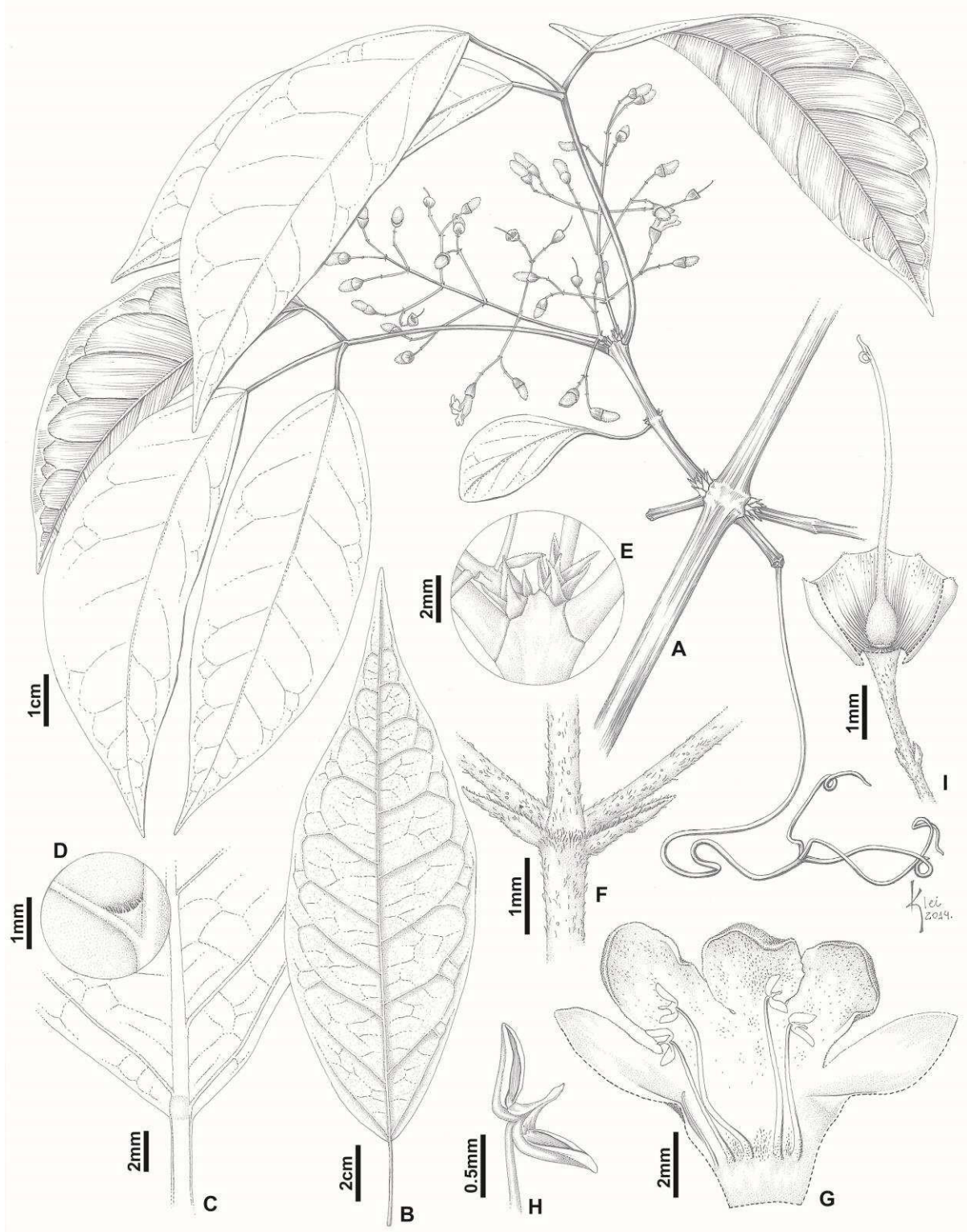


Figure 6. A-I. *Tynanthus espiritosantensis*: A. Habit; B-D. Leaflet showing detail of the pubescent mite-domatia; E. Interpetiolar region, showing the bromeliad-like prophylls of the axillary buds; F. Detail of inflorescence axis showing bracts, simple and peltate trichomes; G. Open corolla showing the androecium; H. Anther; I. Open calyx and gynoecium (D.A. Folli 5931, SPF).

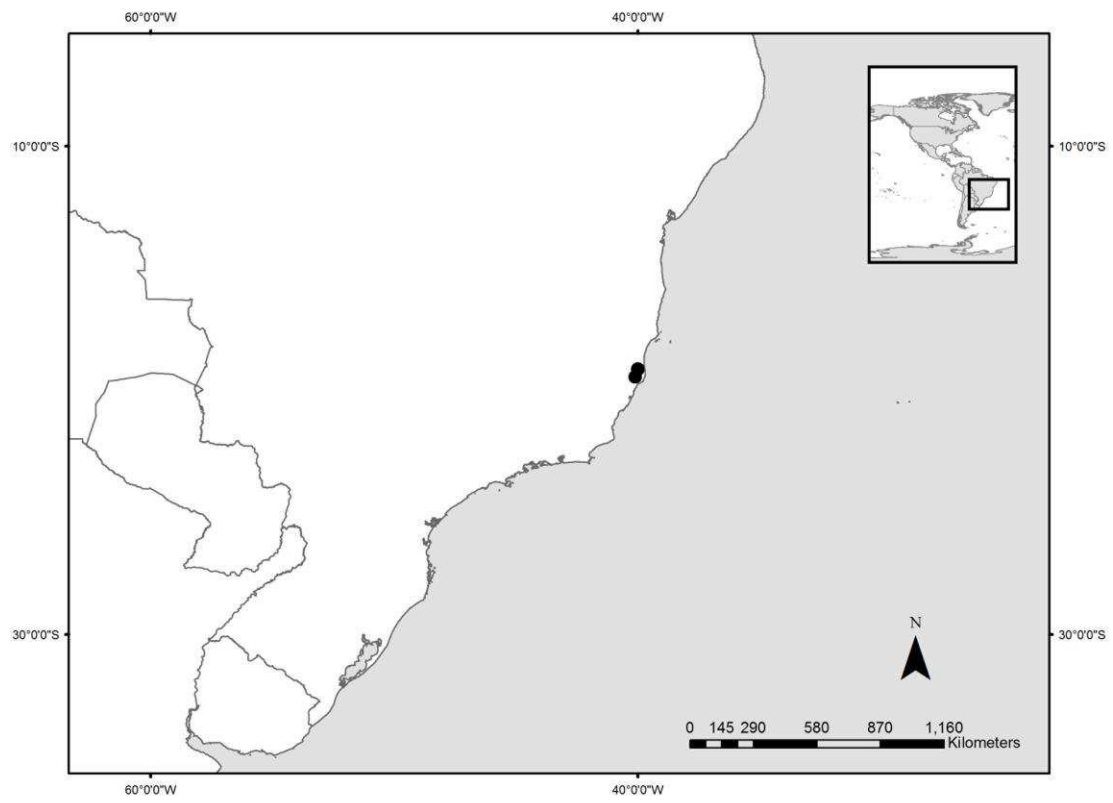


Figure 7. Distribution of *Tynanthus espiritosantensis*.



Figure 8. A-F. *Tynanthus fasciculatus*: A. Habit; B. Detail of tomentose branchetes; C. Calyx with lacinate apex; D. Open corolla showing the androecium; E. Gynoecium (G. Edwall s.n., F 896072); F. Fruit showing the subtetragonal cross section (Mello Barreto 1824, F). G-J. *T. guatemalensis*: G. Habit; H. Interpetiolar region showing the foliaceous prophylls of the axillary buds; I. Flower (E. Contreras 8517, F); J. Fruit (P.H. Gentle 7775, F).

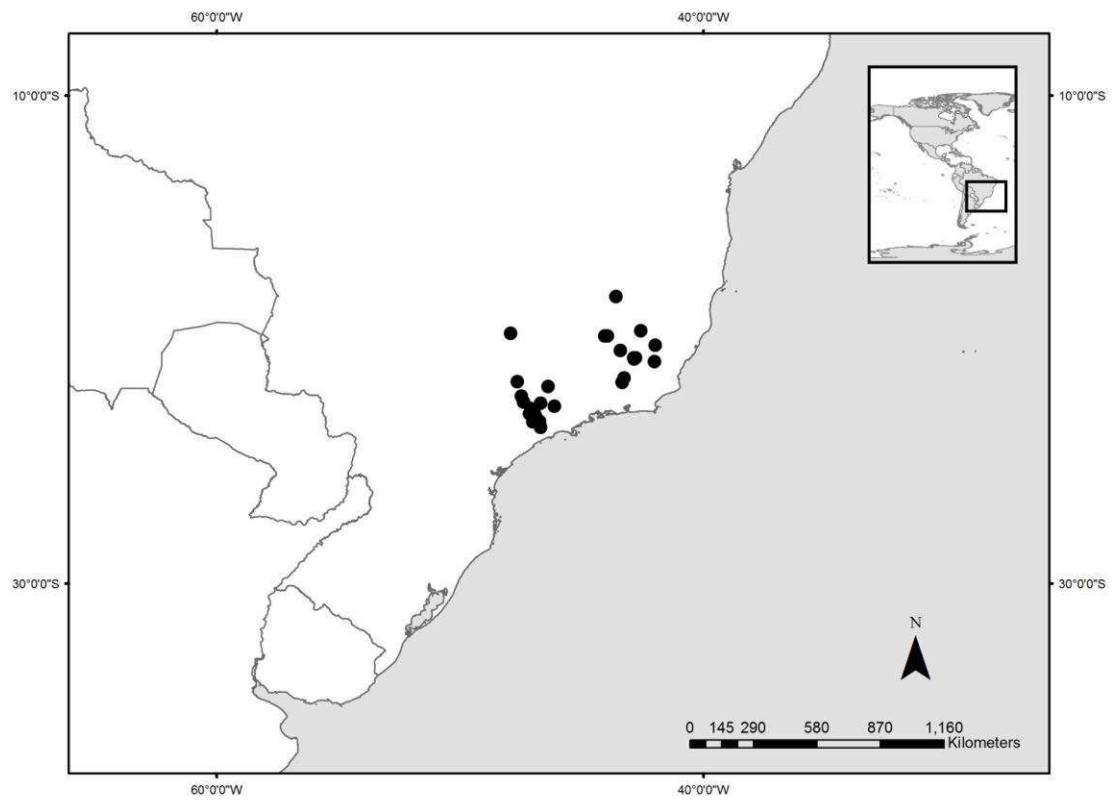


Figure 9. Distribution of *Tynanthus fasciculatus*.

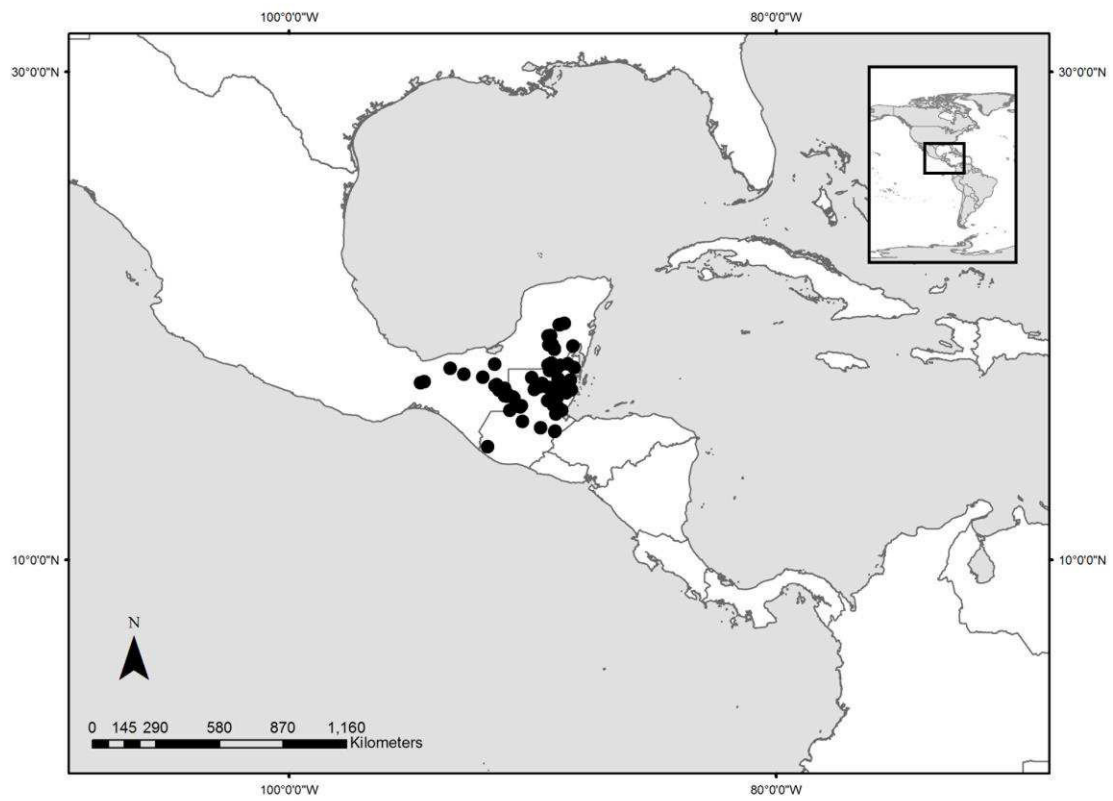


Figure 10. Distribution of *Tynanthus guatemalensis*.

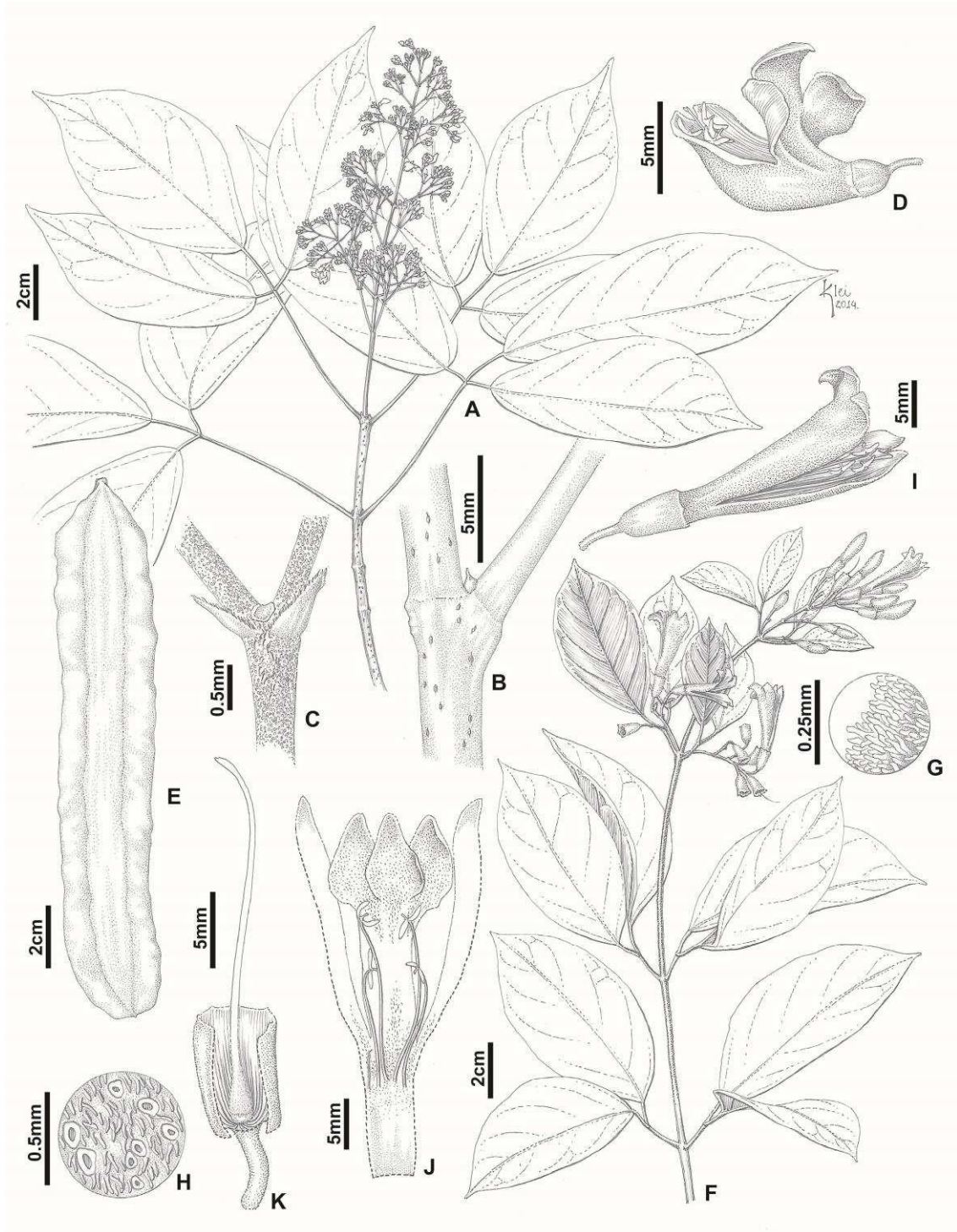


Figure 11. A-E. *Tynanthus labiatus*: A. Habit; B. Petiolar region showing minute prophylls of the axillary buds; C. Detail of inflorescence axis showing the indument and bracts; D. Flower; E. Fruit (J.R. Pirani 3900, SPF). F-K. *T. macranthus*: F. Habit; G. Detail of the densely pubescent branchettes; H. Detail of the interpetiolar glands (R. Lent 42, NY isotype); I. Flower; J. Open corolla showing the androecium; K. Open calyx showing the gynoecium (A. Jiménez M. 2044, NY).

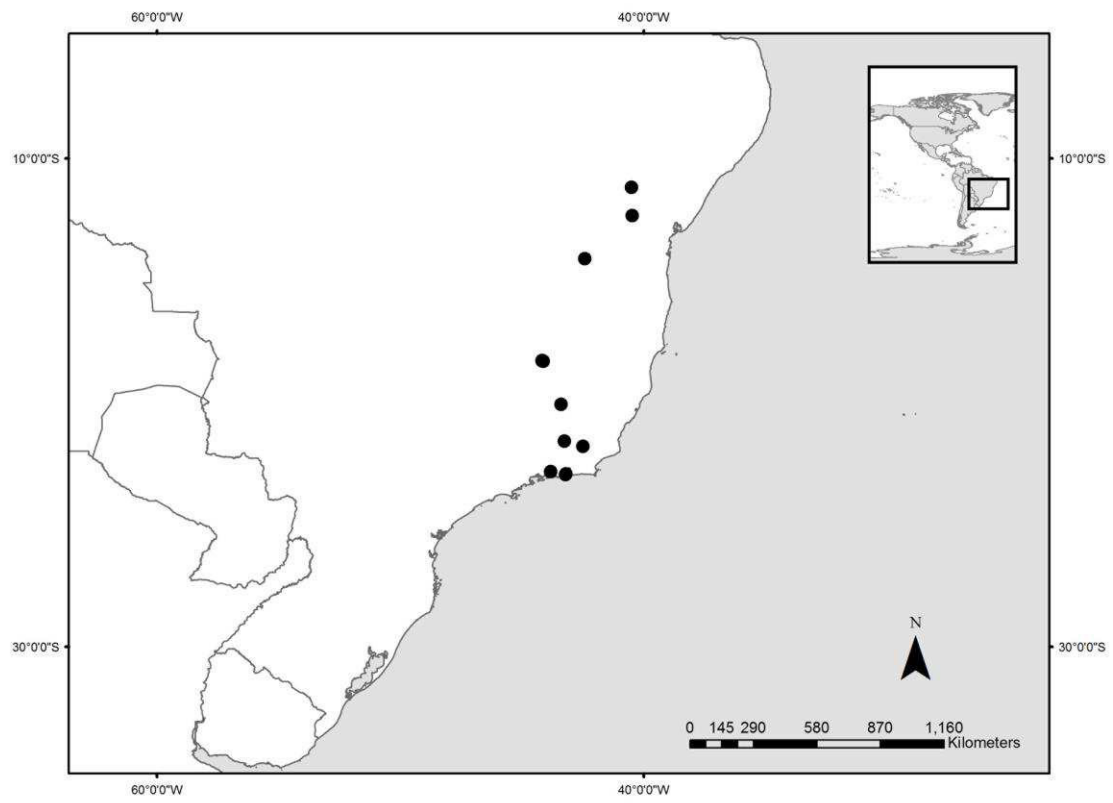


Figure 12. Distribution of *Tynanthus labiatus*.

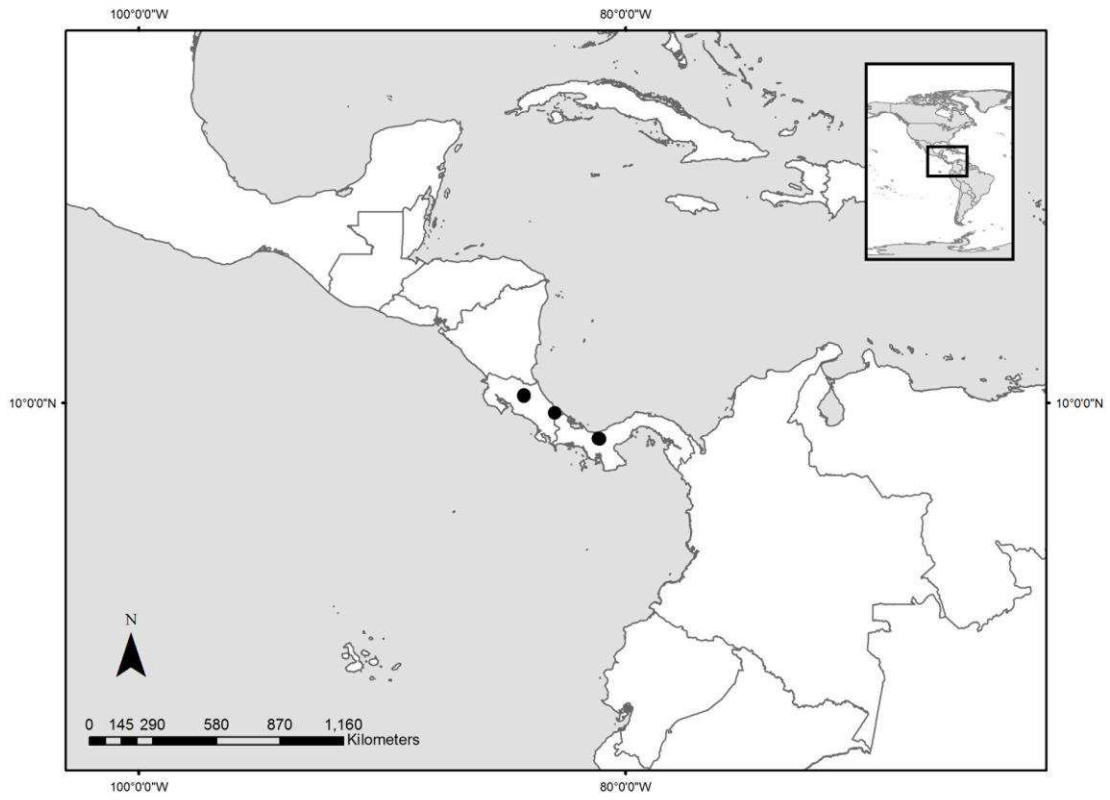


Figure 13. Distribution of *Tynanthus macranthus*.



Figure 14. A-D. *Tynanthus micranthus*: A. Habit; B. Open corolla showing the androecium; C. Open calyx showing the gynoecium (M.C. Medeiros 32, SPF); D. Fruit (J.S. Carneiro 300, FUEL). E-I. *T. panurensis*: E. Habit; F. Interpetiolar region showing the foliaceous prophylls of the axillary buds; G. Inflorescence; H. Flower; I. Fruit (E-F and I: A. Gentry 21066, MO)(G-H: G. Klug 1972, NY).

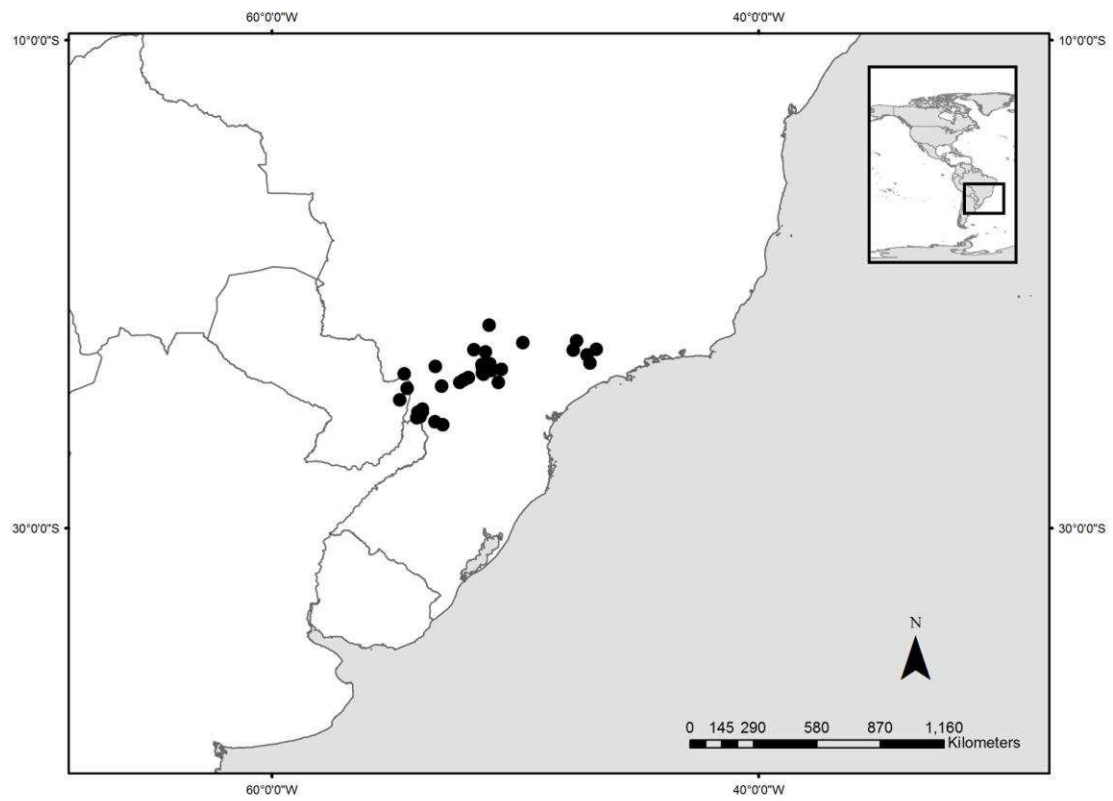


Figure 15. Distribution of *Tynanthus micranthus*.

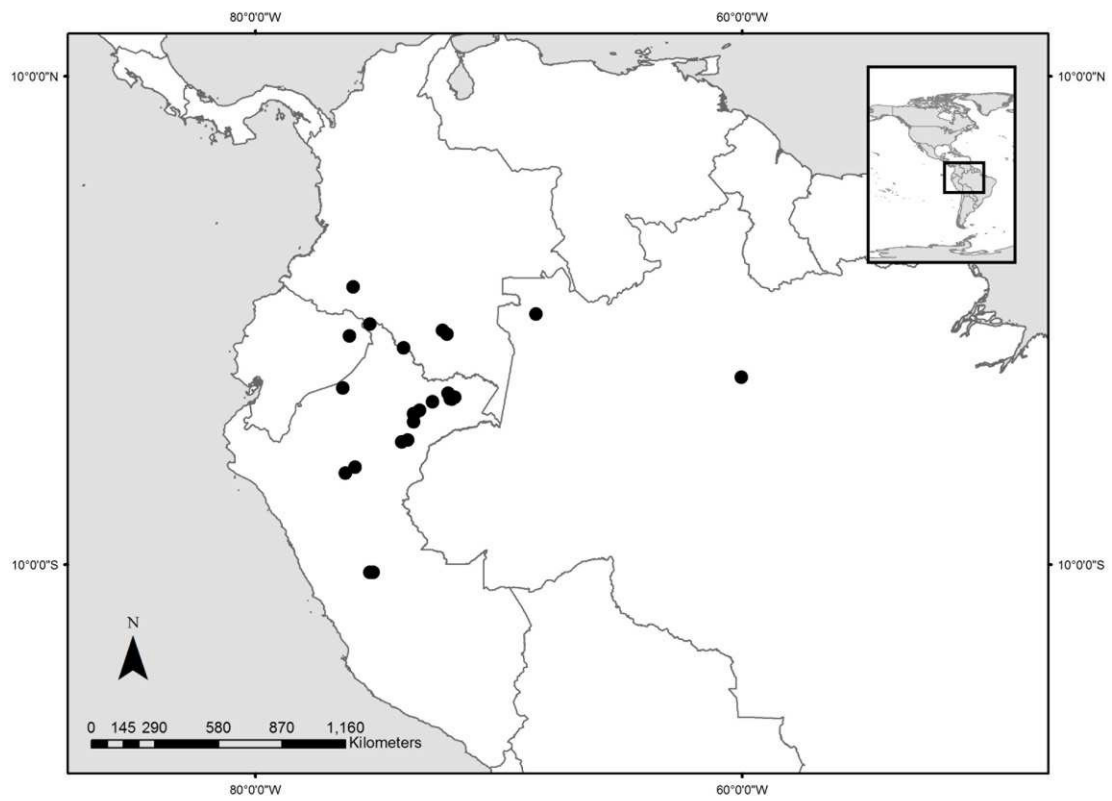


Figure 16. Distribution of *Tynanthus panurensis*.

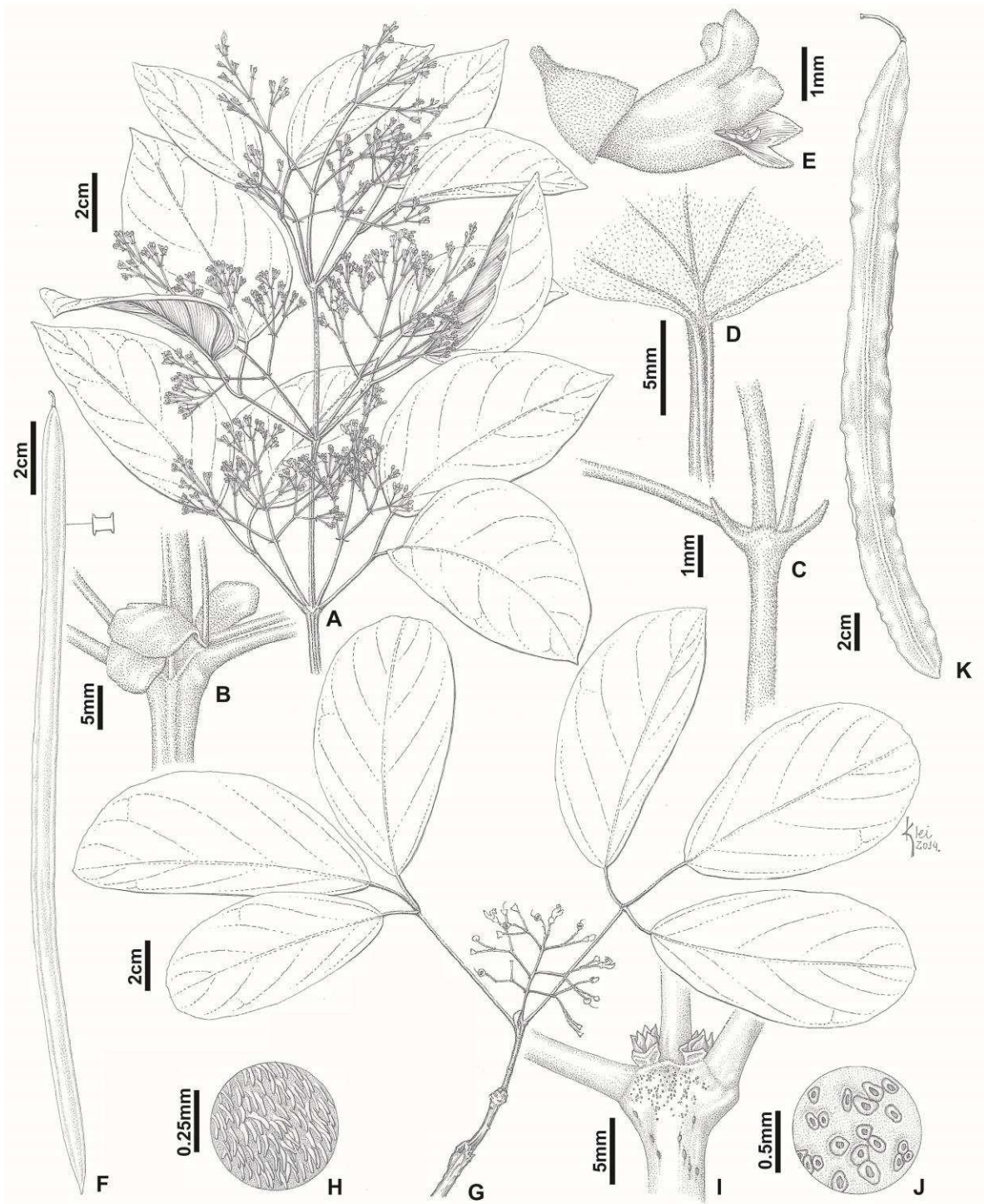


Figure 17. A-F. *Tynanthus polyanthus*: A. Habit; B. Interpetiolar region showing the foliaceous prophylls of the axillary buds; C. Detail of inflorescence axis showing inflorescence bracts; D. Detail of petiolule showing the upper canalicule; E. Flower (M.C. Medeiros 40, SPF); F. Fruit showing the flattened cross section (P. Núñez 11199, MO). G-K. *T. pubescens*: G. Habit; H. Detail of pubescent branchelet (S. Mori 23971, NY); I-J. Interpetiolar region showing patelliform glands; K. Fruit (A. Gentry 25579, F).

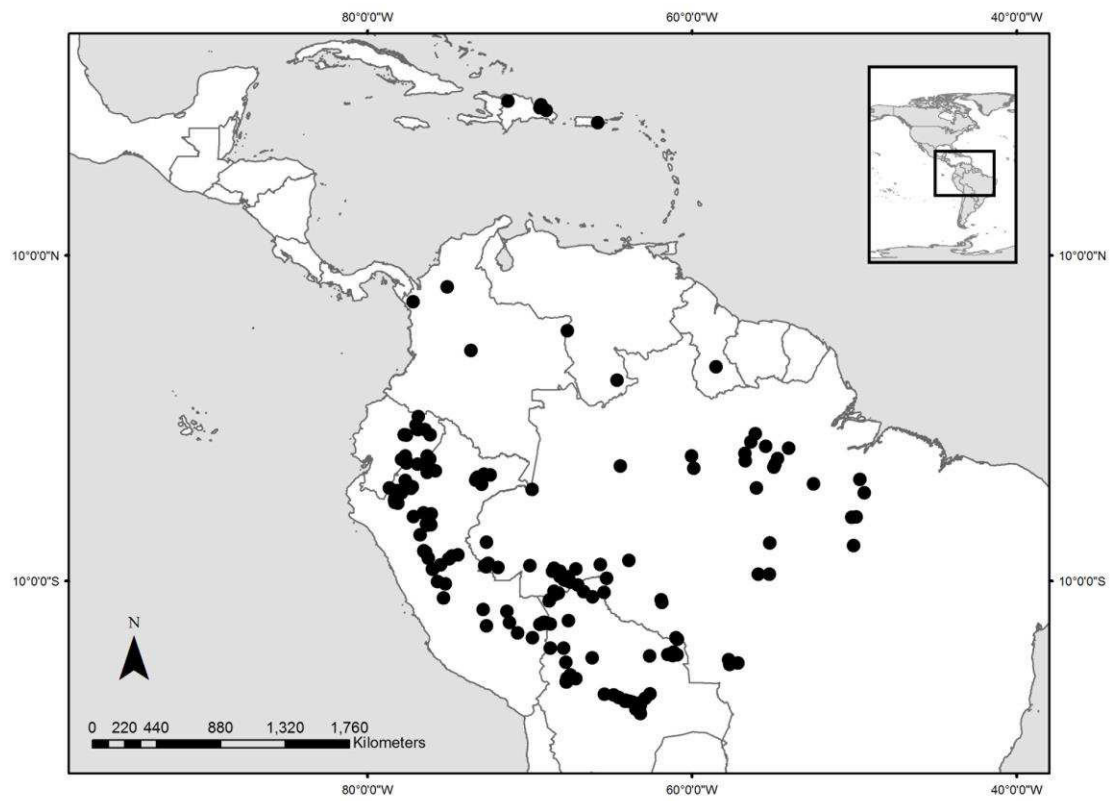


Figure 18. Distribution of *Tynanthus polyanthus*.

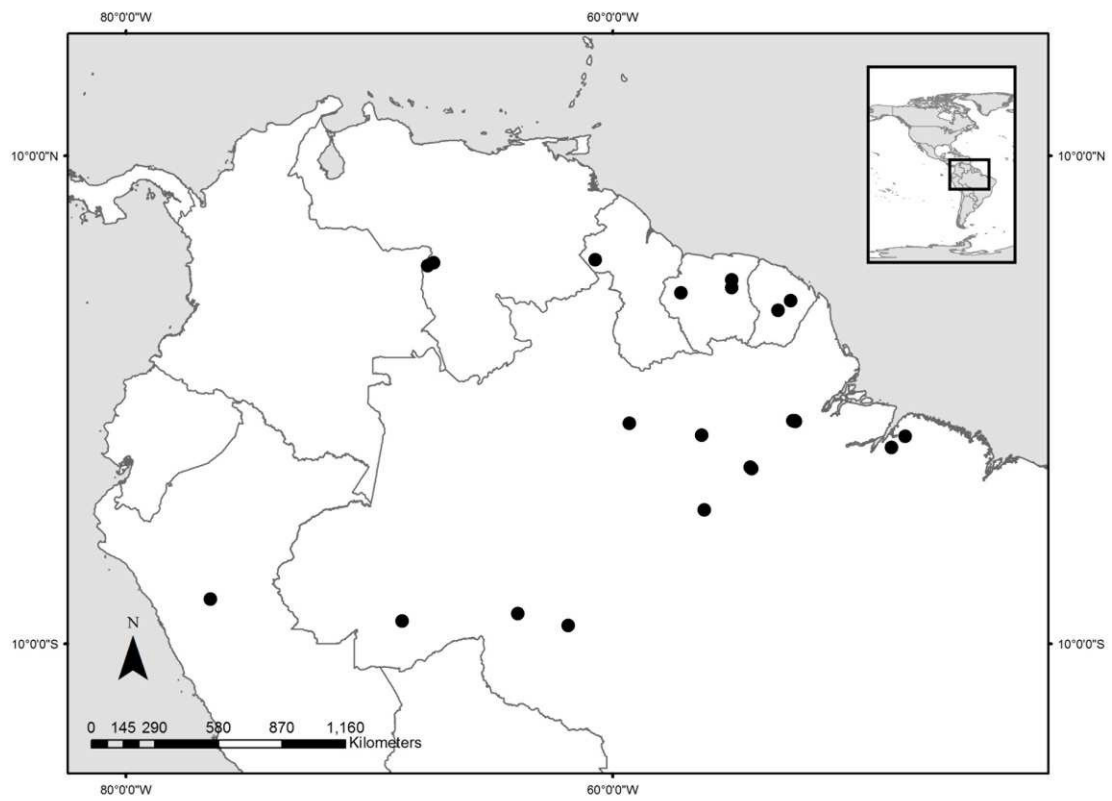


Figure 19. Distribution of *Tynanthus pubescens*.

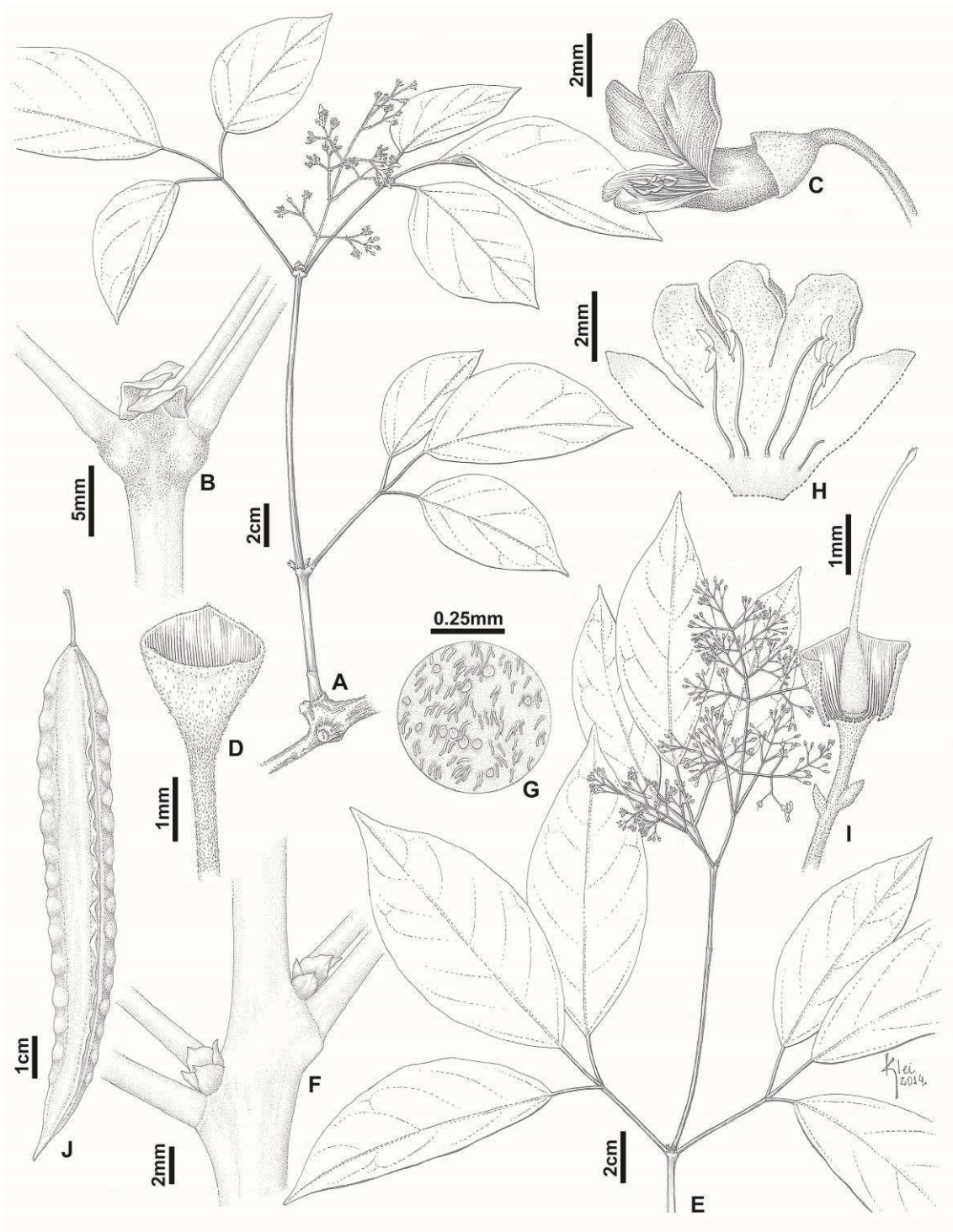


Figure 20. A-D. *Tynanthus sastrei*: A. Habit; B. Interpetiolar region showing the foliaceous prophylls of the axillary buds; C. Flower; D. Calyx with denticulate apex (L. Skog 7043, NY). E-J. *T. schumannianus*: E. Habit; F. Interpetiolar region showing the bromeliad-like prophylls; G. Detail of inflorescence axis indumentum, showing patelliform trichomes; H. Open corolla showing the androecium; I. Open calyx showing the gynoecium (M. Nee 38171, NY); J. Fruit (M. Lewis 37532, MO).

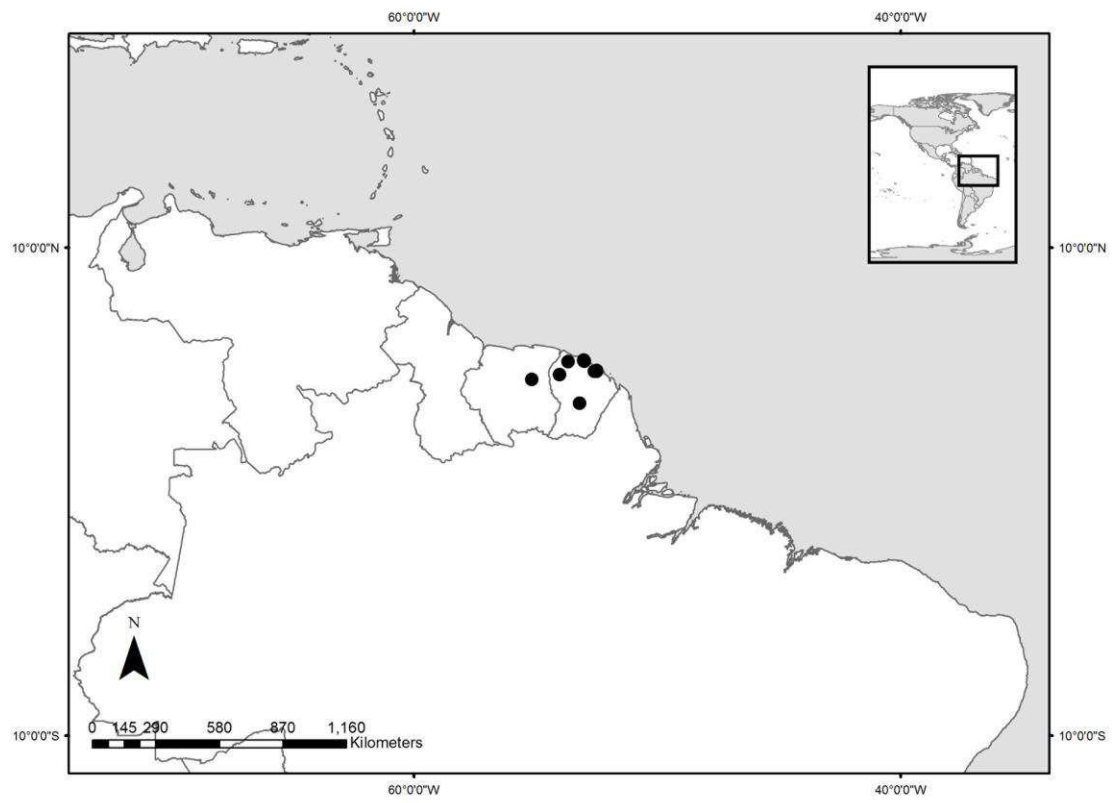


Figure 21. Distribution of *Tynanthus sastrei*.

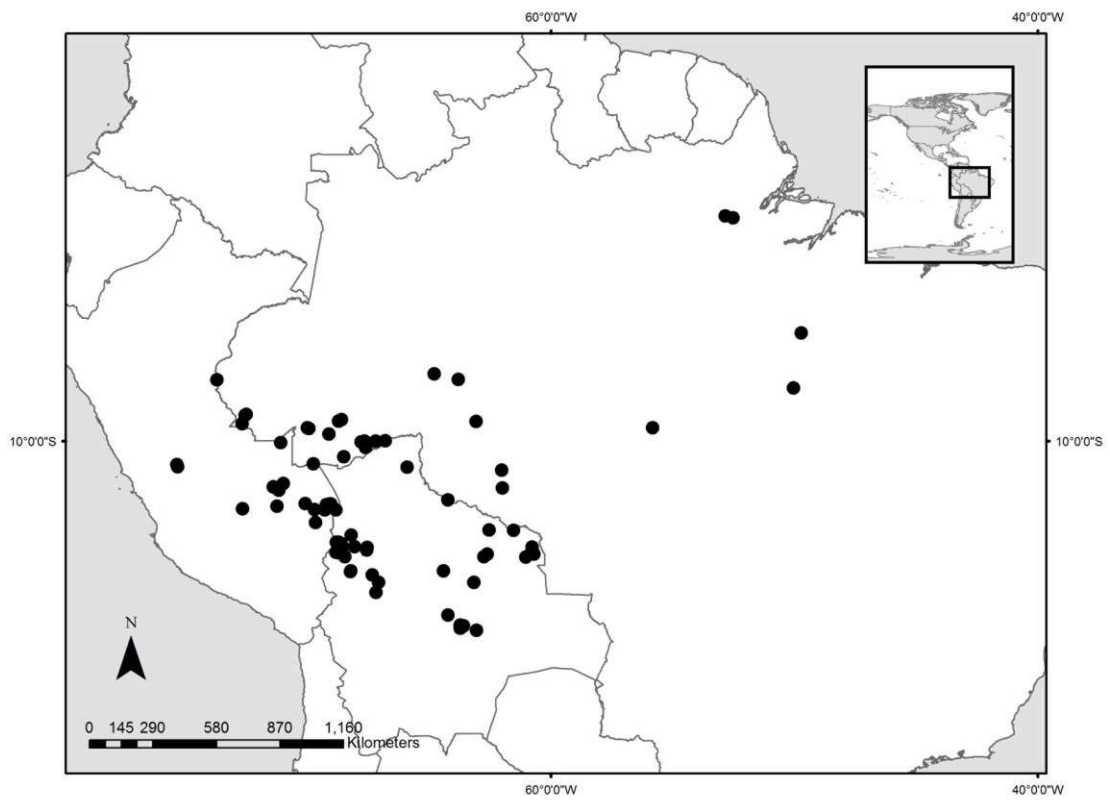


Figure 22. Distribution of *Tynanthus schumannianus*.

Capítulo 4

**Evolution of the ecological niche of *Tynanthus* Miers
(Bignoniaeae, Bignoniaceae)**

Evolution of the ecological niche of *Tynanthus* Miers (Bignoniaceae, Bignoniaceae)

Abstract

Studies on niche evolution allow us to establish how species niches have changed over time as well as to identify how long-term evolutionary processes have led to present-day species distributions. Here, we investigate the patterns of niche evolution in *Tynanthus* (Bignoniaceae, Bignoniaceae) and test the hypothesis that niche conservatism has played an important role in the diversification history of this genus of Neotropical lianas. For that, we perform univariate and multivariate comparisons between species' climatic niches and species' phylogenetic relationships. We encountered considerable divergence in climatic niches among species, indicating that niche conservatism in climatic variables has not played a key role in the diversification of the genus. These results suggest that other ecological factors (e.g., biotic interactions), may have influenced current distribution patterns in the group instead. Our results are used as basis to discuss patterns of ecological niche evolution in the genus and to suggest novel approaches for future analyses.

Keywords. Lianas, neotropical flora, niche conservatism, niche evolution, niche overlap, species distribution patterns

Introduction

The factors determining species distribution patterns in space and time have intrigued ecologists and biogeographers for a long time (Brown *et al.* 1996). It is now clear, that species ranges are determined by a set of abiotic and biotic conditions that are known as a species niche (Hutchinson 1957) which, together with historical factors, seem to have shaped present-day distribution patterns. In this context, it is critical that analyses of niche elements incorporate information on the phylogenetic history of the focal taxa so that a more complete picture of the factors shaping species distributions can be achieved (e.g., Rice *et al.* 2003; Knouft *et al.* 2006; Eaton *et al.* 2008; Kozak & Wiens 2010; Emery *et al.* 2012; Nyári & Reddy 2013). Niche studies based on robust phylogenetic frameworks allow us to identify how long-term evolutionary processes have led to present-day distribution patterns as well as to establish how species niches have changed and evolved over time (Wiens 2011).

Several studies on niche evolution have shown that ecological requirements of lineages are often conserved over time, with closely related species maintaining their ancestral niche traits and often being more ecologically similar than expected based on their phylogenetic relationships; this pattern is known as niche conservatism (see Wiens *et al.* 2010). Nevertheless, niche conservatism is not the rule for all organisms and other studies have also encountered substantial evidence for niche shifts (i.e., niche overdispersion) over time (Losos 2008; Pearman *et al.* 2008; Wiens 2011). Despite the great breath of studies on niche evolution, the exact role of niche conservatism and niche overdispersion remains to be determined.

A better understanding of the level of lability of ecological features is critical for a clearer understanding of community structure (e.g., Stephens & Wiens 2009; Vamosi *et al.* 2009), and species distribution patterns in tropical vs. temperate regions (e.g., Buckley *et al.* 2010; Hawkins *et al.* 2011; Jansson *et al.* 2013), as well as allows for a better evaluation of species' persistence under climate change (e.g., Wiens *et al.* 2009; Maiorano *et al.* 2013), and biological invasions (e.g., Petitpierre *et al.* 2012; Broennimann *et al.* 2014), among others (reviewed by Wiens & Graham 2005; Wiens *et al.* 2010; Peterson 2011). However, studies of Neotropical plant clades, based on robust phylogenies and a detailed understanding of the species niche preferences are still lacking, preventing a complete understanding of the factors that have shaped current distribution patterns in the Neotropical region.

Tynanthus (Bignoniaceae, Bignoniaceae) is a genus of lianas that is widely distributed through the Neotropics (Lohmann & Taylor, 2014; Medeiros & Lohmann in prep.). Species of *Tynanthus* generally have restricted distribution patterns, occurring predominantly in humid forests from Southern Mexico to Southern Brazil (Medeiros & Lohmann in prep.). A taxonomic revision (Medeiros & Lohmann in prep.) and a robust phylogenetic framework based on plastid and nuclear markers were used as basis for a biogeographical study of the genus (Medeiros & Lohmann in prep.). This study indicated that *Tynanthus* originated between 9.4-21.5 Mya, most likely at around 15.3 Mya in Western South America and Central America. Closely related species within *Tynanthus* occupy the same biogeographical region suggesting that ecological niche features might be conserved in the genus, and may have prevented species to expand their ranges both within and outside the individual biogeographical regions (Medeiros & Lohmann in prep.).

In this study, we test the hypothesis that niche conservatism has played a major role in the diversification history of *Tynanthus*. To test this hypothesis, we use climatic variables to estimate the ecological niche of the individual species and a robust phylogenetic framework to investigate patterns of niche diversification within the genus.

Material and methods

Distribution and climatic data. A comprehensive dataset including 1780 georeferenced records of 647 unique localities was assembled from herbarium vouchers for 13 of the 14 species of *Tynanthus* currently recognized (Medeiros & Lohmann in prep.); only *T. espiritosantensis* M.C. Medeiros & L.G. Lohmann was excluded due to the low number of collection records. The total number of unique localities for each species ranged from five (*T. macranthus*) to 193 (*T. polyanthus*); the exact number of records and localities per taxon is presented in Appendix 1. This dataset includes the geographical locations and coordinates included in the specimen labels by collectors. Whenever geographical coordinates were not available, these were georeferenced using the Global Gazetteer Version 2.2 (<http://www.fallingrain.com/world/index.html>) and the database of the Instituto Brasileiro de Geografia e Estatística (<http://www.ibge.gov.br/>). All records were checked using QGIS 2.0.1 (QGIS Development Team; available at <http://qgis.osgeo.org/>).

We used the 19 bioclimatic variables from the WorldClim dataset (Hijmans *et al.* 2005) at 2.5 arc-minutes resolution (roughly 5 km²). All variables were examined for pairwise correlations using Bioestat 5.3 (Instituto Mamirauá; available at <http://www.mamiraua.org.br/>) and calculations were conducted based on values extracted

from sampling points throughout the study area, which was determined by a minimum convex polygon enclosing all species records in QGIS (Fig. 1). This analysis led to selection of six uncorrelated variables (Spearman's correlation < 0.7) that best reflect the climatic tolerances for the species of *Tynanthus*: 'Temperature Seasonality' (bio4), 'Maximum Temperature of the Warmest Month' (bio5), 'Minimum Temperature of the Coldest Month' (bio6), 'Precipitation Seasonality' (bio15), 'Precipitation of the Warmest Quarter' (bio18) and 'Precipitation of the Coldest Quarter' (bio19).

Niche quantification and comparison. Species pairwise comparisons were conducted for the six climatic variables separately. For this comparison, values for the localities of known occurrence of all species were sampled in QGIS and compared through Kruskal-Wallis and subsequent Dunn tests in Bioestat 5.3 (Instituto Mamirauá; available at <http://www.mamiraua.org.br/>). Species density plots were then produced with package sm 5.4 (Bowman & Azzalini 2014) in R 3.0.3 (R Core Team; available at <http://www.r-project.org/>) in order to visualize the distribution of the individual species data for each variable.

We then conducted a multivariate comparison between all species pairs. In those comparisons, niche overlap between taxa was quantified using the PCA-env technique proposed by Broennimann *et al.* (2012), in R. For those analyses, the first two axes of the Principal Component Analysis (PCA) calibrated on the entire climatic space of the study area, including species occurrences, were considered (Broennimann *et al.* 2012). The climatic space delimited by the axes was set to 100 x 100 cells while niche overlap was estimated using Schoener's D metric (Schoener 1970; Broennimann *et al.* 2012). Statistical tests of niche equivalency and similarity were performed (Warren *et al.* 2008). A niche equivalency test was conducted to determine whether the observed overlap between taxa is constant when randomly reallocating the occurrences of the two species (i.e., niches of the two species are identical). On the other hand, the niche similarity test was conducted to determine whether the observed overlap is different from the overlap observed between the niche of one species and niches randomly selected in the environmental space occupied by the other species (i.e., niches of the two species are more similar than expected by chance) (Warren *et al.* 2008; Broennimann *et al.* 2012).

Reconstruction of ancestral climatic variables. We assessed the evolution of the individual climatic variables through ancestral state reconstructions using the R package Phytools 0.3-93 (Revell 2012). We calculated the mean value for each of the six variables per species and conducted ancestral state reconstructions for continuous

characters. For this analysis, we used the Bayesian tree of *Tynanthus* derived from the analysis of sequences of one nuclear (*pepC*) and two plastid markers (*ndhF* and *rpl32-trnL*) (Medeiros & Lohmann in prep.). The phylogenetic hypothesis included one individual of 12 of the 14 species of *Tynanthus* recognized; only *T. espiritosantensis* (for which we did not have sufficient occurrence records) and *T. sastrei* (for which we did not have DNA sequences), were excluded from this analysis. Parameters for phylogeny estimation follow (Medeiros & Lohmann in prep.).

Relationship between phylogenetic distance and niche overlap. We used a Mantel test to check for correlations between niche overlap and phylogenetic distance within *Tynanthus*. For this analysis, we used the matrix of overlap based on Schoener's D metric and patristic distances for all species pairs. All analyses were conducted in the R package Vegan 2.0-10 (Oksanen *et al.* 2013).

Results

Univariate comparisons. Significant differences among *Tynanthus* species regarding all six climatic variables were encountered through a Kruskal-Wallis test ($p < 0.0001$). Subsequent Dunn tests determined significant species differences for each variable (Appendix 2). Three variables, 'temperature seasonality' (bio4), 'minimum temperature of coldest month' (bio6) and 'precipitation of coldest quarter' (bio19), presented more significant than non-significant results (respectively 44, 48 and 52 of the 78 pairwise comparisons; $p < 0.05$), indicating remarkable differences among species niches in these climatic features. The reverse occurred with the other three variables, 'maximum temperature of warmest month' (bio5), 'precipitation seasonality' (bio15) and 'precipitation of warmest quarter' (bio18), all of which presented more non-significant than significant results (50, 46 and 49, respectively), indicating that these variables are not the most important in niche differentiation within the genus.

Density plots illustrate the results from the statistical tests (Fig. 2). In the bio4 plot, for example, it is possible to visualize that *T. croatianus*, *T. densiflorus*, *T. macranthus*, *T. panurensis*, *T. polyanthus*, *T. pubescens* and *T. sastrei* occur predominantly in areas with low temperature seasonality, while the remaining species (i.e., *T. cognatus*, *T. fasciculatus*, *T. guatemalensis*, *T. labiatus*, *T. micranthus* and *T. schumannianus*) occur predominantly in areas with higher temperature seasonality. The bio6 plot shows that *T. cognatus*, *T. fasciculatus* and *T. micranthus* occur with higher density in areas with lower minimum temperature of coldest month than *T. guatemalensis*, *T. labiatus*, *T. macranthus*, *T.*

polyanthus and *T. schumannianus*, which, in turn, present lower values of minimum temperature than *T. croatianus*, *T. densiflorus*, *T. panurensis*, *T. pubescens* and *T. sastrei*. The bio19 plot indicates that *T. cognatus*, *T. fasciculatus*, *T. guatemalensis*, *T. labiatus*, *T. micranthus*, *T. polyanthus* and *T. schumannianus* are mainly distributed in areas with lower precipitation in the coldest quarter than *T. croatianus*, *T. densiflorus*, *T. macranthus*, *T. panurensis*, *T. pubescens* and *T. sastrei*. The bio5, bio15 and bio18 plots, on the other hand, do not show any clear pattern of variation in climatic features among species groups. These plots generally show a high overlap on the density of occurrence, suggesting complex patterns of variation in the curve shapes.

Multivariate comparisons. A principal component analysis (PCA) based on the climatic space of the study area returned two axes that together explain 66.8% of total variation (PC1 = 39.36% and PC2 = 27.44). The contribution of each variable to the axes is presented in Figure 3, as well as the niches of all species analyzed. Density plots illustrate that the niches of the species of *Tynanthus* differ in their position especially along PC1, which is mostly associated with bio4 and bio6; these findings are in agreement with the results derived from the univariate statistical tests previously described. Pairwise overlap ranged from $D=0$ to $D=0.618$ (Table 1). Overlap is low in most cases, with 47 comparisons (around 60% of total) returning a $D < 0.1$. Six of the nine highest values ($D > 0.3$) were obtained for species pairs whose distributions were partially coincident or adjacent (*T. cognatus-T. fasciculatus*, *T. cognatus-T. micranthus*, *T. fasciculatus-T. micranthus*, *T. macranthus-T. polyanthus*, *T. polyanthus-T. pubescens* and *T. polyanthus-T. schumannianus*).

Niche equivalency and similarity tests. The hypothesis of niche equivalency between species pairs was rejected in every case ($p < 0.02$), indicating that none of the species are climatically identical. In the niche similarity tests, most species pairs showed an overlap that falls within the 95% confidence interval of the null distribution. Only in four instances a two-way significant niche similarity was obtained (*T. cognatus-T. fasciculatus*, *T. cognatus-T. micranthus*, *T. guatemalensis-T. schumannianus* and *T. macranthus-T. polyanthus*), indicating that niches were more similar than expected by chance. One-way significant similarity was obtained for *T. fasciculatus-T. labiatus*, *T. fasciculatus-T. macranthus* and *T. polyanthus-T. pubescens*.

Ancestral climatic niche reconstructions. Observed and estimated mean values for each of the six climatic variables are represented by a color gradient in the simplified phylogenetic tree presented in Figure 4. The ancestral condition for the genus

was low to intermediate ‘temperature seasonality’ (bio4). This condition was lower in the ancestral of the panurensis clade, composed of *T. croatianus*, *T. guatemalensis*, *T. densiflorus*, *T. panurensis* and *T. pubescens* (Medeiros & Lohmann in prep.), and higher in the ancestral of the *T. micranthus* + *T. fasciculatus* + *T. labiatus* clade. Furthermore, the most recent common ancestor (MRCA) of the genus presented an intermediate value for the variable ‘maximum temperature in warmest month’ (bio5). The value of bio5 increased in the panurensis + labiatus clade (i.e., *T. schumannianus* + *T. micranthus* + *T. fasciculatus* + *T. labiatus*; Medeiros & Lohmann in prep.), got even higher within the panurensis clade but decreased within the labiatus clade.

As far as the variable ‘minimum temperature in coldest month’ (bio6) is concerned, the ancestral condition is intermediate, increasing within the panurensis clade but decreasing within the *T. micranthus* + *T. fasciculatus* + *T. labiatus* subclade. The MRCA of *Tynanthus* occurred in areas with intermediate values of ‘precipitation seasonality’ (bio15); those values increased in the *T. croatianus* + *T. guatemalensis* subclade and in the ancestor of the labiatus clade, with a subsequent increase within the *T. fasciculatus* + *T. labiatus* subclade. The MRCA of *Tynanthus* also occurred in an area with high values of ‘precipitation of warmest quarter’ (bio18); intermediate values are observed in the MRCA of the panurensis + labiatus clade, with a decrease of those values in the panurensis clade, and increase in the labiatus clade. Finally, the MRCA of *Tynanthus* occupied an area with intermediate values for the variable ‘precipitation of coldest quarter’ (bio19); this variable increased within the panurensis clade and decreased within the labiatus clade.

Phylogenetic distance and niche overlap. Results from the Mantel test indicate a lack of significant correlation between climatic niche overlap and phylogenetic distance within *Tynanthus* ($r=0.16$; $P=0.17$). These results are presented in Figure 5.

Discussion

In this study, we investigate the patterns of niche evolution in *Tynanthus* (Bignoniaceae, Bignoniaceae) and test the hypothesis that niche conservatism has played a major role in the diversification history of this genus. Comparisons of species climatic niches and associated environmental data with information on phylogenetic relationships among the various species recovered considerable divergence in climatic niches among species. The lack of significant conservation of climatic features within the group suggests that other ecological factors such as biotic interactions may have influenced current

distribution patterns in the group. Our results are used as basis to discuss ecological patterns in the genus and to suggest novel approaches for future analyses.

Niche evolution. The analysis of each of the six climatic variables considered indicated that ‘temperature seasonality’ (bio4), ‘minimum temperature of coldest month’ (bio6) and ‘precipitation of coldest quarter’ (bio19) account for the majority of the observed ecological differentiation within *Tynanthus*. These results were obtained through the analysis of the overall geographic distribution of each species; therefore, species with similar niche characteristics are mostly composed by taxa that inhabit the same broad geographical area. For example, the three Atlantic forest species *T. cognatus*, *T. fasciculatus* and *T. micranthus* predominate in areas that are characterized by a higher temperature seasonality, lower minimum temperature of coldest month and lower precipitation of the coldest quarter than the Amazonian *T. densiflorus*, *T. panurensis*, *T. pubescens* and *T. sastrei*. These observations reflect the typical climatic features of each of the biogeographical regions considered (Peel *et al.* 2007; Garreaud *et al.* 2009). In other words, the niche climatic variables considered here generally reflect large-scale biogeographical patterns. However, *T. labiatus* occurs mainly in areas with high temperature seasonality and low precipitation of the coldest quarter, similarly to the other Atlantic forest taxa. Nevertheless, the localities of occurrence of *T. labiatus* show a minimum temperature of the coldest month that is higher than other Atlantic Forest taxa. Differently from ‘temperature seasonality’ (bio4), ‘temperature of the coldest month’ (bio6) and ‘precipitation of the coldest quarter’ (bio19), our results showed that ‘maximum temperature of warmest month’ (bio5), ‘precipitation seasonality’ (bio15) and ‘precipitation of warmest quarter’ (bio18) generally provide less information about the niche differences among species of *Tynanthus*. This is due to the fact that the mean value of these climatic features are not particularly variable in the areas in which most of the *Tynanthus* species occur, especially Amazonia and Central America (Peel *et al.* 2007; Garreaud *et al.* 2009).

Although it is possible to visualize some broad climatic affinities among species of *Tynanthus*, the multivariate comparisons indicate that niche overlap is generally low. The overall divergence in climatic features was also shown by the similarity tests, most of which presented non-significant results, especially in the case of taxa that belong to distinct geographical regions (e.g., *T. cognatus*-*T. sastrei*, $D=0$, $p_{1,2}=0.24$, $p_{2,1}=0.32$; *T. labiatus*-*T. macranthus*, $D=0.048$, $p_{1,2}=0.24$, $p_{2,1}=0.18$), but also for species that occur in adjacent areas (e.g., *T. croatianus*-*T. guatemalensis*, $D=0.004$, $p_{1,2}=0.77$, $p_{2,1}=0.97$; *T. labiatus*-*T. micranthus*, $D=0.071$, $p_{1,2}=0.5$, $p_{2,1}=0.81$) (Table 1).

Many closely related species of *Tynanthus* also occur in the same biogeographical region (Medeiros & Lohmann in prep.). Despite that, no significant relationship was found between niche overlap and phylogenetic distance (Mantel test; $r=0.16$; $P=0.17$). This result suggests that the closely related species that occur in the same biogeographical area likely experienced niche differentiation during the diversification history of the group. In those cases, the diversification of lineages was probably affected by ecological factors other than the climatic ones treated here, especially those acting at smaller spatial scales (Wiens 2011; Crisp & Cook 2012). For instance, biotic interactions such as competition between closely related taxa might be driving species to different microenvironmental niches. It is also possible that competition might explain the relatively reduced range size of some species of *Tynanthus*. In other words, ecological specialization may prevent species from expanding their distribution range, especially in the case of sympatric taxa with similar ecological requirements. Further ecological studies aiming at addressing the competition among species of *Tynanthus* would allow for an adequate test of this prediction. In particular, finer-scale analyses of traits in relation to a variety of environmental variables, including ecological aspects associated with establishment and survival (e.g., soil conditions, host preference, pollinators) (Bazzaz 1991; Schnitzer & Bongers 2002), would further clarify which ecological aspects may lead to competition among species. In the tribe Bignonieae in general, competition for pollinators seems to have had minor effects on community assembly (Alcantara *et al.* 2014). However, this hypothesis should be further tested within other Bignonieae clades with complete phylogenetic sampling such as *Tynanthus*.

Overall, our reconstructions of climatic features indicated that the climatic characteristics of the habitat inhabited by the MRCA of *Tynanthus* were predominantly intermediate, except for the low ‘temperature seasonality’ (bio4) and high ‘precipitation of the warmest quarter’ (bio18). Changes that occurred during the diversification history of *Tynanthus* likely led to the establishment of the current climatic conditions currently occupied by the species of *Tynanthus*. These results received further support from univariate comparisons, and mainly reflected the differentiation between Amazonia+Central America and Atlantic forest species. While the diversification of *Tynanthus* throughout Amazonia and Central America was marked by a decrease in ‘temperature seasonality’ (bio4) and an increase in ‘maximum temperature of warmest month’ (bio5), ‘minimum temperature of coldest month’ (bio6) and ‘precipitation of coldest quarter’ (bio19), the opposite scenario was observed during the diversification of *Tynanthus* throughout the Atlantic forest. No clear pattern was observed with the variables ‘seasonality

of precipitation' (bio15) and 'precipitation of warmest quarter' (bio18); however, some exceptions occurred in specific taxa (e.g., *T. guatemalensis* and *T. schumannianus*; Fig. 4).

Final remarks. Mixed evidence for niche conservatism is available in the literature. While some studies provide convincing evidence for niche conservatism in some lineages (Wiens *et al.* 2010), others show stronger evidence for overdispersion (Losos 2008; Pearman *et al.* 2008; Wiens 2011). These findings indicate that niche conservatism should be explicitly examined instead of assumed a priori (Losos 2008). Recent statistical tests for niche conservatism (e.g., Martínez-Cabrera *et al.* 2012; Ahmadzadeh *et al.* 2013) are providing a more objective means for the test of these hypotheses. In the case of our particular study, initial biogeographical analyses suggested that niche conservatism might be driving species distribution patterns in *Tynanthus* (Medeiros & Lohmann in prep.). Despite that, the detailed studies on climatic niche evolution conducted here indicated an overall climatic differentiation among closely related species within the genus, rejecting a niche conservatism hypothesis. In other words, the occupation of the same broad biogeographic areas by phylogenetically closely related species (Medeiros & Lohmann in prep.) may have been determined by other ecological factors, rather than niche conservatism. This hypothesis remains to be tested with more detailed ecological data. These findings highlight the importance of explicitly testing niche conservatism hypotheses instead of assuming niche conservatism a priori.

The unexpected lack of constancy and evolutionary conservation in niche climatic features reported here only applies to the specific climatic variables and scale of this study. Different results might be encountered when other niche aspects are considered (e.g., ecophysiological) and/or if other spatial scales (e.g., population level) are taken into account. Fine-scale analyses of the distribution pattern of sympatric species would be of particular interest so that habitat use and fine-scale drivers of species distributions could be examined (see Emery *et al.* 2012). Studies of this nature for Neotropical plant clades would be of particular interest given the high levels of diversity encountered in this region and the limited amount of ecological, evolutionary, and biogeographical studies. A synthesis and clear understanding of the exact role of ecology to present-day species distribution patterns will only be achieved once multiple studies, based on a variety of Neotropical taxa are available.

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Table 1. Pairwise comparisons, respective niche overlap (Schoener's D) and niche similarity test p-values. Asterisks indicate significant results ($p < 0.05$). Species names are abbreviated to the four initial letters of the specific epithet.

Species pairs (a-b)	Niche overlap	Similarity a->b	Similarity b->a
cogn-croa	0.001	0.30	0.81
cogn-dens	0.000	0.44	0.38
cogn-fasc	0.376	0.04*	0.02*
cogn-guat	0.142	0.91	0.14
cogn-labi	0.284	0.71	0.53
cogn-macr	0.118	0.55	0.42
cogn-micr	0.406	0.02*	0.04*
cogn-panu	0.071	0.87	0.38
cogn-poly	0.194	0.65	0.53
cogn-pube	0.114	0.83	0.55
cogn-sast	0.000	0.24	0.32
cogn-schu	0.336	0.44	0.10
croa-dens	0.096	0.36	0.24
croa-fasc	0.000	1.23	0.36
croa-guat	0.004	0.77	0.97
croa-labi	0.000	0.75	0.59
croa-macr	0.044	0.81	0.61
croa-micr	0.000	1.11	0.87
croa-panu	0.113	0.63	0.83
croa-poly	0.047	0.46	0.85
croa-pube	0.125	0.46	0.75
croa-sast	0.480	0.06	0.08
croa-schu	0.038	0.91	0.38
dens-fasc	0.000	1.50	1.05
dens-guat	0.000	0.97	1.52
dens-labi	0.000	0.85	0.75
dens-macr	0.001	0.93	0.28
dens-micr	0.000	1.70	1.62
dens-panu	0.012	0.55	0.77
dens-poly	0.003	0.57	0.44
dens-pube	0.028	0.30	0.32

dens-sast	0.199	0.26	0.10
dens-schu	0.001	0.59	0.89
fasc-guat	0.002	0.48	0.59
fasc-labi	0.248	0.02*	0.12
fasc-macr	0.001	0.08	0.04*
fasc-micr	0.339	0.16	0.10
fasc-panu	0.000	0.18	0.93
fasc-poly	0.013	0.16	0.28
fasc-pube	0.001	0.10	0.30
fasc-sast	0.000	0.81	1.45
fasc-schu	0.022	0.48	0.42
guat-labi	0.116	0.42	0.99
guat-macr	0.163	0.08	0.69
guat-micr	0.001	0.36	0.28
guat-panu	0.101	0.20	0.73
guat-poly	0.213	0.06	0.48
guat-pube	0.106	0.79	0.65
guat-sast	0.000	0.83	0.59
guat-schu	0.474	0.02*	0.04*
labi-macr	0.048	0.24	0.18
labi-micr	0.071	0.50	0.81
labi-panu	0.025	0.42	0.89
labi-poly	0.116	0.28	0.87
labi-pube	0.050	0.38	0.61
labi-sast	0.000	0.63	0.69
labi-schu	0.226	0.71	0.20
macr-micr	0.002	0.06	0.32
macr-panu	0.258	0.18	0.12
macr-poly	0.618	0.02*	0.02*
macr-pube	0.184	0.32	0.61
macr-sast	0.010	0.65	0.81
macr-schu	0.257	0.97	0.26
micr-panu	0.000	0.87	1.23
micr-poly	0.024	0.65	0.24
micr-pube	0.002	0.40	0.28
micr-sast	0.000	1.13	1.49
micr-schu	0.085	0.91	0.22

panu-poly	0.203	0.06	0.18
panu-pube	0.092	0.99	0.99
panu-sast	0.018	0.85	0.81
panu-schu	0.139	0.42	0.53
poly-pube	0.330	0.02*	0.10
poly-sast	0.013	0.48	0.50
poly-schu	0.339	0.14	0.08
pube-sast	0.067	0.38	0.32
pube-schu	0.193	0.79	0.97
sast-schu	0.011	0.57	0.59

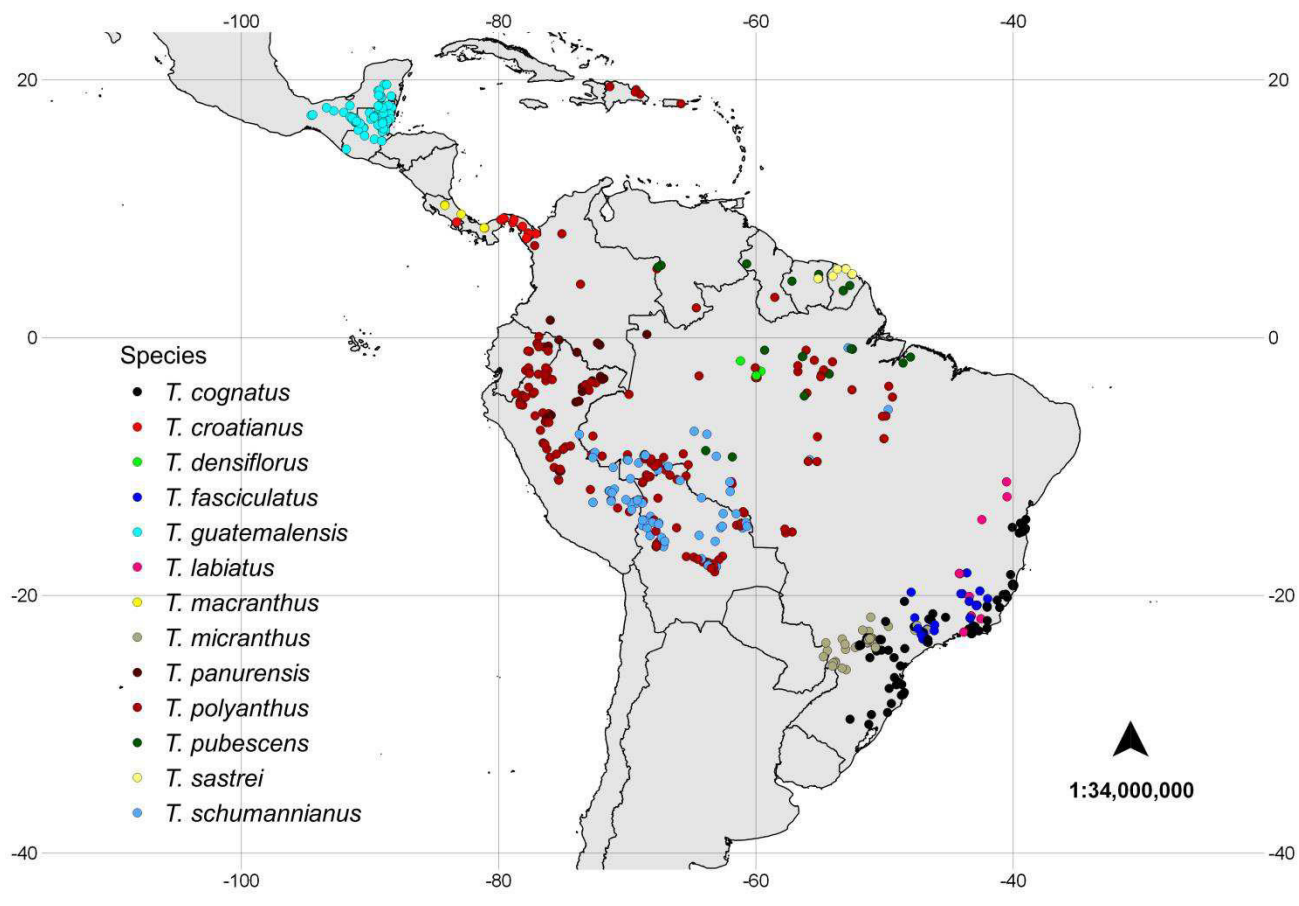
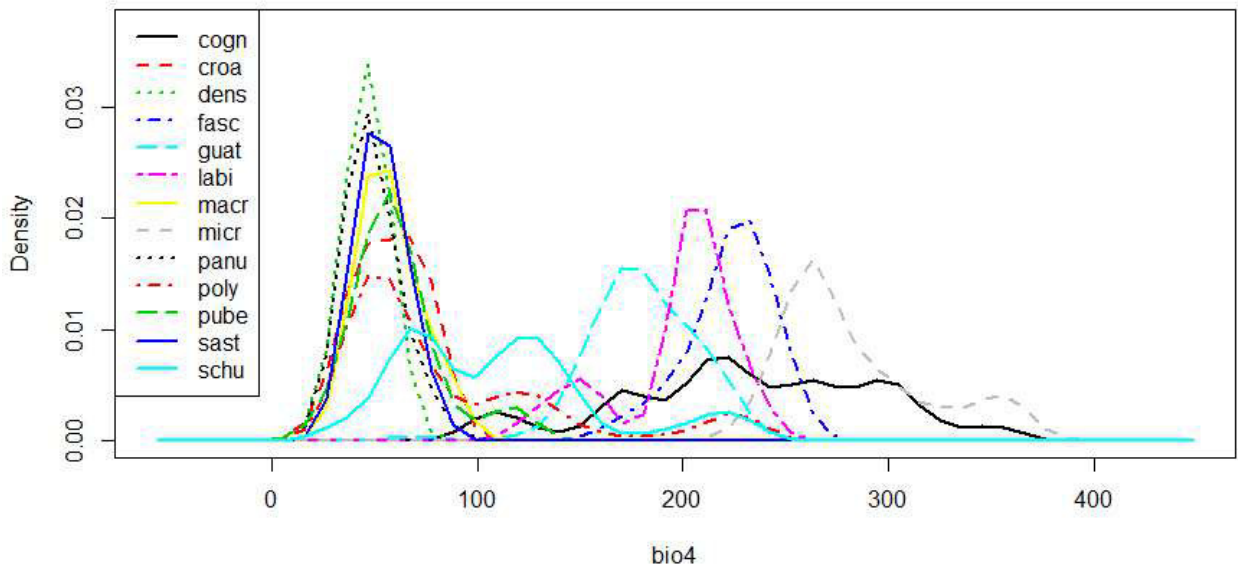
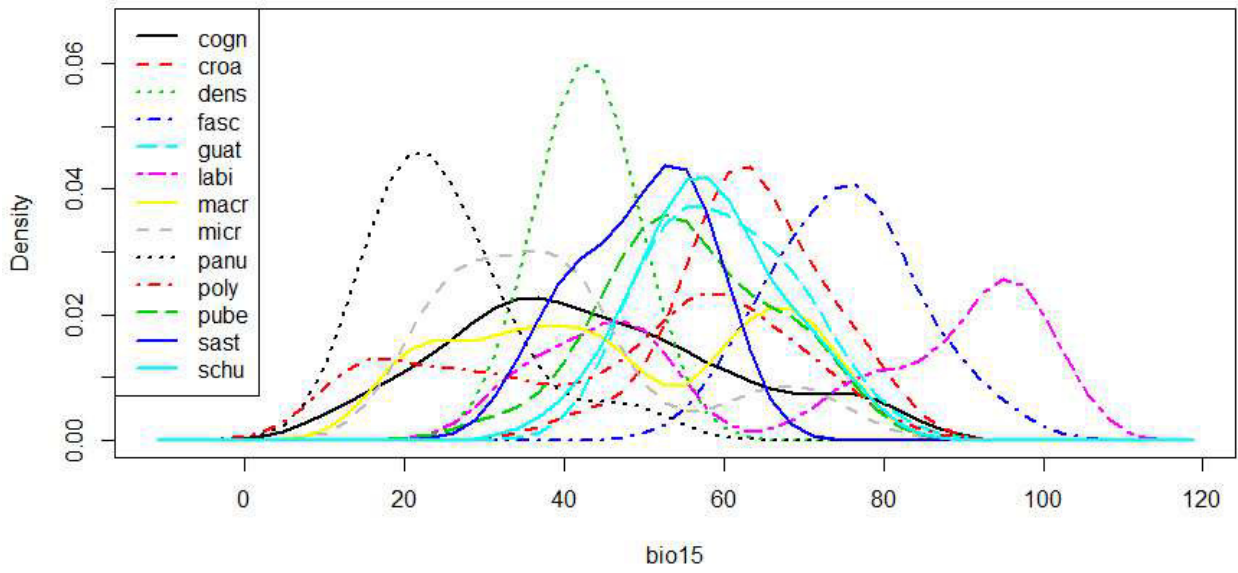
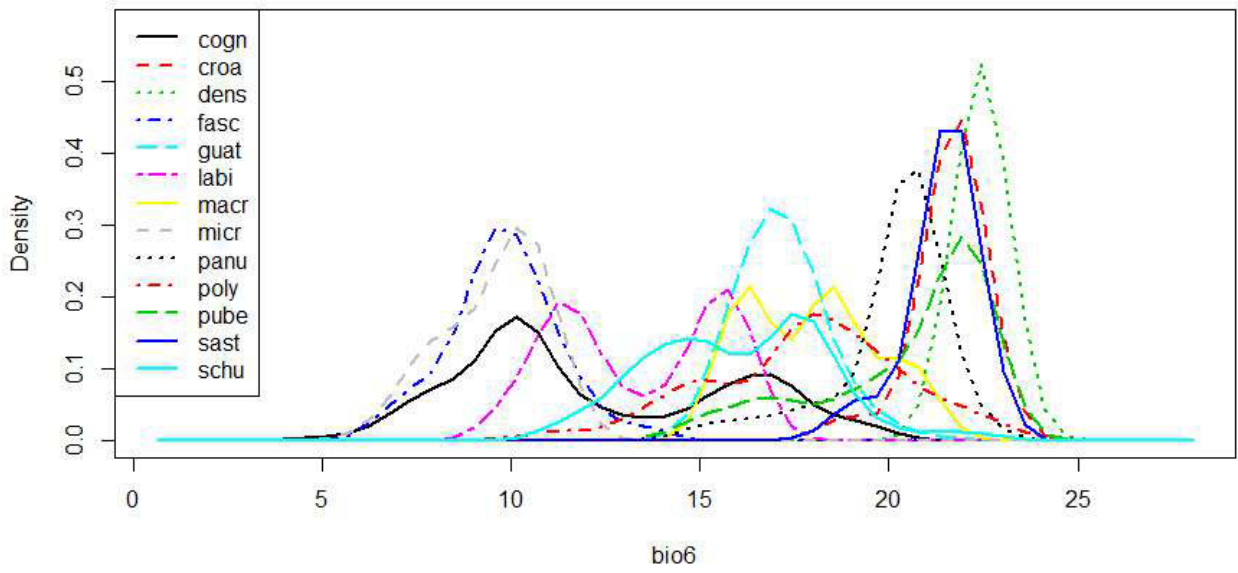


Figure 1. Distribution of the 13 species used in the niche quantifications and comparisons.





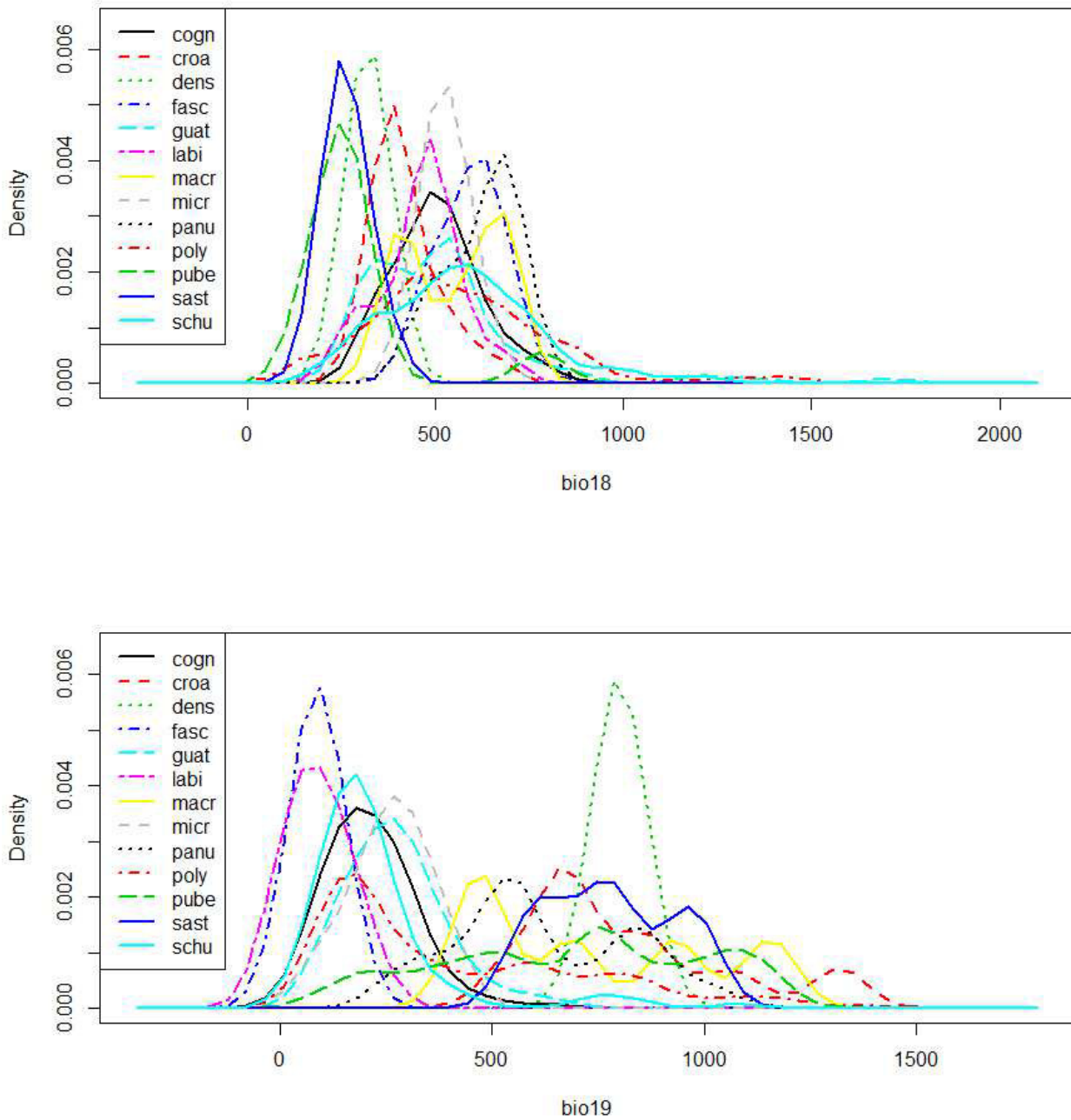
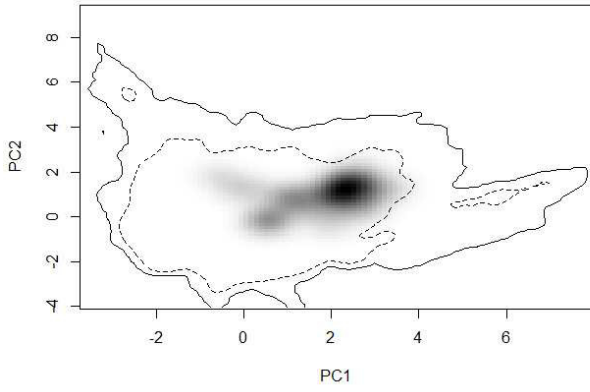
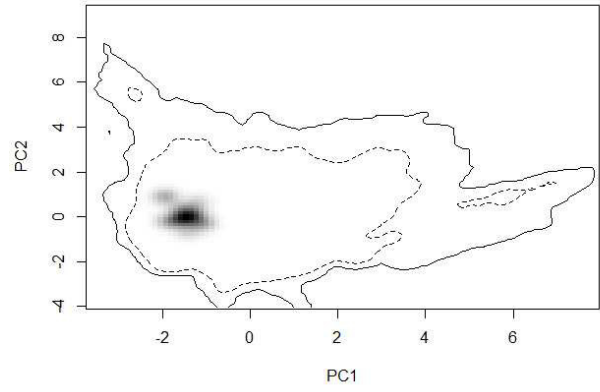


Figure 2. Density plots of the six climatic variables for the 13 species of *Tynanthus* analyzed. bio4: Temperature Seasonality; bio5: Maximum Temperature of the Warmest Month; bio6: Minimum Temperature of the Coldest Month; bio15: Precipitation Seasonality; bio18: Precipitation of the Warmest Quarter; bio19: Precipitation of the Coldest Quarter. Species names are abbreviated using the four initial letters of the specific epithet.

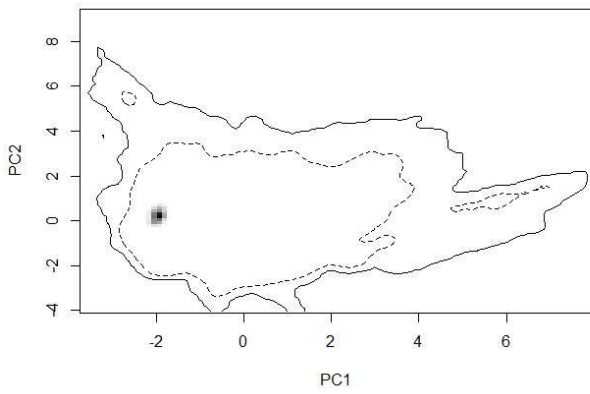
cogn



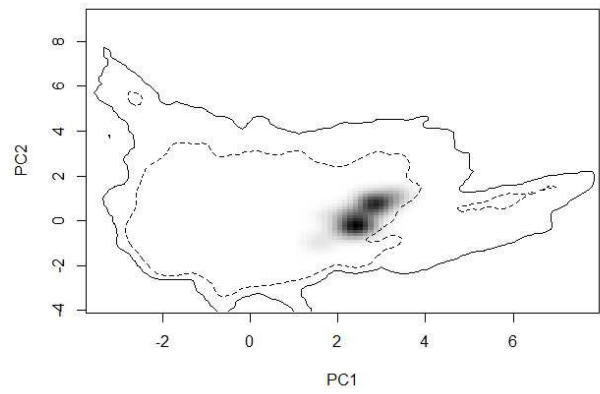
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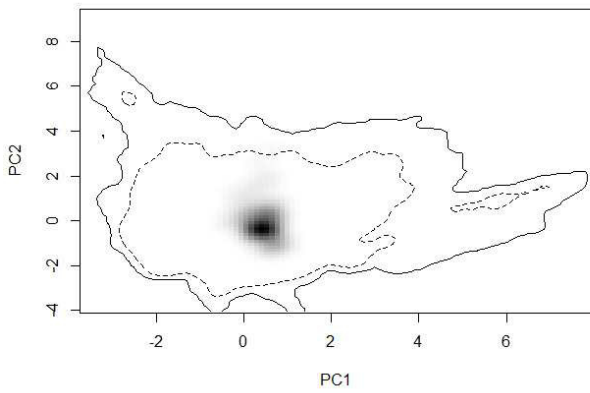
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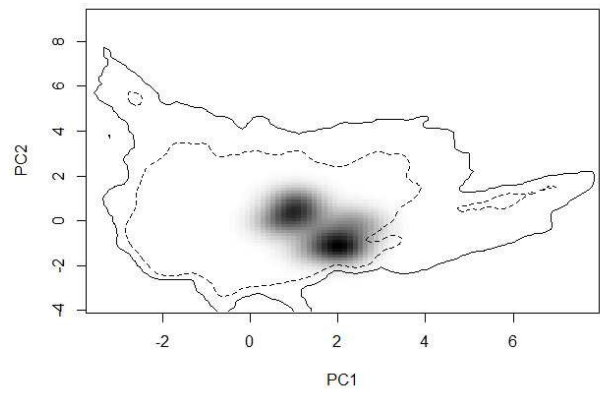
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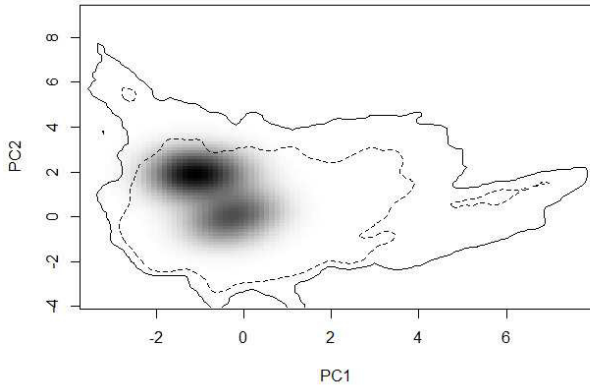
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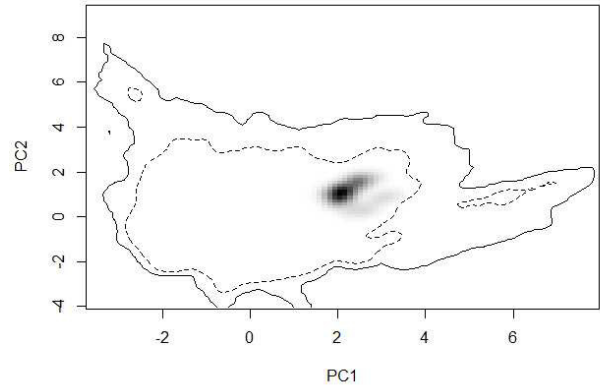
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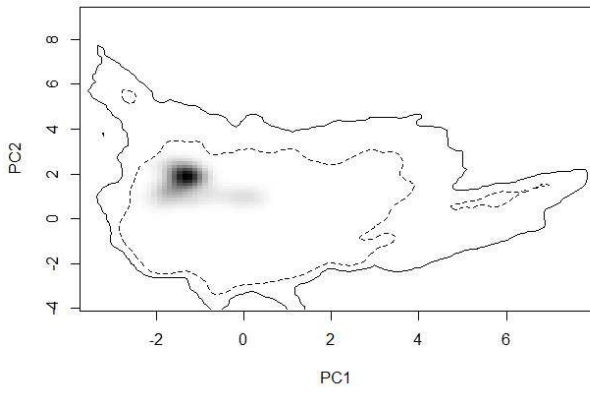
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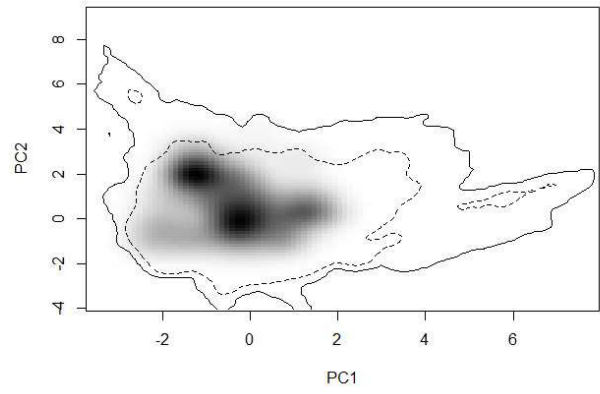
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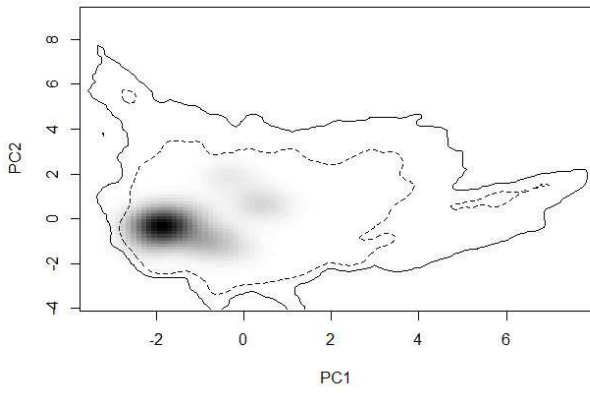
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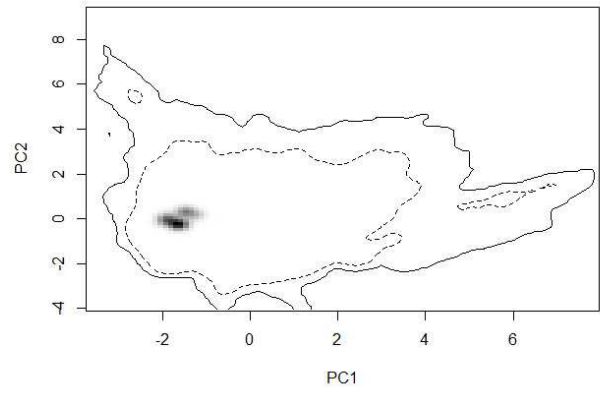
poly



pube



sast



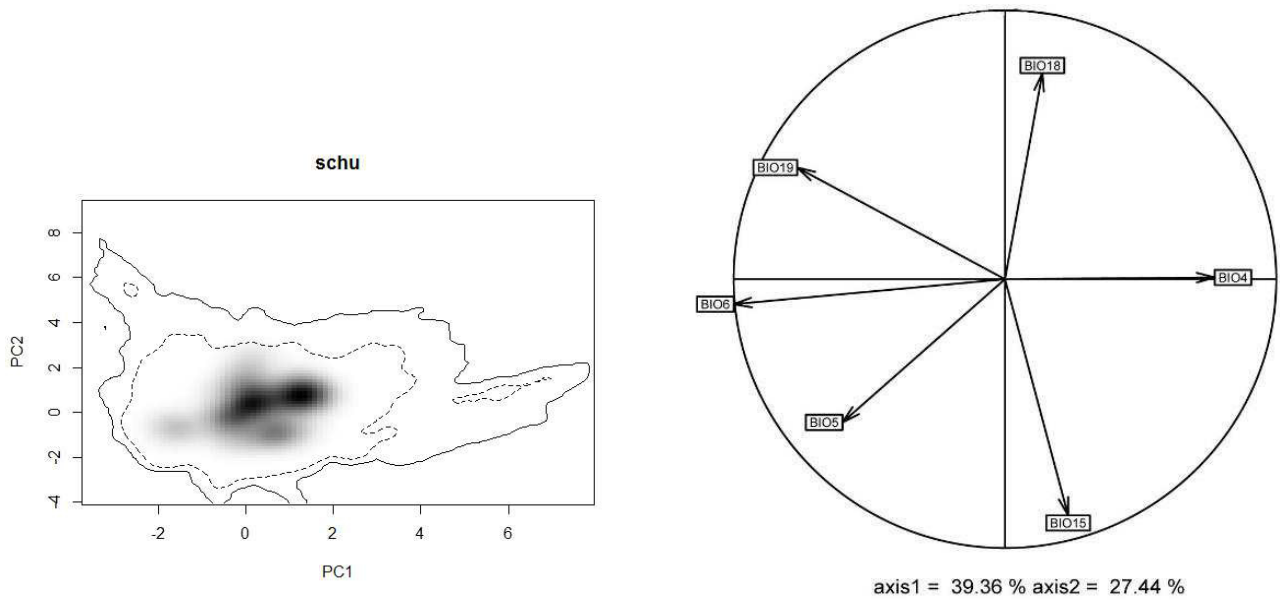
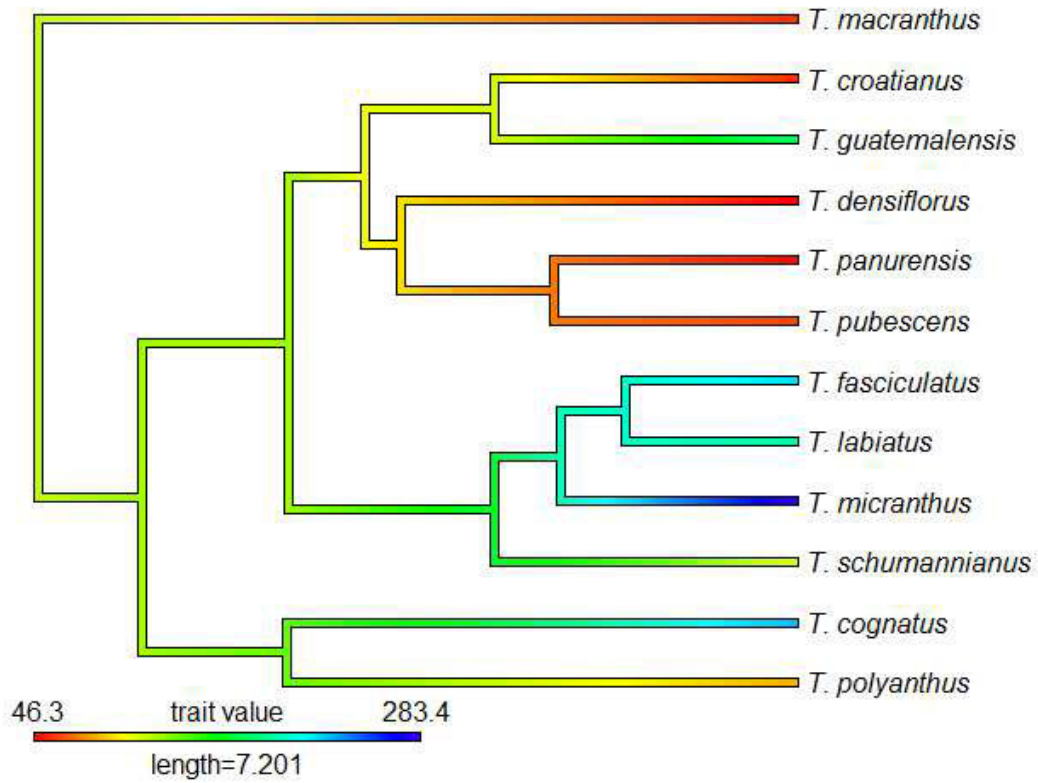
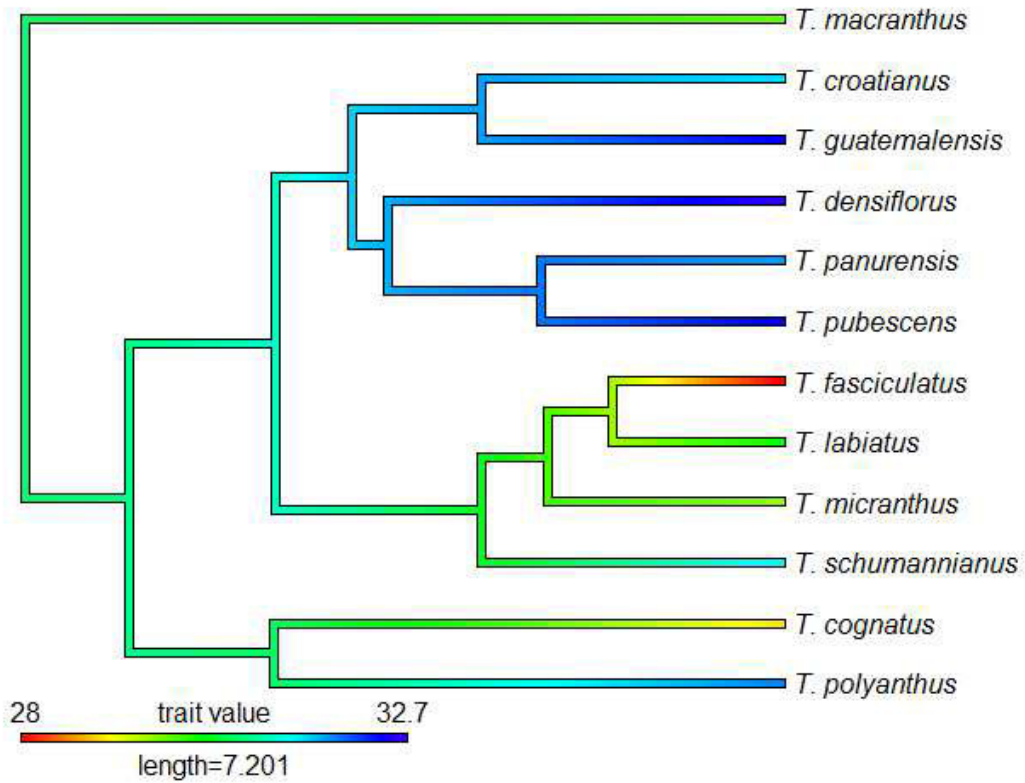


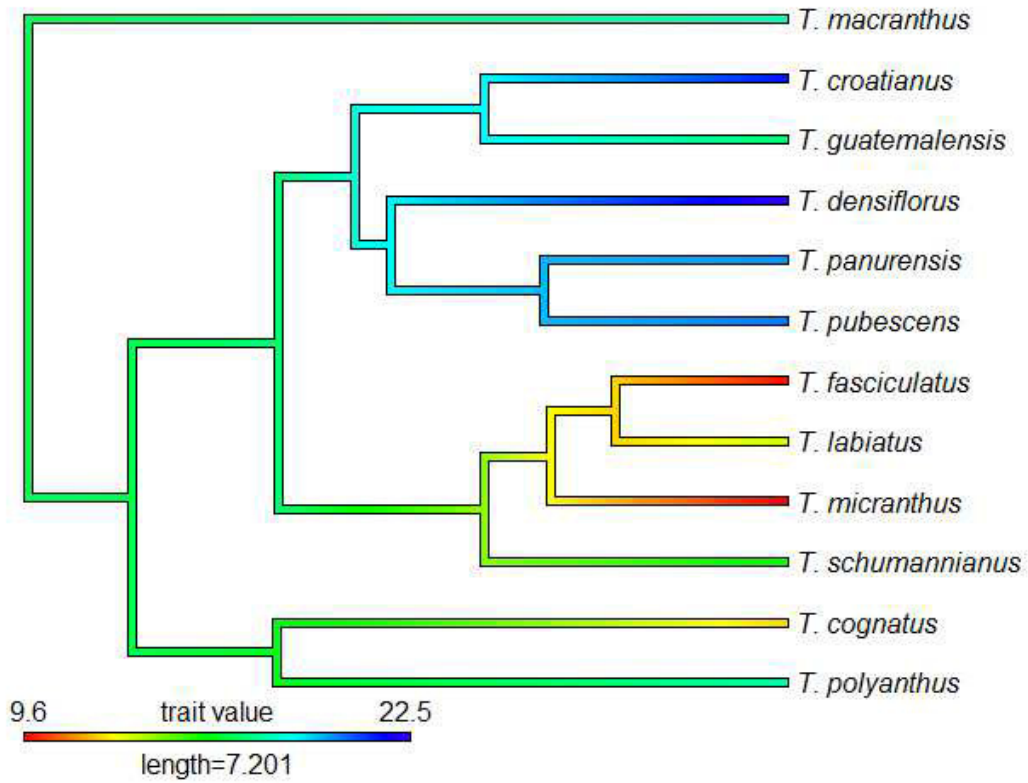
Figure 3. Niches of species of *Tynanthus* in climatic space delimited by the two first PCA axes. Shading represents the density of occurrences of each species by cell. Solid and dashed contour lines show 100 and 50% of the available environment, respectively. The correlation circle illustrates the contribution of the individual climatic variables to the two PCA axes. Species names are abbreviated using to the four initial letters of the specific epithet.



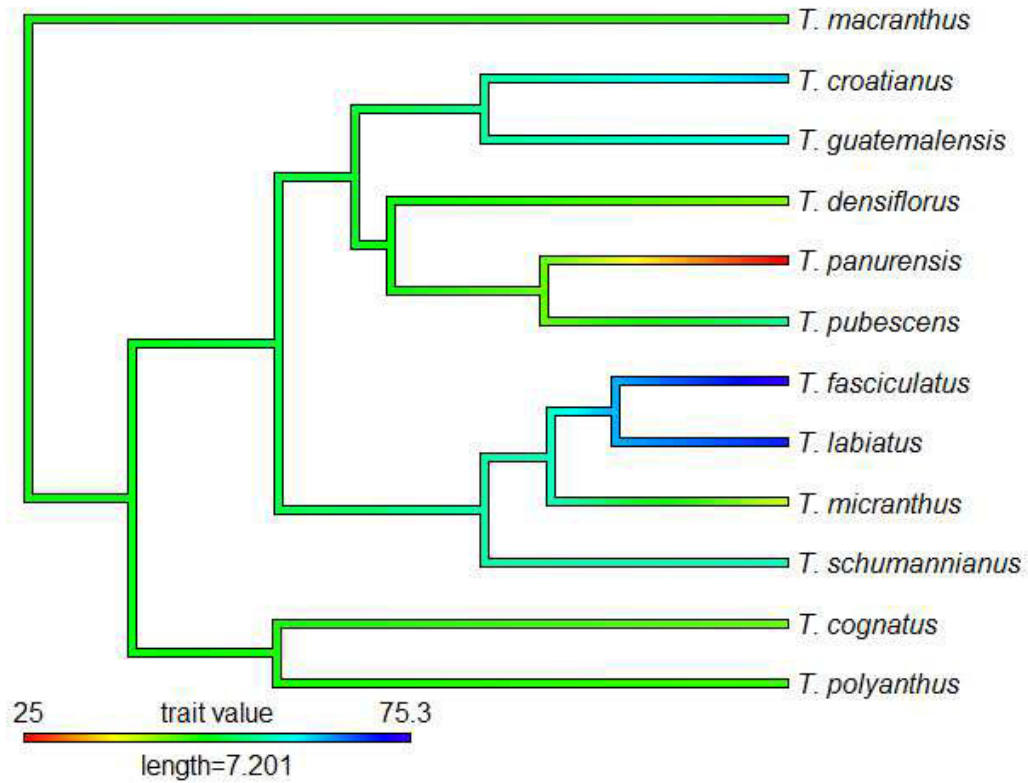
(a)



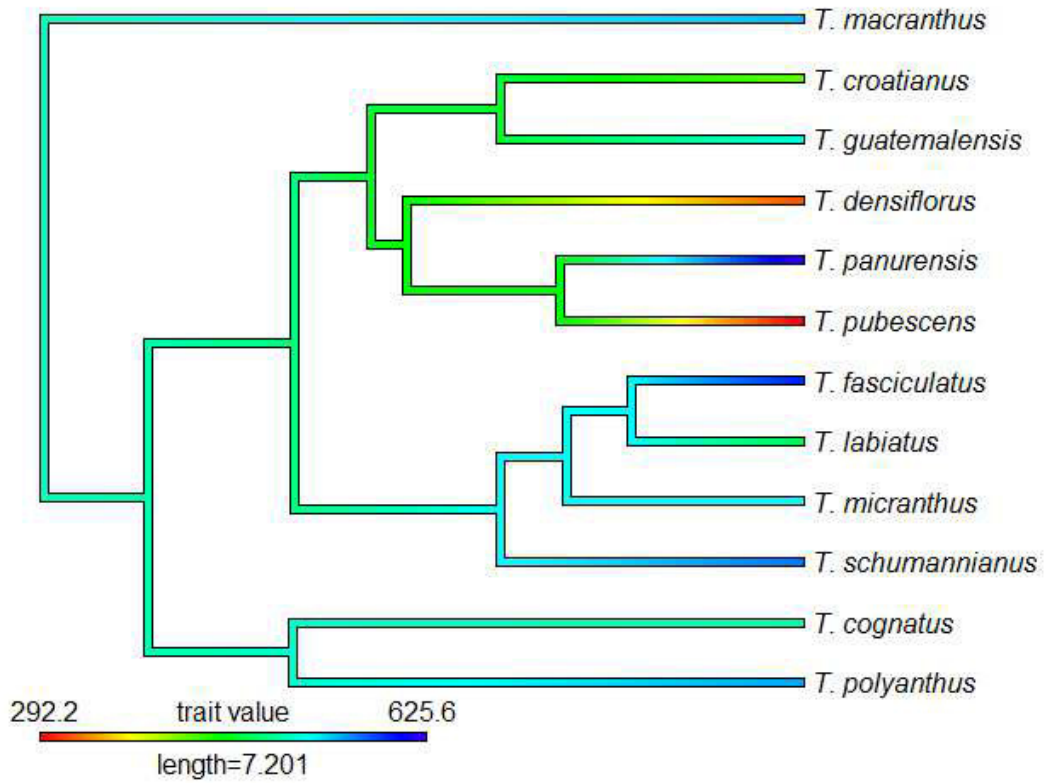
(b)



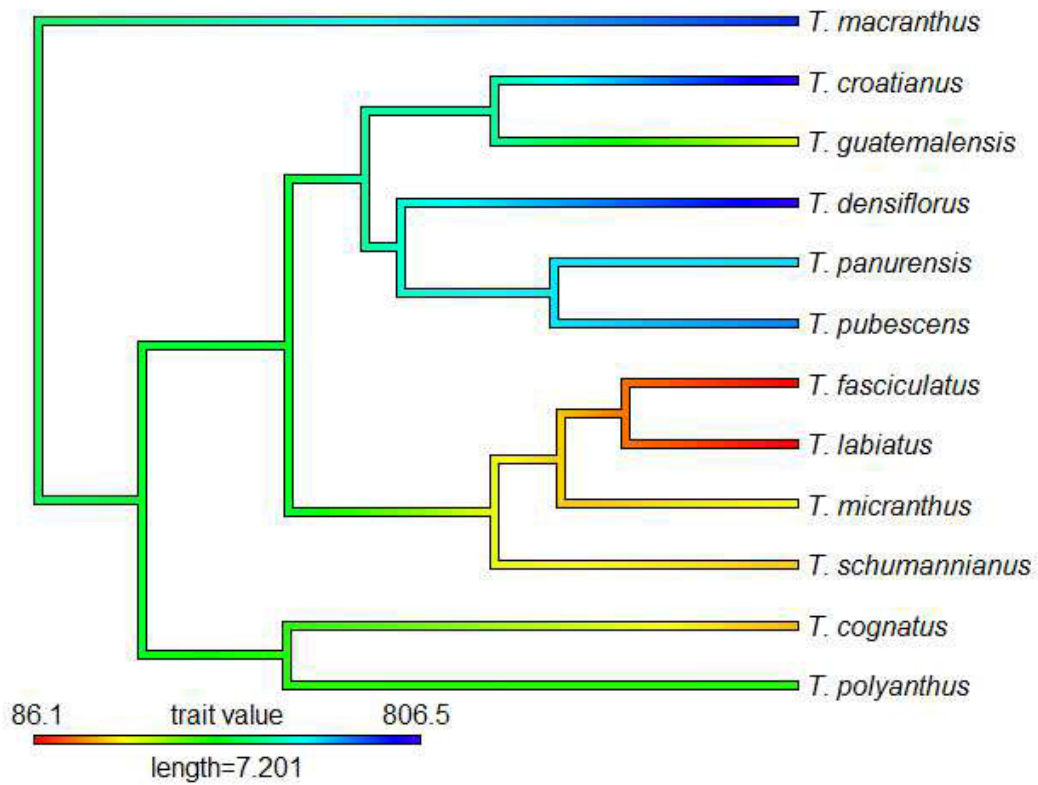
(c)



(d)



(e)



(f)

(See caption in next page)

Figure 4. Ancestral character reconstruction of the mean value for the six climatic variables used in the niche quantification and comparisons: (a) Temperature Seasonality (bio4), (b) Maximum Temperature of the Warmest Month (bio5) (°C), (c) Minimum Temperature of the Coldest Month (bio6) (°C), (d) Precipitation Seasonality (bio15), (e) Precipitation of the Warmest Quarter (bio18) (mm) and (f) Precipitation of the Coldest Quarter (bio19) (mm).

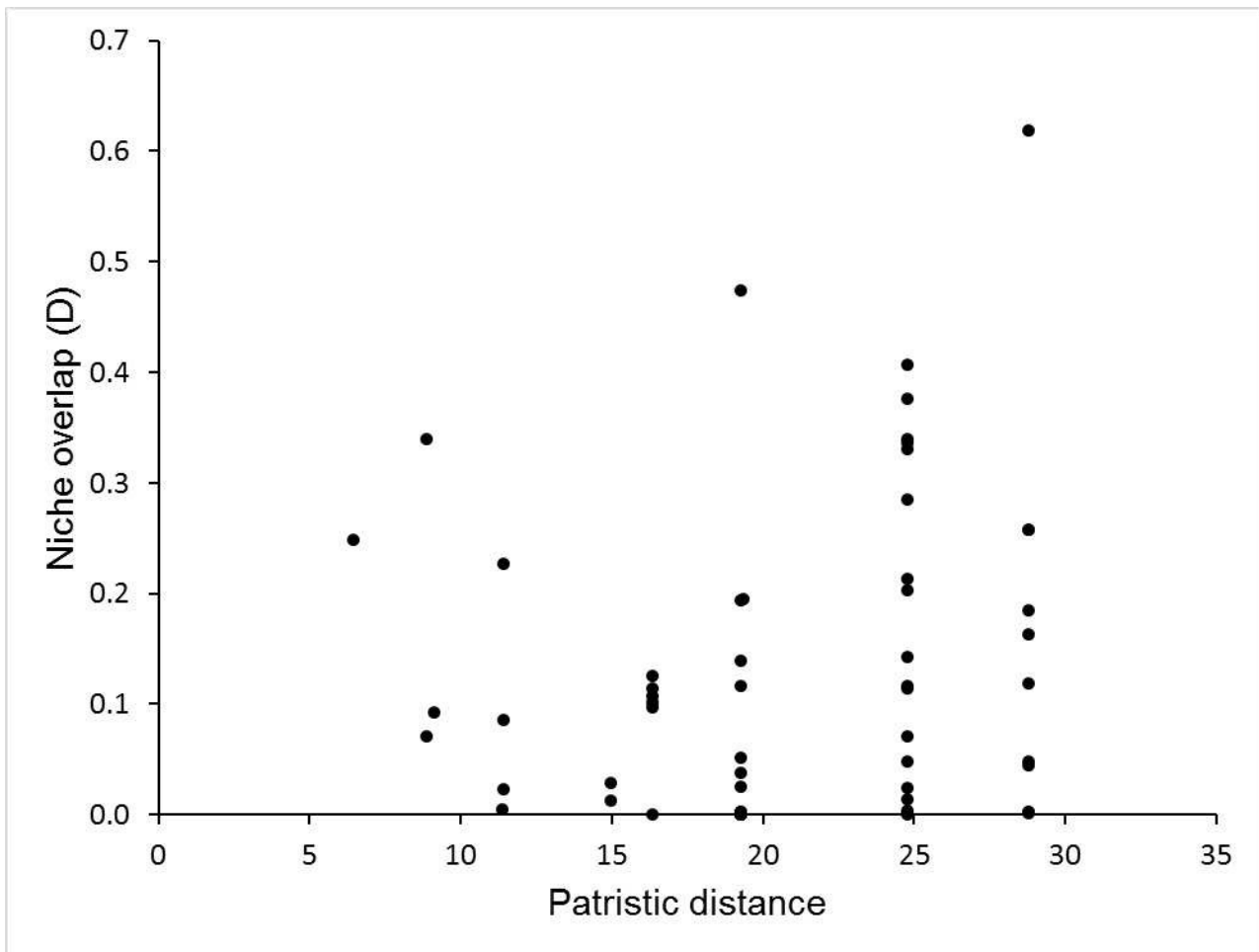


Figure 5. Dispersion diagram illustrating the lack of correlation between the pairwise matrices of niche overlap and patristic distances for the 13 species of *Tynanthus* analyzed.

Appendix 1. Species included in the dataset used for niche quantification and comparison, followed by the number of unique localities.

Species	Localities
<i>Tynanthus cognatus</i> (Cham.) Miers	101
<i>Tynanthus croatianus</i> A.H. Gentry	17
<i>Tynanthus densiflorus</i> M.C. Medeiros & L.G. Lohmann	8
<i>Tynanthus fasciculatus</i> (Vell.) Miers	31
<i>Tynanthus guatemalensis</i> Donn. Sm.	93
<i>Tynanthus labiatus</i> (Cham.) Miers	14
<i>Tynanthus macranthus</i> L.O. Williams	5
<i>Tynanthus micranthus</i> Corr. Mello ex K. Schum	42
<i>Tynanthus panurensis</i> (Bureau) Sandwith	24
<i>Tynanthus polyanthus</i> (Bureau) Sandwith	193
<i>Tynanthus pubescens</i> A.H. Gentry	23
<i>Tynanthus sastrei</i> A.H. Gentry	10
<i>Tynanthus schumannianus</i> (Kuntze) A.H. Gentry	86

Appendix 2. Univariate pairwise comparison results. Significant ($p < 0.05$) and non-significant values (n.s.) of the Dunn tests are indicated. bio4: Temperature Seasonality; bio5: Maximum Temperature of the Warmest Month; bio6: Minimum Temperature of the Coldest Month; bio15: Precipitation Seasonality; bio18: Precipitation of the Warmest Quarter; bio19: Precipitation of the Coldest Quarter. Species names are abbreviated to the four initial letters of the specific epithet.

Species pairs	bio4	bio5	bio6	bio15	bio18	bio19
cogn-croa	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
cogn-dens	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
cogn-fasc	n.s.	n.s.	n.s.	< 0.05	< 0.05	< 0.05
cogn-guat	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	n.s.
cogn-labi	n.s.	n.s.	n.s.	< 0.05	n.s.	< 0.05
cogn-macr	< 0.05	n.s.	n.s.	n.s.	n.s.	< 0.05
cogn-micr	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
cogn-panu	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
cogn-poly	< 0.05	< 0.05	< 0.05	n.s.	n.s.	< 0.05
cogn-pube	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
cogn-sast	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
cogn-schu	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	n.s.
croa-dens	n.s.	n.s.	n.s.	< 0.05	n.s.	n.s.
croa-fasc	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
croa-guat	< 0.05	n.s.	< 0.05	n.s.	n.s.	< 0.05
croa-labi	< 0.05	n.s.	< 0.05	n.s.	n.s.	< 0.05
croa-macr	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
croa-micr	< 0.05	n.s.	< 0.05	< 0.05	n.s.	< 0.05
croa-panu	n.s.	n.s.	n.s.	< 0.05	< 0.05	n.s.
croa-poly	n.s.	n.s.	< 0.05	< 0.05	n.s.	< 0.05
croa-pube	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
croa-sast	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
croa-schu	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
dens-fasc	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
dens-guat	< 0.05	n.s.	< 0.05	n.s.	n.s.	< 0.05
dens-labi	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
dens-macr	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
dens-micr	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05

dens-panu	n.s.	n.s.	n.s.	n.s.	< 0.05	n.s.
dens-poly	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
dens-pube	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
dens-sast	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
dens-schu	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
fasc-guat	n.s.	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
fasc-labi	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
fasc-macr	< 0.05	n.s.	< 0.05	< 0.05	n.s.	< 0.05
fasc-micr	n.s.	n.s.	n.s.	< 0.05	n.s.	< 0.05
fasc-panu	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
fasc-poly	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
fasc-pube	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
fasc-sast	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
fasc-schu	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
guat-labi	n.s.	< 0.05	< 0.05	n.s.	n.s.	< 0.05
guat-macr	< 0.05	n.s.	n.s.	n.s.	n.s.	n.s.
guat-micr	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	n.s.
guat-panu	< 0.05	n.s.	< 0.05	< 0.05	< 0.05	< 0.05
guat-poly	< 0.05	n.s.	n.s.	< 0.05	n.s.	n.s.
guat-pube	< 0.05	n.s.	< 0.05	n.s.	< 0.05	< 0.05
guat-sast	< 0.05	n.s.	< 0.05	n.s.	< 0.05	< 0.05
guat-schu	< 0.05	< 0.05	n.s.	n.s.	n.s.	< 0.05
labi-macr	< 0.05	n.s.	n.s.	n.s.	n.s.	< 0.05
labi-micr	n.s.	n.s.	n.s.	< 0.05	n.s.	< 0.05
labi-panu	< 0.05	n.s.	< 0.05	< 0.05	< 0.05	< 0.05
labi-poly	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	< 0.05
labi-pube	< 0.05	< 0.05	< 0.05	n.s.	n.s.	< 0.05
labi-sast	< 0.05	n.s.	< 0.05	n.s.	n.s.	< 0.05
labi-schu	< 0.05	n.s.	n.s.	n.s.	n.s.	< 0.05
macr-micr	< 0.05	n.s.	< 0.05	n.s.	n.s.	n.s.
macr-panu	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
macr-poly	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
macr-pube	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
macr-sast	n.s.	n.s.	n.s.	n.s.	< 0.05	n.s.
macr-schu	n.s.	n.s.	n.s.	n.s.	n.s.	< 0.05
micr-panu	< 0.05	< 0.05	< 0.05	n.s.	n.s.	< 0.05
micr-poly	< 0.05	< 0.05	< 0.05	n.s.	n.s.	n.s.

micr-pube	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
micr-sast	< 0.05	< 0.05	< 0.05	n.s.	< 0.05	< 0.05
micr-schu	< 0.05	< 0.05	< 0.05	< 0.05	n.s.	n.s.
panu-poly	n.s.	n.s.	< 0.05	< 0.05	n.s.	< 0.05
panu-pube	n.s.	n.s.	n.s.	< 0.05	< 0.05	n.s.
panu-sast	n.s.	n.s.	n.s.	n.s.	< 0.05	n.s.
panu-schu	< 0.05	n.s.	< 0.05	< 0.05	n.s.	< 0.05
poly-pube	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
poly-sast	n.s.	n.s.	n.s.	n.s.	< 0.05	< 0.05
poly-schu	< 0.05	n.s.	< 0.05	< 0.05	n.s.	< 0.05
pube-sast	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
pube-schu	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05
sast-schu	n.s.	n.s.	< 0.05	n.s.	< 0.05	< 0.05

Conclusões Gerais

Esta tese representa o trabalho taxonômico mais abrangente do gênero *Tynanthus* já realizado até os dias de hoje, incluindo uma reconstrução filogenética robusta do grupo (Capítulo 1) e um detalhado tratamento taxonômico (Capítulo 3).

A filogenia do gênero, reconstruída a partir de três marcadores moleculares (*ndhF*, *rpl32-trnL* e *pepC*), esclareceu relações infra-genéricas, contribuindo para decisões taxonômicas importantes, especialmente: (1) a circunscrição de espécies taxonomicamente problemáticas (*T. cognatus*, *T. elegans*, *T. polyanthus* e *T. villosus*), e (2) o reconhecimento de dois novos táxons (*T. densiflorus* e *T. espiritosantensis*; Capítulo 2). A árvore obtida também possibilitou um melhor entendimento do padrão de evolução de características morfológicas e serviu como base para a reconstrução da história biogeográfica de *Tynanthus*. Apesar da grande contribuição da filogenia para um melhor entendimento da história evolutiva do grupo, as análises filogenéticas recuperaram o parentesco entre algumas espécies do gênero com baixa sustentação, indicando a necessidade de trabalhos futuros baseados em um maior número de marcadores moleculares, idealmente com base no sequenciamento de genomas inteiros.

Na monografia de *Tynanthus* são reconhecidas 14 espécies, para as quais são apresentadas descrições morfológicas detalhadas, acompanhadas de dados sobre a fenologia, distribuição geográfica e comentários taxonômicos. Uma chave de identificação e ilustrações para todas as espécies também foram elaboradas, de maneira a facilitar o reconhecimento de todas as espécies.

Esta tese também contribuiu de forma bastante significativa para um melhor entendimento do papel de fatores ecológicos na distribuição geográfica das espécies de *Tynanthus* (Capítulo 4). Enquanto o estudo biogeográfico indicou que o conservantismo de nicho teria atuado de forma significativa na história de diversificação do gênero, o estudo detalhado da evolução do nicho ecológico de *Tynanthus* revelou que a similaridade entre o nicho climático das espécies proximamente aparentadas é baixo. É ainda possível, no entanto, que outros fatores ecológicos não considerados no presente estudo possam ter influenciado os padrões biogeográficos observados atualmente. Futuros estudos sobre as interações entre espécies podem contribuir com informações importantes sobre o papel de outros aspectos ecológicos na distribuição geográfica das espécies.



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