Eric Yasuo Kataoka

Systematics of *Martinella* Baill. (Bignonieae, Bignoniaceae)

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Abstract

Martinella Baill. is a small genus of Neotropical lianas within tribe Bignonieae (Bignoniaceae). The genus is monophyletic, well supported by morphological and molecular characters. Members of *Martinella* have a continuous interpetiolar ridge surrounding the stem, bilobed or 4-5-parted calyces, and minute triangular prophylls of the axillary buds. The most recent taxonomic treatment of *Martinella* recognized three species: *Martinella insignis* A.H. Gentry ex Zuntini & L.G. Lohmann, endemic to the Atlantic Forest of eastern Brazil, *Martinella iquitoensis* A. Samp. [= *Martinella insculpta* Sprague & Sandwith], and *Martinella obovata* (Kunth) Bureau & K. Schum., the latter two are widely distributed species from southern Mexico to Bolivia. Generic circumscription remained unchanged since the description of *Martinella*, although species delimitation and phylogenetic relationships among species within the genus remained unclear or unknown. In this dissertation, I investigated phylogenetic relationships of *Martinella*, and conducted a taxonomic revision. The phylogenetic reconstruction was based on a hybrid approach that combined high throughput sequencing (HTS) with Sanger sequencing data to infer the phylogeny of *Martinella* based on broad sampling of characters and individuals. Three complete and three nearly-complete plastomes were sequenced, assembled, and annotated. In addition, sequences of the plastid markers *ndh*F and *rpl*32-*trn*L and the nuclear marker *pep*C were obtained for additional samples, covering the morphological diversity and geographic distribution of members of the genus. The tree that resulted from the analysis of the complete dataset (Sanger + HTS) is fully resolved, representing the most robust estimate of phylogenetic relationships of *Martinella* to date. This phylogeny identified five main clades that are recognized as five species in the taxonomic revision of the genus. These five species represent the three previously recognized species plus two new species, *Martinella lanuginosa* Kataoka & L.G. Lohmann and *Martinella tomentosa* Kataoka & L.G. Lohmann. The taxonomic revision of the genus presents detailed descriptions for all five taxa, a complete list of synonyms, distribution maps, illustrations, and indications of conservation status for all species recognized. This thesis highlights the importance of in-depth taxonomic studies of selected lineages, especially in megadiverse regions such as the Neotropics, where sampling lacunae still persist.

Keywords: Amazonia, genomics, neotropical region, phylogeny, taxonomy.

Resumo

Martinella Baill. é um gênero pequeno de lianas neotropicais pertencente à tribo Bignonieae (Bignoniaceae). O gênero é monofilético, bem sustentado por caracteres morfológicos e moleculares. Os membros de *Martinella* apresentam uma crista interpeciolar contínua em torno do caule, cálices bilobados ou 4-5-lobados, e profilos da gema axilar triangulares e reduzidos. O tratamento taxonômico mais recente de *Martinella* reconheceu três espécies: *Martinella insignis* A. H. Gentry ex Zuntini & L.G. Lohmann, endêmico da Mata Atlântica do leste do Brasil, *Martinella iquitoensis* A. Samp. [= *Martinella insculpta* Sprague & Sandwith], e *Martinella obovata* (Kunth) Bureau & K. Schum., as duas últimas são amplamente distribuídas do sul do México até a Bolívia. A circunscrição genérica permaneceu inalterada desde a descrição de *Martinella*, embora a delimitação das espécies e as relações filogenéticas dentro do gênero permanecessem pouco claros ou desconhecidos. Nesta dissertação, investiguei as relações filogenéticas de *Martinella* e realizei uma revisão taxonômica. A reconstrução filogenética foi baseada em uma abordagem mista que combinou dados de sequenciamento em larga escala (HTS) e dados de sequenciamento Sanger para inferir a filogenia de *Martinella* com base em uma ampla amostragem de caracteres e indivíduos. Três plastomas completos e três plastomas quase completos foram sequenciados, montados e anotados. Além disso, sequências dos marcadores plastidiais *ndh*F e *rpl*32-*trn*L e do marcador nuclear *pep*C foram obtidas para amostras adicionais, cobrindo a diversidade morfológica e a distribuição geográfica dos membros do gênero. A árvore resultante da análise da matriz de dados completa (Sanger + HTS) é totalmente resolvida, representando a estimativa mais robusta das relações filogenéticas de *Martinella* até o momento. Essa filogenia identificou cinco clados principais que são reconhecidos como cinco espécies na revisão taxonômica do gênero. Essas cinco espécies representam as três espécies previamente reconhecidas, e dois novos táxons, *Martinella lanuginosa* Kataoka & L.G. Lohmann e *Martinella tomentosa* Kataoka & L.G. Lohmann. A revisão taxonômica do gênero apresenta descrições detalhadas de todos os cinco táxons, uma lista completa de sinônimos, mapas de distribuição, ilustrações, e indicações do *status* de conservação de todas as espécies reconhecidas. Esta dissertação destaca a importância de estudos taxonômicos aprofundados de linhagens selecionadas, especialmente em regiões megadiversas como a região neotropical, onde lacunas de amostragem ainda persistem.

Palavras-chave: Amazônia, filogenia, genômica, região neotropical, taxonomia.

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Thesis Outline

This Master's thesis focuses on the systematics of *Martinella* Baill., a genus of Neotropical lianas from tribe Bignonieae (Bignoniaceae). My desire to study biodiversity comes from my fascination for the Neotropical biota, which motivated me to understand its diversity into more depth and to contribute important knowledge in alpha taxonomy. In this study, I investigated the phylogenetic relationships of *Martinella*, and conducted a taxonomic revision of the genus. The main findings of my research are presented in this thesis, which contains an introduction, two chapters, and conclusions. The two chapters correspond to manuscripts that were structured following the guidelines of the scientific journals in which we intend to publish those papers. Further details about these chapters are given below.

Chapter One focuses on the phylogeny of *Martinella*, which was reconstructed based on a combination of high throughput sequencing data (i.e., newly generated sequences of complete or nearly-complete chloroplast genomes), and Sanger sequences of two chloroplast markers (*ndh*F and *rpl*32-*trn*L), and one nuclear gene (*pep*C). Five different datasets were used to reconstruct the phylogeny of the genus under Maximum Likelihood and Bayesian criteria. These analyses led to the most robust phylogenetic tree of *Martinella* to date, which has direct implications for the taxonomy of the genus.

Chapter Two focuses on the taxonomic revision of *Martinella*, which was based on extensive fieldwork, a comprehensive analysis of herbarium specimens, and the phylogenetic information obtained in Chapter One. A general overview on the morphology, taxonomic history, geographic distribution, reproductive biology, economic and ethnobotanical uses is presented. This information is followed by a detailed evaluation of the individual species, including descriptions for all taxa, a full list of synonyms, distribution maps, illustrations, and general comments.

General Introduction

The Neotropical region stands out for its rich biodiversity, even when compared to tropical areas around the world (Antonelli & Sanmartín, 2011). This region includes most of Central and South America, extending from central Mexico to southern Brazil (Morrone, 2014). The Neotropics also comprise a diverse array of ecosystems, ranging from some of the most arid to those with the highest rainfall on the planet (Fiaschi et al., 2015). The striking Neotropical diversity has historically intrigued researchers, which makes studies involving organisms of this region very promising to address evolutionary and biogeographic questions (Hughes et al., 2013).

The Bignoniaceae includes 82 genera and approximately 860 species (Lohmann & Ulloa, 2006 onwards). The family is Pantropical but occurs predominantly in the Neotropics (Olmstead et al., 2009). Members of the Bignoniaceae are trees, shrubs, herbs or lianas that are easily recognized by the compound and opposite leaves, showy and tubular flowers with four didynamous stamens and one staminode, and capsules with winged seeds (Gentry, 1980). Eight major clades are currently recognized: *Tabebuia* alliance, Pantropical clade, and tribes Bignonieae, Catalpeae, Jacarandeae, Oroxyleae, Tecomeae, and Tourretieae (Olmstead et al., 2009). Of these, tribe Bignonieae Dumort. is the largest, encompassing 21 genera and ca. 393 species, nearly half of the known species in the family (Lohmann & Taylor, 2014).

Members of Bignonieae are lianas or shrubs that occur in wet forests of Central and South America, seasonally dry tropical forests and the South American *Cerrados* (Lohmann, 2006). This megadiverse clade is characterized by a stem anatomy with differential cambial activity producing discontinuous 4-32 phloem wedges (Gentry, 1980; Pace et al., 2011; Lohmann & Taylor, 2014). Moreover, members of Bignonieae are readily recognized by the compound and opposite leaves with the terminal leaflet generally modified into a tendril, and by a septicidal capsule (Gentry, 1980; Lohmann, 2006).

Historically, the generic classification of Bignonieae was very unstable (see Figure 1 in Lohmann & Taylor, 2014). This is attributed to the focus of previous classifications on highly variable and homoplastic reproductive characters, such as corolla shape and color, fruit shape and ornamentation (Gentry, 1973; Lohmann & Taylor, 2014). The indication that vegetative characters could be potentially more informative to the generic classification of Bignonieae is relatively recent (Gentry, 1980). This idea was corroborated by a broad phylogenetic study of the whole tribe that

identified certain vegetative characters as putative synapomorphies for many clades (Lohmann, 2006). Few Bignonieae genera remained with a constant circumscription over the last 200 years (see Lohmann & Taylor, 2014). *Martinella* Baill. is one of those few genera whose circumscription remained unchanged since its description by Baillon (1888) (see Table 1 in Lohmann & Taylor, 2014).

Members of *Martinella* are distributed throughout wet forests of Central America and north/northeastern South America (Zuntini & Lohmann, 2014). A continuous interpetiolar ridge on the stems and 2-4-parted calyces represent putative synapomorphies of the genus (Lohmann, 2006; Lohmann & Taylor, 2014). Additional characteristics include: (i) minute and triangular prophylls of the axillary buds, (ii) basal portion of the corolla tube narrower and slightly more elongated than the calyx, (iii) inflated and campanulate corollas, and (iv) hummingbird pollination (*Martinella*-type flower) (Gentry, 1974; Lohmann & Taylor, 2014).

The monophyly of *Martinella* was strongly supported by the molecular phylogeny of tribe Bignonieae based on sequences of two markers (*ndh*F and *pep*C) for the two species recognized at that time, i.e., *Martinella obovata* (Kunth) Bureau & K. Schum and *Martinella iquitoensis* A. Samp. [= *Martinella insculpta* Sprague & Sandwith] (Lohmann, 2006) (Figure 1). The most recent synopsis of the group recognized three lianescent species within the genus (Zuntini & Lohmann, 2014): *Martinella insignis* A.H. Gentry ex Zuntini & L.G. Lohmann, *M. iquitoensis* [= *M. insculpta*], and *M. obovata*. *Martinella insignis* is restricted to northern Atlantic Forest and is known from few records. This species inhabits sandy soils, has membranaceous leaflets, trifid tendrils, "pocket-like" domatia, 5-lobed calyces, and yellow corollas (Zuntini & Lohmann, 2014). *Martinella iquitoensis* [= *M. insculpta*] is widely distributed in the Amazon basin and has been reported to grow on sandy soils. This species has coriaceous leaflets, trifid tendrils, botryoid inflorescences and dark-purple corollas (MacBride, 1961; Zuntini & Lohmann, 2014). *Martinella obovata* is the most widely distributed species, occurring from Central America to southern Amazon, and growing on different soil types. This species is characterized by membranaceous to coriaceous leaflets, trifid tendrils, racemose inflorescence, and lilac/purple corollas (MacBride, 1961; Zuntini & Lohmann, 2014).

Despite the straightforward circumscription of the genus, the delimitation of the Amazonian *Martinella* spp., namely the morphologically diverse *M. iquitoensis* and *M. obovata*, has long been considered problematic. These taxa show overlapping character states such as corolla color, leaflet texture, and tendril type, complicating their correct identification (MacBride, 1961; Zuntini & Lohmann, 2014). Wide geographic distribution and phenotypic plasticity may contribute to such high morphological variation in both species, which led

previous researchers to suggest that these taxa may represent a species complex (Zuntini & Lohmann, 2014).

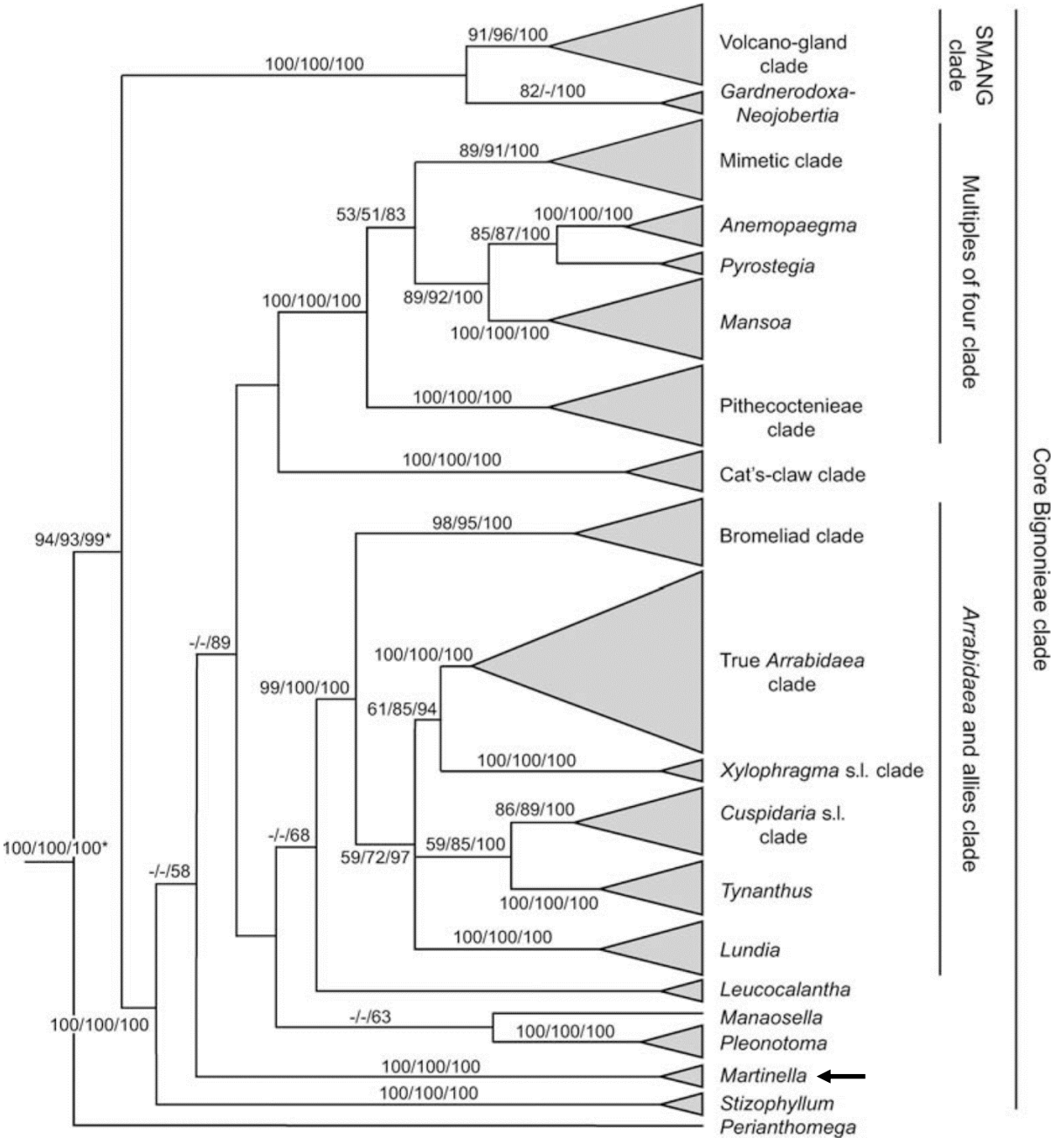

Figure 1. Phylogenetic relationships among the 19 species groups of tribe Bignonieae recovered by Lohmann (2006). The phylogenetic placement of *Martinella* is indicated by a black arrow. Values shown at nodes indicate, respectively, parsimony bootstrap, likelihood bootstrap and posterior probability.

The advent of high throughput sequencing (HTS) technologies is allowing us to rapidly obtain molecular data for a myriad of applications at relatively low costs. The nature of HTS is quantitative as it counts how many times each base has been sequenced (Straub et al., 2012), which then gives the empirical per-base coverage (or sequencing depth) of a given genome

(Sims et al., 2014). Another interesting feature of HTS is that many samples can be pooled together and sequenced in a single run (for a review of applications, see McCormack et al., 2013). Thus, in phylogenetic studies, one would no longer need to choose between sampling more taxa or more characters, as this technique allows us to maximize both. Consequently, the field of Plant Systematics is greatly benefiting from HTS technologies, especially using approaches such as genome skimming (e.g., Straub et al., 2012; Reginato et al., 2016), and target enrichment (e.g., Carlsen et al., 2018; Moore et al., 2018). These applications have recovered robust and highly supported phylogenetic hypotheses, allowing us to address fundamental questions in Plant Systematics.

Recent approaches successfully applied HTS-generated data in combination with data obtained using traditional Sanger sequencing for phylogeny reconstruction (e.g., Williams et al., 2016; Fonseca & Lohmann, 2018). This strategy is particularly interesting as it allows the integration of publicly available sequences of target genes with newly generated HTS data, maximizing character and taxon sampling, thus contributing to advance our understanding about the phylogeny of many plant groups.

This dissertation aimed to: (i) reconstruct phylogenetic relationships of *Martinella* using Sanger and HTS-generated data, and (ii) conduct a taxonomic revision of *Martinella*.

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Conclusions

This Master's thesis focuses on the phylogeny and taxonomic revision of *Martinella*. By combining traditional and novel approaches, we were able to infer the phylogeny of *Martinella* based on HTS and Sanger-generated DNA sequence data. This approach allowed us to assemble complete and nearly-complete chloroplast genomes of *Martinella*, and to construct a comprehensive dataset with over 119,000 characters for samples that represent the known range of geographic distribution. The best phylogenetic estimate of *Martinella* to date was reconstructed using Sanger and HTS datasets. The data obtained here was combined into a super matrix that recovered five main clades that correspond to the three previously recognized species (i.e., *M. insignis*, *M. iquitoensis* [= *M. insculpta*], and *M. obovata*), and two newly described Amazonian species (i.e., *M. lanuginosa*, and *M. tomentosa*). The newly generated complete chloroplast sequences would allow for the development of molecular markers for population genetics studies, especially within the widespread Amazonian species, in the future. Future investigations based on an even higher sampling of individuals (e.g., phylogeography) and a higher sampling of nuclear markers (e.g., target enrichment) can potentially improve support and clarify relationships among populations within the Amazonian clade. These studies are critical for a deep understanding about the origin and maintenance of the Amazonian biodiversity.

The phylogeny of *Martinella* reconstructed here supports the recognition of two new species that were previously identified solely based on morphology. These two new species, *M. lanuginosa* and *M. tomentosa*, were described and illustrated. In addition, the analysis of a comprehensive collection of specimens of *Martinella* allowed us to identify key morphological characters to distinguish *M. insculpta* from *M. obovata* such as the shape of mature stems in cross section (quadrangular in *M. insculpta* vs. cylindrical in *M. obovata*), leaflet texture (coriaceous in *M. insculpta* vs. chartaceous in *M. obovata*), and inflorescence structure (botryoid in *M. insculpta* vs. racemose in *M. obovata*).

This thesis highlights the importance of in-depth taxonomic studies, those of which represent the only way to uncover hidden diversity. These studies are particularly important in megadiverse regions, such as the Neotropics, where many sampling lacunae still remain.