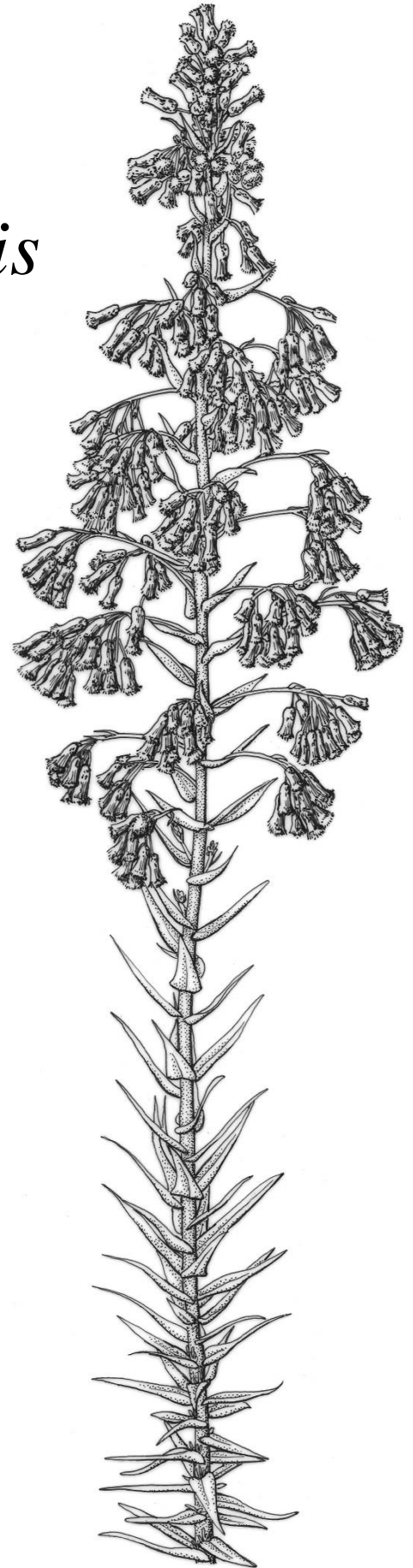


Gustavo Heiden

Systematics of *Baccharis*
(Asteraceae: Astereae)



São Paulo, 2014.

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Systematics of *Baccharis*
(Asteraceae: Astereae)

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Prof. Dr. José Rubens Pirani

*À minha avó Irena Karow Bergmann,
quem primeiro percebeu o quanto eu
admirava as plantas.*

*Não sei pensar a máquina, isto é, faço o meu trabalho criativo primeiramente a lápis.
Depois, com o queixo apoiado na mão esquerda, repasso tudo a máquina com um dedo só.*

– Mas isso não custa muito?

– Custar, custa, mas dura mais...

Mário Quintana,
Da preguiça como método de trabalho.

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RESUMO

Sistemática de *Baccharis* (Asteraceae: Astereae).

Uma hipótese filogenética abrangente sobre *Baccharis*, um gênero Americano predominantemente Neotropical, é necessária para testar seu caráter monofilético e esclarecer suas relações infragenéricas. Devido a sua grande diversidade morfológica e ampla distribuição geográfica, estudos filogenéticos com base em dados moleculares para testar o monofilétismo do gênero e investigar as relações de seus grupos infragenéricos foram aqui conduzidos, permitindo o reconhecimento e a revisão taxonômica de táxons menores e monofiléticos. Desta forma, uma hipótese filogenética sobre *Baccharis* é aqui apresentada, com base em 248 espécies amostradas, quatro regiões do genoma (ETS, ITS, *trnH-psbA*, *trnL-F*) e análises Bayesianas. Os resultados confirmam a subtribo Baccharidinae como uma linhagem monogenérica e sustentam uma definição ampla de *Baccharis s.l.*, monofilético e incluindo todos os gêneros que foram previamente segregados dele. Listagens abrangentes de táxons infragenéricos e de táxons aceitos ao nível de espécie foram compiladas com o objetivo de direcionar uma classificação infragenérica baseada nas relações filogenéticas de *Baccharis*. Sete linhagens principais foram reconhecidas e são tratadas aqui no nível taxonômico de subgênero, e neste processo todos os subgêneros anteriormente reconhecidos tiveram que ser recircunscritos para constituírem táxons monofiléticos. O levantamento de nomes publicados nas categorias taxonômicas de seção e série totalizaram 68 seções e 13 séries, novas seções e novos posicionamentos ao nível de seção são propostos para acomodar táxons que não correspondiam a qualquer das seções previamente descritas, enquanto que 22 seções foram sinonimizadas. Estes procedimentos permitiram reconhecer 47 seções, embora seja esperado que esse número diminua com a realização de futuros estudos baseados em maior amostragem. Os nomes aceitos ao nível de espécie totalizaram 433 táxons que foram posicionados na categoria infragenérica mais inclusiva possível à luz dos dados disponíveis atualmente. *Baccharis* subgen. *Tarchonanthoides* Heering, um grupo restrito aos campos e savanas do sudeste da América do Sul, foi definido como um alvo adequado para uma revisão taxonômica precursora devido ao número reduzido de espécies, área de ocorrência restrita quando comparado aos demais subgêneros e distinção morfológica. Esta é a primeira tentativa de proceder a revisão taxonômica de um subgênero de *Baccharis* em concordância com um sistema filogenético e livre de qualquer limitação geográfica. A recircunscrição de *Baccharis*

subgen. *Tarchonanthoides* envolve a sinonimização de *Lanugothamnus*, e a exclusão de uma seção do subgênero, no sentido de torná-lo monofilético. Outras ações nomenclaturais e taxonômicas são necessárias como a designação de lectótipos, a proposição de um novo status, novas combinações, novas sinonimizações e o esclarecimento de conceitos de espécie previamente aplicados de forma equivocada para alguns nomes de espécies. Duas seções recircunscritas e 13 espécies são aceitas nesta revisão taxonômica de *B.* subgen. *Tarchonanthoides*, um grupo diversificado nas vegetações abertas do Sudeste da América do Sul, ocorrendo no Brasil, Uruguai, Argentina e Paraguai. Descrições morfológicas dos táxons infragêneros são fornecidas, assim como uma chave taxonômica, descrições, dados sobre etimologia, distribuição e habitats, fenologia, estado de conservação, nomes em vernáculo e listas de espécimes examinados, pranchas em nanquim, fotografias e mapas de distribuição para todas as espécies aceitas no subgênero. Paralelamente aos objetivos principais, expedições exploratórias a campo e o estudo de espécimes em herbários possibilitaram a descrição de oito novas espécies: *Baccharis dichotoma*, *B. hemiptera*, *B. magnifica*, *B. napaea*, *B. nebularis*, *B. obdeltata*, *B. simplex* e *B. umbellata*.

ABSTRACT

Systematics of *Baccharis* (Asteraceae: Astereae).

A comprehensive phylogenetic hypothesis for the predominantly Neotropical American genus *Baccharis* is necessary to test its monophyly and clarify the infrageneric relationships within the genus. Given its great morphological diversity and wide geographic distribution, phylogenetic studies based on molecular data to test the monophyly of the genus and investigate the relationships of its infrageneric groups are here proposed, allowing the recognition and taxonomic revision of smaller and monophyletic taxa. Therefore, a phylogenetic hypothesis for *Baccharis* is provided based on 248 species sampled, four molecular regions (ETS, ITS, *trnH-psbA*, *trnL-F*) and Bayesian analyses. The results confirm subtribe Baccharidinae as a monogeneric lineage, and support a wide definition of *Baccharis s.l.*, monophyletic and including all genera that were previously segregated from it. Comprehensive lists of infrageneric taxa and taxa accepted at species level were compiled to move towards a phylogeny-based infrageneric classification of *Baccharis*. Seven main lineages were recovered, treated here at subgeneric level, and in this process all subgenera recognized before had to be recircumscribed to constitute monophyletic taxa. A survey of names published in the ranks of sections and series accounted 68 sections and 13 series; new sections are described and new statuses at the rank of section are proposed to accommodate taxa not corresponding to any previously described section, while 22 sections were considered synonyms. This procedure allowed the recognition of 47 sections, though this number is supposed to decrease after future studies are accomplished with a larger sampling. The names accepted at species level totalize 433 taxa that were here assigned to the most inclusive infrageneric category possible in the light of the data currently available. *Baccharis* subgen. *Tarchonanthoides* Heering, a group restricted to the southeastern South American grasslands and savannas, was chosen as a good target to first tackle for a taxonomic revision, due its small size, restricted area of occurrence when compared to the remaining subgenera, and morphological distinctiveness. This is the first attempt to provide a taxonomic revision of a subgenus of *Baccharis* according to a phylogenetic framework, and under no geographic constraint. The recircumscription of *Baccharis* subgen. *Tarchonanthoides* involves the synonymization of *Lanugothamnus*, and the exclusion of one section in order to keep the subgenus monophyletic. Other taxonomic and nomenclatural actions necessary are designation of lectotypes, a new status and new combinations, new synonymizations and

clarification of the species concepts formerly misapplied to some names. Two recircumscribed sections and 13 species are accepted within the taxonomically revised *B.* subgen. *Tarchonanthoides*, which diversified mainly in open vegetations from southeastern South America in Brazil, Paraguay, Uruguay and Argentina. General morphological descriptions of the infrageneric taxa are provided, as well as a taxonomic key, descriptions, data on etymology, distribution and habitats, phenology, conservation status, ethnobotany and vernacular names, and a list of specimens examined, line drawings, pictures and maps of distribution for all accepted species within this subgenus. Alongside the main goals, exploratory fieldwork and study of herbaria specimens allowed the description of eight new species: *B. dichotoma*, *B. hemiptera*, *B. magnifica*, *B. napaea*, *B. nebularis*, *B. obdeltata*, *B. simplex* and *B. umbellata*.

INTRODUCTION

INTRODUCTION

1. Background

Baccharis (Asteraceae: Astereae: Baccharidinae) is an American, predominantly Neotropical, genus broadly characterized by the leaves and stems covered by a tufted indumentum, which is composed of trichomes with adjoining basal cells, and by the occurrence of dioecy (Müller 2006). The genus is profusely diversified in a variety of environments, usually as an important element in several plant formations (Giuliano 2001). The most important centers of species richness are the Andes from Colombia to central Chile and central Argentina, and the mountainous areas of southeastern Brazil, Uruguay, and eastern Paraguay (Müller 2006).

Despite its significance in Neotropical vegetations, since De Candolle (1836), *Baccharis* has never been target of an overall taxonomic revision. The most comprehensive works are compilations of accepted scientific names and synonyms. The number of species recognized within the genus is controversial, ranging from 354 fide Müller (2013) to ca. 500 species fide Malagarriga (1976). Most of the contemporary studies on *Baccharis* appeared as part of floras and geographically limited taxonomic works. Recent alterations in the circumscription of *Baccharis* do not rely on extensive taxonomic revisions, neither in phylogenies. Broad circumscriptions of *Baccharis* were proposed by Nesom (1988) and Müller (2006) with the merging of monoecious (*Baccharidastrum* Cabrera), gynodioecious (*Heterothalamus* Less.), and polygamous taxa (*Baccharidiopsis* G.M. Barroso). On the other hand, Hellwig (1993, 1996) proposed some generic segregates from *Baccharis*. These proposals of segregation were not followed by the subsequent authors, except Deble et al. (2004) and Deble (2012), who accepted most of the previously published generic segregates of *Baccharis* and separated *B. wagenitzii* (F.H. Hellw.) Joch.Müll. into the monospecific genus *Heterothalamulopsis* Deble, A.S. Oliveira & Marchiori, and *Baccharis* subgen. *Tarchonanthoides* sensu Müller (2006), segregated into the genus *Lanugothamnus* Deble.

Concerning the infrageneric classification, the most recent proposals were published by Giuliano (2001, 2005, 2011), Giuliano and Nesom (2003) or Nesom (1990), on a sectional basis focusing mainly in Argentinean or North American taxa, while Müller (2006), focused on a subgeneric scheme, first concentrating on the Bolivian species, accepting four out of five subgenera established by Heering (1904, 1905) and rejecting the sectional classification proposed by Cuatrecasas (1967), who relied mostly on the Colombian species. Müller (2006) assumed as a starting point the infrageneric taxa of Nesom (1990) and the genera segregated

by Hellwig (1993, 1996), accepting four out of five subgenera established by Heering (1904a, b; Heering 1905). In his scheme, Müller (2006) recognized three subgenera as probably monophyletic (*Baccharis* subgen. *Baccharis*, *B.* subgen. *Pteronioides* Heering and *B.* subgen. *Tarchonanthoides* Heering), while he considered *B.* subgen. *Molina* (Pers.) Heering as a possible paraphyletic assemblage. Later, Müller (2010, 2013) expanded the subgeneric classification formerly applied to Bolivian species to its list of accepted species, subspecies and varieties of the whole genus.

Zanowiak (1991) conducted a cpDNA RFLP phylogenetic study of 23 representatives of the subtribe Baccharidinae. The phylogenetic analysis made by Zanowiak (1991) placed *B. vanessae* R.M.Beauch. as sister of a clade composed by *Conyza* L., *Erigeron* L., *Exostigma* Sancho and the remaining of the subtribe Baccharidinae, where *Archibaccharis* and *Heterothalamus* Less. emerged as a clade sister to the remaining species of *Baccharis*, while *Baccharidastrum* nested within *Baccharis*. Later, the analysis performed by Karaman-Castro & Urbatsch (2009) placed *Baccharis* and *Heterothalamus* as sisters in a clade basal to the polytomy which contains *Hinterhubera* Sch.Bip. ex Wedd., while in the analysis of Sancho & Karaman-Castro (2008), Baccharidinae emerged as a monophyletic group, sister of the South-American Podocominae. Recently, Brouillet et al. (2009) published the largest phylogeny of Astereae based on ITS markers and stated that the results did not support the monophyly of Baccharidinae (comprising *Archibaccharis*, *Baccharis* and *Heterothalamus*), nor of *Baccharis s.l.* However, only nine species of the subtribe in its traditional circumscription (e.g. including *Archibaccharis* and *Baccharis s.l.*) and six of *Baccharis*, in a narrow sense, were sampled, hence the authors assumed that a thorough phylogenetic study within the genus is in need to corroborate or refuse its alleged monophyly.

A comprehensive phylogenetic hypothesis for *Baccharis* is necessary to test its monophyly and clarify the infrageneric relationships within the genus. Given its great morphological diversity and wide geographic distribution, I propose to perform phylogenetic studies based on molecular data to test the monophyly of the genus and investigate the relationships of its infrageneric groups, allowing the recognition and taxonomic revision of smaller and monophyletic taxa. *Baccharis* subgen. *Tarchonanthoides* Heering, a group restricted to the southeastern South American grasslands and savannas, is a good target to first tackle for a taxonomic revision due its small size, restricted area of occurrence when compared to the remaining subgenera, and morphological distinctiveness.

2. Aims

- Test the monophyly of *Baccharis* and its infrageneric taxa, investigate the relationships among them, and provide the first phylogeny based proposal of infrageneric classification for the genus, including an updated checklist of taxa accepted at species level.
- Prepare the taxonomic revision of *Baccharis* subgen. *Tarchonanthoides*, a group from the Southeastern South American open vegetations, including general morphological description of the infrageneric taxa, a taxonomic key, descriptions, data on etymology, distribution and habitat, phenology, conservation status, ethnobotany and vernacular names, and list of specimens examined, as well as line drawings, pictures and maps of distribution for each accepted species.
- Proceed to the description of new species found alongside the previous main goals of the proposed work.

3. Structure of the thesis

The thesis is composed by the Introduction, two chapters, the Conclusion and the appendices. The new names and new combinations of taxa presented in this thesis were or will be published in scientific journals.

- Chapter 1 presents the first step towards an infrageneric classification for the genus *Baccharis* based on robust phylogenetic data (plastidial and nuclear), including an updated checklist of accepted names classified under the new infrageneric framework proposed. The manuscript is planned to be submitted to the journal *Taxon* and is co-authored by Daniele Silvestro, Alexandre Antonelli and José Rubens Pirani.
- Chapter 2 is an assembly of two already published papers and one manuscript planned to be submitted, all of them dealing with taxonomic studies in *Baccharis* subgen. *Tarchonanthoides*, a group from the southeastern South American open vegetations. Part 2.1 is a synopsis and notes for *Baccharis* subgen. *Tarchonanthoides* (Asteraceae: Astereae), published in *Phytotaxa* in co-authorship with José Rubens Pirani. Part 2.2 regards to two new combinations in *Baccharis* (Asteraceae: Astereae) published in *Phytoneuron*. Part 2.3 is the taxonomic revision of the recircumscribed *Baccharis* subgen. *Tarchonanthoides* in co-authorship with José Rubens Pirani and planned to be submitted to *Phytotaxa*.
- The appendices comprise a compilation of seven published papers or accepted manuscripts dealing with eight new species of *Baccharis* described along the development of

the current work. Appendix 1 describes a new dwarf shrubby species of *Baccharis* from southeastern Brazil, published in *Brittonia* in co-authorship with Leonardo Dias Meireles. Appendix 2 describes a new species of *Baccharis* from the high altitude grasslands of Parque Nacional do Caparaó, Southeastern Brazil, published in *Candollea* along with Ângelo Alberto Schneider. Appendix 3 describes a new species of *Baccharis* endemic to the highest summits of Paraná, Southern Brazil, published in *Phytotaxa* and co-authored by Osmar dos Santos Ribas. Appendix 4 describes a new species from the subtropical highlands of southern Brazil, published in *Phytotaxa* with José Rubens Pirani. Appendix 5 describes a striking new species of *Baccharis* endemic to the summits of Serra do Caparaó, southeastern Brazil, in collaboration with Lúcio de Souza Leoni and Jimi Naoki Nakajima, accepted for publication in *Phytotaxa*. Appendix 6 describes two new species of *Baccharis* with single-flowered female capitula from the Serra do Cipó, Minas Gerais, Brazil, and Appendix 7 describes a new species of *Baccharis* from the mountains of southern Brazil, both co-authored by José Rubens Pirani and accepted for publication in *Phytotaxa*.

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CONCLUSIONS

CONCLUSIONS

The retrieved phylogenetic hypothesis for *Baccharis* based on four molecular regions (ETS, ITS, *trnH-psbA*, *trnL-F*) and Bayesian analyses confirms subtribe Baccharidinae as a monogeneric group, and support a wide definition of *Baccharis s.l.*, monophyletic and including all genera previously segregated from it.

A comprehensive revision of formerly published infrageneric taxa and taxa accepted at species level, allied with the results of the phylogenetic analyses, constitutes the first attempt to move towards a phylogeny-based infrageneric classification of *Baccharis*. Seven main lineages were recovered and treated at subgeneric level, and all the subgenera recognized before had to be recircumscribed in order to be monophyletic groups. Three of these subgenera roughly match previous subgeneric concepts while two of them are synonyms. Two earlier segregated genera and two formerly existing sections were moved to the subgeneric rank. The survey of names published in the ranks of sections and series accounted 68 sections and 13 series. Four new sections had to be described and three new statuses had to be transferred to the rank of section to accommodate taxa not corresponding to any previously described sections, while 22 sections were considered synonyms resulting in the recognition of 47 sections. The list of names accepted at species level totalized 433 taxa that were assigned to the most inclusive infrageneric category possible in the light of the data currently available.

The first attempt to prepare a modern taxonomic revision of a subgenus of *Baccharis* according to a phylogenetic framework and under no geographic constraint was made through the study of *Baccharis* subgen. *Tarchonanthoides*. This subgenus was initially the target of a synopsis disentangling the main nomenclatural and taxonomic problems, with the proposition of a new combination and designation of lectotypes to keep the stability of the names. Secondly, two new combinations were provided to species belonging to the subgenus, but not described originally in *Baccharis*, and finally the recircumscription of *B.* subgen. *Tarchonanthoides* based on phylogenetic grounds was proposed, demanding the synonymization of *Lanugothamnus*, and the exclusion of one section in order to keep the subgenus monophyletic. Other taxonomic changes resulted from the accomplished taxonomic revision as new synonyms were proposed and the application of long term misapplied names was corrected. The taxonomic revision deal with 13 accepted species within the subgenus, which has a history of diversification mainly in open vegetations from southeastern South America in Brazil, Paraguay, Uruguay and Argentina.

Exploratory field work allied to study of herbarium specimens allowed the recognition of eight new species of *Baccharis*, belonging to five of the seven main lineages recognized within the genus. The new species found confirm that much of the biodiversity of the group is still cryptic, and uncover how critical it is to understand the systematics and evolution of the genus.

Since *Baccharis* is monophyletic in its broader sense, it is confirmed that building a strong infrageneric classification scheme is critical to achieve advances in the knowledge of infrageneric and interspecific evolutionary relationships within the genus. The first overall scheme of infrageneric classification for *Baccharis* will allow the taxonomic revision of smaller monophyletic groups. The compilation of accepted names and its positioning within an infrageneric framework of classification will enable recognition of undersampled lineages and taxa of unclear relationships to be target of subsequent investigations.

A more comprehensive tree allowing a completely phylogeny-based classification of *Baccharis* will be achieved after a sampling focusing on the missing type species of already described generic segregates and infrageneric taxa, and on the several species unplaced at subgeneric levels. The current recognition of seven monophyletic lineages at the rank of subgenus and of 47 groups at the rank of section will help to access the taxonomic revision of clades within *Baccharis*, but it is also expected that the number of sections recognized will decrease as the knowledge of the whole group proceeds. The availability of the first big picture phylogeny for this megadiverse Neotropical genus unveils the possibility to investigate hypothesis of evolution of characters, and to explore the biogeographical information hidden within the evolutionary history of the largest genus of tribe Astereae in forthcoming works.