Systematics and Evolution of
Chresta Vell. ex DC.
(Vernonieae, Asteraceae)

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Systematics and Evolution of *Chresta* Vell. ex DC. (Vernonieae, Asteraceae)

Sistemática e Evolução de *Chresta* Vell. ex DC. (Vernonieae, Asteraceae)

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Aos meus pais, Cíntia e Roberto e à minha avó, Judith,
meus pilares.

Magno amore in familiam
Synantherearum captus...

—Lessing, 1829

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RESUMO

Chresta pertence à tribo Vernonieae e apresenta dezoito espécies distribuídas nos domínios da Caatinga, Cerrado e Mata Atlântica. A extensa variabilidade de caracteres observada no gênero fez com que suas espécies fossem atribuídas a diversos gêneros distintos e até mesmo classificadas em diferentes grupos dentro da tribo. Tentativas anteriores de definir a posição do gênero em relação a outras subtribos de Vernonieae não foram bem-sucedidas. Nesse trabalho, apresentamos uma nova filogenia para *Chresta*, baseada numa amostragem taxonômica completa da qual obtivemos centenas de marcadores moleculares e, pela primeira vez, métodos filogenômicos são aplicados a um grupo neotropical de Asteraceae. Essa análise confirma a monofilia de *Chresta*, resolve as relações infragenéricas com alto suporte, e define com sucesso o grupo-irmão do gênero, embora as relações dessa linhagem com Lychnophorinae e Lepidaploinae ainda sejam duvidosas. Usamos as árvores obtidas para reconstruir estados ancestrais de dez caracteres morfológicos selecionados face a sua provável relevância na história do grupo, e assim propomos um cenário biogeográfico no qual a diversificação do grupo pode ter ocorrido. Também usamos marcadores de microssatélites para estudar a genética de populações de cinco espécies da Caatinga que apresentam populações naturalmente isoladas, devido a sua restrição a afloramentos rochosos de área limitada. Essas espécies apresentam diferentes padrões, variando no grau de diversidade e estruturação genética. Esses dados permitem uma discussão do impacto relativo de fatores como distância espacial, preferência de substrato, tamanho populacional e capacidade de dispersão, sobre o fluxo gênico entre as populações analisadas. Também apresentamos uma sinopse ilustrada do gênero, com uma nova classificação infra-genérica filogenética, condensando o conhecimento acumulado até o momento sobre *Chresta*. A sinopse inclui descrição de quatro espécies novas, chave de identificação das 18 espécies aceitas e três táxons infragenéricos, sinonímia completa, ilustrações e mapas de distribuição das espécies, bem como seu status de conservação atual.

Palavras-chave: Chrestinae, Compositae, filogenia, genética de populações, sinopse.

ABSTRACT

Chresta belongs to tribe Vernonieae, subtribe Chrestinae, and presents eighteen species distributed in the Caatinga, Cerrado and Mata Atlântica domains. Its species display a fairly wide range of characters that led the species to be ascribed to several distinct genera, sometimes also classified into different groups inside the tribe. Attempts to define the position of the genus in relation to other Vernonieae subtribes and to understand the relationships within the genus have so far been unsuccessful. In this work, we present a novel phylogeny for *Chresta*, based on a complete set of sampled taxa from which hundreds of molecular markers were assessed, and for the first time, phylogenomics methods are applied to a Neotropical group of Asteraceae. We confirm the monophyly of *Chresta* and resolve infrageneric relationships with high support for all clades. We also successfully define the sister group to the genus, although the relations of this whole lineage with Lychnophorinae and Lepidaploinae are still doubtful, and. We use the obtained trees to reconstruct ancestral states of ten selected characters, which seem to have played an important role during the history of the genus, and propose a biogeographical scenario where the diversification of the group may have taken place. We also use evidence from microsatellite markers to study the population genetics of five species from the Caatinga that naturally present isolated populations restricted to narrow rupicolous habitats. These species present contrasting patterns, varying in their degree of genetic diversity and structuring, and this data enable us to discuss the relative impact of factors such as spatial distance, substrate preference, population size and dispersal ability on the genetic flow among the populations assessed. We also present an illustrated synopsis of the genus, with a new phylogenetic infrageneric classification, summarizing the accumulated knowledge about *Chresta* so far. We provide descriptions of four new species, a key for identification of 18 accepted species and three infrageneric taxa, synonyms, illustrations and distribution maps of the species, as well as their current conservation status.

Keywords: Chrestinae, Compositae, phylogeny, population genetics, synopsis.

GENERAL INTRODUCTION

Asteraceae (or Compositae) is one of the largest families of Angiosperms, with around 24,000 species and ca. 1700 genera (~10% of all spermatophytes), distributed in the whole world, except for Antarctica (Funk et al. 2009). Peculiar characters of the family, such as flowers organized in capitula, the fused anthers, the secondary pollen presentation and fruits of the type cypsela with pappus, have contributed to it being acknowledged as natural group since the Middle Age (Small 1919); its monophyly was posteriorly confirmed in several molecular and morphologic phylogenetic analysis (e.g. Jansen & Palmer 1987, Lundberg & Bremer 2003; Keeley & Robinson 2009). Around 2000 species are found in Brazil, 65% of which are endemic to this country (Brazil Flora Group 2015).

The family is currently subdivided in 12 subfamilies and 28 tribes (Panero & Funk 2002), with Vernoniae being one of the largest tribes, with ~129 genera e ~1100 espécies (Keeley & Robinson 2009). Vernoniae was initially delimited by Cassini (1816), based on several characters, including the dorsally curved style arms that are common in the group (Cassini 1819), with the general delimitation being sparsely changed since then. The monophyly of Vernoniae was corroborated in several phylogenetic analyses (e.g. Keeley & Jansen 1991, 1994; Kim & Jansen 1995; Kim et al. 1998; Keeley et al. 2007) and the tribe is currently placed in subfamily Cichorioideae. Recently analysis using large genomic datasets, however, put the monophyly of Cichorioideae in doubt (Mandel et al. 2017), indicating that relationships in that part of the family might not be as stable as it was once thought.

Besides the presence of thin styles, with filiform and pilose arms, other important features of tribe Vernoniae are the variety of habits, from herbs to trees, the phylotaxy that is usually alternate and the discoid, homogamous capitula that usually present purple, lilac or white florets (Keeley & Robinson 2009). One remarkable feature is the widespread presence of secondary heads (i.e. syncephalia) in the tribe, which occur in ca. 14 genera, mostly from the New World (Loeuille et al. 2015a); this character has been historically used to further divide the tribe into subtribes (e.g. Baker 1873). Vernoniae is found in the American continent, in Africa and Asia, and the main diversity centers are Brazil and Africa. Members of the tribe show a peculiar tolerance for soils with unusual composition, such as those with high contents of iron, bauxite and dolomite (Keeley & Robinson 2009). In Brazil, the tribe is especially representative in the Cerrado phytogeographical domain, where many species occupy the *campos rupestres*, an herbaceous and shrubby type of vegetation found in high elevations, in sandy and rocky soils (Loeuille et al 2015a, b).

Among the Brazilian taxa is *Chresta*, composed by 18 species of herbs, subshrubs and shrubs distributed in the Caatinga, Cerrado and Atlantic Forest. Species of the genus are frequently found in rock outcrops and other types of dry and rocky soils. Some of the features that define *Chresta* are the presence of syncephalia, which can have different morphologies, the indument composed of T-shaped trichomes, the non-sclerified cells on the anther appendages, pappus composed of several series of setose elements and a variety of underground systems.

The first phylogenetic studies in Vernoniae were mainly focused on the monophyly and composition of the mega-genus *Vernonia*, which grouped ca. 1000 species, until its dismemberment after several taxonomic (several treatments by Robinson, but specially 1999a, b, c) and phylogenetic works (Kim & Jansen 1995, Keeley & Turner 1990, Keeley et al. 2007), resulting in many monotypic and small genera and a new circumscription for *Vernonia*, containing ca. 20 species (Keeley &

Robinson 2009). More recently, phylogenetic studies were used to investigate the origin of syncephaly in the American taxa of tribe (Loeuille et al. 2015a) and also to understand the relationships within Lychnophorinae, one of the most representative subtribes in Brazil (Loeuille et al. 2015b). These more recent study helped clarify many of the relationships within South American taxa, but still left some unresolved issues, mainly due to poor resolution and support.

Chresta was sampled in two previous phylogenies (Keeley et al. 2007, Loeuille et al. 2015a), which showed the genus to be monophyletic, but placed doubt about its relationships with other Vernoniaceae subtribe, mainly Lychnophorinae and Vernoniinae. The relationships within the genus showed the presence of two clades, one with Caatinga species and other with Cerrado species, but the internal resolution was not enough to draw conclusions about morphological evolution within the genus.

Molecular phylogenetic studies in Asteraceae have been challenging, mainly due to the abundant polyploidization in the family, both ancient and current, what makes the identification of orthologous nuclear markers difficult (Badouin et al. 2017, Mandel et al. 2017). Besides, the chloroplast genome (plastome) in the family has been shown to be highly conserved at the sequence level, reducing its usefulness in studies of closely related taxa (Shaw et al. 2005, Timmee et al. 2007).

The advances on sequencing techniques in the last two decades (Mardis 2008), with the development of parallel, high-throughput sequencing (Delseny et al. 2010), has been seen as promising to tackle these types of issues (Bräutigam & Gowik 2010), using different approaches, like shotgun sequencing, RADseq (Davey & Blaxter 2010), and Hyb-Seq (Weitemeier et al. 2014) for different types of data. Methods that combine targeting of specific genomic regions with large-scale sequencing are the most promising methods for phylogenetic studies, as they allow the sequencing of hundreds of markers at once and use DNA as source, instead of RNA, as in transcriptome sequencing. On the other hand, they require previous information about the regions of interest, such as a reference genome or EST database. A set of probes based on sunflower ESTs has been developed to be used across the Asteraceae (Mandel et al. 2014), with promising results (Mandel et al. 2015, 2017).

Whereas phylogenies allow the study of the genus as a whole, having species as terminals of the analysis, when this morphological variation is observed among members of a same species, studies focusing on population genetics and phylogeography are more informative. Field observations and study of herbarium collections have evidenced interesting cases of infraspecific variation in the group of *Chresta* species from the Brazilian Caatinga.

Chresta artemisiifolia, *C. harleyi* H.Rob., *C. hatschbachii* H.Rob. and *C. subverticillata* all occur in a short stretch of Espinhaço Septentrional and Chapada Diamantina (Alkmim 2012), where they form distinct populations delimited by the rock outcrops where they occur. These four species are morphologically similar, what raises interesting questions about the patterns of occupation and speciation in fragmentary rocky environments in the Caatinga.

Chresta martii (DC.) H.Rob. has a wider distribution, forming three geographic clusters around the Northern portion of Rio São Francisco. The geographic clusters are very isolated from each other, and there are some morphological differences between populations in each one of them, with plants on the western portion of the distribution being robust, profusely ramified, with wide leaves, while the plants on the eastern end are smaller, with less ramifications and more delicate, narrower leaves. This geographical separation associated to morphological differentiation is an interesting setting to study effects of gene flow and reproductive isolation in natural populations.

This has implications for conservation, as small, isolated populations often show strong population structuring, with little genetic variation among members of a given population, but with some variation among members of different populations (Gitzendanner & Soltis 2000). Regarding *Chresta* species from the Caatinga, the majority of their populations are outside of conservation units, sometimes presenting scarce populations, each with a restricted number of individuals, practically isolated from other populations of the same species, posing a challenge to their conservation.

Phylogenomics datasets have been used in the past few years as a source for microsatellite mining, as they usually present large portions of coding and non-coding portions of the genome, facilitating the process of developing and validating these markers (Jennings et al. 2011). Computational resources can be used to identify putative repetitive regions, even allowing the comparison with homologous sequences from other species, thus contributing to the development of microsatellite markers transferable among different species, which is an advance to studies comparing multiple species. Even though the advances in sequencing have brought over new methods to study populations, like RAD-Seq and Pool-Seq (Schlötterer et al. 2014), microsatellites are still widely used, proving to be valuable resources in several types of population studies (Hodel et al. 2016).

In face of the accumulated knowledge about *Chresta*, and with the possibility of applying new methods and new approaches to study the relationships of the genus with other Vernoniae subtribes, as well as the intraspecific relations within the genus, this work proposed to study the systematics and evolution of *Chresta* and summarize the current knowledge about its species. The results of each study are organized in the following chapters:

Chapter 1 presents a new phylogenetic hypothesis for *Chresta*, reevaluating the relationships within Vernoniae, focusing on other representative Brazilian taxa. The target capture method developed by Mandel et al. (2014) was used to obtain a molecular matrix composed by ca. 700 nuclear markers, which provided complete resolution and good support for almost all nodes. The resulting tree was used to study morphological evolution in the genus, through mapping of different character states. The phylogeny was also used to propose a biogeographical scenario explaining the occupation of the Caatinga and Cerrado by the genus. This part of the study was conducted in partnership with the Mandel Lab at the University of Memphis, TN, USA, and will be co-authored by Dr. Benoit Loeuille, Dr. Jennifer Mandel and Dr. José R. Pirani.

Chapter 2 is divided in two parts; Part A contains the process of developing and validating microsatellite markers transferable among species of *Chresta* from the Caatinga, which will be co-authored by Dr. José R. Pirani and Dr. Jennifer Mandel. Part B presents a population genetics study of five Caatinga species, focusing on genetic diversity and structuring among populations of these species, aiming to understand what processes are at play on the speciation in this group. This part will be co-authored by Dr. Benoit Loeuille, Dr. José R. Pirani and Dr. Jennifer Mandel. This chapter is also a product of the partnership with the University of Memphis.

Chapter 3 summarizes all the taxonomic and systematics knowledge of the genus in a synopsis, also proposing a new infra-generic classification. The synopsis is also an attempt to standardize the nomenclature within the genus, as no comprehensive treatments have been published since the 1980s, when it was split into five different taxa, and because new species and synonyms were published in the last two decades. This chapter also presents illustrations of species that were not previously illustrated, as well as maps and photographs, and also evaluation of conservation status for all species. It will be co-

authored by Marcelo T. Kubo, Dr. Benoit Loeuille and Dr. José R. Pirani.

Chapter 4 is divided in three parts and presents four new species of *Chresta*. Part A contains a paper already published in the period *Phytotaxa* (Siniscalchi et al. 2016), describing *C. filicifolia*, the only species endemic to the Atlantic Forest in the genus. Part B contains a work that is already submitted at *Systematic Botany*, containing two new species of the Caatinga. Part C contains another paper that will be submitted to *Phytotaxa*, describing a new species from Bahia, fruit of a partnership with researchers from the herbarium HVASF, in Petrolina, Pernambuco.

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FINAL CONCLUSIONS

In the last decades, phylogenetic studies have been used to study the evolution of morphological characters and biogeographical history of different groups, greatly increasing the knowledge about the current biodiversity and the evolutionary processes that acted on them. As one of the richest families of Angiosperms, Asteraceae is an important target for these studies, as the understanding of how this diversity came to be can also increase our knowledge about the diverse environments where they occur, and about how shifts in morphology can boost diversification.

The tribe Vernonieae is very diverse in Brazil, especially in drier environments, like the Cerrado, *campos rupestres*, rock outcrops and in the Caatinga. *Chresta* is a remarkable member of the tribe, found on the Caatinga, Cerrado and Mata Atlântica, presenting from widely distributed species like *C. scapigera* and *C. sphaerocephala*, to narrow endemics like *C. hatschbachii* and *C. souzae*. The morphological variety found in the group, expressed in different combinations of characters like leaf morphology, pattern of synflorescence branching, syncephalium morphology and growth, floret color and pollen type, has led to different interpretations of its taxonomy, with the species being kept in different genera (e.g. Candolle 1836, MacLeish 1984, 1985a, b) or united in the same genus (e.g. Gardner 1842, Baker 1873, Robinson 1999). The relationships of *Chresta* to other Vernonieae genera has also been a point of discussion, with the genus being grouped in the Lychnophorinae (e.g. Baker 1873) or as part of *Vernonia* (Lessing 1831) or even as a separate tribe (e.g. Robinson 1999), due to the unusual combination of characters like syncephalia, typical of Lychnophorinae, with the pollen type more commonly found in other Vernonieae. Previous phylogenies did not elucidate the position of *Chresta* in Vernonieae with certainty, due to a lack of resolution and support (e.g. Keeley et al. 2007, Loeuille 2015).

With the present study, we obtained a well resolved and supported phylogeny of *Chresta*, using Phylogenomics methods that provide hundreds of markers (Mandel et al. 2014), and used the phylogeny as a basis to study the evolution of the characters and biogeography in the genus. We verified that all taxonomic treatments that separated *Chresta* species in multiple genera relied in non-monophyletic groupings, thus supporting *Chresta* as a single unit. Also, most of the characters used to divide these genera, like the ramification of the synflorescence or floret color, actually arose multiple times in the phylogeny or suffered reversals. Also, we recovered a biogeographical history depicting an early diversification of *Chresta* in the Caatinga area with posterior expansion into the adjacent Cerrado.

We also used five rupicolous, isolated and fragmentary species of *Chresta* from the Caatinga to study microevolutionary processes that may be underway in their populations, aiming to delineate general patterns of diversification. We found that although these species share several similarities in morphology and environmental requirements, they differ in their genetics, varying in the degree of isolation between populations and intensity of effects of genetic drift and inbreeding. These results have implications on conservation strategies for these species, as they may require different strategies to be protected.

In order to summarize the knowledge obtained during these studies, we also present an illustrated synopsis of the genus, proposing a new infrageneric classification based on the clades obtained in the phylogeny. We propose a wide circumscription for *Chresta*, containing eighteen species divided into two subgenera and three sections, defined by molecular synapomorphies and morphological

characteristics.

With this study, we hope to contribute to the general knowledge of Asteraceae in Brazil and also to the understanding of the evolution and history of the plant biota of the phytogeographical domains that compose the Brazilian landscape. We also expect that our results will serve as a model for the incorporation of new methods and approaches to phylogenetic studies.

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