



## Hidden in the dry woods: Mapping the collection history and distribution of *Gymnanthes boticario*, a well-collected but very recently described species restricted to the dry vegetation of South America

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### Abstract

Botanists estimate that 80 to 90% of existing plant species have already been described and it is expected that most undescribed species are rare or narrow endemic ones. Here we map the geographical distribution of *Gymnanthes boticario*, a species described in 2010, and show that the species is not only widespread, but was well-collected in the Caatinga semiarid vegetation prior to its description. During a revision of the genus *Gymnanthes* we also found collections of *G. boticario* in the Brazilian Mato Grosso do Sul state (in Pantanal ecoregion), in Paraguay (in Cerro León dry forests) and in Bolivia (in Chiquitano dry forest ecoregion) in a pattern that closely resembles the Pleistocenic Arc Hypothesis. We map the continental distribution of *G. boticario*, report the first records of it for Bolivia, Paraguay and the Brazilian Pantanal and show the rich data available in herbaria for a plant only recently described.

**Key words:** Bolivia, Brazil, Chiquitano, Ecoregions of South America, Hippomaneae, Paraguay

### Introduction

#### *The Pleistocenic Arc Hypothesis*

South America has a large number of different vegetation types and ecosystems, ranging from superhumid rainforest such as the Amazonian and Atlantic forests to deserts in Chilean and Peruvian coasts (Cabrera & Willink 1973, Olson *et al.* 2001). Distributed throughout South America, there are also many disjunct areas where semiarid conditions prevail, and in which there is a shortage in water availability for most of the year (Pennington *et al.* 2000, 2006a, Prado 2000). Of these, the Caatinga dry formation, a variable complex of semiarid vegetation that occupies most of the Northeastern region of Brazil, is the largest area, with some 800,000 km<sup>2</sup> (Prado 2003, IBGE [Instituto Brasileiro de Geografia e Estatística] 2004).

During part of the twentieth century, biogeographers assumed that the tropical semiarid Caatinga in Brazil and subtropical, frost prone semiarid Chaco in Argentina and Paraguay were ecologically similar and shared floristic links (Cabrera & Willink 1973, Rizzini 1979, Prado & Gibbs 1993). In a seminal paper, Prado & Gibbs (1993) tested the alleged floristic similarity between Caatinga and Chaco, plotting species distributions and showing that the links between Caatinga and Chaco were negligible, but that there were, however, many

disjunct distributions between Caatinga and other dry formations of South America. While the flora of Chaco was almost entirely different, Caatinga shared species with dry formations such as the Chiquitano dry forests in Bolivia, the dry valleys of the Andes in Bolivia, Peru, Ecuador and Colombia and the dry coast of Venezuela (Prado & Gibbs 1993, Pennington *et al.* 2000, Prado 2000). Prado & Gibbs (1993) explained the large number of disjunct taxa between these widely separated semiarid areas with the following scenario. During the Pleistocene glaciations the climate was drier, causing wet forests to reduce in area and dry formations to spread to a much larger extent (Werneck *et al.* 2011). After the glaciations, with a wetter climate, dry formations reduced in area and were split into separate nuclei (Pennington *et al.* 2000; Werneck *et al.* 2011). But as a legacy of their joint history, they now share a number of species, genera and lineages. Based on these shared taxa, Prado (2000) and Pennington *et al.* (2000) suggested that these semiarid disjunct areas should be considered a single, large phytogeographical domain called Seasonally Dry Tropical Forest (SDTF) or Dry Plant Formations (Sarmiento 1975).

Sarmiento (1975) had already called attention to the similarities between dry vegetation formations across South America. And, based on the many floristic disjunctions recorded by Prado & Gibbs (1993), it was proposed that distant dry forests of South America shared floristic links and a common history, leading this idea to be the focus of much debate in the last 20 years (Prado & Gibbs 1993, Pennington *et al.* 2000, 2006b, Dirzo *et al.* 2011). Criticism of the hypothesis has emerged too. Mayle (2006) argued that the pollen data available to date are not consistent with the Pleistocene Arc Scenario and suggested that multiple long distance dispersal events between Caatinga and other dry formations could also explain the observed pattern. The debate continues and while some prefer to consider the possibility of multiple dispersal events (e.g. Mayle 2006), others admit that at least between the dry Caatinga and Chiquitano areas there is support for a more widespread occurrence of dry vegetation in the past (e.g. Linares-Palomino *et al.* 2011). In any case there is a striking number of disjunct occurrences of species or lineages known to be present in the Caatinga and other dry vegetation of America, but which do not occur in the Cerrado savannas nor in the wet forests between them (see examples in Prado & Gibbs 1993, Taylor & Zappi 2004 and Lewis *et al.* 2006).

### ***Gymnanthes boticario* in Caatinga and beyond**

Historically, the semiarid Caatinga was one of the most scientifically overlooked areas of Brazil. Assumed to be poor in species diversity and endemism, few efforts to study its flora and establish nature reserves were made up to the 1990s, and even now less than 2% of its area is protected by Nature Reserves (Tabarelli & Vicente 2002, Castelletti *et al.* 2003). Studies in Caatinga intensified sharply in the last decade and now show that the Caatinga is a semiarid area rich in plant diversity and with many endemic genera and species [e.g. the monotypic genera *Holoregmia* Nees von Esenbeck (1821: 300) (Harley *et al.* 2003) and various species of Fabaceae (Queiroz 2009), Cactaceae (Taylor & Zappi 2004) and Euphorbiaceae (Lucena & Alves 2010)]. In 2002 a first synthesis of the plant biodiversity in the Caatinga was prepared (Sampaio *et al.* 2002), and in 2006 a general catalogue of the plant species was published (Giulietti *et al.* 2006), recognizing 5344 species in the Brazilian semiarid region and 1511 species in the Caatinga *sensu stricto* vegetation. A new list of species was published in 2010 as part of the List of Plants of Brazil, recording 4320 Angiosperms for the semiarid region of Brazil (Caatinga Phytogeographical Domain, or Caatinga *sensu lato*) (Forzza *et al.* 2010). Several new species have been published since this recent comprehensive list, including the subject of this paper, *G. boticario*.

*Gymnanthes boticario* Esser, M.F.Lucena & M.Alves (2010: 345) is a Euphorbiaceae species, of the Hippomaneae tribe, recently described from the Caatinga vegetation in Northeastern Brazil (Esser *et al.* 2010). The plant is easily recognized in the genus by the presence of indumentum, usually serrate (rarely entire) margins of the leaves, the short petiole, densely tomentose ovary and sessile fruits. In the protologue, 14 collections from Bahia, Ceará, Pernambuco, Piauí and Rio Grande do Norte states are cited, indicating that the plant has a wide distributional range. During a general revision of *Gymnanthes* Swartz (1788: 6) by the first author, dozens of other specimens of this plant were recorded in many herbaria, demonstrating a surprising amount of unpublished distributional data available about such a newly recognized

plant, and stimulating us to map the occurrences of it. A study visit to G, K and M herbaria revealed new records for Mato Grosso do Sul state, Brazil, Bolivia and Paraguay, indicating that this new species is not only well collected, but also quite widely distributed in South America, with a pattern that matches closely the Pleistocenic Arc proposed by Prado & Gibbs (1993). Our purposes are thus 1) to record the history of collections made of *G. boticario* up to its description, exploring the factors that may cause a widely collected plant to remain unrecognized a long time before description; 2) to map the known distribution of the plant, revealing its ecological preferences; 3) to report the first records for *G. boticario* for the dry forests of Pantanal ecoregion in Mato Grosso do Sul, Brazil; for Paraguay, in Cerro León dry forests; and also for Bolivia, in Chiquitano dry forests, also contributing to the Catalogue of Vascular Plants of Bolivia, now in preparation; and 4) to discuss the implications of this new disjunct record for the hypothesis of the Pleistocenic Arc.

## Material & Methods

### How many years and how many collections are necessary to allow for a new species to be recognized?

To determine the amount of data available and the geographical distribution for *Gymnanthes boticario* up to the year of the species description, we consulted material deposited in the herbaria ALCB, B, BM, BR, CEPEC, EAC, G, GUA, HRB, HUEFS, HVASF, IPA, JPB, K, M, MAC, OXF, P, PEUFR, RB, TEPB, UFP, UFRN, Z and also received by loan material from ASE, BA, BHCB, CESJ, CEN, CH, CIB, COR, CRI, CTES, ESA, F, FLOR, FURB, HB, HRCB, HUFU, HXBX, HUM, IAC, IBGE, ICN, IAN, INB, INPA, JBSD, LD, LIL, LPB, MBM, MBML, MEXU, MICH, PACA, PMG, R, RBR, SMDB, SP, SPF, UB, UEC, UFMT, UPCB, VIC, VIES, XAL, WU (acronyms follow Index Herbariorum 2012). As *G. boticario* was only recently recognized, we consulted with special attention material labeled as “undetermined” in Euphorbiaceae, and collections under closely related and/or morphologically similar genera and families [especially *Actinostemon* Mart. ex Klotzsch (1841: 184), *Microstachys* Jussieu (1824: 48), *Sebastiania* Sprengel (1821: 118), and Salicaceae]. Collections labeled under *Gymnanthes* sp. were always evaluated, as part of a revision of *Gymnanthes* in progress by the first author and we built a database of all recorded sheets with the taxonomic and geographical data associated with the collections (herbarium code, collecting locality, names previously applied to herbarium sheets etc). The list of consulted material is presented in Appendix 1.

### Mapping the distribution of *Gymnanthes boticario*

From each collection in the consulted herbaria we recorded the following geographical data from the sheets: GPS coordinates when available, locality and town of collection and Brazilian State or Bolivian/Paraguayan department. When GPS coordinates were recorded we plotted the points in a GIS environment and checked if the point was within the political borders reported on the sheet. Collections without GPS coordinates or for which coordinates were clearly wrong were mapped using the geographical location of the town or a more specific locality reported on the specimen label (a known mountain, or a national park).

To understand the biogeographical pattern of distribution of *G. boticario* we selected from the Olson *et al.* (2001) map of ecoregions of the world, the dry formations of South America using the definitions and maps presented by Sarmiento (1975) and Pennington *et al.* (2006b). We plotted the dry formations together with the Cerrado, Pantanal and Chaco ecoregions and then added to the map the collection locations of *G. boticario*.

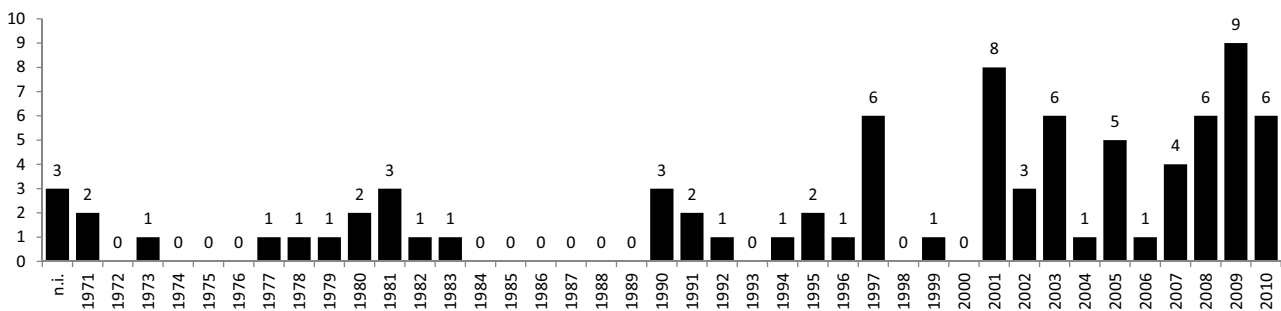
## Results

### How many years and how many collections are necessary to allow for a new species to be recognized?

The first collection of *Gymnanthes boticario* we are aware was made in 1971, but the species was described only in 2010 (Esser *et al.* 2010). So at least 39 years elapsed from the first collection to the description [Fig. 1]. Up to 2010 there were 82 collections of *G. boticario* available in 18 herbaria [Fig. 2], with 50 further duplicates distributed to 21 herbaria [Fig. 3], resulting in a total of 132 sheets in 25 herbaria in six

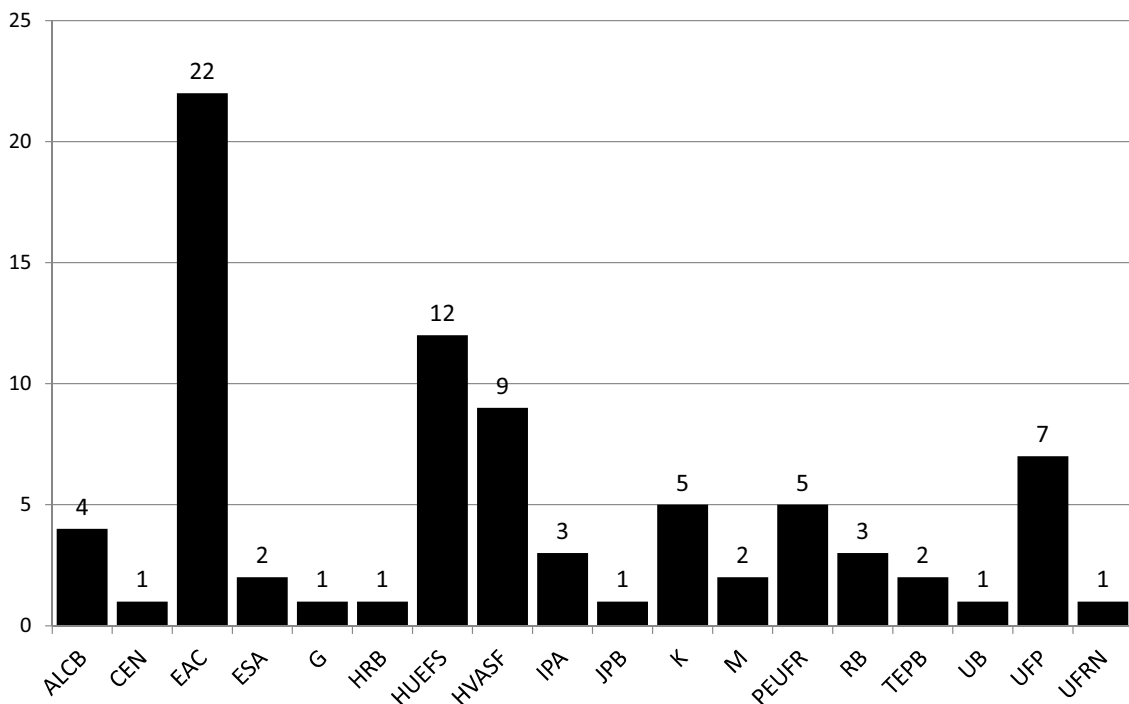
countries (Bolivia, Brazil, Germany, Switzerland, United Kingdom, United States) up to the year of the description of the species. Two further collections (*Oliveira & A. Laurênio 211* and *Siqueira-Filho et al. 2663*, not included in the statistics presented here, but listed in the examined material—Appendix 1) were made after 2010. Most of the collections were labeled as *Gymnanthes* sp. (27 sheets) or *Sebastiania* sp. (25 sheets). The other names applied were Euphorbiaceae (15), *Actinostemon* sp. (8), *Sebastiania* cf. *serrata* (3), *S.* aff. *brasiliensis* (2), *S. vestita* (1) and *Maprounea* sp. (1) [Fig. 4]. Up to 2010, when *G. boticario* was described, the 82 collections available already covered five of the eight recognized subregions of Caatinga (called by Velloso *et al.* 2002 “ecorregions” of Caatinga) and seven of the ten Brazilian states where Caatinga vegetation occurs (as well as one collection in Cerro León, Paraguay; two collections for the Brazilian Pantanal, in Mato Grosso do Sul state; and two collections in the Chiquitano dry forests in Bolivia) [Figs. 5–7]. However, only 17% of these collections had been examined by the authors of *G. boticario* in the protologue, because they were not attempting a monographic approach, but simply citing collections to hand at that time.

**Number of collections of *G. boticario* per year up to 2010**



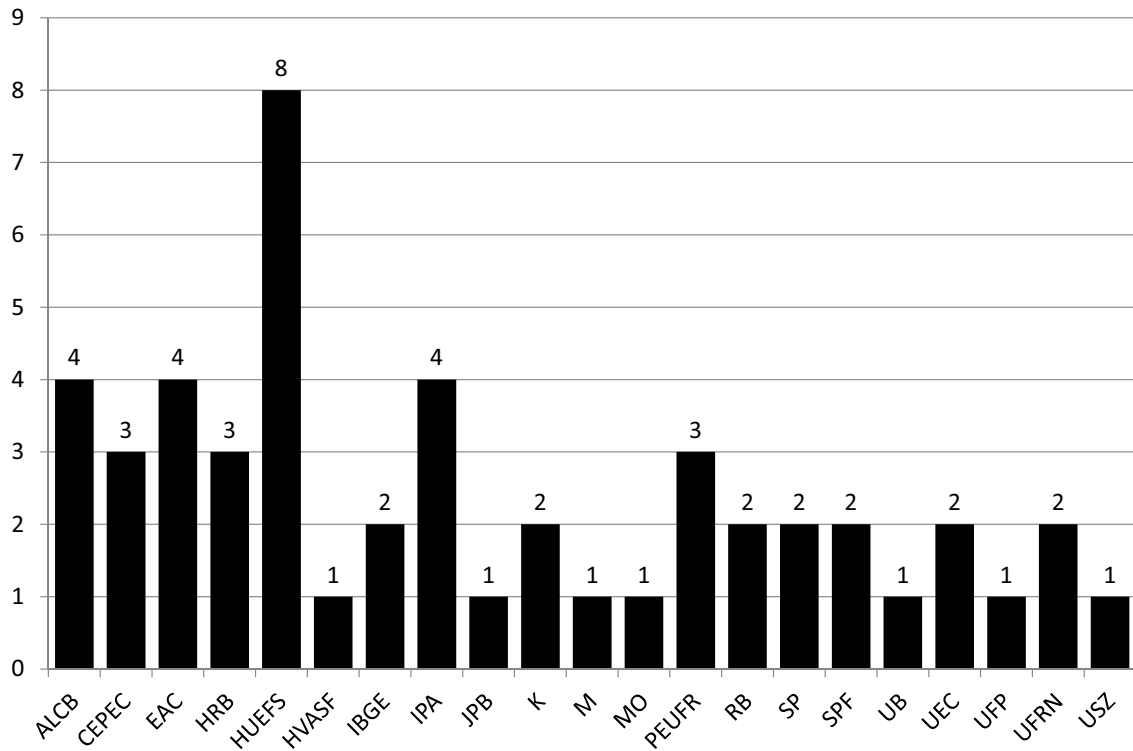
**FIGURE 1.** Number of collections per year of *Gymnanthes boticario* up to 2010, when the species was described.

**Number of available collections of *G. boticario* in different herbaria up to 2010**



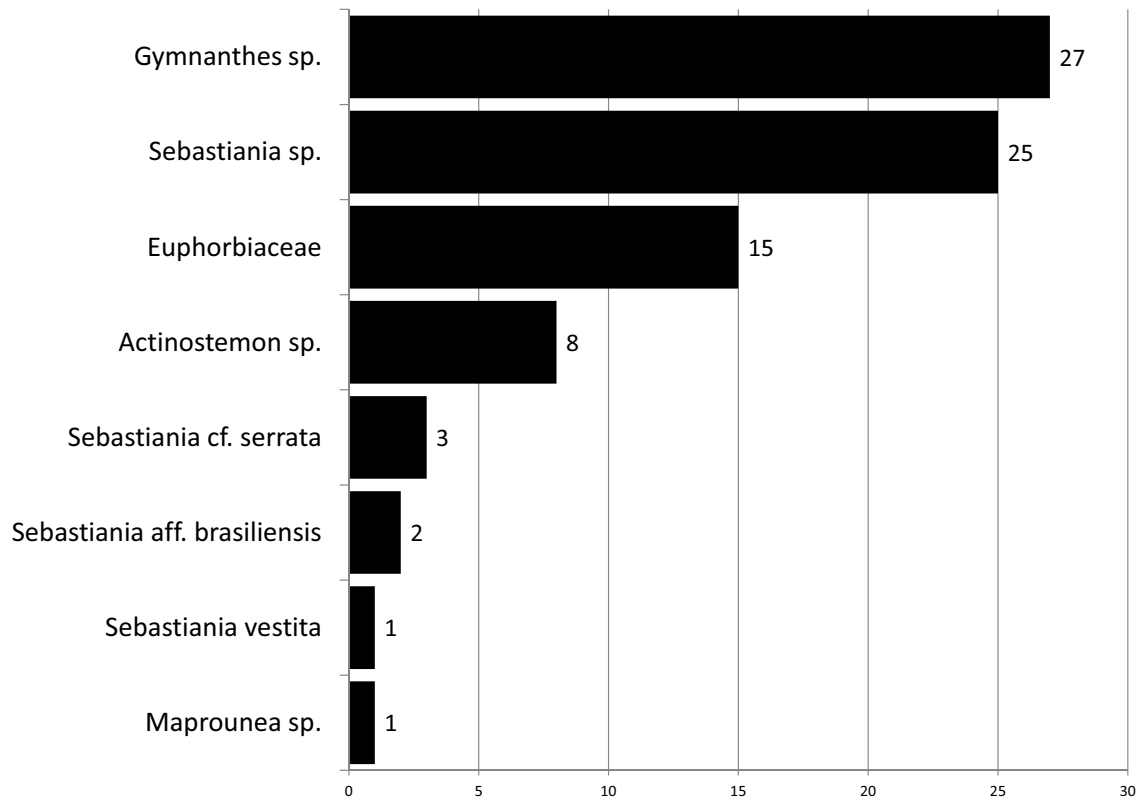
**FIGURE 2.** Number of collections of *Gymnanthes boticario* available in the consulted herbaria up to 2010, when the species was described.

**Number of available duplicates of *G. boticario* in different herbaria up to 2010**



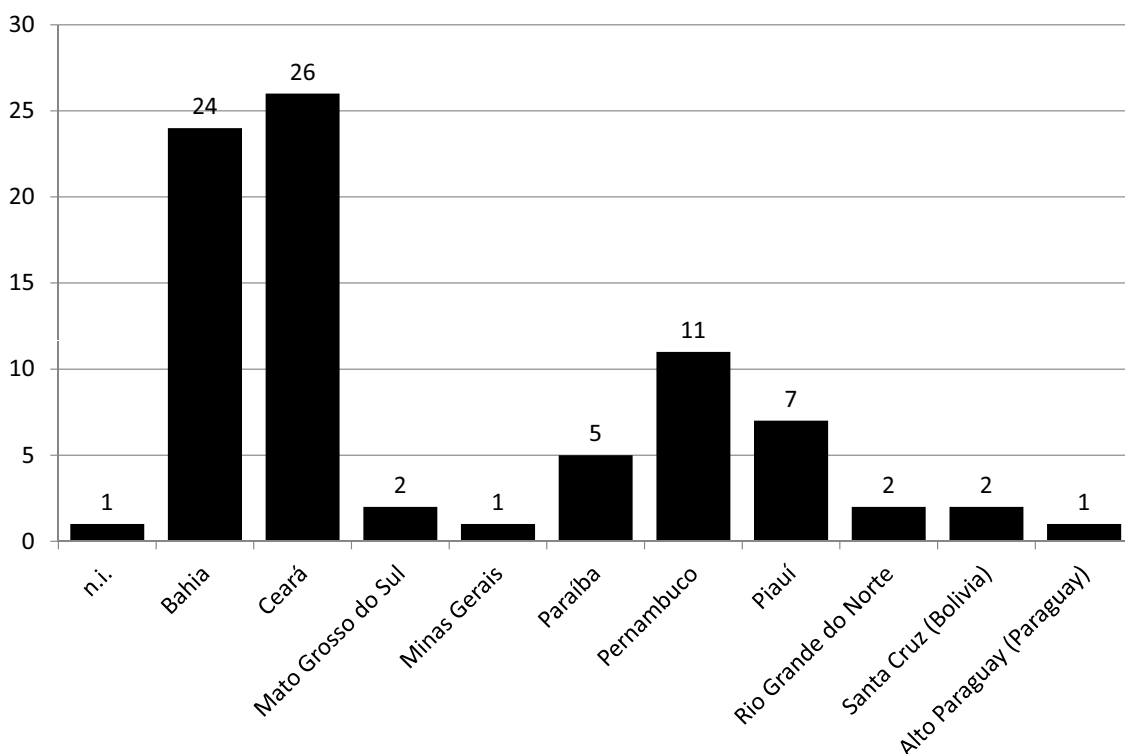
**FIGURE 3.** Number of duplicates of *Gymnanthes boticario* available in the consulted herbaria up to 2010, when the species was described

**Names applied in herbarium sheets to *G. boticario* up to 2010**



**FIGURE 4.** Names applied to *Gymnanthes boticario* on herbarium sheets before recognition as a new species

**Number of collections of *G. boticario* per Brazilian state or Paraguayan/Bolivian department up to 2010**

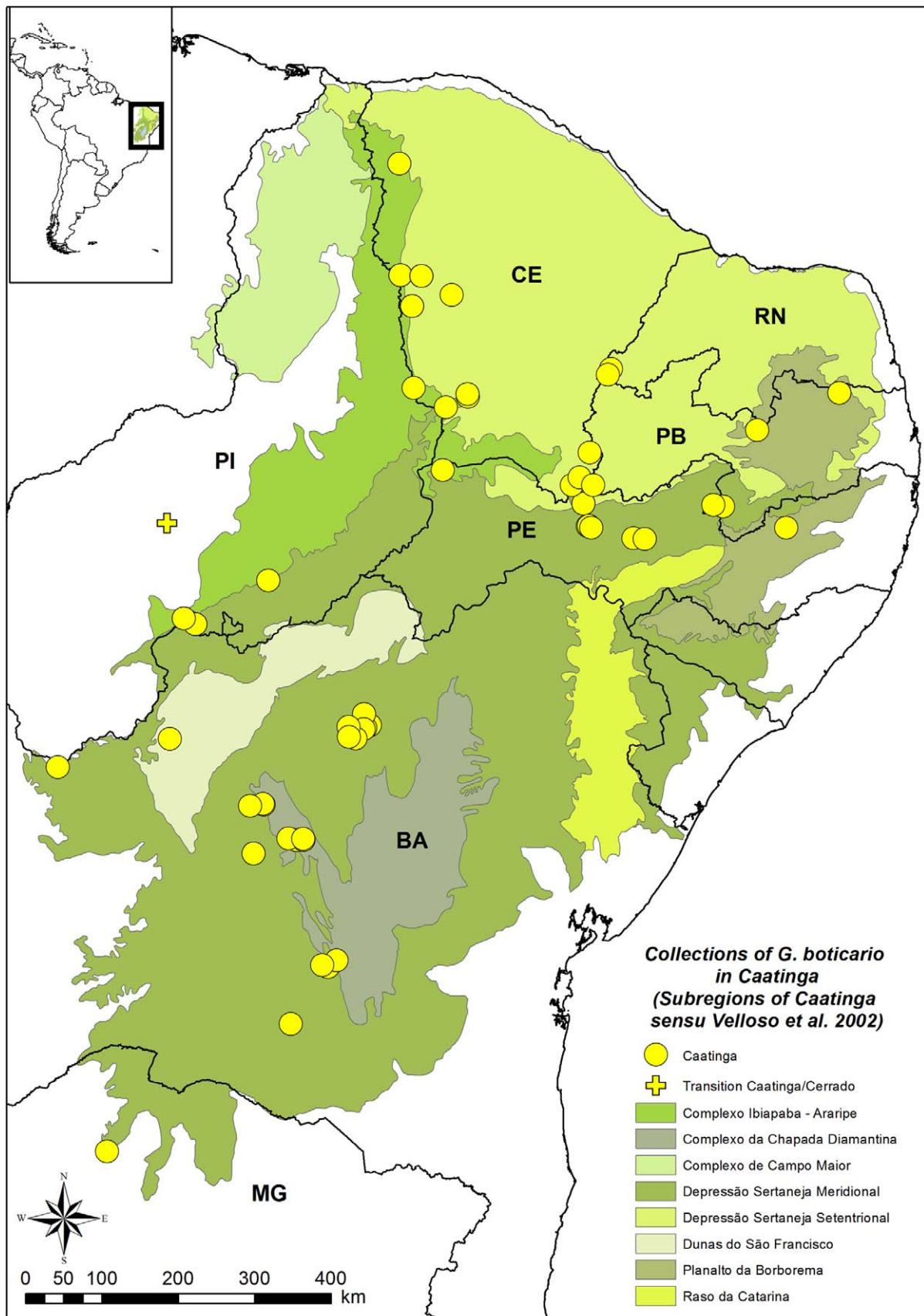


**FIGURE 5.** Number of collections of *Gymnanthes boticario* in each Brazilian state or Paraguayan/Bolivian department available in herbaria up to 2010, when the species was described.

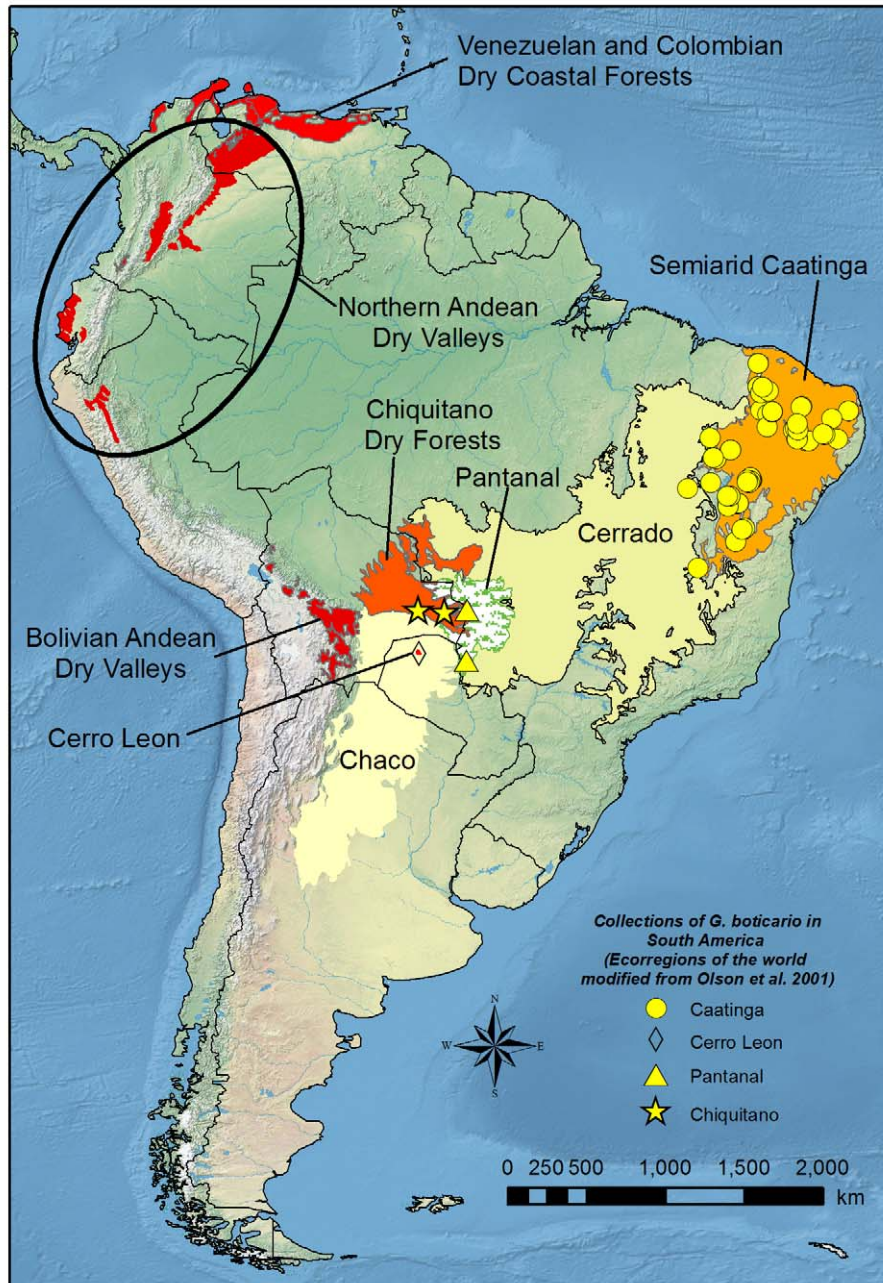
### Mapping the distribution of *Gymnanthes boticario*

The distribution of the *G. boticario* in northeastern Brazil was clearly related to the Dry Caatingas, and not to the Cerrado savannas or the Atlantic rainforests which are together the three main Phytogeographical Domains of Northeastern Brazil. We found 77 collections of *G. boticario* in the semiarid region of Brazil, all of them related to the Caatinga or at most to the ecotonal areas to Cerrado, but none in Cerrado vegetation or Atlantic rainforest itself. One collection was from an ecotonal area between Caatinga and Cerrado (*Fernandes & Matos s.n.*, Eliseu Martins, Piauí).

Piauí, Bahia and Minas Gerais have extensive areas of Cerrado vegetation, but all collections we encountered in these states were made in the Caatinga or at most in ecotonal areas, showing the preference of *G. boticario* for dry vegetation [Fig. 6]. This preference is even more evident when we analyze the distribution of the plant in the South American continent as a whole [Fig. 7]. The only other points we could locate outside the Caatinga were in the Cerro León, Alto Paraguay department; in the Bolivian department of Santa Cruz; and in the Brazilian state of Mato Grosso do Sul (collections made close to the Bolivian and Paraguayan borders). These areas represent respectively the Cerro León dry forests of Northern Paraguay; the Chiquitano Dry Forest ecoregion; and dry forests of hilly areas of the Pantanal ecoregion (in the case of the collections *Prance et al. 26151* and *Bernardi 20426*). The Chiquitano and Caatinga are considered by Pennington *et al.* (2000) as SDTF. The Cerro León is a particular vegetation that occurs inside the Chaco ecoregion, but has a flora related to dry forest and not to the surrounding Chaco (it is, in a certain sense, an enclave of dry forests within the Chaco—Prado & Gibbs 1993, Werneck *et al.* 2011). In the Pantanal, known primarily as a wetland, there are many patches of dry forests (deciduous or semideciduous forests) that occur in hills scattered across the landscape and harbor a flora which species come from both the Cerrado and from other dry formations of South America (Prance & Schaller 1982, Damasceno Júnior *et al.* 2009). The distribution of *G. boticario*



**FIGURE 6.** Distributional map of *Gymnanthes boticario* in the semi-arid Caatinga of Northeastern Brazil, showing that when the species was described in 2010 collections were already available for seven of the ten Brazilian states where Caatinga occurs, including five of its eight Ecoregions (sensu Velloso *et al.* 2002). States where we recorded the species: PI- Piauí; CE: Ceará; RN: Rio Grande do Norte; PB: Paraíba; PE: Pernambuco; BA: Bahia; MG: Minas Gerais (Map elaboration: M.F. Moro).



**FIGURE 7.** Mapped distribution of *Gymnanthes boticario* in South America, a species typical of dry forests, including the first recorded occurrences to Bolivia, in the Chiquitano dry forests, to Paraguay, in the Cerro León, and to Mato Grosso do Sul, in the Pantanal (Map elaboration: M.F. Moro).

adheres closely to the distribution expected by the model of the Pleistocenic Arc, which argues that during drier glacial times dry formations expanded to a larger extent than the actual one (Werneck *et al.* 2011) and constituted a larger arc of dry vegetation surrounding the wet forests, Cerrado and the Chaco. According to the model, these dry formations fragmented again in wetter post glacial times and the dry areas became isolated [see actual distribution in Fig. 7], but retained some floristic elements that were separated by this vicariance event.



## Discussion

### How many years and how many collections are necessary to allow for a new species to be recognized?

Most plant species published as new to science in recent years are described from relatively small ranges, often based on just a few herbarium collections (Joppa *et al.* 2011), leading sometimes to the assumption that species remaining to be described are narrow endemics and that most of the “common” plants have been already published. But here we have a case of common, widely distributed and well collected newly described species. Although widely collected in Brazil, almost four decades elapsed between the time of the earliest known collection of *G. boticario* and the time of its publication. This elapsed time may seem long but is, in fact, close to recently published estimates of the mean time that species in general remain undescribed after first collected (Bebber *et al.* 2010), and reinforces the importance of the continuing taxonomic work in Brazil as a means of revealing the many new plants waiting to be discovered (Pimm *et al.* 2010), not all of them particularly rare, as shown here.

Why did *Gymnanthes boticario* lie undiscovered in so many herbaria for so long? Our results show that in 33% of the collections, it had been correctly identified to genus level [27 collections were deposited in herbaria as *Gymnanthes* sp.—see Fig. 4] and in a similar number of cases it had been assigned to a closely related genus (25 collections of *Sebastiania* sp.) or simply assigned to family level (15 collections as Euphorbiaceae) [Fig. 4]. It seems that “generalist” botanists were succeeding in getting the material correctly determined to or close to the genus level. Which factors resulted in a long delay in recognizing *G. boticario* as new to science? Unclear taxonomic boundaries and the dearth of specialists and monographs for the Hippomaneae tribe are obvious reasons.

Bebber *et al.* (2010) show how continuous intensive taxonomic work in a particular group can increase efficiency in recognizing new species. When the first monograph for Neotropical Chrysobalanaceae was completed, the mean time for recognizing new species was 35 years, while the mean time for recognizing new species in subsequent works on this group was only 10.5 years (Bebber *et al.* 2010). Hippomaneae is a large group in the Euphorbiaceae family (33 genera and 330 species worldwide; 13 genera and about 120 species in Brazil; Esser 2012) and lacks much taxonomic input. For the 13 Brazilian genera of Hippomaneae, only five have recently published revisions, and *Gymnanthes* is recognized as one of the critical genera, both in Brazil and the world (Esser 2012, Secco *et al.* 2012), so it is not surprising that new species in this group are a long time waiting to be recognized.

Moreover, before the 1990s Caatinga was poorly studied, but in the last decade the number of publications about Caatinga has increased and a large number of syntheses, catalogues, taxonomic treatments and new species have been published (Sampaio *et al.* 2002, Taylor & Zappi 2004, Giulietti *et al.* 2006, Queiroz 2009, Forzza *et al.* 2010). The discovery of narrow endemic species are happy surprises, but as shown in our distribution map and consulted material list [Figs. 5–6; Appendix 1] *Gymnanthes boticario* is a widespread and well collected plant in Caatinga. It is clear that more taxonomic effort is needed in this region of Brazil (Pimm *et al.* 2010). Fortunately this need is beginning to be addressed and not only has more taxonomic work been undertaken there in the last two decades, but also many new species have been recognized recently (e.g. Carneiro-Torres *et al.* 2011)

### Mapping the distribution of *Gymnanthes boticario*

As our distribution maps make clear, *Gymnanthes boticario* is widespread in the Caatinga and has a marked preference for dry formations. All collections of *G. boticario* are material coming from SDTF (sensu Pennington *et al.* 2000) or at most from their ecotonal areas to Cerrado or dry forests within Pantanal. But we didn't find evidence of *G. boticario* occurring in Cerrado vegetation itself. In Piauí, Bahia and Minas Gerais states, Cerrado and Caatinga are contiguous and the Cerrado covers large areas (IBGE [Instituto Brasileiro de Geografia e Estatística], 2004). If *G. boticario* was also a characteristic element of Cerrado vegetation we would expect at least some collections there. Moreover we didn't locate any collections from central Brazil. The species seems to be absent from Cerrado areas and reappears only in the dry Chiquitano forests in

Bolivia, in the dry forests of Cerro León, in Paraguay, or in dry forests in the Pantanal of Mato Grosso do Sul. Both Caatinga and Chiquitano are part of the SDTF that according to the model of Prado & Gibbs (1993) were part of the once extensive arc of dry forests of South America (Werneck *et al.* 2011), which could explain the large number of disjunctions observed between these areas.

The collection Prance *et al.* 26151 was made in the Pantanal, close to the border with Bolivia, in a site now belonging to the Mato Grosso do Sul state, Corumbá municipality (the state of Mato Grosso was split in two in 1979 and the place where Prance *et al.* collected is now Mato Grosso do Sul). Describing the site of this collection Prance & Schaller (1982) deemed it a mosaic of vegetation and a confluence of different floras, where elements of Cerrado, Amazonia and Chaco flora mix. This area is also on the outskirts of the Chiquitano Dry Forest ecoregion (Olson *et al.* 2001), an area of ecological tension. So it is not surprising that the *G. boticario* was found there. Bernardi made his collection of *G. boticario* in the “Cerro Pedrera, riacho Navileque, Paraguay” (Bernardi 20426). But Navileque river is located in Brazilian territory, in the Pantanal ecoregion. Lorenzo Ramella (from herbarium G) kindly provided us with a transcription of Bernardi’s notes of his field trips, and it seems clear that he, while collecting in Paraguay, entered many kilometers in Brazilian territory without realizing he had done so. So we could locate two collections of *G. boticario* to the Pantanal ecoregion in Mato Grosso do Sul state. Pantanal is one of the largest wetland areas in the world, but within the flooded areas there are hills which are never flooded and harbor dry forests (Damasceno Júnior *et al.* 2009). These show a diverse flora, mixing species of Cerrado and dry forests, that are interspersed with swampy vegetation and gallery forests (Prance & Schaller 1982, Damasceno Júnior *et al.* 2009). Prance’s collection is recorded as being made from forest on slopes in higher areas and Bernardi’s collection was made in higher areas of a hill (cerro, in Spanish). These never-flooded areas have dry forests in the slopes (Prance & Schaller 1982) and are thus the type of environment where *G. boticario* could be expected outside Caatinga.

An interesting collection was made in the Cerro León in Paraguay. This mountain supports dry forests, but is completely surrounded by the Chaco plains. While the Chaco plains have a flora very different from the dry formations of South America, Cerro León has different soil types and many plant species shared with other dry formations of the continent (Prado & Gibbs 1993). *Gymnanthes boticario* is a new example of the links of Cerro León with disjunct dry areas.

It should be noted that the Cerrado ecoregion is not a homogeneous vegetation type. Within the Cerrado one can find the typical cerrado *sensu stricto* vegetation, which has a savannah physiognomy, but also grasslands (campo limpo e campo sujo), arboreous cerrado (cerradão), gallery forests, and a different type of dry forest, which is known as deciduous calcareous dry forests (or limestone outcrop vegetation, Mata Seca em solo Calcário; Ribeiro & Walter 2008). Floristic and phytosociological studies in these dry deciduous forests within the Cerrado have collected many taxa typical of the semiarid Caatinga that do not occur in Cerrado *sensu stricto*. Examples are *Aspidosperma pyrifolium* Martius (1824: 60), *Commiphora leptophloeos* (Martius 1828: 393) Gillett (1980: 582) and *Cavanillesia arborea* (Willd.) Schumann (1886: 327) (Felfili *et al.* 2007, Lima *et al.* 2010, Carvalho & Felfili 2011). If *Gymnanthes boticario* does occur within the Cerrado Phytogeographical Domain, we would expect it to be in these calcareous dry forests within the Cerrado, not in Cerrado vegetation itself. Collecting *G. boticario* in the limestone forests would lend even more support to the Pleistocenic Arc hypothesis, as these small patches of dry forests within the Cerrado can be seen as the remnants of the dry vegetation that once covered much larger areas of South America.

An alternative hypothesis to the Pleistocenic Arc is that many different taxa made independent long distance migrations through the Cerrado to other dry formations of South America. Mayle (2006) concluded in favor of this idea because available pollen data were not congruent with the model of the Pleistocenic Arc. But he also acknowledged that the palynological data is, as yet, very incomplete and a newer-evaluation is desirable once more information is available. Linares-Palomino *et al.* (2011) compared floristic resemblances of many of the dry nuclei in Latin America. They concluded that relatively close areas showed reasonable floristic congruence, but that the whole set of South American dry areas cannot be joined in a single floristic unit because of large differences among them. They identified four major SDTF regions and one of these four comprised the Chiquitano forest, Caatinga and other Brazilian SDTFs.

It is striking that disjunct distributions that conform to the Pleistocenic Arc (not only species, but also subgeneric level occurrences) are reported in many cases among Cactaceae (Taylor & Zappi 2004), Leguminosae (Lewis *et al.* 2006) and also other families (Prado & Gibbs 1993). *G. boticario* conforms well to this model. Moreover Linares-Palomino *et al.* (2011) found a reasonable similarity between Chiquitano forest and Caatinga, and Lima *et al.* (2010) and Carvalho & Felfili (2011) report some disjunctions between limestone dry forests within Cerrado and Caatinga. Perhaps the true scenario is a much more complex dynamic in the past of the continent, with large scale community migrations at some times (maybe not only in the Pleistocene) combined with long distance dispersal events. In this case, the limestone dry forests within Cerrado could represent either remnants of a former larger dry area or stepping stone environments allowing dry forest species to cross the Cerrado. In either case we predict that new records for *G. boticario* will be found in the limestone outcrop forests within the Cerrado.

It is remarkable for *G. boticario* to be so specific to dry formations. It occurs in many disjunct SDTF sites in South America, including small patches of seasonal forests within the Pantanal and in Cerro León hills, which is surrounded by Chaco vegetation, but we could find no evidence of it occurring in other vegetation of the continent as cerrado *sensu stricto*, Chaco or rain forests. Probable new sites to collect this plant are the limestone outcrop dry forests within Cerrado and Bolivian Andean dry valleys. If this species is collected in these sites, it will strengthen even more the plant as a Pleistocenic Arc distribution model.

## Conclusion

*Gymnanthes boticario* is an example of reasonably common and well collected plant that took a long time to be recognized as new. This illustrates the fact that the plants remaining to be described are not necessarily narrow endemics or plants from remote and unpopulated areas. The plant occurs in readily accessible places and had been available for many years in different herbaria prior to recognition, showing the need for more specialist work on Caatinga plants.

Regarding the plant's distribution, it can now be listed among the many cases of dry formation specialists recorded separately from distant patches of SDTFs of South America (Prado & Gibbs 1993, Taylor & Zappi 2004, Lewis *et al.* 2006). We make the first record of *Gymnanthes boticario* in Bolivia and Paraguay and bring to light collections of it in slope forests of hills (cerros) in Pantanal, also making the first record for the state of Mato Grosso do Sul, Brazil. Further collecting in the limestone dry forests within Cerrado and in the Dry Andean Bolivian Valleys are predicted to yield new records of the plant.

Up to date *G. boticario* conforms well to the model proposed by the Pleistocenic Arc hypothesis, but this, of course, does not prove it. As highlighted by Mayle (2006), long distance dispersal could also explain this pattern, although many repeated disjunct patterns (Prado & Gibbs 1993) makes this unlikely. Maybe a more complex model will be needed for understanding historical vegetation shifts in South America, taking into account both vegetational shifts and possible long distance dispersal events. Genetic comparisons between populations may be an interesting tool to address these questions and we suggest *Gymnanthes boticario* as a good candidate for future population genetic studies.

## Acknowledgements

Luciana Oliveira thanks the Re flora Project (Historical Rescue and Virtual Herbarium for the Knowledge and Conservation of Brazilian Flora) that permitted the data interchange between Royal Botanic Gardens, Kew and Brazilian researchers. She also thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the PhD. grant and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Capes) for the international interchange grant awarded to her. M.F. Moro thanks the Fundação de Amparo à Pesquisa do Estado de São Paulo (Fapesp 2009/14266-7 and 2011/22498-5) for providing him a

PhD. grant and an international interchange grant. We are grateful to Luciano Paganucci de Queiroz (State University of Feira de Santana), Domingos Benício Cardoso (State University of Feira de Santana), Ary Teixeira de Oliveira-Filho (Federal University of Minas Gerais), Darién E. Prado (National University of Rosario/CONICET), R. Toby Pennington (Royal Botanic Gardens, Edinburgh), Gwilym P. Lewis, Gill Challen and Raymond M. Harley (Royal Botanic Gardens, Kew), Arnildo Pott (Federal University of Mato Grosso do Sul), and Fernanda P. Werneck (Brigham Young University) for their kind attention in discussing some of the ideas expressed in this paper and providing more literature references and suggestions for improvement; we also thanks Alain Chautems and Lorenzo Ramella (Conservatoire et Jardin Botaniques de la Ville de Genève), Arnildo Pott (UFMS) and Maria Pena Chocarro (Natural History Museum, London) for helping us to locate collection points in the Bolivian/Paraguayan/Brazilian border. Lorenzo Ramella kindly provided us with a transcription of the field notes of Bernardi collections, what allowed us to determine that the “Paraguayan” collection made by him was in fact made in Brazil.

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## Appendix—specimens examined

*Gymnanthes boticario*: **BOLIVIA. Santa Cruz**: Chiquitos, 7 km de San Jose em la salida de Taperas a Roboré, 10 November 2007, *Wood et al.* 23844 (K, USZ); Nascente del río Santo Corazon, 7 km ao N de Santo Corazon, 26 April 1997, *Fuentes et al.* 1811 (MO). **BRAZIL. Bahia**: Abaíra, Estrada para Catolés, ca 14,5 Km da rodovia, 3 February 2005, *Paula-Souza et al.* 5374 (ESA); Mendonça de Daniel Abreu, 12 January 1994, *Ganev* 2811 (HUEFS); Estrada Catolés-Ribeirão, próximo ao Mendonça, ca 3 Km de Catolés, 24 October 1992, *Ganev* 1336 (HUEFS, K). Barra do Mendes, Povoado São Bento, 25 October 2009, *Melo et al.* 6849 (ALCB, HUEFS); Estrada para Canarina, localidade Carretão, 15 December 2009, *Melo et al.* 7499 (ALCB, HUEFS); Serra do Escalavrado, 20 February 2001, *Moraes* 200 (HUEFS). Brotas de Macaúbas, 3 October 2005, *Melo et al.* 4091 (HUEFS). Buritirama, 6 April 1978, *Assis* 147 (RB). Caetitê, São Francisco, caminho para Lagoa Real, 8 February 1997, *Saar et al.* 5245 (ALCB, CEPLAC, IBGE, K, UEFS, USP). Formosa do Rio Preto, Fazenda Santa Luzia, 25 February 2005, *Xavier & Guedes* 330 (ALCB). Gentio do Ouro, Cerro, 6 October 2002, *Jost et al.* 560 (HRB, HUEFS); Cerro, 5 May 2002, *Tourinho et al.* 23 (HUEFS, HRB); Currálinho, Sítio Coqueiro, 26 May 2009, *Oliveira et al.* 4211 (UNIVASF). Irecê/Barra do Mendes, Barra dos Mendes divisa com Ipupiara, 25 October 2009, *Guedes et al.* 16119 (ALCB, HUEFS). Sento Sé, 29 April 1981, *Orlandi* 386 (RB); Alta do tabuleiro, 27 January 2010, *Oliveira & Maciel* 4684 (UNIVASF). Umburanas, Barra dos Alegres, Caminho para riacho da Barra, 28 January 2010, *Fontana et al.* 6420 (UNIVASF); Bela Vista, Estrada Delfino/Sento Sé, Morro dos Cactos, 25 March 2004, *Moraes* 659 (HUEFS); Estrada Delfino-Mimoso de Minas, 20 Km de Delfino, 8 March 1997, *Giulietti et al.* 6127 (ALCB, CEPEC, HUEFS, K); Delfino (município de Umburanas), Rio Salitre, 23 May 2008, *Melo et al.* 5715 (HUEFS); encosta e vale do rio dos Morins, afluente do rio Salitre, 23 May 2008, *Melo et al.* 5711 (HUEFS); Estrada Delfino-Mimoso de Minas, 20 Km de Delfino, 8 March 1997, *Harley et al.* 6123 (ALCB, CEPEC, IBGE, K, UEFS, USP); Barra dos Alegres, caminho para o Riacho da Barra, 28 January 2010, *Carvalho-Sobrinho et al.* 2619 (UNIVASF). 3 October 2005, *Melo et al.* 4093 (HUEFS). **Ceará**: Aiuaba, Estação Ecológica, 25 June 1982, *Viana s.n.* (EAC); Estação Ecológica de Aiuaba, 25 January 2005, *Lemos & Matias* 289 (HUEFS, K) Flamengo, 7 January 1997, *Andrade et al.* 273 (EAC); Flamengo, 11 December 1997, *Andrade et al.* 250 (PEUFR). Brejo Santo, Estrada para DNOCS, 3 February 2009, *Carvalho-Sobrinho et al.* 1870 (UNIVASF, UFP); Reservatório Porcos, 27 April 2009, *Oliveira et al.* 4012 (UNIVASF). Crateús, RPPN Serra das Almas, 18 July 2001, *Bruno & Sobrinho* 276 (EAC, PEUFR); Serra das Almas, s.d., *Lima-Verde* 1199 (EAC); RPPN Serra das Almas, 6 April 2001, *Bruno & Sobrinho* 6 (EAC); RPPN Serra das Almas, 7 May 2003, *Costa* 118 (EAC); RPPN Serra das Almas, 5 May 2003, *Costa* 12 (EAC); RPPN Serra das Almas, 8 March 2003, *Costa* 42 (EAC, UFRN); RPPN Serra das Almas, 9 May 2003, *Costa* 294 (EAC); RPPN Serra das Almas, 6 September 2001, *Bruno & Sobrinho* 8 (EAC, UFRN); Serra das Almas, s.d., *Lima-Verde* 1033 (EAC); Serra das Almas, s.d., *Lima-Verde* 965 (EAC); Serra das Almas, 27 February 1995, *Lima* 27 (EAC); Serra das Almas, sítio Gameleira região Centro-Sul, 8 February 2008, *Silveira s.n.* (EAC, HUEFS). Independência, Chapada do Angical, 13 May 1983, *Angélica s.n.* (EAC). Mauriti, Povoado Poço, aqueduto do Boi, 19 May 2010, *Oliveira* 4901 (UNIVASF); Santo Antônio, 27 April 2009, *Oliveira* 3998 (UNIVASF). Novo Oriente, Baixa Fria, Serra da Ibiapaba, 9 March 1991, *Araújo* 376 (EAC, PEUFR); Planalto da Ibiapaba, 3 August 1990, *Araújo* 150 (EAC, IPA, PEUFR). Ubajara, Planalto da Ibiapaba, 5 January 1995, *Araújo* 1078 (EAC); Miudinho, Planalto da Ibiapaba, 30 July 1990, *Araújo* 112 (EAC, IPA); Chapada da Ibiapaba, entre Ubajara e cachoeira, 29 November 1990, *Fernandes et al. s.n.* (EAC); Entre São José de Belmonte e Jati, 13 May 1971, *Heringer et al.* 737 (ESA, IPA, RB, UB). **Mato Grosso do Sul**: Cerro Pedrera, Rio Navileque, 50–60 Km N de Fuerte Olimpio, Alto Paraguai, 30 March 1980, *Bernadi* 20246 (G) [By mistake reported as Paraguay, but almost certainly collected in Brazil, as Navileque river in completely inside Brazilian territory, but not so far from Paraguay. Apparently the collector entered Brazilian territory without noticing]; Acorizal, Rio Paraguai, 11 June 1979, *Prance et al.* 26151 (CEN) [The Mato Grosso was split in two states in 1979. Prance collected in Acorizal farm, in Corumbá municipality, in an area now in Mato Grosso do Sul state]. **Minas Gerais**: Januária, 16 November 1980, *O. Filho* 85 (HRB). **Paraíba**: Araruna, Parque Estadual da Pedra da Boca,

subida para a Pedra da Boca, 9 December 2003, *Pessoa & Lima* 89 (HUEFS, IPA, JPB); Parque Estadual da Pedra da Boca, subida para a Pedra da Boca, 9 December 2003, *Pessoa & Lima* 84 (IPA). Junco do Seridó, 21 February 1999, *Schindwein* 927 (JPB). Monteiro, Serra do Cruzeiro, 21 April 2010, *Oliveira & Silva* 4843 (UNIVASF); Fazenda Olho d'água dos Silva, 13 May 2009, *Carvalho-Sobrinho et al.* 2202 (UNIVASF). **Pernambuco:** Araripina, Chapada do Araripe, Estação Experimental IPA, 8 December 2008, *Cardoso et al.* 2366 (HUEFS). Betânia, 4 April 2001, *Gomes* 811 (PEUFR); Serra do Catolé, Sítio Catolé (08°13'53,4"S 38°07'07.2"W' 635m) 21 May 2012, *Oliveira & Laurênio* 211; Serra dos Arrombados, na subida da serra, 24 May 1971, *Heringer et al.* 883 (IPA, RB, UB); Betânia/Floresta, Fazenda Rabeca, 8 April 2001, *Costa et al.* 241 (PEUFR). Brejo da Madre de Deus, Bituri, Serra da Piedade, 15 June 1973, *Andrade-Lima* 7395 (IPA). Mirandiba, Serrotinho, 9 February 2007, *Lucena et al.* 1679 (M, UFP); 19 July 2008, *Pinheiro* 1075 (UFP); 19 July 2008, *Pinheiro* 1084 (UFP); Fazenda Areias, 31 May 2006, *Lucena et al.* 1461 (UFP). São José do Belmonte, entre as localidades de Agreste e Mandante, 16 May 2001, *Laurênio et al.* 1831 (PEUFR); entre as localidades de Agreste e Mandante, 16 May 2001, *Laurênio et al.* 1822 (PEUFR). **Piauí:** Caracol, Estrada para a Serra das Confusões, 19 November 1981, *Fernandes & Nunes s.n.* (EAC); PARNA Serra das Confusões, Sobrado, 9 December 2011, *Siqueira-Filho et al.* 2663 (UNIVASF); PARNA Serra das Confusões, trecho das Andorinhas, 9 April 2009, *Martinelli et al.* 16323 (RB, SP); Entre as serras das Confusões e Caracol, 20 November 1981, *Rezende s.n.* (TEPB). Coronel José Dias, PARNA Serra da Capivara, 24 April 2007, *Lucena & Silva* 1693 (M, UFP); PARNA Serra da Capivara, próximo a entrada principal da guarita, 24 April 2007, *Lucena & Silva* 1696 (K, M, MO, SP, UFP). Eliseu Martins, Núcleo Colonial do INCRA, Pico do Gurguéia, 14 December 1977, *Fernandes & Matos s.n.* (EAC, UEC). Pimenteiras, Planalto da Ibiapaba, 24 May 1996, *Araújo* 1247 (EAC). **Rio Grande do Norte:** Cel. João Pessoa, Mata Redonda, 19 July 1991, *Figueiredo et al.* 396 (EAC, TEPB). Venha Ver, Serra de São José, 4 August 2010, *Roque* 835 (UFRN). **PARAGUAY. Alto Paraguay:** Proposed Biosphere Reserve "Gran Chaco": Cerro León, dwarf forest on rocks, 10 February 2002, *Zardini & Rivas* 58529 (M).