Morphology, phylogeny and biogeography of *Turnera* L. (Turneraceae)

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Cladistic analyses are made based on morphological characters and chromosome basic numbers in order to test the monophyly of the nine series of genus *Turnera* (Turneraceae). Series *Annulares* and *Turnera* are monophyletic, and also series *Anomalae* with the exception of two species with unknown fruit and seed morphology. Series *Microphyllae* and *Papilliferae* should be merged, and also series *Salicifoliae* and *Stenodictyae* together with some species of series *Capitatae*. The *Capitatae* split in several groups and series *Leiocarpae* is unresolved. The *Turnera sidoides* complex should be separated into a new series. Biogeographic analyses show that the major diversification of the genus took place in the Chaquean subregion, with vicariance and dispersal events to other Neotropical subregions and Africa.

KEYWORDS: Africa, America, biogeography, phylogeny, *Turnera*

INTRODUCTION

The genus *Turnera* belongs, along with nine other genera, to Turneraceae (Arbo, 2007). At present it comprises over 135 species in America and 2 in Africa, and was arranged by Urban (1883) into nine series. On the basis of floral structure these series can be divided in two groups. In the first one, including *Annulares*, *Capitatae*, *Leiocarpae*, *Microphyllae*, *Papilliferae*, *Salicifoliae* and *Stenodictyae*, the floral tube is formed by the adnation of the calyx and petal-claws, with the staminal filaments adnate only at the base. In the second group, with series *Turnera* (= *Canaligerae* Urb.) and *Anomalae*, the floral tube has five nectar pockets formed by the marginal adnation of each staminal filament to the petal-claws up to the throat (Arbo, 2005).

Each series is well characterized by morphological features (Table 1). The series *Salicifoliae* has wide glabrous or glabrescent leaves, yellow flowers with glabrous or barely pilose ovary, and seeds with obvious piliform papillae (Arbo, 1997). Most species of the series *Stenodictyae* show prominent petiolar nectaries, floral peduncle well developed and pedicel lacking, wide involucral prophylls, pilose ovary, granulose pericarp, and seeds glabrous or with piliform papillae (Arbo, 1997). The seeds of series *Annulares* are unmistakable, very short, almost globose, with a prominent and slightly concave chalaza. In *Microphyllae* and *Papilliferae* the seeds are obovoid, reticulate or striate; stipitate glandular hairs are exclusive to series *Papilliferae*, while *Microphyllae* has sessile-capitate glandular hairs. The leaves of *Microphyllae* are small, with the stipules adnate to the foliar base. Flowers of series *Capitatae* are gathered in short, capitate inflorescences (Arbo, 2000).

Most species of series *Leiocarpae* have nectaried leaves and epiphyllous flowers, usually lacking a pedicel. They frequently have single-flowered inflorescences, though in many taxa the leaves are reduced to bracts and the internodes between them are very short, making up capitate inflorescences. The fruit is generally smooth, and the seeds are reticulate. *Turnera sidoides*, placed by Urban (1883) in series *Leiocarpae*, has leaves without nectaries and granulose fruits, a floral peduncle almost free or linked to the petiole and the pedicel usually developed. It has five subspecies in a large distribution area, being the only American species of the genus below 29° S. Its seeds are unique in the family, with crested seed coat (Arbo, 1985). The ontogenic study showed that the pattern is developed by the exotesta, unlike the seeds of the other species, where the pattern is set by the relative size and arrangement of the exotegmen sclereids and the endotesta cells (Gonzalez, 2000). *Turnera sidoides* is an autopolyploid complex ($2x$–$8x$), with three of its subspecies showing diploid populations. However, they represent only 15% of the total, since 63% of the populations sampled are $4x$ (Solís Neffa & Fernández, 2001).

In series *Turnera* flowers are epiphyllous and solitary, the pedicel is absent, the leaves show basal marginal nectaries, the fruit is granulose, naked, and the seeds are glabrous and reticulate. Series *Turnera* was divided in two subseries based upon seed morphology: in subseries *Turnera* the chalaza is apical, blunt, not prominent, while in subseries *Umbilicatae* it is prominent, concave, with intermediate or rapheal orientation (Arbo, 2005).

Finally, most species of series *Anomalae* have well-developed stipules and flowers either solitary or gathered in racemose inflorescences. The fruit is frequently

Table 1. Summary of morphological features of the series of genus *Turnera*. Species of dubious taxonomic position are included separately.

Taxon	Capitate glandular hairs	Foliar nectaries	Epiphyllous flowers	Pedicel	Petals ligule	Nectar pockets	Staminal filaments cohesion	Ovary	Pericarp	Seed shape	Seed coat	Seed epidermic papillae	Chalaza
Ser. Microphyllae	Sessile	No	No	No	No	No	Free/ wanting	Pilose	Rugose	Curved obovoid	Reticulate	Absent	Blunt not concave
Ser. Papilliferae	Stipitate	No	No	No	No	No	Free	Pilose	Rugose	Curved obovoid	Reticulate	Absent	Blunt not concave
T. sidoides	Micro	No	Yes/no	Yes	No	No	Free	Pilose	Rugose	Curved obovoid	Crested	Piliform	Blunt not concave
Ser. Leiocarpae	Micro Sessile	Yes/no	Yes	No	No	No	Free	Pilose	Smooth	Curved obovoid	Reticulate	Absent/ other	Blunt not concave
Ser. Capitatae	Micro	Yes	Yes/no	No	Yes/no	No	Free	Pilose	Smooth/ rugose	Curved obovoid	Reticulate/ striate	Polymor.	Prominent concave
T. rubrobracteata	Micro	Yes	Yes	Yes	No	No	Irregular	Pilose	Rugose	Curved obovoid	Reticulate	Absent	Prominent concave
Ser. Stenodictyae	Micro	Yes	No	Yes	No	No	Free	Pilose	Rugose	Curved obovoid	Striate	Piliform/ other	Prominent concave
Ser. Salicifoliae	Sessile Micro	Yes/no	No	Yes/no	No	No	Free	Glabrous	Smooth/ rugose	Curved obovoid	Reticulate/ striate	Polymor.	Prominent concave
Ser. Annulares	Sessile Micro	Yes	No	No	No	No	At base	Pilose	Smooth/ rugose	straight globose	Reticulate	Other	Prominent concave
Ser. Anomalae	Micro	Yes/no	Yes/no	No	No	Yes	Up to throat	Pilose	Smooth/ rugose	Curved obovoid	Reticulate/ striate	Piliform/ other	Prominent concave
Subser. Umbilicatae	Micro	Yes	Yes	No	No	Yes	Up to throat	Pilose	Rugose	Curved obovoid	Tenui-reticulate	Absent	Prominent concave
Subser. Turnera	Micro	Yes	Yes	No	No	Yes	Up to throat	Pilose	Rugose	Curved obovoid	Reticulate	Absent	Blunt not concave

covered by the withered perianth. The seeds usually have concave prominent chalaza, and the epidermis is generally papillose (Arbo, 2005).

Genus *Turnera* shows three basic chromosome numbers: $x = 7$, $x = 5$ and $x = 13$. The plesiomorphic basic number would be $x = 7$, being the number found in all the studied species of *Piriqueta*. All the analyzed species of series *Salicifoliae*, *Stenodictyae*, *Microphyllae* and *Leiocarpae* have $x = 7$, one of two species of the series *Papilliferae* has $x = 13$, while series *Turnera* has $x = 5$. Polyploidy has played an important role in the evolution of the genus: ploidy levels range from $2x$ to $10x$ and some species show two to several autoploid cytotypes. The chromosome analyses of parental accessions and hybrids have demonstrated that several species of subseries *Turnera* are allopolyploids, including *T. grandidentata* (Urb.) Arbo ($2n = 4x = 20$ chromosomes), *T. campaniflora* Arbo, Shore & Barrett, *T. occidentalis* Arbo & Shore, *T. orientalis* (Urb.) Arbo, *T. ulmifolia* L., *T. velutina* Presl ($2n = 6x = 30$ chromosomes), *T. aurelii* Arbo and *T. cuneiformis* Poir. ($2n = 8x = 40$ chromosomes). In subseries *Umbilicatae*, three species have been studied. Regretfully, there are no chromosome counts of any species of the series *Anomalae*, *Annulares* and *Capitatae* (Shore & al., 2006).

The first molecular phylogeny for 37 taxa of *Turnera* was constructed using sequences of the internal transcribed spacer region (ITS) of nuclear ribosomal DNA (Truyens & al., 2005).

The phylogenetic analysis indicated that series *Turnera* is monophyletic. Neither series *Microphyllae* and *Papilliferae*, however, are monophyletic, forming a clade together with two species of series *Anomalae*. Breeding system evolution was mapped onto the phylogeny assuming distyly to be ancestral in *Turnera*, and showed that self-compatible homostyly evolved at least three times in the genus (Truyens & al., 2005).

With the aim of exploring the phylogenetic relationships in *Turnera*, and to test the monophyly of its series, cladistic analyses were conducted on a matrix of morphological characters and chromosome basic numbers. As indicated by Goloboff & al. (2008), down-weighting of morphological characters according to their homoplasy produces more strongly supported groups and more stable results. Therefore, we performed an implied weight search strategy to obtain a hypothesis of evolution for the genus *Turnera*. In addition, a biogeographic analysis was performed in order to reconstruct the distribution history of the species of *Turnera*.

MATERIALS AND METHODS

Plant material. — Ninety-two taxa belonging to the nine series of genus *Turnera* were analyzed. *Turnera rubrobracteata*, a species of uncertain position because of its unusual combination of characters, was also included (Table 1; Appendix 1 in the online version of this article). All known hybrid allopolyploid species were excluded. Seven species of the related genus *Piriqueta* were selected as outgroups (Appendix 1 in the online version of this article). Morphological data were gathered from live material and herbarium specimens. From these observations, forty-eight characters were scored (Appendix 2 in the online version of this article).

Phylogenetic analyses. — A data matrix with 99 taxa and 48 characters was built and deposited in TreeBase (PIN number 11482, submitter Shirley Espert). Eight characters were treated as additive: stipules development, insertion mode of stipules, type of inflorescence, degree of development of prophylls, cohesion of sepals, number of ovules per placenta, seed coat areoles, chalaza orientation and length of epiphyllum hairs.

The dataset was analyzed using T.N.T. ver. 1.0 (Goloboff & al., 2003a), with different implied weighting schemes. In order to explore the occurrence of monophyletic groups under different concavity constants (k), a range of k from 3 to 9 was used. These are the usual values when using implied weighting; a k of 3 penalizes homoplastic characters harder than a concavity constant of 9. The searching procedure involved 100 random addition sequences followed by a combined strategy of sectorial searches, tree drifting and tree fusing due to the large number of taxa analyzed. Jackknife values (JK) were estimated by resampling the matrix 1,000 times, with a 36 % removal probability (Farris & al., 1996). Finally, the fit of each character on the consensus tree was calculated using the command CSCORES.

In some analyses, constraints of monophyly on internal *Turnera* clades were applied. This was done to test how much the optimal length differed with the length obtained when no constraints were used.

Biogeographic analyses. — The geographic areas of the species of *Turnera* and their phylogeny were used to reconstruct their distribution history. Areas were assigned according to the American regional division devised by Morrone (2001); species distribution is shown in Appendix 1 (see online version of this article). This information was gathered from Arbo (1997, 2000, 2005).

The input tree for these analyses was randomly chosen from one of the most parsimonious trees obtained with concavity constants of 7. The trees obtained with different k values were almost identical to the ones obtained with a constant of 7, and when biogeographic analyses were performed on them, results didn't differ. Two methods of biogeographic reconstruction were applied. First, areas were treated as unordered multi-state characters and optimized onto the topology using Winclada (Nixon, 2002). With this method no biogeographic event is favored (i.e., all transformations have equal cost). Second, the program DIVA (Dispersal Vicariance Analysis; Ronquist, 1996, 1997) was used, which differs from the Winclada optimization procedure by favoring vicariance events and minimizing the number of dispersals and extinctions.

RESULTS

Phylogenetic analyses. — The implied weighting search resulted in three trees under a k of 3, nine most parsimonious trees (MPT) under a k of 5, fifteen trees when a k of 7 was applied, and finally, ten MPT were obtained under a k of 9. Since the monophyly of a group unsupported in some very close values of k cannot be considered as firmly established (Goloboff & al. 2008), a strict consensus of all these trees was obtained (Fig. 1). In this cladogram, *Turnera* is recovered as monophyletic but with very low support (under 50% JK). The synapomorphy that distinguishes the genus (Fig. 1A) is the lack of a crown in the flower (i.e., no appendices on the perianth pieces).

Individual fits for all the morphological characters were calculated for the consensus tree. Sixty-five percent of the characters retain more homology than homoplasy (i.e., their fit values are > 0.5). Seven features adjust perfectly to the tree: leaf blade, ovary indumentum, basic chromosome number, aril pilosity, presence of floral nectar pockets, seed shape and seed coat design.

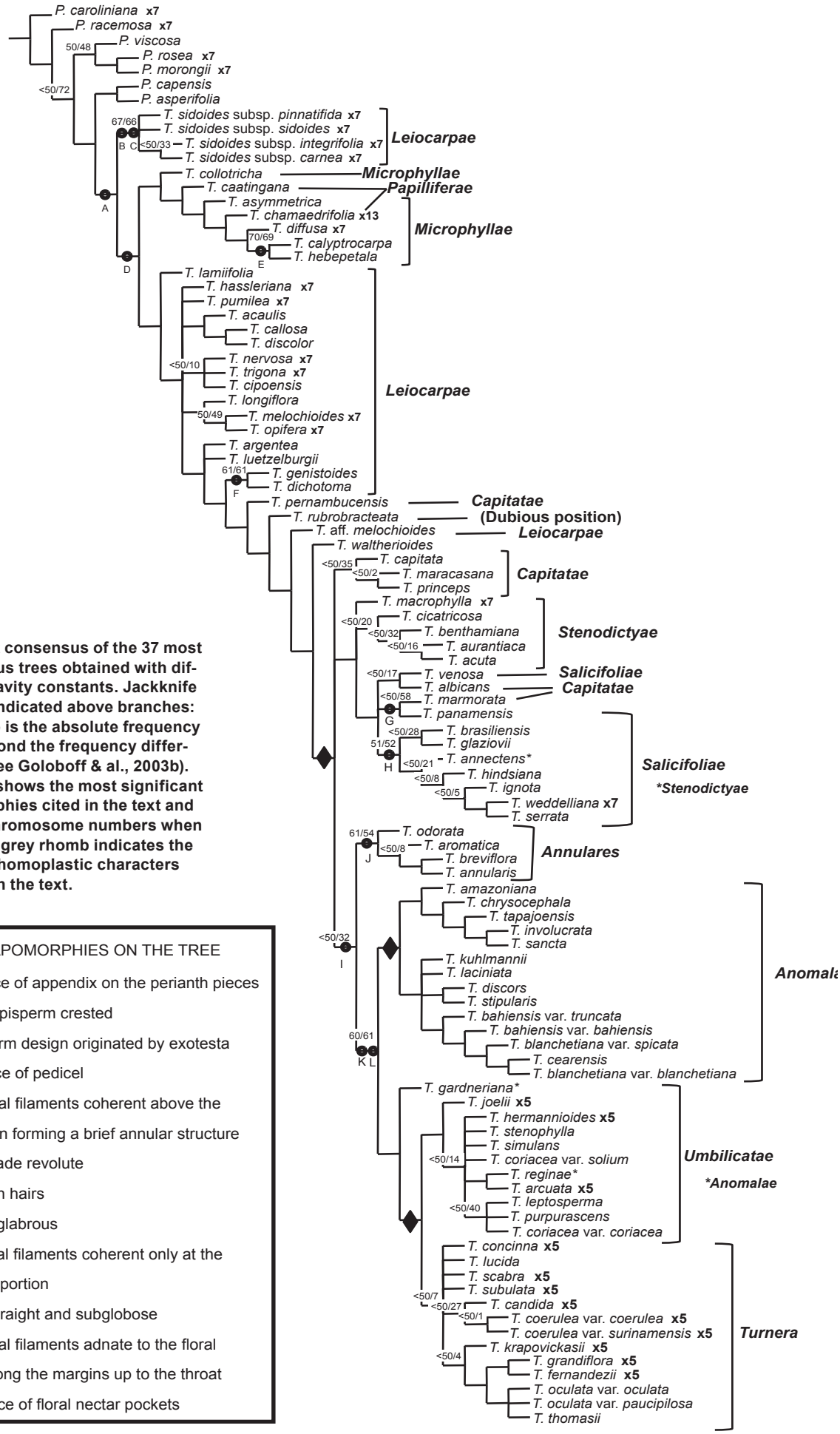


Fig. 1. Strict consensus of the 37 most parsimonious trees obtained with different concavity constants. Jackknife values are indicated above branches: the first one is the absolute frequency and the second the frequency difference (GC, see Goloboff & al., 2003b). This figure shows the most significant synapomorphies cited in the text and the basic chromosome numbers when known. The grey rhomb indicates the nodes with homoplastic characters discussed in the text.

SYNAPOMORPHIES ON THE TREE

A: Absence of appendix on the perianth pieces

B: Seed episperm crested

C: Episperm design originated by exotesta

D: Absence of pedicel

E: Staminal filaments coherent above the adnation forming a brief annular structure

F: Leaf blade revolute

G: Aril with hairs

H: Ovary glabrous

I: Staminal filaments coherent only at the adnate portion

J: Seed straight and subglobose

K: Staminal filaments adnate to the floral tube along the margins up to the throat

L: Presence of floral nectar pockets

Interestingly, the sequence in which the different series come up in the subsequent nodes is the same in all the trees obtained with different searching strategies. The clade formed by the subspecies of *T. sidoides* is the best supported one (67% JK), and it is the sister group to all other species of *Turnera*, with two synapomorphies: crested seeds, and seed coat design determined by the exotesta (Fig. 1: B, C). The synapomorphy present in all other species is the lack of a floral pedicel (Fig. 1: D).

Series *Microphyllae* and *Papilliferae* are not monophyletic, arising together at the next node as a monophyletic clade. *Turnera collotricha* (*Microphyllae*), the only species in *Turnera* with glandular hairs similar to those of *Piriqueta*, is sister to the other species. *Turnera calyptrocarpa* and *T. hebepetala* show one synapomorphy: staminal filaments joined at the base forming an annular structure (Fig. 1: E).

The sister clade to *Microphyllae* and *Papilliferae* includes all the other taxa of *Turnera*. Species of series *Leiocarpae*, some species of the series *Capitatae*, and *T. rubrobracteata*, of dubious position, remain unresolved on the consensus tree.

An important group of species is assembled by two homoplastic characters: sepals coherent up to the middle, and 4–15 ovules per placenta. Three main clades arise in this group; in two of them the staminal filaments are free, while the third is characterized by the cohesion of the staminal filaments only at the adnate portion (Fig. 1: I). In the first two clades, the ligulate species of series *Capitatae* (*T. capitata*, *T. maracasana* , *T. princeps*) integrate one group, and the other is conformed with series *Stenodictyae* and *Salicifoliae* and some species of series *Capitatae*. Series *Stenodictyae* is polyphyletic, while *Salicifoliae* is paraphyletic. The synapomorphy which gathers the species of series *Salicifoliae* (excluding *T. panamensis* which is polymorphic and *T. venosa*) is the glabrous ovary (Fig. 1: H).

In the sister clade with staminal filaments coherent (Fig. 1: I), series *Annulares* is monophyletic (support of 61% JK), with one synapomorphy: seed shape, straight and globose (Fig. 1: J). The remnant species are gathered in a clade (support of 60% JK) by two synapomorphies: staminal filaments adnate along the margins to the perianth tube up to the throat, and the nectariferous pockets (Fig. 1: K, L). Two homoplastic characters gather the species of series *Anomalae*: floral peduncle lacking, and striate-reticulate seeds. This series is monophyletic excluding *T. gardneriana* and *T. reginae*, which cluster with series *Turnera*.

Series *Turnera* is monophyletic, sharing the following homoplastic characters: floral peduncle adnate to the petiole and solitary epiphyllous flowers. This result is consistent with the molecular phylogenetic analysis of Truyens & al. (2005).

Subseries *Umbilicatae* is monophyletic, including *T. reginae* (*Anomalae*), and subseries *Turnera* is monophyletic as well. The shape and orientation of the chalaza are the characters that differentiate them.

Biogeographic analyses. — The areas of the ancestral nodes were reconstructed with DIVA and with a parsimony optimization (Fig. 2). Both analyses coincide in almost all the node assignments, except for ten of them (arrows on Fig. 2). In this case, only the DIVA reconstruction is shown.

Twelve vicariance events and twenty dispersals are required to explain the present distribution of the species of *Turnera*. According to both biogeographic analyses the genus originated in the Chaquean subregion of the Neotropical region.

DISCUSSION

Our results indicate that *Turnera sidoides* should be singled out of series *Leiocarpae*, to constitute a separate series. In the molecular phylogenic analysis, however, *T. sidoides* is not a separate lineage, and not at the basal node (Truyens & al., 2005), so its taxonomic position remains uncertain.

Series *Microphyllae* and *Papilliferae* are not recovered as monophyletic, this phylogenetic analysis indicates that they should be merged. *Turnera diffusa* ($2n = 14$) is the only species of *Microphyllae* with known chromosome number. The basic chromosome number $x = 13$, found in *T. chamaedrifolia*, was probably derived by means of aneuploidy from a polyploid $2n = 4x = 28$ (Fernández, 1987). This analysis suggests that this polyploid would have belonged to series *Microphyllae*. Regretfully, the chromosome number of *T. caatingana*, the other species of series *Papilliferae*, is not known. The molecular phylogenetic analysis of Truyens & al. (2005) showed the closeness of *T. diffusa* and *T. chamaedrifolia* (support of 100%).

Although the species of *Leiocarpae* remain unresolved, when a new analysis was performed constraining the monophyly of *Leiocarpae*, the cladograms found had almost the same fit of those obtained when no constraints were applied. The analyzed species of *Leiocarpae* are grouped in a clade near *T. sidoides* in Truyens & al. (2005).

Urban (1883) gathered in series *Capitatae* most of the species with capitate inflorescences but stated that it was an artificial group. Arbo (2000) excluded from this series *T. blanchetiana* and *T. stipularis*, placing them instead in series *Anomalae*, as well as *T. dichotoma*, suggesting that it should be placed in series *Leiocarpae*. Nevertheless, the remaining species obviously are not a natural group. The species of *Capitatae* split in several groups, some of them cluster with *Salicifoliae* and *Stenodictyae*,

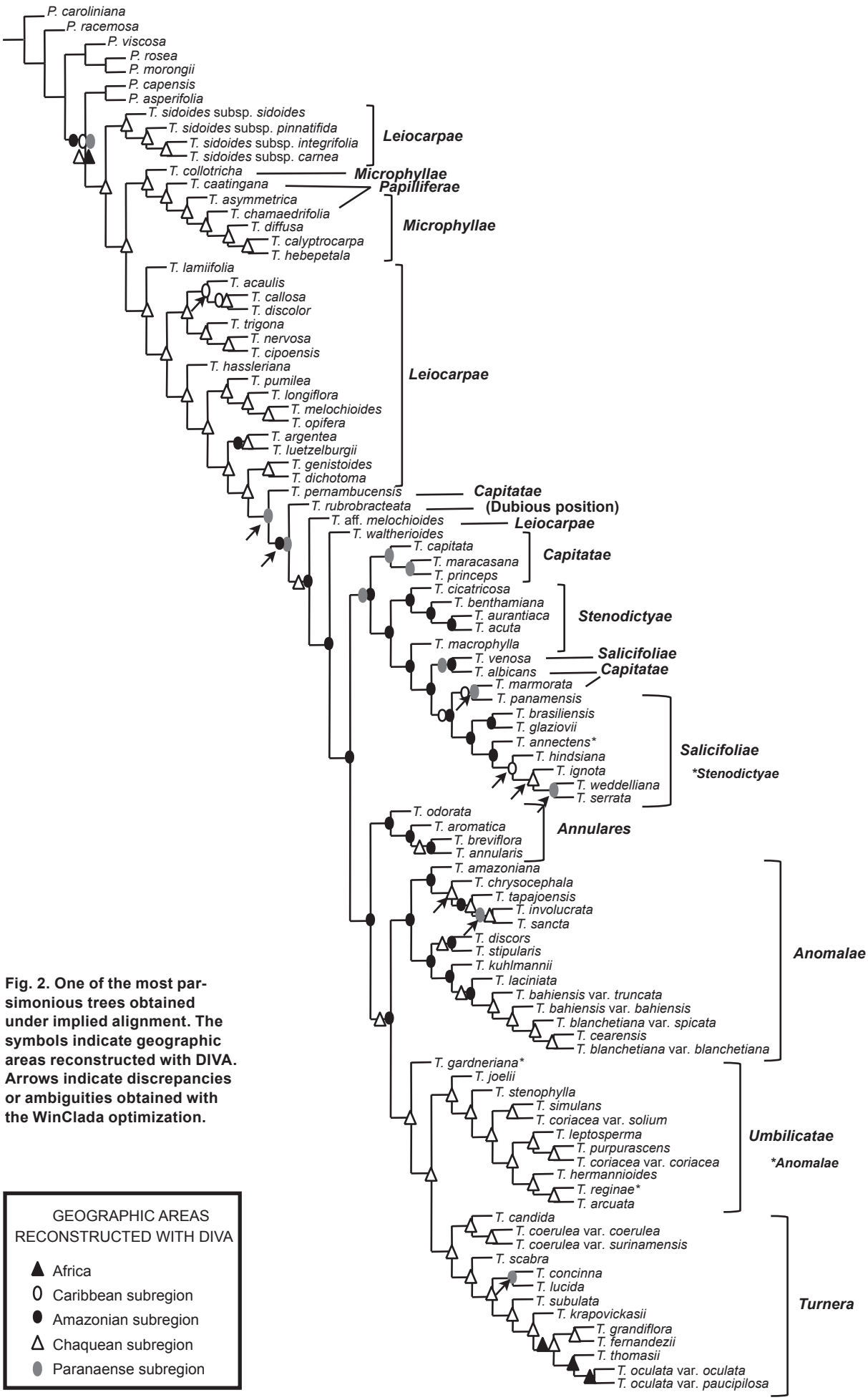
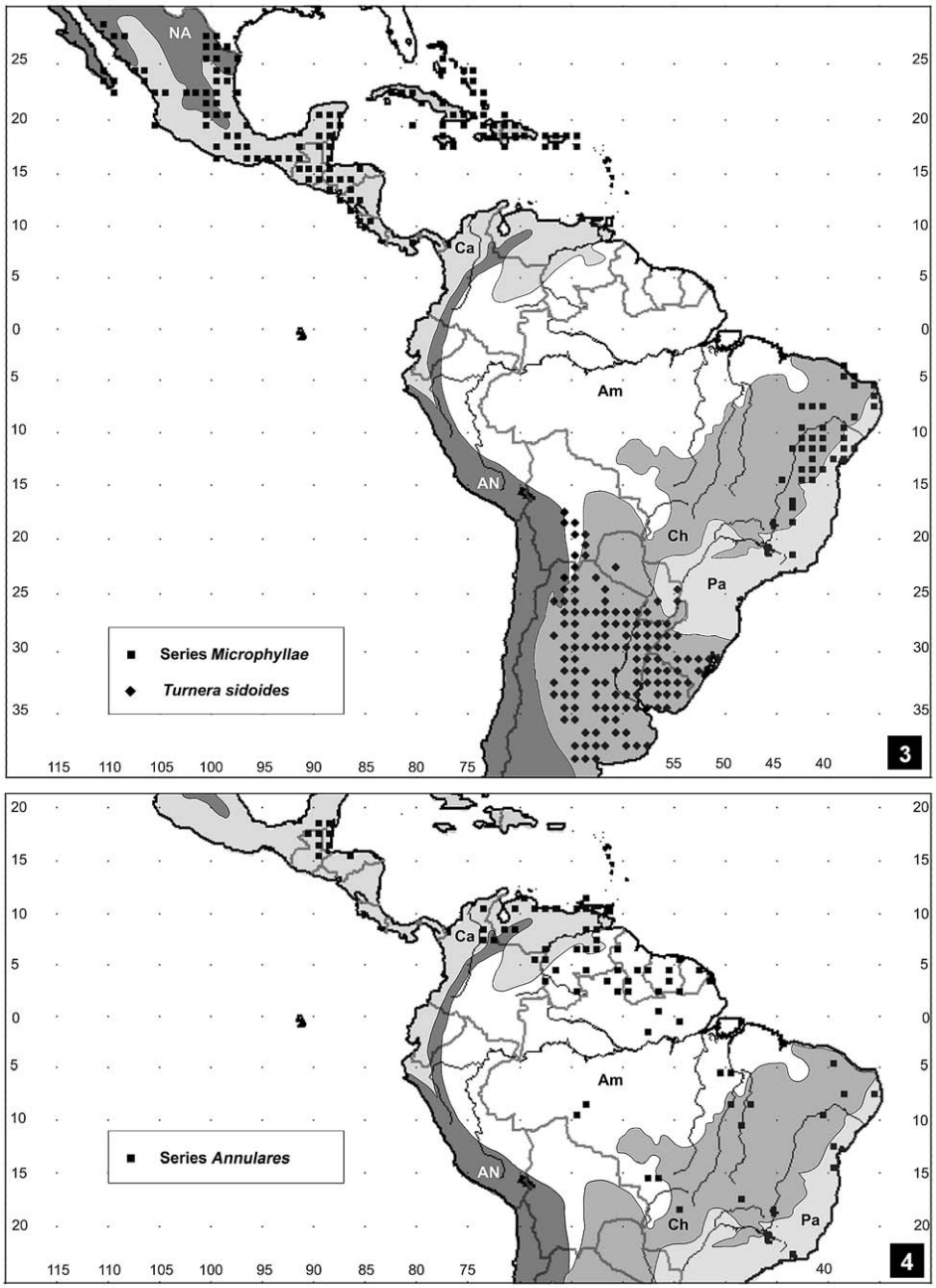


Fig. 2. One of the most parsimonious trees obtained under implied alignment. The symbols indicate geographic areas reconstructed with DIVA. Arrows indicate discrepancies or ambiguities obtained with the WinClada optimization.

some with *Leiocarpae*. Only the ligulate-flowered species, *T. capitata*, *T. maracasana* and *T. princeps*, remain together forming a monophyletic clade (support of 50% JK), a result consistent with the molecular phylogenetic analysis of Truyens & al. (2005), in which this group is the sister clade to all the other species of *Turnera*.

Series *Stenodictyae* and *Salicifoliae* are not monophyletic; our results indicate that both series should be merged with some species of *Capitatae*. Urban (1898) considered the uncertain position of *T. venosa* was between *Stenodictyae* and *Capitatae*, and its possible relationship with *T. glaziovii* Urb. of series *Salicifoliae*. Arbo (2000) placed *T. venosa* in the latter series and showed that series *Salicifoliae* and *Capitatae* share important morphological characters.

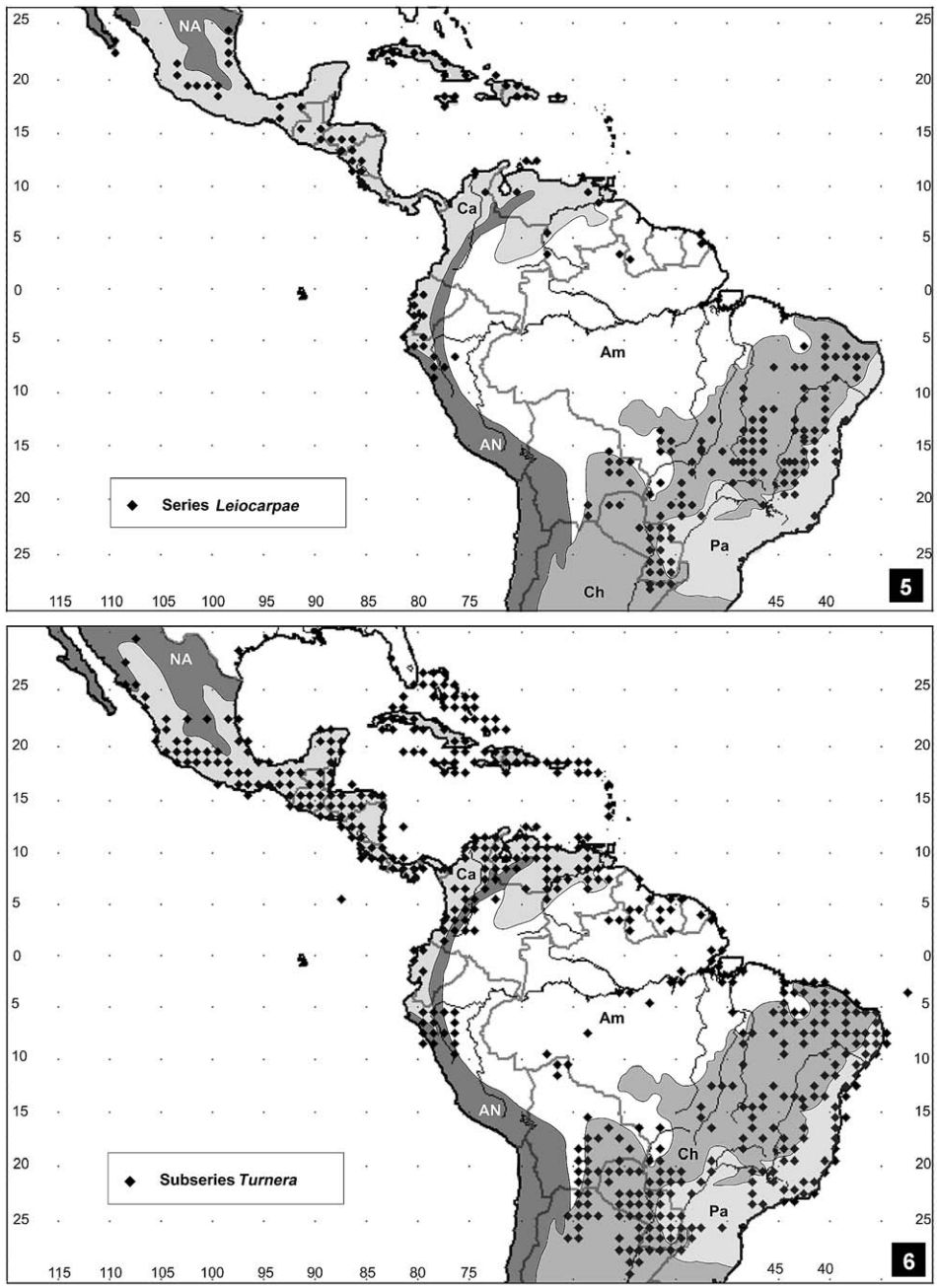
The present analyses show the monophyly of series *Annulares* (Fig. 1: J) and its closeness to series *Anomalae* and *Turnera*. The monophyly of series *Turnera*, evidenced



Figs. 3+4. Present distribution of *Turnera sidoides*, series *Microphyllae* and *Annulares*. Biogeographic areas: Am, Amazonian subregion; AN, Andean; Ca, Caribbean subregion; Ch, Chaquean subregion; NA, Nearctic; Pa, Paranaense subregion.

in the molecular phylogenetic analysis (Truyens & al., 2005), is confirmed. Series *Anomalae* and subseries *Umbilicatae* are monophyletic as well, with the exception of *T. gardneriana* and *T. reginae*, which remain in doubtful position (clustered with series *Turnera*) until their fruits and seeds are known. Although most of the series proposed by Urban (1883) are not monophyletic, this study verifies the significance of morphology in the understanding of the phylogenetic relationships in *Turnera*.

Biogeographic analyses. — *Turnera* seems to have started its diversification in America, where more than 120 species are known at present. The lineages that diverge near the root of the tree are the *T. sidoides* complex on one hand, and series *Microphyllae* and *Papilliferae* on the other. Probably the distribution area of their ancestor was the Chaquean subregion of Neotropical region. At present *T. sidoides* occurs mainly in Chaquean grasslands and open forests in Bolivia, Argentina, Paraguay,



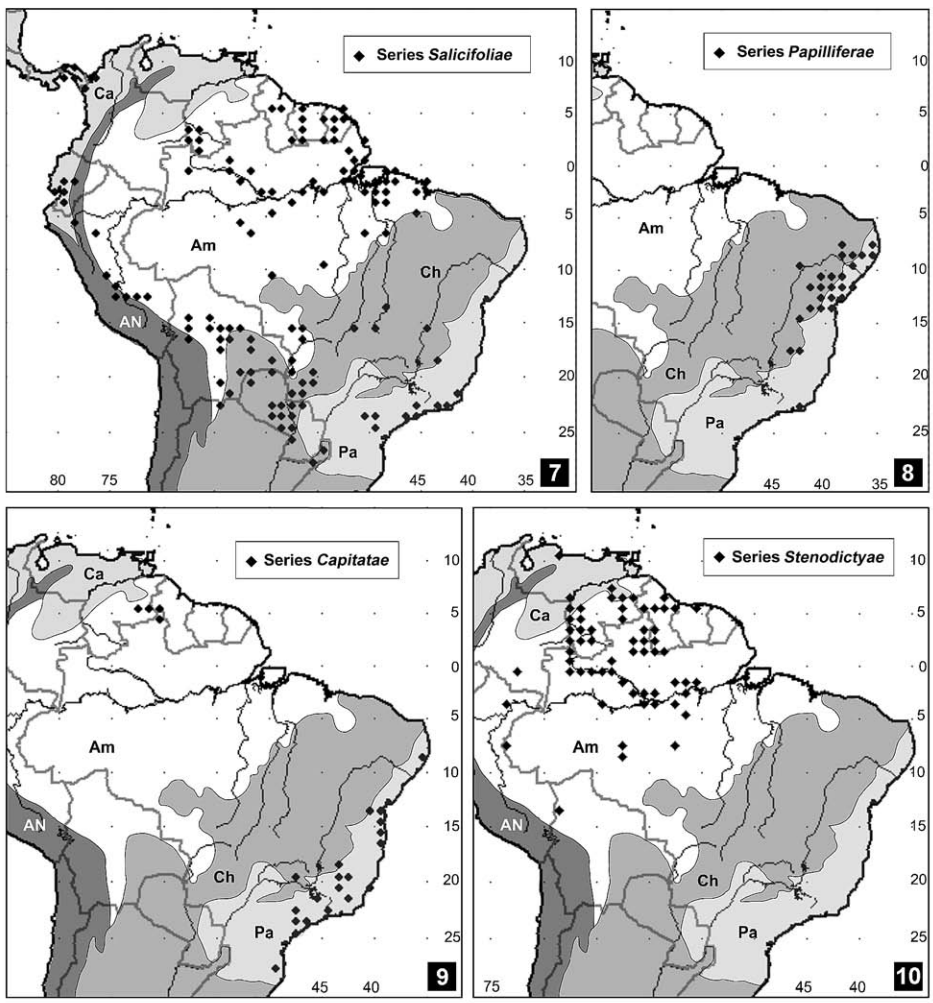
Figs. 5+6. Present distribution of series *Leiocarpae* and subseries *Turnera*. Biogeographic areas: Am, Amazonian subregion; AN, Andean; Ca, Caribbean subregion; Ch, Chaquean subregion; NA, Nearctic; Pa, Paranaense subregion.

Uruguay and SE Brazil (Fig. 3). Speranza & al. (2007) proposed for the *T. sidoides* complex three putative refugial areas associated with the orographical systems of Uruguay and NW Argentina, taking into account the chloroplast DNA variation, the present distribution of diploids and polyploids, and the historical events that determined the diversification of the South American lowlands flora.

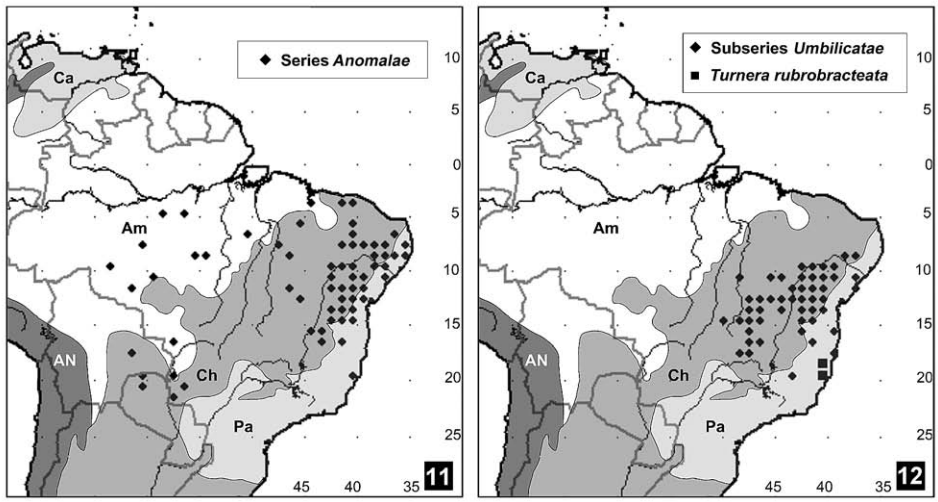
The biogeographic analysis indicates that diversification of the series *Microphyllae* and *Papilliferae* took place in the NE area of the Chaquean subregion, where at present several endemic species occur. The species of *Microphyllae* and *Papilliferae* are restricted to NE Brazil, mainly in "caatinga", *T. asymmetrica* and *T. caatingana* are endemic to Bahia, *T. collotricha* is endemic to Minas Gerais, and *T. hebepetala* grows in a limited area of Bahia and Piaui. *Turnera diffusa* is the only species in this group with a large, disjunct range, occurring in NE Brazil, Mesoamerica, the Caribbean, Mexico and Texas. It is one of the few species of the genus which have reached the Neartic Region (Fig. 3).

At the subsequent nodes several species of *Leiocarpae* arise that currently occur in the "cerrados", grasslands and "campos rupestres" of the Chaquean subregion. Two dispersal events are inferred, one to the Caribbean subregion (*T. callosa* to Mexico, *T. acaulis* to Cuba), one to the Amazonian subregion (*T. argentea*, endemic to Venezuela) (Fig. 5). The next dispersal event inferred is to the Paranaense subregion where *T. pernambucensis* (endemic to Pernambuco, series *Capitatae*) and *T. rubrobracteata* (endemic to Espirito Santo) occur (Figs. 9, 12).

By means of a dispersal event the ancestor of the ligulate species of series *Capitatae*, series *Stenodictyae* and series *Salicifoliae* would have recolonized the Paranaense subregion. At the subsequent nodes, there are vicariance events to the Amazonian and Chaquean subregions. The



Figs. 7–10. Present distribution of series *Salicifoliae, Papilliferae, Capitatae* and *Stenodictyae*. Biogeographic areas: Am, Amazonian subregion; AN, Andean; Ca, Caribbean subregion; Ch, Chaquean subregion; Pa, Paranaense subregion.



Figs. 11 + 12. Present distribution of series *Anomalae,* subseries *Umbilicatae* and *Turnera rubrobracteata*. Biogeographic areas: Am, Amazonian subregion; AN, Andean; Ca, Caribbean subregion; Ch, Chaquean subregion; Pa, Paranaense subregion.

ligulate species of *Capitatae* arise through a vicariance event in the Paranaense subregion, where *T. maracasana* is endemic to Bahia and *T. princeps* to Minas Gerais (Fig. 9).

The ancestor of *Salicifoliae* (Fig. 7) and *Stenodictyae* (Fig. 10) would have developed in the Amazonian subregion, where the diversification of these series took place. In this clade, there were several dispersal events to the Paranaense, Caribbean and Chaquean subregions. At present there are several endemic taxa: *T. panamensis* to Panama, *T. hindsiana* subsp. *hindsiana* to Ecuador, *T. ignota* to Minas Gerais (*Salicifoliae*) and *T. albicans* and *T. marmorata* to Bahia (*Capitatae*).

From the ancestor of the remnant series, in the Amazonian subregion, arises series *Annulares*, in which *T. aromatica* shows a disjunct area, living also in Mexico and the neighboring Mesoamerican countries. At present series *Annulares* has extended to the Caribbean, Chaquean and Paranaense subregions, but its diversification started also in the Amazonian subregion (Fig. 4).

The ancestor of the other clade would have expanded to the Chaquean subregion, the ancestor of series *Anomalae* arose in the Amazonian subregion by means of a vicariance event, and the ancestor of series *Turnera*, *T. gardneriana* and *T. reginae* developed in the Chaquean subregion.

The diversification of series *Anomalae* occurred in the Amazonian and Chaquean subregions, with one dispersal to the Paranaense subregion. The known distribution of most taxa is limited: *T. bahiensis* and *T. involucrata* are endemic to Bahia, *T. blanchetiana* var. *subspicata* occurs in Mato Grosso do Sul and Western Paraguay, *T. chrysocephala* in Bahia and Piaui, *T. discors* and *T. kuhlmanniana* are endemic to Roraima, *T. laciniata* and *T. tapajoensis* to Para, *T. stipularis* to Maranhão and *T. sancta* to Espirito Santo (Fig. 11).

Series *Turnera* branched out in the Chaquean subregion. The diversification of subseries *Umbilicatae* took place in the Chaquean subregion (Fig. 12) where most species are endemic to narrow areas of Bahia (*T. joelii*, *T. stenophylla*, *T. simulans*, *T. leptosperma*), Goias (*T. arcuata*, *T. purpurascens*) or Minas Gerais (*T. coriacea*).

The diversification of subseries *Turnera* came about in the Chaquean subregion. Then there was a dispersal event to subregion Paranaense, where *T. lucida* is endemic to the "restingas" of Rio de Janeiro and Espirito Santo, and a dispersal-vicariance event to Africa where *T. thomasii* and *T. oculata* occur. Both varieties of *T. coerulea* have disjunct areas, growing in Mexico and South America. Interestingly, the areas of most species of this subseries are broad and show considerable overlapping in the Neotropical region.

The chromosome studies of hybrids demonstrated that within subseries *Turnera* reticulate evolution occurred, with *T. aurelii*, *T. campaniflora*, *T. cuneiformis*, *T. grandidentata*, *T. occidentalis*, *T. orientalis*, *T. ulmifolia* and *T. velutina* being allopolyploids (Shore & al, 2006). Presently, the geographic area of subseries *Turnera* is almost the same as the area of genus *Turnera* (Fig. 6) except for the *T. sidoides* complex (Fig. 3) which ranges southwards to 38° S.

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Appendix 1. Species of *Turnera* L. and outgroup taxa analyzed, their geographic distribution, and the assigned area.

Acronyms for the geographic distribution: Argentina (Chaco: CH; Corrientes: CO; Formosa: FO; Jujuy: JU; Salta: SA; Santa Fe: SF; Tucumán: TU). **Bolivia** (Beni: BE; Chuquisaca: CH; Santa Cruz: SC; Tarija: TA). **Brazil** (Acre: AC; Alagoas: AL; Amapá: AP; Amazonas: AM; Bahia: BA; Ceará: CE; Distrito Federal: DF; Espirito Santo: ES; Goías: GO; Maranhão: MA; Mato Grosso do Sul: MS; Mato Grosso: MT; Minas Gerais: MG; Pará: PA; Paraíba: PB; Parana: PR; Pernambuco: PE; Piauí: PI; Rio de Janeiro: RJ; Rio Grande do Norte: RN; Rio Grande do Sul: RS; Rondônia: RO; Roraima: RR; Santa Catarina: SC; São Paulo: SP; Sergipe: SE; Tocantins: TO). **Mexico** (Aguas Calientes: AC; Chiapas: CH; Chihuahua: CI; Guerrero: GU; Jalisco: JA; Mexico: ME; Michoacán: MI; Morelos: MO; Nayarit: NA; Oaxaca: OA; Puebla: PU; Quintana Roo: QR; San Luis Potosí: SP; Sinaloa: SI). **Paraguay** (Eastern Paraguay: EP; Western Paraguay: WP). **Venezuela** (Amazonas: AM; Bolívar: BO).

Acronyms for the biogeographic Regions/Subregions (Morrone, 2001): Neartic: NA. Andean: AN. Neotropical: Caribbean subregion: Ca; Amazonian subregion: Am; Chaquean subregion: Ch; Paranaense subregion: Pa. Africa: AF.

Dubious position. *T. rubrobracteata* Arbo. Brazil: ES. **Pa**

Turnera series ***Anomalae*** Urb.
T. amazonica Arbo. Brazil: AM, MT. **Am**
T. bahiensis Urb. Brazil: BA. **Ch, Pa**
T. bahiensis var. *truncata* Arbo. Brazil: BA, CE. **Ch**
T. blanchetiana Urb. var. *blanchetiana*. Brazil: BA, CE, MG, PB, PE, PI, RN. **Ch, Pa**
T. blanchetiana var. *subspicata* Urb. Brazil: MS; Paraguay: WP. **Am, Ch**
T. cearensis Urb. Brazil: AL, BA, CE, MA, MG, PA, PE, SE. **Am, Ch, Pa**
T. chrysocephala Urb. Brazil: BA, PI. **Ch**
T. discors Arbo. Brazil: RO. **Am**
T. gardneriana Arbo. Brazil: GO. **Ch**
T. involucrata Arbo. Brazil: BA. **Ch**
T. kuhlmanniana Arbo. Brazil: RO. **Am**
T. laciniata Arbo. Brazil: PA. **Am**
T. reginae Arbo. Brazil: MA. **Ch**
T. sancta Arbo. Brazil: ES. **Pa**
T. stipularis Urb. Brazil: MA. **Ch**
T. tapajoensis Moura. Brazil: PA. **Am**

Turnera series ***Annulares*** Urb.
T. annularis Urb. Brazil: BA, RJ, PB, PE. **Ch**, **Pa**
T. aromatica Arbo. Mexico: QR; Belize; Guatemala; Honduras; Colombia; Venezuela; Trinidad & Tobago; Guyana. **Ca, Am** (disjunct area)
T. breviflora Moura. Colombia; Northern Venezuela; Brazil: PA. **Ca, Am**
T. odorata Rich. Colombia; Venezuela; Trinidad & Tobago; Guyana; Suriname; French Guiana; Brazil: AP, AM, CE, GO, MA, MT, MS, PA, RJ, RO, RR, TO. **Ca, Am, Ch**

Turnera series ***Capitatae*** Urb.
T. albicans Urb. Brazil: BA. **Pa**
T. capitata Cambess. Brazil: MG, RJ, SC, SP. **Ch, Pa**
T. maracasana Arbo. Brazil: BA. **Ch**
T. marmorata Urb. Brazil: BA. **Pa**
T. pernambucensis Urb. Brazil: PE. **Pa**
T. princeps Arbo. Brazil: MG. **Ch**
T. waltherioides Urb. Venezuela: BO; Brazil: RR. **Am**

Turnera series ***Leiocarpae*** Urb. ($x = 7$)
T. acaulis Griseb. Cuba. **Ca**
T. aff. *melochioides* Cambess. Brazil: GO. **Ch**
T. argentea Arbo. Venezuela: AM. **Am**
T. callosa Urb. Mexico. **Ca**
T. cipoensis Arbo. Brazil: MG, Serra do Cipo. **Ch**
T. dichotoma Gardner. Brazil: MG. **Ch**
T. discolor Urb. Brazil: MT, GO. **Ch**
T. hassleriana Urb. Bolivia; Brazil: MS; Paraguay; Argentina: MI. **Ch, Pa**
T. genistoides Cambess. Brazil: MG. **Ch**
T. lamiifolia Cambess. Brazil: GO, MG. **Ch**
T. longiflora Cambess. Brazil: GO, MG, TO. **Ch**
T. luetzelburgii Sleumer. Brazil: BA. **Ch**
T. melochioides Cambess. Brazil: AL, AM, BA, GO, CE, MA, MG, MS, MT, PA, PB, PE, PI, RN, SE, TO; Paraguay. **Am, Ch, Pa**
T. nervosa Urb. Paraguay; Argentina: CO, MI. **Ch, Pa**
T. opifera Mart. Brazil: BA, MG. **Ch**
T. pumilea L. Mexico; Caribbean Islands; Mesoamerica; Colombia; Venezuela; Guyana; Ecuador; Peru; Bolivia; Brazil; Paraguay; Argentina. **NA, Ca, Am, Ch, Pa, AN**
T. sidoides L. subsp. *sidoides*. Brazil: RS; Uruguay. **Ch**
T. sidoides subsp. *carnea* (Cambess.) Arbo. Paraguay; Argentina; Brazil: RS; Uruguay. **Ch, Pa**
T. sidoides subsp. *integrifolia* (Griseb.) Arbo. Paraguay; Argentina; Brazil: RS; Uruguay. **Ch**
T. sidoides subsp. *pinnatifida* (Poir.) Arbo. Bolivia; Paraguay; Argentina; Uruguay. **Ch, Am, AN**
T. trigona Urb. Brazil: GO, MG. **Ch**

Turnera series ***Microphyllae*** Urb. ($x = 7$)
T. asymmetrica Arbo. Brazil: BA. **Ch**
T. calyptrocarpa Urb. Brazil: BA, CE, MG, PE, PI, RJ, SE. **Ch, Pa**

Appendix 1. Continued.

T. collotricha Arbo. Brazil: MG. **Ch**
T. hebepetala Urb. Brazil: BA, PI. **Ch**
T. diffusa Willd. ex Schult. U.S.A.: TE; Mexico; Mesoamerica; Caribbean Islands; Brazil: BA, CE, PE, RN. **NA, Ca, Ch** (disjunct area)

Turnera series ***Papilliferae*** Urb. (x = 13)
T. caatingana Arbo. Brazil: BA. **Ch**
T. chamaedrifolia Cambess. Brazil: AL, BA, MG, PB, PE, SE. **Ch, Pa**

Turnera series ***Salicifoliae*** Urb. (x = 7)
T. brasiliensis Willd. ex Schult. Guyana; Suriname; Brazil: AP, GO, MA, MT, PA. **Am, Ch**
T. glaziovii Urb. Suriname; French Guyana; Brazil: AP, AM, PA. **Am**
T. hindsiana Benth. subsp. *hindsiana.* Ecuador. **Ca**
T. ignota Arbo. Brazil: MG. **Ch**
T. panamensis Urb. Panama; Colombia. **Ca**
T. serrata Vell. Brazil: MG, RJ, SP, SC. **Pa**
T. venosa Urb. Venezuela; Brazil: AM, PA, RR. **Am**
T. weddelliana Urb. & Rolfe. Ecuador; Peru; Bolivia; Brazil: MT, MS; Paraguay: EP, WP. **Ca, Am, Ch, Pa, AN**

Turnera series ***Stenodyctiae*** Urb. (x = 7)
T. acuta Willd. ex Schult. Colombia; Venezuela; Peru; Brazil: AC, AM, RR. **Ca, Am**
T. annectens Arbo. Venezuela: AM, Cerro Sipapo. **Am**
T. aurantiaca Benth. Guyana; Brazil: AC, AM, RR. **Am**
T. benthamiana M.R. Schomb. Guyana; Brazil: RR. **Am**
T. cicatricosa Arbo. Venezuela: AM, BO; Guyana. **Ca, Am**
T. macrophylla Urb. Venezuela: AM; Brazil: AM, PA, RO; Bolivia: BE. **Am**

Turnera series ***Turnera***
Subseries ***Turnera*** (x = 5)
T. candida Arbo. Brazil: BA, MG, PI. **Ch, Pa**
T. coerulea DC. var. *coerulea*. Mexico: AC, CI, GU, JA, ME, MI, MO, NA, PU, SI; Brazil: AP, BA, CE, GO, MA, MT, MS, PA, PI, RR, SE, TO; Bolivia: CH, SC, TA. **Am, Ca, Ch, Pa, NA** (Disjunct area)
T. coerulea var. *surinamensis* (Urb.) Arbo & Av. Fernández. Mexico: CH, NA, OA, SP, SI; Guyana; Suriname; Brazil: AP, AM, BA, CE, GO, MA PA, PI, TO. **Ca, Am, Ch** (disjunct area)
T. concinna Arbo. Bolivia: SC; Brazil: MS; Paraguay: EP. **Ch, Pa, Am**
T. fernandezii Arbo. Brazil: MS; Paraguay: EP. **Ch, Pa**
T. grandiflora (Urb.) Arbo. Brazil: MS; Paraguay: EP, WP; Argentina: CH, CO, FO, SA, SF. **Ch, Pa, Am**
T. krapovickasii Arbo. Bolivia: CH, SC, TA; Paraguay: WP; Argentina: JU, SA, TU. **Am, Ch**
T. lucida Urb. Brazil: ES, RJ. **Pa**
T. oculata Story var. *oculata*, Africa: Angola, Namibia. **AF**
T. oculata var. *paucipilosa* Oberm. Africa: Namibia. **AF**
T. scabra Millsp. Mexico; Mesoamerica; Puerto Rico; Haiti; Dominican Republic; Netherlands Antilles; Grenada; Colombia; Venezuela; Guyana; Ecuador; Brazil. **Ca, Am, Ch, Pa, AN**
T. subulata Sm. U.S.A.; Panama; Netherlands Antilles; Dominica; Saint Vincent & Grenadines; Saint Lucia; Trinidad & Tobago; Colombia; Venezuela; French Guyana; Ecuador; Brazil. **Ca**, **Am, Ch, Pa, AN**
T. thomasii (Urb.) Story. Africa: Kenya. **AF**
Subseries ***Umbilicatae*** Arbo (x = 5)
T. arcuata Urb. Brazil: DF, GO. **Ch**
T. coriacea Urb. var. *coriacea*. Brazil: MG: Serra do Cipo. **Ch**
T. coriacea var. *solium* Arbo. Brazil: MG: Serra do Cipo. **Ch**
T. hermannioides Cambess. Brazil: BA, GO, MG, PE, PI, SE, TO. **Ch, Pa**
T. joelii Arbo. Brazil: BA. **Ch**
T. leptosperma Urb. Brazil: BA. **Ch**
T. purpurascens Arbo. Brazil: DF, GO. **Ch**
T. simulans Arbo. Brazil: BA. **Ch**
T. stenophylla Urb. Brazil: BA: Serra de Açuruá. **Ch**

Piriqueta (x = 7)
P. asperifolia Arbo. Brazil: BA. **Ch**
P. capensis (Harvey) Urb. Africa: South Africa. **AF**
P. cistoides subsp. *caroliniana* (Walter) Arbo. U.S.A.: FL; Mexico; Caribbean Islands; Colombia; Venezuela; Guyana; Bolivia; Brazil. **Ca, Am, Ch, Pa**
P. morongii Rolfe. Bolivia; Paraguay; Brazil: MS; Argentina: CO. **Ch**
P. racemosa (Jacq.) Sw. Caribbean Islands; Colombia; Venezuela; Brazil; Paraguay. **Ch, Pa**
P. rosea (Cambess.) Urb. Brazil: GO, MG, MS, MT, SP; Paraguay. **Ch, Pa**
P. viscosa Griseb. Caribbean Islands; Mesoamerica; Colombia; Venezuela; Guyana; Brazil; Bolivia. **Ca, Am, Ch, Pa**

Appendix 2. Morphological characters and their states

0. Tector hairs: simple (0); stellate and simple (1); porrect-stellate, stellate and simple (2).
1. Glandular hairs: absent (0); stipitate-capitate (1); microcapitate (2); sessile-capitate (3); clavate (4).
2. Glandular setiform emergences: absent (0); present (1).
3. Stipules degree of development: absent or rudimentary (0); short (1); long (2).
4. Stipules location: absent (0); at both sides of the leaf base (1); joint to the base or to the petiole (2).
5. Leaf base: not prominent (0); prominent and persistent (1).
6. Petiole: present (0); absent (1).
7. Extrafloral nectaries: absent (0); present (1).
8. Leaf blade, adaxial face indumentum: with hairs (0); glabrous (1).
9. Leaf blade: expanded (0); revolute (1).
10. Inflorescence: cymose (0); solitary flower (1); racemose (2).
11. Floral peduncle: free or barely joint at the base to the petiole (0); joint to the petiole up to the middle or more (1); absent (2).
12. Prophylls: absent or rudimentary (0); narrow with a visible middle vein (1); narrow to wide with several veins (2); leafy with multiple veins (3).
13. Pedicel: present (0); absent (1).
14. Sepals cohesion: up to a quarter of their length (0); up to half of their length (1); up to three quarters of their length (2).
15. Basal portion of the calyx tube external face: with hairs (0); glabrous (1).
16. Petal's color: pink (0); salmon (1); white or white-blue (2); ivory or creamy (3); yellow (4); yellow-orange (5); orange-red (6).
17. Petal dark basal spot: absent (0); present (1).
18. Appendix on the perianth pieces: crown (0); ligule on petals (1); absent (2).
19. Staminal filaments indumentum: glabrous (0); with hairs (1).
20. Staminal filaments cohesion: free (0); joined only at the adnate portion (1); joined above the adnation forming a brief annular structure (2); joined above the adnation irregularly, at different heights (3).
21. Staminal filaments, adnation to floral tube: joined only at the base (0); free (1); joined along the margins up to the throat (2).
22. Ovary indumentum: with hairs (0); glabrous (1).
23. Anthers: dorsifixed (0); basifixed (1).
24. Anthers apex shape: obtuse (0); acute (1).
25. Anthers apex indumentum: glabrous (0); with hairs (1).
26. Ovules per placenta: 16 or more (0); 4 to 15 (1); 1 to 3 (2).
27. Length of the gyneceum: shorter than the corolla (0); equal or larger than the corolla (1).
28. Style pilosity: glabrous (0); with hairs (1).
29. Fruit exocarp: smooth, minutely spotted or areolate (0); warted, granulate or tuberculate (1).
30. Fruit: naked (0); dressed with the withered perianth (1).
31. Seed coat: reticulate (0); reticulate with prominent knots (1); striated (2); crested (3).
32. Seed epidermis: with short cylindrical papillae (0); smooth (1); with other papillae (2).
33. Seed coat areoles: with 2 punctiform cavities (0); with 1 punctiform cavity (1); without cavities (2).
34. Seed, chalaza shape: blunt, not prominent (0); prominent (1).
35. Seed, chalaza surface: not concave (0); concave (1).
36. Seed, chalaza orientation: apical (0); intermediate (1); rapheal (2).
37. Aril, cell type: smooth (0); papillose (1).
38. Chromosome basic number: $x = 7$ (0); $x = 13$ (1); $x = 5$ (2).
39. Plant type: herb (0); not herb (1).
40. Breeding system: homostyly (0); distyly (1).
41. Simple hairs: unicellular (0); multicellular in one row (1).
42. Aril pilosity: glabrous (0); with hairs (1).
43. Floral nectar pockets: absent (0); present (1).
44. Seed shape: neither straight nor subglobose (0); straight and subglobose (1).
45. Epiphyllous flowers: absent (0); present (1).
46. Episperm design originated by: endotesta and exotegmen (0); exotesta (1).
47. Epiphyllum hairs length: absent (0); ≤ 50 µm (1); ≥ 50.1 µm (2).