



# A brainstorm on the systematics of *Turnera* (Turneraceae, Malpighiales) caused by insights from molecular phylogenetics and morphological evolution



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## ABSTRACT

With 145 species, *Turnera* is the largest genus of Turneraceae (Malpighiales). Despite several morphotaxonomic and cytogenetic studies, our knowledge about the phylogenetic relationships in *Turnera* remains mainly based on morphological data. Here, we reconstruct the most comprehensive phylogeny of *Turnera* with molecular data to understand the morphological evolution within this group and to assess its circumscription and infrageneric classification. We analyzed two nuclear and six plastid markers and 112 taxa, including species and infraspecific taxa, 97 from *Turnera*, covering the 11 series of the genus. Bayesian inference, maximum parsimony and maximum likelihood analyses show that *Turnera*, as traditionally circumscribed, is not monophyletic. The genus is divided into two well-supported independent clades; one of them is sister to the genus *Piriqueta* and is here segregated as the new genus *Oxossia*. According to our reconstructions, *Turnera* probably evolved from an ancestor without extrafloral nectaries and with solitary, homostylous flowers with yellow petals. The emergences of extrafloral nectaries and distyly, both common in extant taxa, played an important role in the diversification of the genus. An updated infrageneric classification reflecting the relationships within *Turnera* is now possible based on morphological synapomorphies and is here designed for further studies.

## 1. Introduction

Turneraceae, Malesherbiaceae, and Passifloraceae s.s. (Malpighiales) form a well-supported clade (e.g., [Davis and Chase, 2004](#); [Korotkova et al., 2009](#); [Wurdack and Davis, 2009](#); [Sun et al., 2016](#)). The three families share the presence of a corona and flowers with a hypanthium ([APG II, 2003](#)) and have been treated together as Passifloraceae s.l. ([APG III, 2009](#); [APG IV, 2016](#); [Maas et al., 2019](#)). [Tokuoka \(2012\)](#), however, unequivocally demonstrated that Turneraceae, Malesherbiaceae, and Passifloraceae s.s. are, independently, well-supported clades, each with a broad set of diagnostic characters. Splitting stigmas, for example, are a possible synapomorphy of Turneraceae ([Shore et al., 2006](#)) and most species in the family have heterostylous flowers.

More recently, [Maas et al. \(2019\)](#) described a new monospecific genus, *Pibiria* Maas, in a new monogeneric subfamily of Passifloraceae s.l., *Pibirioidae* M.W.Chase & Christenh. Their phylogenetic analyses

were based on three plastid DNA regions and showed *Pibiria flava* Maas well supported as sister to the other Turneraceae (as “Turneroideae”). Nevertheless, they did not sample the monospecific genus *Adenoa* Arbo, which also diverged at the initial evolution of Turneraceae ([Thulin et al., 2012](#); see also our results below). Therefore, the actual phylogenetic position of *Pibiria* is still questionable and treating the Turneraceae at the family level or within Passifloraceae s.l. is only a question of convenience.

*Turnera* L. is the largest genus of Turneraceae, with 143 American and two African species ([Fig. 1](#)). It is recognized mainly by the absence of a corona at the base of petals and sepals, and most species of *Turnera* have extrafloral nectaries on petioles or at the base of leaf blades, opposite and well developed prophylls, and epiphyllous flowers, i.e. with the peduncle adnate to the petiole ([Arbo, 2007](#)). *Turnera* is also remarkable because of the distyly, expressed in most species, and the polyploidy, present in approximately 60% of the species whose chromosome number is known (e.g., [Shore et al., 2006](#)).

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**Fig. 1.** Morphological diversity in the series of the genus *Turnera*. A-B: ser. *Anomalae*. A. *T. blanchetiana*; B. *T. cearensis*. C-J: ser *Leiocarpae*. C. *T. sidoides* subsp. *integrifolia*; D. *T. humilis*; E. *T. lamiifolia*; F. *T. fissifolia*; G. *T. longiflora*; H. *T. pinifolia*; I. *T. rosulata*; J. *T. trigona*. K: ser *Microphyllae*, *T. diffusa* var. *diffusa*. L: ser *Papilliferae*, *T. chamaedrifolia*. M: ser *Salicifoliae* I, *T. serrata* var. *serrata*. N: ser *Salicifoliae* II, *T. brasiliensis*. O-P: ser *Sessilifoliae*. O. *T. dichotoma*; P. *T. revoluta*. Q-R: ser *Stenodictyae*, *T. acuta*. S-W: ser *Turnera*. S: subser. *Umbilicatae* I, *T. purpurascens*; T-V: subser. *Turnera*. T. *T. candida*; U. *T. subulata*; V. *T. ulmifolia* var. *ulmifolia*; W: subser. *Umbilicatae* II, *T. arcuata*. Photos A, B, K, L, P, U by L.Rocha; C by T.N.Cabreira; D, I by C.Bitencourt; E-H, J, O, S, T, W by H.Moreira; M by D.Gonzaga; N by J.A.Teixeira; V by J.L.Costa-Lima.

**Urban (1883)** published the most comprehensive taxonomic treatment of Turneraceae and recognized nine series in the genus *Turnera*: ser. *Annulares*, ser. *Anomalae*, ser. *Capitatae*, ser. *Leiocarpace*, ser. *Microphyllae*, ser. *Papilliferae*, ser. *Salicifoliae*, ser. *Stenodictyae*, and ser. *Turnera* ('*Canaligerae*'). Since then, two additional series were proposed (**Arbo, 2008**): ser. *Conciliatae* and ser. *Sessilifoliae*. These 11 series of *Turnera* are defined mainly on the basis of morphoanatomy, particularly concerning their seeds and floral nectaries (e.g., **Gonzalez and Arbo, 2004, 2013; Gonzalez, 2010**).

Despite important advances in genetic and microevolutionary studies in the genus *Turnera* (e.g., **Barrett, 1978; Arbo and Fernández, 1983, 1987; Fernández and Arbo, 1989, 1990, 1993, 1996, 2000a, 2000b; Solís-Neffa and Fernández, 1993, 2000, 2001; Fernández and Solís Neffa, 2004; Shore et al., 2006; Speranza et al., 2007; Moreno et al., 2015**), the genus has not yet been broadly explored phylogenetically. Morphological and chromosome number cladistics (**Arbo and Espert, 2009; Arbo et al., 2015**) weakly supported *Turnera* as monophyletic and showed that its infrageneric classification needs revision. Among the phylogenetic studies with molecular data in *Turnera* (e.g., **Truyens et al., 2005; Chafe, 2009; Thulin et al., 2012; López et al., 2013**), the most comprehensive included 35 out of the 145 species of the genus and represented seven of the 11 series. Their sampling has been mainly concentrated in *Turnera* ser. *Turnera*, which is the only series supported as monophyletic so far, and their results did not strongly support the monophyly of the genus *Turnera*.

Here, we reconstruct the phylogeny of the genus *Turnera* to assess its circumscription and provide a new morphological basis for an updated infrageneric classification (Rocha et al., in prep.). We sampled 70% of the taxonomic diversity in *Turnera*, almost three times more than any molecular studies so far, and represented all 11 series of the genus. Sequences of six plastid and two nuclear markers were used, expanding the sampling of the most used markers (the nuclear ITS and the plastid *trnT-F*) and adding others (the nuclear ETS and the plastid *psbA-trnH*, *trnD-E*, and *trnY-T*), which are used for the first time to investigate *Turnera* in this study. The data set was analyzed with Bayesian inference (BI), maximum parsimony (MP), and maximum likelihood (ML). Morphological evolution and taxonomic implications were discussed based on the recovered phylogeny, which enabled us to explore important questions, such as how the reproductive system evolved in *Turnera* and how critical morphological characters may have affected diversification in lineages of the genus.

**Table 1**  
Primers and protocols used to amplify the DNA regions.

Region	Primers	Protocol	Notes
ITS	ITS-92(F) 5'- AAG GTT TCC GTA GGT GAA C-3' ITS-75(R) 5'- TAT GCT TAA ACT CAG CGG G-3'	94 °C for 3 min, 28 × (94 °C for 1 min, 60 °C for 1 min, 72 °C for 2.30 min), 72 °C for 7 min	<a href="#">Desfeaux et al. (1996)</a>
ETS	ETS-B(F) 5'-ATA GAG CGC GTG AGT GGT G-3' 18S-IGS(R) 5'-GAG ACA AGC ATA TGA CTA CTG GCA GGA TCA ACC AG-3'	94 °C for 3 min, 30 × (94 °C for 1 min, 55 °C for 1 min, 72 °C for 2 min), 72 °C for 7 min	ETS-B ( <a href="#">Baldwin and Markos, 1998</a> ); 18S-IGS (A. Yen, University of Washington, unpubl.)
<i>psbA-trnH</i>	PsbA(F) 5'-GTT ATG CAT GAA CGT AAT GCT C-3' TrnH(R) 5'-CGG GCA TGG TGG ATT CAC AAA TC-3'	80 °C for 5 min, 30 × (95 °C for 1 min, 53 °C for 1 min, 65 °C for 4 min), 65 °C for 5 min	<a href="#">Sang et al. (1997)</a>
<i>trnT-L</i>	trnL-A(F) 5'-CAT TAC AAA TGC GAT GCT CT-3' trnL-B(R) 5'-TCT ACC GAT TTC GCC ATA TC-3'	94 °C for 2 min, 35 × (94 °C for 50 sec, 60 °C for 25 sec, 72 °C for 1.25 min), 72 °C for 3 min	<a href="#">Taberlet et al. (1991)</a>
<i>trnL-intron</i>	trnL-C(F) 5'-CGA AAT CGG TAG ACG CTA CG-3' trnL-D(R) 5'-GGG GAT AGA GGG ACT TGA AC-3'	94 °C for 3 min, 28 × (94 °C for 1 min, 56 °C for 1 min, 72 °C for 2.30 min), 72 °C for 7 min	<a href="#">Taberlet et al. (1991)</a>
<i>trnL-F</i>	trnL-E(F) 5'-GGT TCA AGT CCC TCT ATC CC-3' trnL-F(R) 5'-ATT TGA ACT GGT GAC AGC AG-3'	94 °C for 2 min, 35 × (94 °C for 50 sec, 60 °C for 25 sec, 72 °C for 1.25 min), 72 °C for 3 min	<a href="#">Taberlet et al. (1991)</a>
<i>trnD-E</i>	trnD(F) 5'-ACC AAT TGA ACT ACA ATC CC-3' trnE(R) 5'-AGG ACA TCT CTC TTT CAA GGA G-3'	94 °C for 5 min, 36 × (94 °C for 50 sec, 54 °C for 50 sec, 72 °C for 1.30 min), 72 °C for 5 min	<a href="#">Shaw et al. (2005)</a>
<i>trnY-T</i>	trnY(F) 5'-CCG AGC TGG ATT TGA ACC A-3' trnT(R) 5'-CTA CCA CTG AGT TAA AAG GG-3'	94 °C for 5 min, 36 × (94 °C for 50 sec, 54 °C for 50 sec, 72 °C for 2 min), 72 °C for 5 min	<a href="#">Shaw et al. (2005)</a>

## 2. Material and methods

### 2.1. Taxonomic sampling

We sampled approximately two thirds of the species and infraspecific taxa in *Turnera* (97), covering the morphological and geographical diversity of the genus and representing all infrageneric taxa: ser. *Annulares* (2 taxa of 4 species), ser. *Anomalae* (6/14), ser. *Capitatae* (7/11), ser. *Conciliatae* (1/1), ser. *Leiocarpace* (37/57), ser. *Microphyllae* (3/5), ser. *Papilliferae* (2/2), ser. *Salicifoliae* (5/13), ser. *Sessilifoliae* (2/2), ser. *Stenodictyae* (3/9), ser. *Turnera* subser. *Turnera* (21/19) and ser. *Turnera* subser. *Umbilicatae* (8/8); apart from *Turnera callosa* (type of ser. *Leiocarpace*), we sampled all type-species of these series. We also included the other American genera of Turneraceae that are closely related to *Turnera* ([Chafe, 2009; Thulin et al., 2012](#)): *Adenoa* (1 species), *Erblichia* Seem. (1), and *Piriqueta* Aubl. (6); to cover the phylogenetic range of *Piriqueta*, we sampled species that diverged at the initial evolution of the genus and species that are more derived ([Chafe, 2009](#)), (see Appendix A, for voucher information). Two African genera of Turneraceae, *Tricliceras* Thonn. ex DC. (2 species) and *Mathurina* Balf. f. (1) were also included. The outgroup consisted of species of *Malesherbia* Ruiz & Pav. (Malesherbiaceae), *Adenia* Forssk., *Passiflora* L., and *Paropsis* Noronha ex Thouars (Passifloraceae s.s.), representing the two families that are closer related to Turneraceae and commented above (see also [Thulin et al., 2012; Tokuoka, 2012](#)).

### 2.2. DNA extraction, amplification and sequencing

Total DNA was extracted from leaves of herbarium specimens (70%) or dehydrated on silica gel using Dneasy Plant Mini Kit (Quiagen, Valencia, CA, USA) or 2 × CTAB method ([Doyle and Doyle, 1987](#)). Markers were selected by known variability or number of parsimony informative characters ([Truyens et al., 2005; Speranza et al., 2007; Thulin et al., 2012; López et al., 2013](#); see Table 1 for primer sequences and amplification protocols). PCR reactions were performed using the TopTaq Master Mix Kit (QIAGEN GmbH, Hilden, Germany) according to the manufacturer's protocol, for a final volume of 10 µL, including 1.98 µL of TBT-PAR [trehalose, bovine serumalbumin (BSA), polysorbate-20 (Tween-20)] ([Samarakoon et al., 2013](#)), to avoid secondary conformations, for ITS they also included 0.3 µL of DMSO 99.5% (dimethyl sulfoxide).

PCR products were purified with PEG 11% (polyethylene glycol) (Paithankar and Prasad, 1991) and sequenced in both directions, using the Kit Big Dye Terminator 3.1 (Applied Biosystems), with the same primers used in PCR. Electropherograms were generated by the automatic capillary sequencer ABI3130XL, at the Laboratório de Sistemática Molecular de Plantas (LAMOL), Universidade Estadual de Feira de Santana (UEFS), Bahia, Brazil. Sequences from previous studies (Truyens et al., 2005; Speranza et al., 2007; Thulin et al., 2012; López et al., 2013) were obtained from GenBank (Appendix A, see supplemental data with the online version of this article).

### 2.3. Alignment and phylogenetic analyses

We used Geneious 5.3.6 (Drummond et al., 2010) to check electropherograms and edit contigs. Assembled sequences (see Appendix A, for voucher information) and sequences from GenBank were aligned using MUSCLE (Edgar, 2004) in Geneious platform, with manual adjustments. We analyzed four data sets: 1) plastid, 2) nuclear, 3) plastid + nuclear, and 4) plastid + nuclear + morphology. Terminals without sequences of particular regions were maintained because missing data usually do not negatively affect analyses (Wiens, 2006 and references therein).

Maximum parsimony (MP) analyses were performed in PAUP 4.0b10 (Swofford, 2002), using a heuristic search with 1,000 replicates, random taxon addition, and tree-bisection reconnection algorithm (TBR), saving up to 15 trees per replicate; a second search was performed, using as starting trees those saved in the first round, using the same parameters of search and saving a maximum of 10,000 trees, all characters were equally weighted and unordered (Fitch, 1971). The non-parametric Bootstrap (BS-MP) support (Felsenstein, 1985) was estimated with 1,000 replicates according to the above-mentioned heuristic search parameters.

Bayesian inference (BI) analyses were performed in MrBayes 3.2.6 (Ronquist et al., 2012), with two simultaneous runs and four chains in each run (one cold and three hot each), for 10 million generations, saving one tree every 1,000 generations; the best-fitting substitution models for each partition were selected using the Akaike Information Criterion (AIC), implemented in jModelTest 2.1.5 (Darriba et al., 2012) (Table 2). For convergence diagnostics, we visualized the MrBayes output files in Tracer v.1.5 (Rambaut et al., 2014) and accepted only trees after the standard deviation between the divided frequencies reached values < 0.01 and estimated sample size (ESS) > 200. Thus, the first 3 million generations trees of each run were excluded as burn-in in MrBayes 3.2.6 and the remaining trees from both runs summarized in a majority-rule (50%) consensus, where the frequency of a branch represents its posterior probability (PP).

Maximum Likelihood (ML) analyses were performed in RAxML 8.1.20 (Stamatakis, 2014), using GTRGAMMA as the evolutionary model for all partitions; we did not estimate the proportion of invariant

(PInvar) sites because the combination of GAMMA and PInvar may disturb the optimization of parameters as they cannot be optimized independently from each other. Branch support was established through 1,000 bootstrap replications (BS-ML).

All analyses of MP, BI, ML were performed at Cyberinfrastructure for Phylogenetic Research (Cipres Science Gateway; Miller et al., 2010) and the trees edited in FigTree 1.4.3 (Rambaut, 2012).

### 2.4. Morphological ancestral character reconstruction

Morphological evolution and inferred synapomorphies are investigated through ancestral state reconstructions for 23 vegetative and reproductive characters (Table 3), selected from the 90 characters in Arbo et al. (2015). Priority was given to those characters more commonly used in the taxonomy of Turneraceae, especially for *Turnera* circumscription and infrageneric classification. Character coding was performed based on the literature (Arbo, 1997, 2000, 2005, 2008), direct examination of herbarium specimens (stored in HUEFS; Thiers, 2018, continuously updated), and field observations. The reconstructions (Maddison and Maddison, 2005) were performed in Mesquite 3.04 (Maddison and Maddison, 2014), using the parsimony criterion, which is less susceptible to equivocal reconstructions when terminals are polymorphic; all morphological characters were equally considered, unordered and unweighted. We optimized morphological characters onto 1,000 trees, a sample with the last 500 trees of each independent run of the BI analysis with combined molecular data set (plastid + nuclear). Frequency of optimizations for each node was summarized, through pie charts, onto the majority-rule consensus tree (50%) of the BI analysis with combined nuclear and plastidial data.

## 3. Results

### 3.1. Molecular data analyses

The nuclear data set (ITS1 + 5.8S + ITS2 and ETS) included 105 terminals and 1,225 bp (565 parsimony informative characters, ca. 46%). The plastid data set (*psbA-trnH*, *trnT-L*, *trnL* intron, *trnL-F*, *trnD-E*, and *trnY-T*) included 105 terminals and 4,082 bp (1,169 parsimony informative characters, ca. 28%). The combined molecular data set included 112 terminals and 5,307 bp (1,734 parsimony informative characters, ca. 32%) (Table 2).

Topologies from MP, BI, ML analyses as well as MP and BI analyses with nuclear + plastidial + morphological data (Appendix B, Fig. B1–5) recovered similar clades, but three hard conflicts (i.e. PP > 0.95 and MP/ML-BS > 80%) between plastid and nuclear data sets: 1) *Piriqueta densiflora* var. *densiflora* is nested in *Piriqueta* with the plastid data set but nested in *Turnera* with the nuclear data set; 2) *Turnera bahiensis* var. *bahiensis* is in ser. *Anomalae* with the plastid data set but sister to the rest of *Turnera* with the nuclear data set; and 3) *Turnera*

**Table 2**

Summary of phylogenetic analyses and selected nucleotide substitution models based on AIC. N, number of taxa; Align., length of the aligned molecular matrix; PI, number of parsimony informative characters; L, length of most parsimonious tree; CI, consistency index; RI, retention index.

DNA marker	N	Align. (bp)	PI (%)	L	CI	RI	Model
ITS	99	771	315 (40,8%)	2115	0.4	0.7	ITS1/ITS 2 GTR+I+G 5.8S SYM+I+G
ETS	67	454	253 (55,7%)	1117	0.5	0.8	GTR+I+G
<i>psbA-trnH</i>	71	465	211 (45,3%)	749	0.6	0.8	GTR+I+G
<i>trnT-L</i>	74	592	222 (37,5)	774	0.7	0.8	GTR+G
<i>trnL-intron</i>	101	830	189 (22,7%)	776	0.6	0.8	GTR+I+G
<i>trnL-F</i>	95	387	106 (27,3%)	386	0.6	0.8	GTR+G
<i>trnD-E</i>	79	754	207 (27,4%)	687	0.7	0.9	GTR+I+G
<i>trnY-T</i>	49	1054	237 (22,4%)	610	0.8	0.9	GTR+I+G
Combined nuclear	105	1225	568 (46,3%)	3276	0.4	0.5	Mixed
Combined plastidial	105	4082	1175 (28,7%)	4304	0.6	0.8	Mixed
Combined (all data)	112	5307	1743 (32,84%)	7693	0.5	0.8	Mixed

**Table 3**

List of morphological characters and the state coding used in the ancestral state reconstructions.

Character	States
1. Glandular trichomes	(0) absent; (1) stipitate-capitate; (2) microcapitate; (3) sessile-capitate; (4) clavate; (5) setiform
2. Stipule length	(0) up to 0.4 mm; (1) 0.5–2 mm; (2) 2.1–6 mm; (3) length > 6 mm
3. Extrafloral nectaries	(0) absent; (1) present
4. Inflorescence type	(0) cymose branching; (1) spike to head; (2) raceme; (3) solitary flower
5. Flower morphs (A: androecium; G: gynoecium)	(0) 1 morph: homostylous [A = G]; (1) 2 morphs: heterostylous long-styled and short-styled; (2) 3 morphs: long-styled, short-styled and mid-styled [A = G]
6. Epiphyllous flowers	(0) absent; (1) present
7. Peduncle	(0) present, free or barely joined at the base to the petiole; (1) present, joined to the petiole up to the middle or more; (2) absent
8. Pedicel	(0) present; (1) absent
9. Petal color	(0) pink or lilac; (1) salmon; (2) white or white-blue; (3) ivory or creamy; (4) yellow; (5) yellow-orange; (6) orange-red; (7) red
10. Petal dark basal spot	(0) absent; (1) present
11. Perianth appendices	(0) corona free, inserted between petals and stamens; (1) corona fixed on perianth at the throat; (2) ligule on petals; (3) absent
12. Staminal filament indument	(0) glabrous; (1) Pilose
13. Stamen connation to each other	(0) free; (1) connate only at the adnate portion; (2) connate irregularly above adnation, at different heights; (3) connate above adnation in a slender annular structure
14. Stamen adnation to the petals	(0) free or almost so; (1) external face adnate at the base or up to 1/3 of the length; (2) adnate along the margins briefly or up to the throat
15. Nectar pockets	(0) absent; (1) present
16. Ovary indument	(0) pilose all over; (1) some hairs at the top; (2) totally glabrous
17. Style indument	(0) glabrous; (1) pilose
18. Fruit exocarp	(0) smooth, minutely spotted or areolate; (1) warty, granulate or tuberculate
19. Seed coat (episperm)	(0) reticulate; (1) striate-reticulate; (2) striate; (3) crested; (4) foveolate
20. Seed coat areoles	(0) with two pointshaped cavities; (1) with one pointshaped cavity; (2) just concave, without pointshaped cavities; (3) absent
21. Chalaza shape	(0) obtuse; (1) pulvinate; (2) conical; (3) different
22. Chalaza surface	(0) not concave; (1) concave
23. Chalaza surface orientation (in lateral view)	(0) apical; (1) intermediate/oblique; (2) raphal/lateral

*odorata* arises within ser. *Leiocarpae* with the plastid data set, but sister to ser. *Stenodictyae* with the nuclear data set (Fig. 2). The exclusion of these terminals increased branch supports, but did not affect the general topologies (Appendix B, Figs. B5–7). The BI total evidence analysis (plastid + nuclear + morphological data sets) resolved more derived clades (e.g., within ser. *Turnera*), but produced clades with less support. Our discussion focused on the results from the BI analysis with combined molecular data, which is more resolved and shows higher support for most clades (Fig. 3).

The genus *Turnera* is diphytic, with a well-supported clade, formed by species of ser. *Capitatae*, ser. *Conciliatae*, ser. *Microphyllae*, and ser. *Annulares* (henceforth, *Capitatae* clade; PP = 1/MR-BS = 90%/ML-BS = 98%), closer to the genus *Piriqueta* (1/98/100), in BI and ML analyses. Within the *Capitatae* clade, the monotypic ser. *Conciliatae* is sister to a clade formed by *Turnera annularis* (ser. *Annulares p.p.*), ser. *Microphyllae p.p.*, and ser. *Capitatae p.p.* The other clade (*Turnera* core group; 1/99/100) comprises 1) the complex *Turnera sidoides* (1/90/99); 2) ser. *Salicifoliae*, forming a grade; 3) ser. *Leiocarpae* (1/98/100); 4) ser. *Sessilifoliae* (1/100/100); 5) ser. *Papilliferae* (1/95/100); 6) ser. *Anomalae* (1/100/100); 7) ser. *Stenodictyae* (1/86/99); and 8) ser. *Turnera* (1/100/100), including the subser. *Umbilicatae*, forming a grade, and subser. *Turnera* (1/59/88). The complex *Turnera sidoides* is strongly supported as sister to the rest of the *Turnera* core group (1/99/100), forming a basal grade with ser. *Salicifoliae*. The ser. *Sessilifoliae* is sister to the clade *Papilliferae-Microphyllae p.p.* (1/100/100) and together they are sister to a clade that consists of ser. *Anomalae*, ser. *Annulares p.p.*, ser. *Stenodictyae*, and ser. *Turnera*. The clade *Stenodictyae-Annulares p.p.* and ser. *Turnera* form a clade (1/81/99) that is weakly supported as sister to the ser. *Anomalae* (0.68/−/−).

### 3.2. Morphological reconstruction analyses

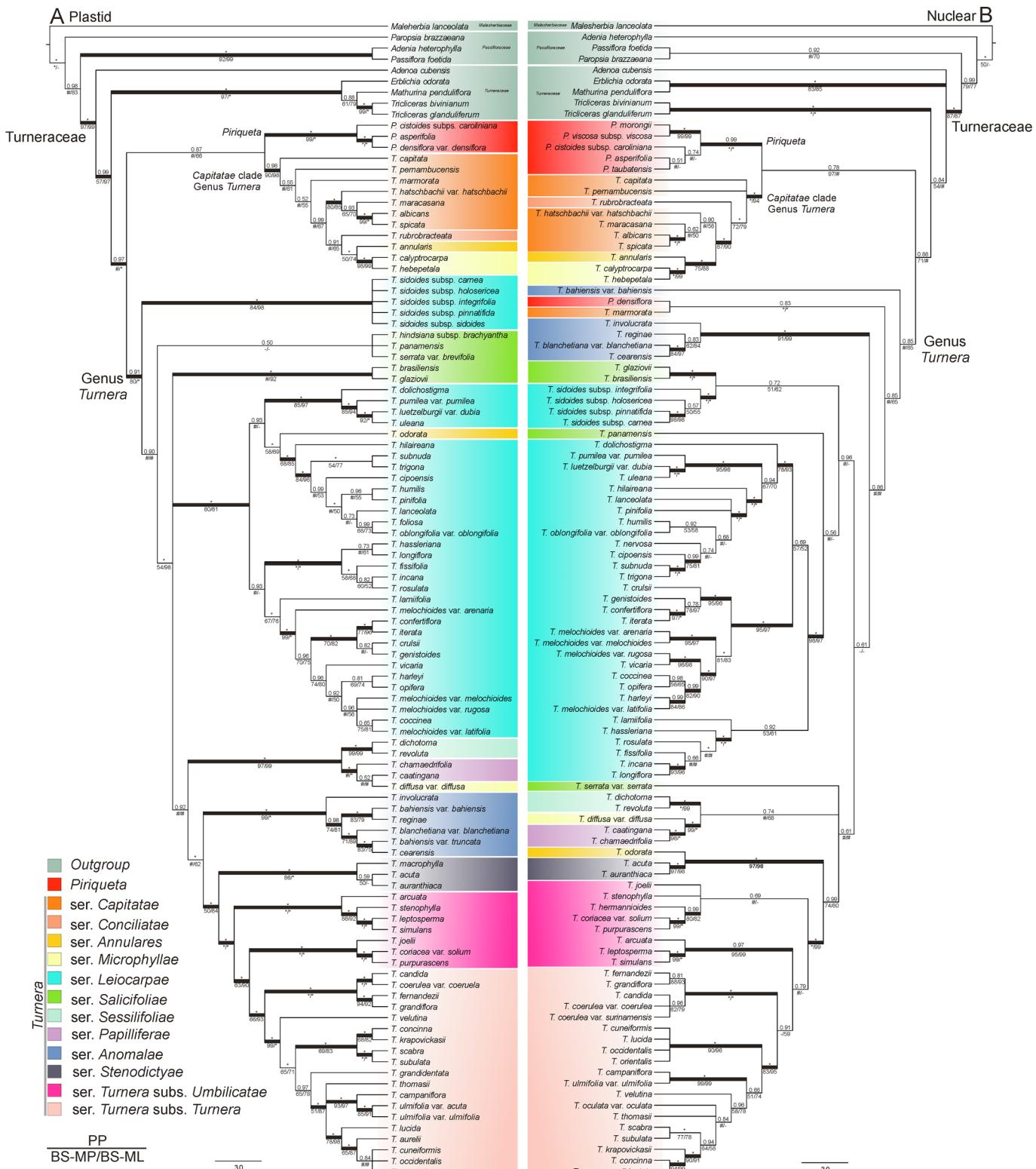
We summarize the potential synapomorphies that are discussed throughout the text onto the BI majority-rule consensus (Fig. 4). All character state (Table 3) reconstructions are shown individually in

Appendix C (Fig. C1–C23, available online). Most characters show some degree of homoplasy, but can be useful to define clades when combined with other characters. For instance, extrafloral nectaries (EFNs) are most common in lineages of Turneraceae (Fig. 5A) that have capitate glandular trichomes (Fig. 5B). The evolution of inflorescence in Turneraceae probably differed from what has been thought so far (see discussion): solitary flowers seem to be the ancestral state in the family and was conserved in many lineages, whereas compaction of floral branches and racemization occurred independently in some groups (Fig. 6). The genus *Piriqueta* can be defined by setiform glandular trichomes (character 1: state 5) and an annular corona at the flower throat, at the base of petals and sepals (11:1), both found exclusively in this group. The *Capitatae* clade has six morphological synapomorphies (Fig. 4), whereas the morphologically diverse *Turnera* core group apparently does not have any.

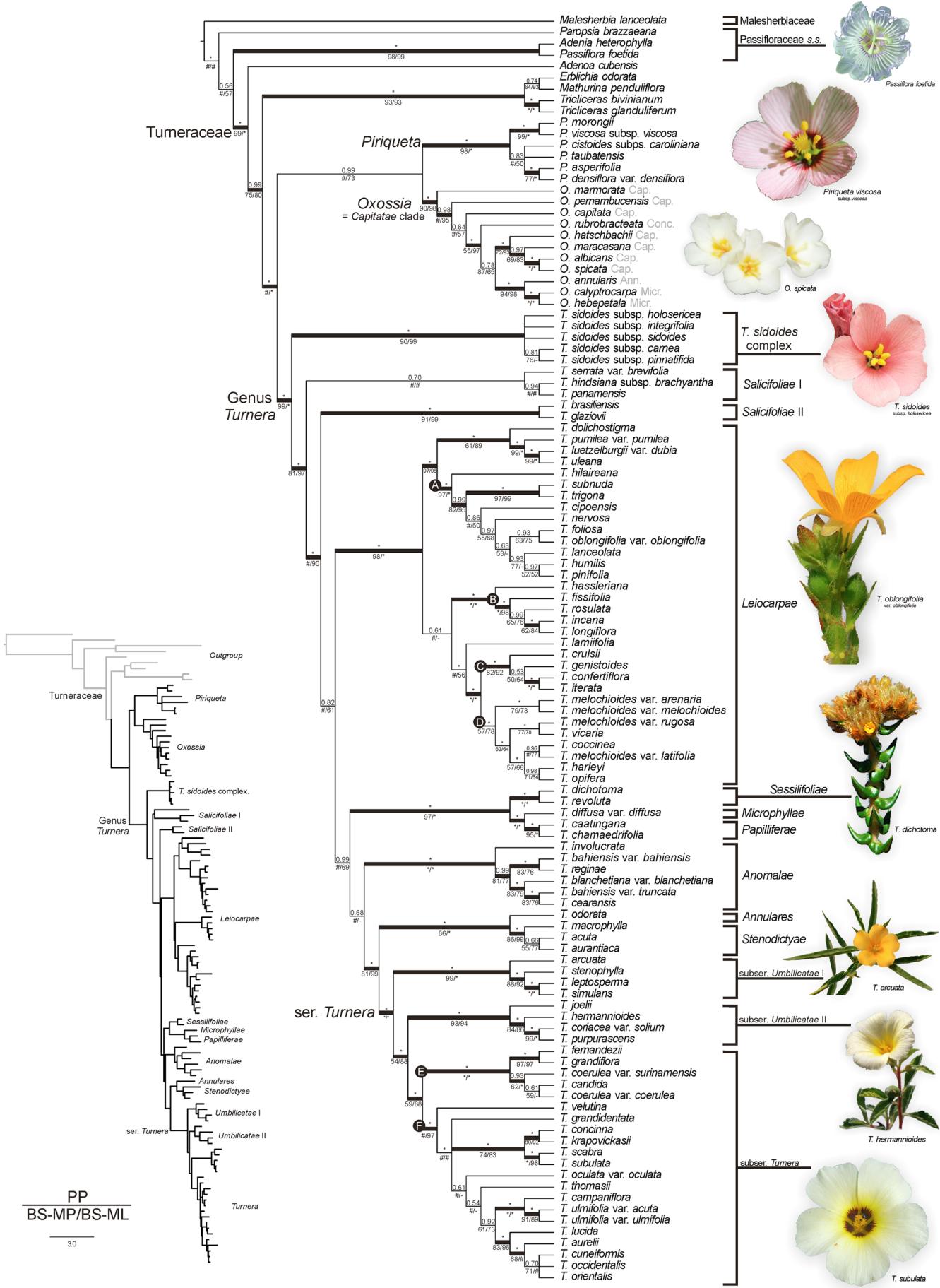
### 4. Discussion

Although the 11 series of *Turnera* are morphologically well-defined (Urban, 1883; Arbo, 1997, 2000, 2005, 2008), our results support only five of them: *Anomalae*, *Sessilifoliae*, *Papilliferae*, *Stenodictyae* and *Turnera*. Some clades and infrageneric taxonomic arrangements suggested by previous phylogenetic studies with molecular (Truyens et al., 2005) and morphological data sets (Arbo and Espert, 2009; Arbo et al., 2015) are confirmed, but relationships among them are mostly new. Here, we performed the first reconstruction of ancestral states in Turneraceae based on a phylogeny recovered with molecular data to support the taxonomy of the genus *Turnera*.

Below, we briefly address the evolution of most relevant morphological traits in the systematics of Turneraceae. Then, we assess the correspondence of *Turnera* circumscription and infrageneric classification with clades recovered in this study as basis for an updated classification of the genus reflecting phylogenetic relationships and supported by morphological synapomorphies (Rocha et al., in prep.).



**Fig. 2.** Majority-rule consensus trees derived from Bayesian analyses of (A) the plastid (*psbA-trnH*, *trnT-L*, *trnL-F*, *trnL* intron, *trnD-E*, and *trnY-T*) and (B) nuclear (ITS and ETS) data sets. Traditional series and subspecies of *Turnera* are represented by different colors. Values above branches are posterior probabilities (PP) and below branches are the bootstrap support (BS) percentages from maximum parsimony (left) and maximum likelihood analyses (right). Thicker branches are supported by PP ≥ 95% and BS ≥ 80%; \* indicates PP = 1 or/and BS = 100%; - indicates BS < 50% and # groups that are not recovered in MP or ML analyses.



(caption on next page)

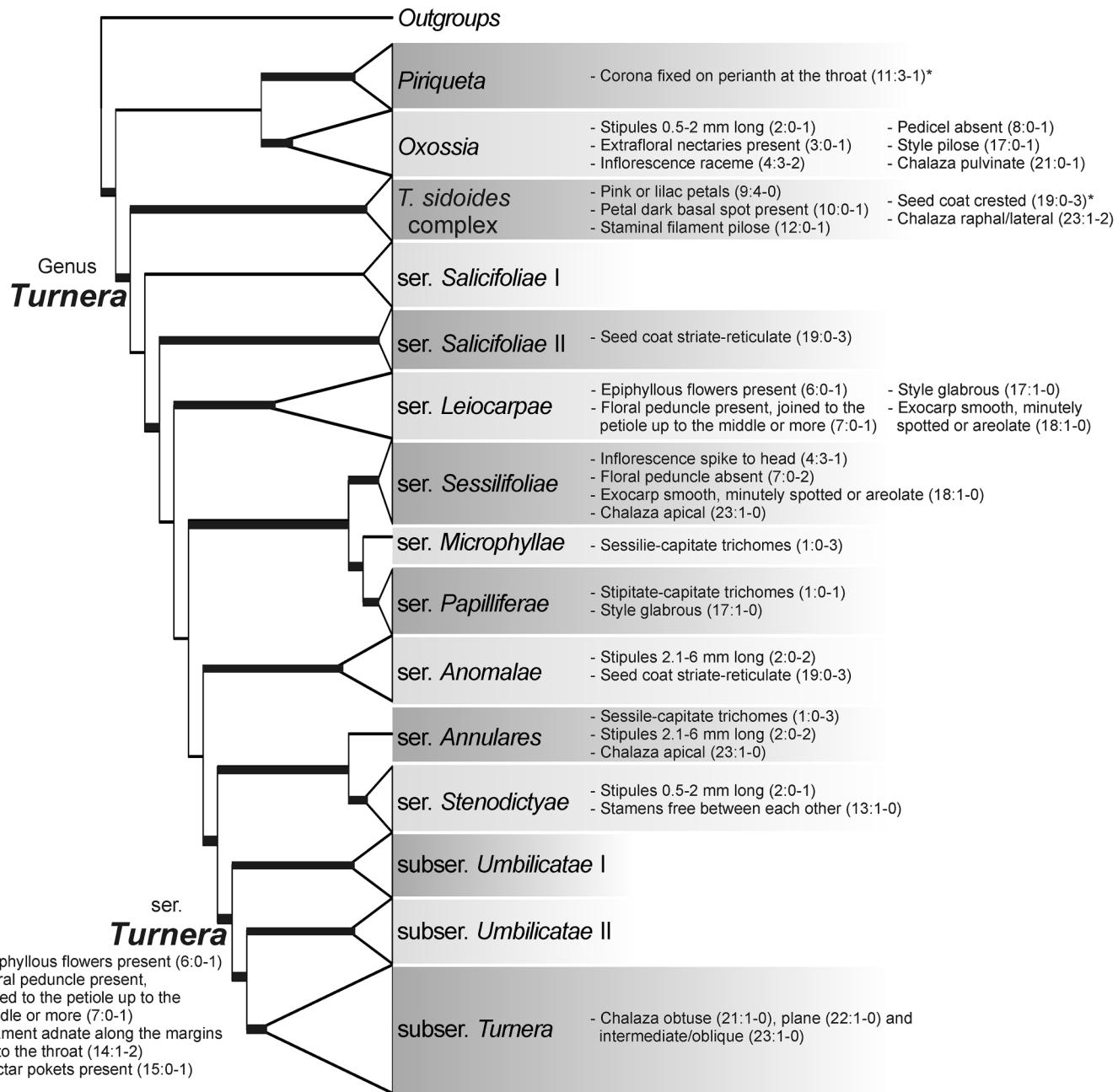
**Fig. 3.** Majority-rule consensus tree and phylogram (left) from the Bayesian analysis with combined nuclear and plastid data sets showing the new generic circumscription of the American Turneraceae, with the new genus *Oxossia* segregated from the genus *Turnera*. Values above branches are posterior probabilities (PP) and below are the bootstrap (BS) percentages from maximum parsimony (left) and maximum likelihood analyses (right). Thicker branches are supported by PP  $\geq 95\%$  and BS  $\geq 80\%$ ; \* indicates PP = 1 and/or BS = 100%; - indicates BS < 50% and # groups that are not recovered in MP or ML analyses; In *Oxossia*, the series of *Turnera* to which the species were traditionally classified are indicated at right: Cap. = ser. *Capitatae*, Conc. = ser. *Conciliatae*, Ann. = ser. *Annulares*, Micr. = ser. *Microphyllae*. Pictures show the general morphology of lineages discussed in the text. Photo of *Passiflora foetida* by L.Rocha; *Piriqueta viscosa* subsp. *viscosa* by C. Pinheiro; *Oxossia spicata* by J.L.Costa-Lima; *Turnera sidoides* subsp. *holosericea* by T.N.Cabreira; *T. oblongifolia*, *T. dichotoma*, *T. arcuata*, *T. hermannioides* by H.Moreira; *T. subulata* by L.Rocha.

#### 4.1. Morphological evolution

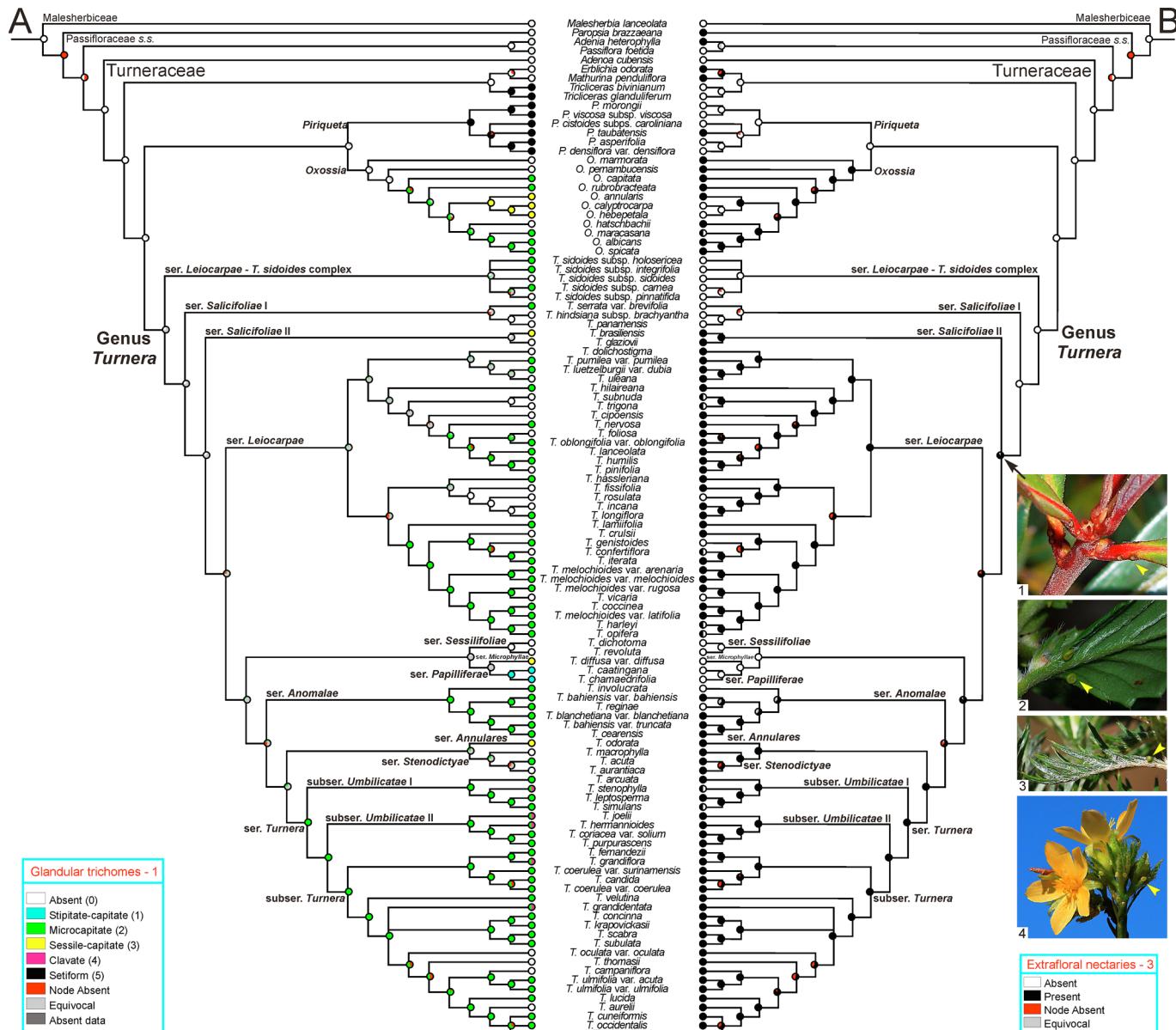
##### 4.1.1. Extrafloral nectaries (EFNs)

Approximately 4,000 species, including those in Turneraceae and Passifloraceae s.s., have EFNs (Weber and Keeler, 2013). We restrict the discussion to EFNs associated to petioles and leaves (Fig. 5B). Our reconstruction shows the absence of EFNs as the ancestral condition in

Turneraceae, Passifloraceae s.s., and Malesherbiaceae, with multiple independent origins during the evolution of these families. In Turneraceae, EFNs occur in lineages that are more derived and diverse, and seem to be associated with increased diversification rates (Marazzi et al., 2006; Weber and Agrawal, 2014). Lineages with few species usually lack EFNs, such as those corresponding to the ser. *Papilliferae*, ser. *Sessilifoliae*, and the *T. sidoides* complex (Fig. 3); on the other hand,



**Fig. 4.** Summary of relationships among the largest American genera of Turneraceae and the infrageneric taxa of the genus *Turnera* (Fig. 3), showing their morphological synapomorphies (character : character state change), \* indicates exclusive synapomorphy. Thicker branches are supported by PP  $\geq 95\%$  and BS  $\geq 80\%$ .



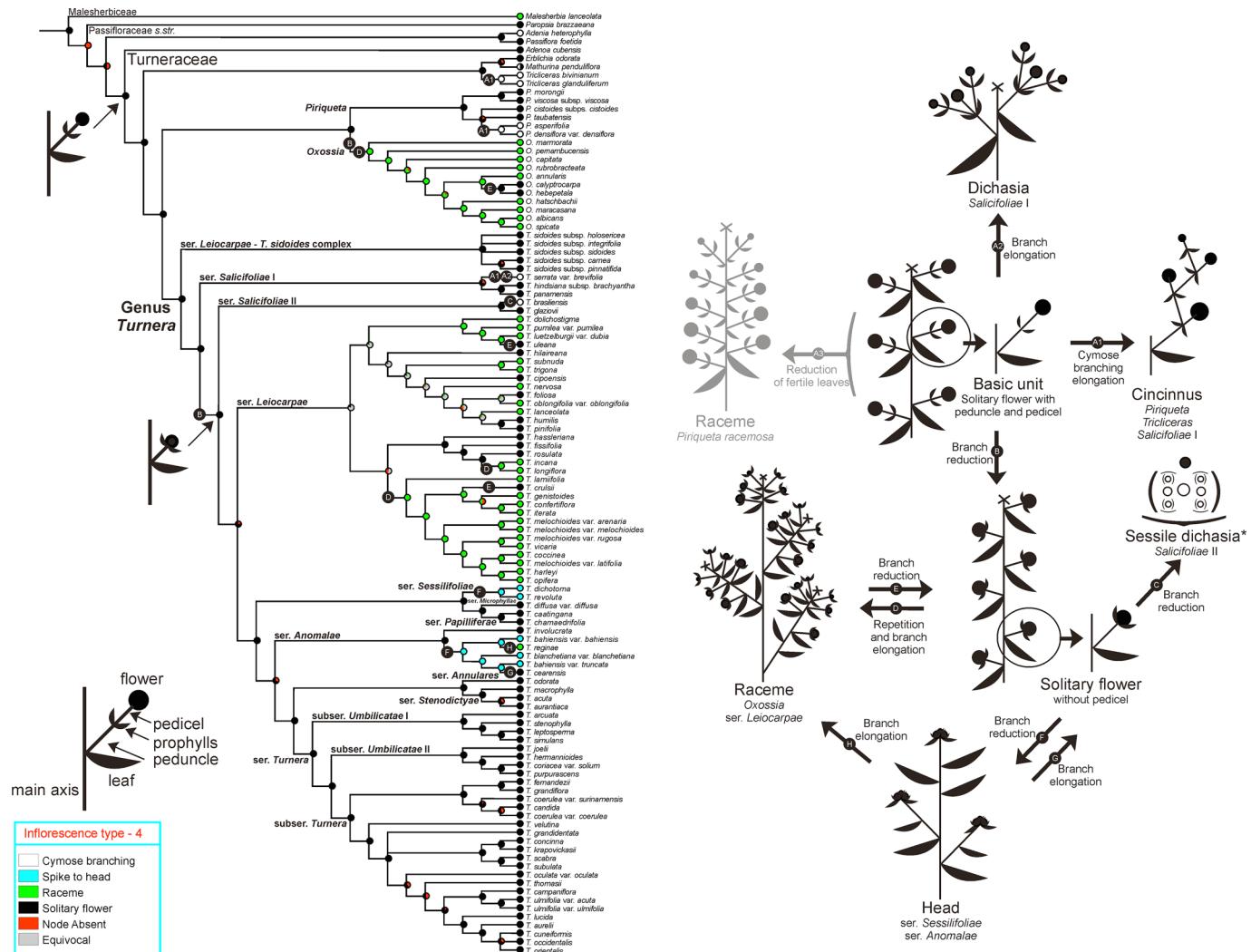
**Fig. 5.** Parsimony ancestral state reconstructions of the glandular trichomes (A) and the extrafloral nectaries (B) in Turneraceae, Malesherbiaceae, and Passifloraceae s.s. on the 50% majority-rule consensus tree from the IB analysis with combined nuclear and plastid data sets; circles indicate the frequency of states on the last 1,000 post-burnin trees from the BI phylogenetic analysis. Pictures show extrafloral nectaries in representatives of *Turnera*. Photos 1. *T. glaziovii*, by C.Silva; 2. *T. simulans*, by L.Pataro; 3. *T. fissifolia*, 4. *T. trigona*, by H.Moreira.

EFNs prevails in the large ser. *Leiocarpae* and ser. *Turnera*. Accordingly, the genus *Passiflora*, whose diversity of EFNs is evident (Ulmer and MacDougal, 2004), also stands out as the largest genus of Passifloraceae s.s. The association between EFNs and higher diversity has also been noted in *Senna* (Marazzi and Sanderson, 2010), but not in *Chamaecrista* (Conceição et al., 2009) and *Mimosa* (Simon et al., 2011) as lineages with EFNs are not necessarily richer in species in these two genera.

EFNs are often associated with plant defense, mainly with help by ants (Bronstein, 1998; Chamberlain and Holland, 2009; Trager et al., 2010). However, they (or their secretory function) are often lost (Nogueira et al., 2012), which affects this association as ants patrol the plants looking for nectar. In Turneraceae, the appearance of abundant setiform or capitate glandular trichomes (Fig. 5A), suggesting a compensatory selection, in which glandular trichomes would replace EFNs for plant protection (Levin, 1973; Conceição et al., 2009; Glas et al., 2012). In the genus *Piriqueta*, the setiform glandular trichomes are often sticky, and may hinder or prevent the movement of insects across the

plant, possibly reducing herbivory (Levin, 1973; Morais-Filho and Romero, 2010), similar to species without extrafloral nectaries but with many glandular trichomes in the genera *Passiflora* (T.S. Nunes, pers. comm.) and *Chamaecrista* (Conceição et al., 2009), and the tribe Bignonieae (Nogueira et al., 2013). In ser. *Microphyllae* and ser. *Papilliferae*, capitate glandular trichomes with mentholic odor keep insects away (L. Rocha, pers. obs.), directly increasing the resistance of plants to herbivory and/or pathogens (Glas et al., 2012). Since species with abundant glandular trichomes are widely distributed and sometimes ruderal (e.g. *Piriqueta duarteana*, *P. guianensis*, *Turnera chamaedrifolia*, and *T. diffusa* var. *diffusa*), it is possible that these attributes also contribute to the occupation of new environments (Arbo, 1995, 2000). EFNs also occur in plants with microcapitate glandular trichomes, but these trichomes are inconspicuous, not glutinous or odoriferous, such as setiform, capitate-sessile or capitate-stipitate trichomes; in these cases, EFNs may represent only an additional advantage against herbivory.

In addition to the glandular trichomes, EFNs also seem to contribute



**Fig. 6.** Parsimony ancestral state reconstruction of the inflorescence in Turneraceae, Malesherbiaceae and Passifloraceae s.s., on the 50% majority-rule consensus tree from the IB analysis with combined nuclear and plastid data sets; circles indicate the frequency of states on the last 1,000 post-burnin trees from the BI phylogenetic analysis. An interpretation of the evolution of the cymose and racemose inflorescences are shown at right with pictures showing the general inflorescence morphology evolution.

to the plant reproductive success (Villamil et al., 2019) and the expansion of species distribution (Cuautle et al., 2005). ENFs close to the flowers of *Turnera velutina* (subser. *Turnera*), for instance, can distract ants from reproductive structures, reducing ant-pollinator conflicts (Villamil et al., 2019). In *T. ulmifolia* (subser. *Turnera*), besides nectar from ENFs, ants are attracted by the elaiosomal aril and collect seeds, increasing their dispersion capacity (Dutton et al., 2016). Actually, how ENFs and trichomes are ecologically and evolutionarily associated to plant defense and diversification (Lengyel et al., 2009, 2010; Nogueira et al., 2015) remains a poorly explored issue.

#### 4.1.2. Inflorescences

The inflorescence architecture has been widely used in the taxonomy of Turneraceae (Urban, 1883; Arbo, 1997, 2000, 2005, 2007, 2008). A flowering shoot in Turneraceae has foliage leaves or relatively small, bract-like leaves, and each of these leaves has a single flower or a group of flowers in its axil. This group of flowers can have a cymose (i.e., dichasial or monochasial) or a racemose ramification. In the terminology of Arbo (e.g., 1985, 1997), who did a number of extensive and careful studies on morphology of Turneraceae, these axil products are defined as inflorescences. Here, we decided to use the same terminology to alleviate comparisons between all these Turneraceae publications. However, we should also mention that recent treatments

of inflorescence morphology preferably use the terminology by Weberling (1989), which is in some way better suited for larger scale (angiosperm-wide) comparisons (see also Endress, 2010). In this terminology, the entire flowering shoot of *Turnera* would be defined as an inflorescence. It is a raceme in the single-flower case. It is a thyrs in the cyme case. And it is a double raceme or double spike in the case of racemose ramification of the first-order lateral axes.

Apparently, it was assumed an ancestral state with cymose units in Turneraceae from which solitary flowers evolved by branch suppression and reduction; thus, racemes in this family would represent inflorescences with reduced partial inflorescences. Our analyses suggest a different history, in which solitary flowers would be plesiomorphic (Fig. 6). Inflorescences in most lineages of Turneraceae, mainly *Piriqueta* and most series of *Turnera*, would then have evolved from solitary flowers and not from cymose inflorescences. The inflorescence evolution then followed different processes. In lineages that diverged initially, e.g. *Piriqueta* and *Tricliceras*, *Turnera* ser. *Salicifoliae* I, the elongation of the main axis, and proliferation of branches (peduncles and pedicels) in the axil of prophylls, increased the structure, resulting in independent origins of inflorescences with cymose branches (dichasia and cincinnus; Fig. 6, steps A1, A2). Rarely only flower proliferation in the axil of prophylls, resulting in sessile dichasia in *T. brasiliensis*, *Salicifoliae* II (Fig. 6, C). In contrast, in the most derived



**Fig. 7.** Representation of the diversity in the new genus *Oxossia*. A: *O. annularis*. B-C: *O. calyptrocarpa*. D: *O. maracasana*. E-F: *O. marmorata*. G-H: *O. pernambucensis*. I: *O. spicata*. J. *O. rubrobracteata*. Photos A. by J.Jardim; B-C. by C.Pinheiro; D. by L.Daneu; E-F: E.Matos; G-H. by A.Zelenski; J. by R.Perdiz.

lineages racemization, branch reduction/loss (Fig. 6, B), and compaction prevailed (Wyatt, 1982; Harris, 1999; Feng et al., 2011), resulting in the dense racemes found in ser. *Capitatae* (= *Oxossia*), ser. *Leiocarpae*, and some species in ser. *Anomalae*, as well as the head and spikes of ser. *Sessilifoliae*. However, in *Piriqueta*, the racemization may have occurred by reduction of fertile leaves in branches with solitary flowers (Fig. 6, A3). Transition between different inflorescence types is still possible through such mechanisms (Fig. 6, F, G, H). At most derived nodes of the genus *Turnera*, the ancestral condition was conserved, but pedicels were lost and peduncles became recaulescent to the leaf or bract petiole (epiphyllous flower, character 6, see Table 3).

Changes in the expression of floral meristem regulatory genes (Coen and Nugent, 1994; Liu et al., 2013; Benloch et al., 2015) may have played a significant role in shaping the inflorescence architecture in Turneraceae. These genes can be activated or deactivated through environmental or ecological-physiological conditions (Prusinkiewicz et al., 2007). This could explain the high diversity of inflorescences in ser. *Leiocarpae*, whose distribution covers different levels of environmental pressure. The origin of epiphyllous flowers and racemization seems to have played an important role in the diversification of *Turnera*, as racemes, heads and spikes increase floral accessibility by visitors in environments where pollinators are limited (Iwata et al., 2012; Schmitt,

1983). Overall, the diversification of inflorescence architectures probably affected the reproductive success and thus drove the evolution of Turneraceae, but this matter still requires further studies.

#### 4.1.3. Floral morphs

Turneraceae, Passifloraceae s.s., and Malesherbiaceae are distinguished by particular floral morphs. Heterostyly is found exclusively in Turneraceae, and has been interpreted as the ancestral condition, as well as in several other families (e.g., Schoen et al., 1997; Church, 2003; Graham and Barrett, 2004; Tippery et al., 2008; Kissling and Barrett, 2013), although reconstructions may have been negatively affected by outgroup selection. Distyly appeared at least twice in Turneraceae: in the African Clade A and in the predominantly American Clade B (Fig. C5). With more species from Africa, Chafe's (2009) ancestral reconstruction for Turneraceae, was equivocal, but a single origin was suggested because distyly requires a greater number of factors, including a "supergene", for example (Schoen et al., 1997; Barrett and Shore, 2008).

Our reconstruction shows multiple reversals to homostyly in *Piriqueta* and *Turnera*: ser. *Leiocarpae* (*T. pumilea* var. *pumilea*), ser. *Papilliferae* (populations of *T. chamaedrifolia*), ser. *Stenodictyae* (*T. macrophylla*), *Turnera sidoides* complex, and some species of ser.

*Turnera*. Chafe (2009) pointed to homostyly as a derived condition in *Piriqueta* and *Turnera* and highlighted at least three independent origins in the former and five in the latter genus. Truyens et al. (2005) also assumed homostyly as a derived condition in *Turnera*, but relationships among homostylous species in this study did not improve our understanding of its evolution, whether homostyly comes from a single or from multiple origins, for instance. Our analysis does not allow safe conclusions for deeper nodes in ser. *Turnera*, e.g. subser. *Turnera*, due to equivocal reconstructions. Furthermore, topologies from nuclear and plastid data sets suggested different histories, something also found by López et al. (2013), probably as a result of reticulate evolution. However, based on the combined data analysis, at least three transitions to homostyly in the subseries are inferred: *Turnera candida*, *T. velutina*, and Clade C (Fig. C5). These transitions are also associated with self-compatibility, low genetic diversity among populations (Barrett, 2013), and polyploidy (e.g., Guggisberg et al., 2006; Naiki, 2012). Nevertheless, the combination of homostyly and polyploidy is not always confirmed, as in other groups (e.g., *Amsinckia*; Schoen et al., 1997; Naiki, 2012, and references therein); in *Piriqueta*, for instance, polyploid species always show distyly (Shore et al., 2006). Therefore, it is still premature to suggest a causal relationship between polyploidy and homostyly evolution in Turneraceae.

#### 4.1.4. Petal color

Petal color is central in plant systematics and ecology (Fenster et al., 2004), but the evolution of this character remains unexplored in Turneraceae. Our reconstruction showed that the ancestral state in Turneraceae, Passifloraceae s.s., and Malesherbiaceae probably is ivory or cream petals (Appendix C, Fig. C.9). Nevertheless, the range of petal colors in the latter two families is enormous (Ricardi, 1967; Krosnick et al., 2013) and a larger sampling of them would possibly change this result. Most lineages of Turneraceae evolved from ancestors with yellow petals, with multiple transitions to other colors, such as white, orange, or red. Nevertheless, some lineages conserved the ancestral color, which explains its high representation in *Turnera*. Petals in yellow and orange-yellow shades may exhibit patterns of UV absorption that can be perceived by many floral visitors (Lunau et al., 1996; Briscoe and Chittka, 2001; Papiorek et al., 2016), increasing the reproductive capacity of these plants (Gómez et al., 2014). Lineages whose petals changed from yellow to any other color tend to have fewer species and in some cases a more restricted distribution; for example, *Turnera fissifolia* (bluish-white petals), *T. rosulata* (lilac), and *T. coccinea* and *T. longiflora* (red petals) are all endemic to the Cerrado. This pattern suggests that yellow is a plesiomorphic color for petals in Turneraceae and changes in this character probably reduced the potential of diversification (Smith et al., 2010).

White or bluish-white petals are synapomorphies of clade *Capitatae* (= *Oxossia*), independently appearing in a group of the genus *Turnera* (subser. *Turnera*) (Fig. 7), and we point to at least four other independent origins of this petal color in the genus. The pink or lilac petals are synapomorphies of the *Turnera sidoides* complex. These changes, in particular, seem to asymmetrically affect patterns of diversity and distribution, but also many other morphological attributes probably affected the current diversity of these groups. Within the clade *Capitatae* (= *Oxossia*), for example, the shift from yellow to white petals seems to be associated with higher diversity and wider distribution; in this lineage, however, floral visitation and reproductive success may be favored by the chromatic contrast between the white blade and yellow base of petals. This chromatic contrast may work as nectar guides for floral visitors (Lunau et al., 1996). In the subser. *Turnera*, the white petal lineage is less diverse (5 species), but widely distributed (Arbo, 2005). This group, however, has flowers with nectariferous pockets (Fig. C15) and with yellow or dark (blue) basal spot or blue lines (Fig. C10) on petals.

The prevalence of yellow petals and the multiple origins of other colors in addition to nectar guides are probably associated to

pollination (Fenster et al., 2004). However, a possible influence of pleiotropy (Rausher, 2008; Smith and Goldberg, 2015), gene drift (Zufall and Rausher, 2004), and pigment interaction (Ellis and Field, 2016; Ng and Smith, 2016) cannot be discarded.

## 4.2. Towards an updated classification

### 4.2.1. *Capitatae* clade: The new genus *Oxossia*

In Truyens et al. (2005) and Thulin et al. (2012), the genus *Turnera* was weakly supported and the ser. *Capitatae* was recovered as sister to the rest of the genus. In the morphological analysis of Arbo and Esper (2009), the species of this series appeared dispersed in clades with species of ser. *Salicifoliae* and ser. *Stenodictyae*, while in Arbo et al. (2015), ser. *Capitatae* appeared in a polytomy with ser. *Annulares*, ser. *Stenodictyae*, and ser. *Salicifoliae*. According to our analyses, ser. *Capitatae* is not monophyletic; three species of this series form a basal grade, whereas the other species form a clade, sister to a group composed of *T. calyptrocarpa*, *T. hebetepetala* (ser. *Microphyllae*) and *T. annularis* (ser. *Annulares*). Furthermore, the clade *Capitatae* is closer to the genus *Piriqueta* than to the other species of *Turnera* and so the genus *Turnera*, as traditionally circumscribed, is not monophyletic.

The presence of a ligule in species of the clade *Capitatae* and the genus *Piriqueta* can be interpreted as an evidence of their close relationship. Four species of *Turnera* ser. *Capitatae* (*T. capitata*, *T. maracasana*, *T. hatschbachii*, and *T. princeps*) have a ligule at the base of petals (11:2) anatomically similar to the corona found in *Piriqueta* (11:1). However, these ligules arise only on petals (Gonzalez, 2001), whereas the corona consists of 10 lobes, five on sepals and five on petals (Arbo, 1995); ligules also occur in ser. *Salicifoliae* and genera *Tricliceras* and *Erblichia* (Arbo et al., 2015). Although comprising species of ser. *Capitatae*, ser. *Conciliatae*, ser. *Annulares* (*T. annularis*), and ser. *Microphyllae* (*T. calyptrocarpa* and *T. hebetepetala*), this clade can be defined by six morphological synapomorphies, well developed stipules (> 0.5 mm) (2:1), presence of pairs of extrafloral nectaries (3:1) (rarely absent), (sub)sessile flowers (8:1) in racemose inflorescences (4:1) (rarely solitary), pilose styles (17:1), which can be geniculate, and pulvinate chalaza (21:1) (Fig. 4). Most species have flowers with white corolla (8:2), becoming yellow towards the base, and pilose stamens (12:1) (Fig. 7).

There are three main possibilities to taxonomically represent these relationships. First, including *Piriqueta* under the synonymy of *Turnera*, which would require 46 new combinations, producing a highly heterogeneous genus, no longer recognized by the porrect-stellate tector trichomes and petals with corona. Second, transferring the species of the clade *Capitatae* to *Piriqueta*, which would require only 15 new combinations, but then *Piriqueta* would no longer be recognized by the characteristics mentioned above, which so promptly define the genus. Third, segregating the species of clade *Capitatae* into a new genus, which would also require only 15 new combinations, maintaining most of the morphological identity of the genera *Turnera* and *Piriqueta*. Here, we argue for this third possibility and propose the new genus *Oxossia* (see below; Fig. 7), which represents a morphologically and geographically cohesive lineage (Table 4).

### 4.2.2. *Turnera sidoides* complex

*Turnera sidoides* comprises five subspecies of perennial rhizomatous herbs, widespread in Pampas, seasonally dry tropical forests and woodlands, in the Bolivian Chaco, southern Paraguay, southernmost Brazil, and from Uruguay up to 39°S in Argentina (Arbo, 1985, 2005; Solís Neffa, 2010; BFG, 2015). *Turnera sidoides* can be recognized mainly by the leaves without extrafloral nectaries (3:0), flowers with developed pedicel (8:0), and fruits with granular exocarp (18:1), and have six morphological synapomorphies (Fig. 4), of these, seeds with a crested surface (19:3) is unique in the family (Arbo, 2008; Gonzalez and Arbo, 2013). Subspecies are separated by indument, leaf shape, and petal color (Arbo, 1985), traits whose variations are also evident in

**Table 4**

Morphological comparison between *Oxossia* and the phylogenetically closely related genera, *Turnera* and *Piriqueta*. Differences between the traditionally circumscribed groups within *Turnera* are listed.

	<i>Oxossia</i>	<i>Turnera</i>	<i>Piriqueta</i>
Stipule size	> 0.5 mm long	Absent to rudimentary, rarely 4.5 mm long	Absent to rudimentary
Leaf size	(0.4–)2.5–22.5 cm long	Variable, rarely up to 24.5 cm long (series <i>Salicifoliae</i> )	Variable, rarely up to 10 cm long
Leaf nectaries	Present or absent	Present or absent	Absent, rarely present
Inflorescence	Racemose, rarely solitary flower	Solitary flower, racemose, rarely cymose branching	Cymose or solitary flower, rarely racemose
Petal color	White, rarely yellow, pink, or red	Often yellow or orange yellow, rarely white, red, or pink.	Yellow, pink, rarely white, orange reddish
Perianth appendices	Absent or ligule on the petals.	Absent, rarely ligule on the petals (series <i>Salicifoliae</i> )	Corona on the petals and sepals
Staminal filament indument	Pilose, rarely glabrous	Glabrous, rarely pilose	Glabrous
Stamen connation to each other	Free between each other, connate irregularly above adnation, only at the adnate portion or above adnation in a slender annular structure	Free between each other or connate only at the adnate portion	Free between each other
Style indument	Pilose	Glabrous or pilose	Glabrous or pilose
Fruit exocarp	Warted, granulate, rarely smooth	Warted to smooth	Warted to smooth
Occurrence	Rain forests and restingas of the Atlantic forest, Amazon, rarely Caatinga or Cerrado	Wide, with centers of endemism in the Cerrado	Wide, with centers of endemism in the Caatinga

ploidy levels, 2x–8x ( $n = 7$ ) (Kovalsky et al., 2018 and references therein).

The species is treated in ser. *Leiocarpae* (Arbo, 2008), although Truyens et al. (2005) pointed to the fragility of this relationship by recovering its subspecies in a well-supported clade, unresolved among several series of the genus *Turnera*. The species appeared as sister to the rest of the genus *Turnera* in Arbo and Espert (2009), but nested in ser. *Leiocarpae* in Arbo et al. (2015). Here, we support *T. sidoides*, including its subspecies, as monophyletic and diverging at the base of the genus *Turnera*, apart from ser. *Leiocarpae*. This position is also supported by morphology and is congruent with cytogenetic data (e.g., Solis Neffa and Fernández, 2000; Gonzalez and Arbo, 2013); thus, a new series will be proposed to represent this lineage (Rocha et al., in prep.).

#### 4.2.3. *Salicifoliae* grade

Traditionally, the ser. *Salicifoliae* is characterized by glabrous or glabrescent indumentum, usually large leaves, flowers with yellow corolla, ovary glabrous, rarely sparse-pilose, fruits with tuberculate exocarp, seeds with filiform papillae, and pulvinate, concave chalaza, oriented towards the raphe side. It also comprises all the species of the genus with flowers in dichasial (Arbo, 1997; Arbo and Espert, 2009). In our analyses, the species of ser. *Salicifoliae* form a basal grade. Since two species of this series have a ligule on the petals (11:2), which is possibly a plesiomorphy, this relationship is not surprising. Phylogenetic relationships of ser. *Salicifoliae* were essentially unknown: the three species analyzed by Truyens et al. (2005) diverged in a polytomy, along with other species of the genus *Turnera*; the series was not recovered as monophyletic in Arbo and Espert (2009) and Arbo et al. (2015), with species emerging closer to ser. *Capitatae* and ser. *Stenodictyae*, both with similar floral structures.

The first clade to diverge in the *Salicifoliae* grade (*Salicifoliae* I) includes species with petioles without extrafloral nectaries (3:0), well-developed peduncles and pedicels (8:0) and ligulate petals (11:2). Thus, *Turnera serrata* var. *brevifolia*, *T. hindsiana* subsp. *brachyantha* and *T. panamensis*, together with morphologically similar taxa, should represent a new series (Rocha et al., in prep.). The second clade of this series to diverge (*Salicifoliae* II) includes *T. glaziovii* (type of the series) and *T. brasiliensis*. These species also emerged together in Arbo and Espert (2009). The clade is characterized by 1–8 pairs of extrafloral nectaries (rarely inconspicuous) on petiole (3:1), sessile, solitary flowers or flowers in short-pedunculate or sessile dichasial or abbreviated spike (8:1), corolla without ligule (11:3), and glabrous ovary (16:2). Therefore, ser. *Salicifoliae* should be restricted to species of this clade.

#### 4.2.4. *Leiocarpae* clade

The ser. *Leiocarpae* is the most species-rich in the genus *Turnera*. It comprises 57 species, distributed from Mexico to Argentina, with most species in Brazil (50 species), mainly in the Cerrado and Caatinga (Arbo, 2008; Arbo and Mazza, 2011). In Truyens et al. (2005), species of ser. *Leiocarpae* appeared in two clades unresolved with other series of the genus. In Arbo and Espert (2009), species of this series appeared in three distantly related groups, whereas in Arbo et al. (2015), the series was recovered as monophyletic, provided that ser. *Sessilifoliae* was included in it (see discussion below). These studies did not recover ser. *Leiocarpae*, and showed the need of its recircumscription, segregating the *T. sidoides* complex from it, which is strongly supported by our results. The 33 species and infraspecific taxa of the series sampled here formed a clade, sister to a large group composed of seven series, and is defined by three morphological synapomorphies: epiphyllous flowers (6:1), solitary or in racemose inflorescences, glabrous styles (rarely pilose) (17:0) and smooth exocarp (18:0) (Fig. 4). Although we have not sampled the species type of the series (*T. callosa*), its morphological similarity with *T. crulsii* and *T. hassleriana* supports the placement of this species in ser. *Leiocarpae*.

According to our results, ser. *Leiocarpae* should include species with generally rudimentary stipules (developed only in *T. incana*, *T. longiflora*, and *T. lamijifolia*), leaves with extrafloral nectaries (rarely absent, in *T. genistoides*, *T. vicaria*, and *T. rosulata*) (3:1), epiphyllous (6:1) and no pedicellate (8:1) flowers, stamens free from each other (13:0), fruits with smooth exocarp (18:0) (rarely rugose, in *T. melochioides* var. *rugosa*), and reticulate seeds (19:0). The series shows a high taxonomic diversity in the Cerrado, and we recovered three lineages (clades A, B and C in Fig. 3) predominantly endemic to this phytogeographic domain. They probably had a long history in the Cerrado and show several adaptations to fire-prone savanna (Simon et al., 2009; Bond and Midgley, 2012; Simon and Pennington, 2012), such as flowering and fruiting driven by fire regimes, xylopodium, and dwarf habit (e.g., *T. humilis*, *T. rosulata*, and *T. fissifolia*; Fig. 1D, F, I).

The four varieties of *T. melochioides* are included in a phylogenetic study for the first time (Fig. 3, clade D) and, contrasting to the groups established by Arbo (2008), they are recovered in distant clades of ser. *Leiocarpae*, suggesting that *T. melochioides* comprises at least three independent lineages and its circumscription should be reviewed. Nevertheless, this species is so widely distributed and morphologically variable that a new taxonomic circumscription will require phyogeographic studies or phylogenetic analyses with multiple accessions of varieties.

#### 4.2.5. *Sessilifoliae* clade

The ser. *Sessilifoliae* includes only two species of subshrubs or shrubs, restricted to the campos rupestres (rocky grasslands) and savannas of the Espinhaço Range, in Minas Gerais, Brazil. Characterized by four morphological synapomorphies: sessile flowers (7:2), gathered in terminal head or spikes (4:1), fruits with smooth or very slightly rugose exocarp (18:0), and chalaza oriented towards the apex of the seed (23:0) (Fig. 4). Moreover, the species in this series also present xylopodium, tomentose stems, no glandular trichomes (1:0), small and sessile leaves with revolute margins, without extrafloral nectaries (3:0), traits often found in groups adapted to dry campos rupestres and fire-prone savannas (Ratter et al., 1997; Lusa et al., 2014; Loeuille et al., 2015). These species were formally circumscribed in ser. *Capitatae*, because of the inflorescence architecture (Urban, 1883, 1893), being later transferred to ser. *Leiocarpae* (Arbo, 2000) because of exocarp ornamentation, until Arbo (2008) finally proposed their formal recognition in a separate series.

Arbo and Espert (2009) sampled only one species of ser. *Sessilifoliae*, which appeared with *T. genistoides* (ser. *Leiocarpae*). Arbo et al. (2015) supported the monophyly of the series and its close relationship with ser. *Leiocarpae*, as they share fruits with smooth or slightly rugose exocarp. Here, we also recovered *Sessilifoliae* as monophyletic, but as sister to a clade composed of ser. *Microphyllae* and ser. *Papilliferae*, a relationship morphologically supported by leaves generally small, extrafloral nectaries absent (3:0), and seeds with obtuse chalaza (21:0).

#### 4.2.6. *Papilliferae-Microphyllae* p.p. clade

The ser. *Papilliferae* is strongly supported as sister to *Turnera diffusa* var. *diffusa* (ser. *Microphyllae*). This relationship is morphologically supported by the leaves usually small and aromatic, without extrafloral nectaries (3:0), and seeds with obtuse chalaza (21:0), plus trichomes capitate, glandular, sessile or stipitate (character 1; Fig. C.1). Their close relationship was also pointed out by Truyens et al. (2005), as well as Arbo and Espert (2009) and Arbo et al. (2015), who suggested the synonymization of the two series. However, none of these studies have recovered ser. *Papilliferae* as monophyletic as here. The series includes only two species, associated mainly to the Caatinga domain, in Northeast Brazil, one of them endemic to the biome, *T. caatingana*. These species are characterized by rudimentary stipules (2:0), small to medium leaves (up to 10 cm long), solitary flowers (4:3), only the peduncle developed (4–14 mm length), free or briefly adnate (up to 2 mm) to the petiole (7:0), petals creamy with vinaceous base, and generally short seeds (1.4–1.7 mm long) with obtuse chalaza (21:0), plus stipitate-capitate glandular trichomes (1:1) and glabrous styles (17:0) are morphological synapomorphies (Fig. 4).

Thus, the ser. *Microphyllae* should only include the three shrubby species with yellow corolla (Arbo, 2000) that occur mainly in the Caatinga and campos rupestres, across northeastern Brazil and Minas Gerais. One of them (*T. diffusa*), however, is widespread in dry forests throughout Mesoamerica, Caribbean, Mexico, and southern United States (Texas) (Arbo, 2000). They are characterized by small (up to 5 cm long) and aromatic leaves, small stipules (0.5–1 mm long) (2:1), adnate to the base of petiole, and sessile-capitate glandular trichomes (1:3), its only morphological synapomorphy (Fig. 4). *Turnera collotricha* (not sampled here) is the only species of the genus with setiform glandular trichomes, a trait typical to the genus *Piriqueta* (Arbo, 1995, 2000). In Arbo et al. (2015), the species emerged close to *T. diffusa*, and according to leaves, stipules, and flowers, it should remain in ser. *Microphyllae*.

#### 4.2.7. *Anomalae* clade

The ser. *Anomalae* comprises 14 species, most of them in the Caatinga dry woodlands and Amazonian rainforests, with some others endemic to the Cerrado (*T. reginae*) or Atlantic rainforest (*T. sancta*). In general, they are characterized by sessile or only slightly pedunculate flowers, which are solitary or gathered in head (Fig. C4), and seeds with

papillose epidermis, pulvinate (21:0) and concave (22:0) chalaza. The ancestral reconstruction analyses also showed that well developed stipules (2:2) and striate-reticulate seeds (19:1) are morphological synapomorphies of the series (Fig. 4). Similar to ser. *Turnera*, the floral tube of ser. *Anomalae* is formed by the adnation of calyx, corolla, and filament margins usually up to the corolla throat (14:2), resulting in five nectar pockets, between stamens and the sepals of the same radius (15:1), forming an appendicular hypanthium (Gonzalez, 2001; Arbo, 2005; Arbo et al., 2015). The two species of the series sampled by Truyens et al. (2005) formed a clade with *T. calyptrocarpa* (until then classified in ser. *Microphyllae*), in a polytomy with other series of *Turnera*, whereas Arbo and Espert (2009) and Arbo et al. (2015) supported the monophyly of ser. *Anomalae* and their close relationship with ser. *Turnera*, because of their floral structure (see discussion below). Our results suggest, but with weak support, that ser. *Anomalae* is close to a morphologically heterogeneous clade, composed of ser. *Stenodictyae*, ser. *Annulares*, and ser. *Turnera*, sharing the extrafloral nectaries (3:1) and seeds with pulvinate chalaza (21:1) with most of these groups, and the floral nectar pockets with ser. *Turnera*, which is probably a convergence.

We did not obtain good quality DNA of the Amazonian species of ser. *Anomalae*. Morphologically, they contrast with the species from Caatinga and Cerrado sampled here, which have medium size leaves (up to 10 cm long), terminal inflorescences, and yellow or orange corolla. The Amazonian species, on the other hand, have large leaves (up to 14 cm long in *T. amazonica* Arbo), axillary head (e.g., *T. stipularis*) and white corolla (*T. kuhlmanniiana* and *T. discors*). Therefore, the inclusion of Amazonian species in phylogenetic analyses is still required to understand their relationships within the genus; up to then, it seems appropriate to maintain them in this series.

#### 4.2.8. *Stenodictyae-Annulares* p.p. clade

The species of ser. *Stenodictyae* form a well-supported clade, sister to *T. odorata* (ser. *Annulares*). This relationship is supported by the presence of extrafloral nectaries in both series (3:1), solitary flowers (4:3), peduncles free from petiole (7:0), and pilose stamens (12:1) and styles (17:1). On the other hand, in analyses with morphological data, the two series appear phylogenetically distant. In Arbo and Espert (2009), ser. *Stenodictyae* appeared in two lineages within a clade composed of ser. *Salicifoliae* and ser. *Capitatae*, whereas species of ser. *Annulares* formed a clade, close to ser. *Anomalae* and ser. *Turnera*. The ser. *Annulares* was supported as monophyletic in Arbo et al. (2015), close to a clade with ser. *Stenodictyae*, ser. *Salicifoliae*, and ser. *Capitatae*. In our analyses, the clade comprising ser. *Annulares* and ser. *Stenodictyae* is sister to ser. *Turnera*, although few morphological similarities support this relationship.

The ser. *Stenodictyae* includes shrubs up to 3 m high, growing in wet forests, 'igapós' and floodplains in northern Amazonia. It is mostly characterized by large peduncles, prophylls with pairs of lateral appendices, sometimes laciniate, yellow-orange or orange-reddish corolla, fruits with granular exocarp, and seeds with concave chalaza (22:1). The presence of small stipules (0.5–2 mm long) (2:1) and free stamens (13:0) are morphological synapomorphies of the series (Fig. 4). Our analyses involved species of the major morphological groups of the series, i.e., species with large leaves and stipules (*T. macrophylla*), short peduncles and small stipules (*T. acuta*), and those with long peduncles (*T. aurantiaca*). In spite of this, a more comprehensive sampling may reveal new patterns and synapomorphies for this series; up to then, the current classification should be followed.

The ser. *Annulares* occurs in Amazon savannas and rainforests, as well as in dry and wet forests in southern Mexico and northern Central America (Arbo, 2005). It can be recognised by sessile-capitate glandular trichomes (1:3), and developed stipules (> 2.1 mm long) (2:3), the morphological synapomorphies of the series (Fig. 4). In addition, they also present bractless solitary flowers, with yellow or orange-yellow corolla, glabrous stamens (12:0), which are connate only at the portion

adnate to the floral tube (13:1), glabrous styles (17:0), fruits with verrucous or softly tuberculate exocarp (18:1), reticulated seed (19:0), and areoles without punctiform cavities (20:2). This series should be restricted to only *T. odorata*, *T. aromatica*, and *T. breviflora*.

#### 4.2.9. *Turnera* clade

The species of ser. *Turnera* are characterized by epiphyllous flowers (6:1), with peduncle adnate to petiole up to the middle or more (7:1). The stamens are adnate to the petal claws usually up to the throat (14:2) and are connate to each other only up to this portion, i.e. up to the floral tube to which they are adnate, as in ser. *Anomalae* (13:1), forming nectar pockets (15:1). Other common characters in this series are rudimentary stipules (2:0), leaves with extrafloral nectaries (3:1), fruits with granular exocarp (18:1), and reticulate seeds (19:0) (see Fig. 4 for summary of morphological synapomorphies of the series). The close relationship between ser. *Turnera* and ser. *Anomalae* was supported by the five nectar pockets (Arbo and Espert, 2009; Arbo et al., 2015), but different from Arbo et al. (2015), they are recovered as convergent in the two series here and not as an evidence of their relationship. In agreement with Truyens et al. (2005) and López et al. (2013), our data also support the monophyly of the ser. *Turnera*, with subser. *Umbilicatae* forming a grade with two well-supported clades and subser. *Turnera* forming a clade.

The species of subser. *Umbilicatae* occur in seasonally dry forests, savannas, and campos rupestres of Brazil. They are characterized by seeds with umbilicate, pulvinate chalaza, concave (22:1), and usually oriented towards the raphal side (23:2). By sampling all species of this subseries, we could show that it needs to be recircumscribed to comprise only the clade *Umbilicatae* I, which diverges at the root of ser. *Turnera* and includes the type of the subseries (*T. arcuata*). This taxon will contain the species with entire or serrate leaves, often with narrow teeth, and small extrafloral nectaries (up to 1.3 mm diam.), sometimes lacking in basal leaves, and petals without a dark basal spot (10:0). Species of the other clade, *Umbilicatae* II, have crenate or serrate leaves, often with broad teeth, and larger extrafloral nectaries (up to 2.3 mm diam.), and should be segregated into a new subseries. None of these clades have been recovered in previous phylogenetic studies, only *T. joelii* and *T. hermannioides*, with raphal aril (Gonzalez and Arbo, 2013), emerged together in Arbo et al. (2015).

The species of subser. *Turnera* have seeds with rounded, obtuse chalaza (21:0), not or only slightly concave (22:0), obliquely oriented (23:1) or oriented towards the apex of the seed (23:0). It is the most geographically widespread group of the genus, occurring in most environments throughout the New World and with two African species. The monophyly of the subseries was already supported by cytogenetic, morphological and molecular studies (Fernández 1987, 1997; Truyens et al., 2005; Fernández et al., 2010; Fernández and Arbo, 1989, 1990, 1993, 1996, 2000a, b). Our results also confirm the existence of two groups separated by petal color (Fig. 3): blue-white (9:2) in clade E and yellow or cream (9:3 or 4; bluish-white only in *T. thomasii*) in clade F. The African taxa *T. oculata* var. *oculata* and *T. thomasii* appeared close to the group with homostylous flowers, yellow or cream petals, which is widely distributed in America.

## 5. Conclusions and perspectives

In this study, we evaluated generic and infrageneric circumscriptions in *Turnera*, based on a taxonomically comprehensive and well resolved molecular phylogenetics and morphological synapomorphies. By exploring the initial evolution of the genus, the ser. *Capitatae* together with other species of *Turnera* was resolved closer to the genus *Piriqueta*, supporting its segregation into the new genus *Oxossia*. The lineages *Turnera sidoides* complex and ser. *Salicifoliae* form the basal grade in the genus *Turnera*; thus, pedunculate, pedicellate flowers and ligulate petals are confirmed as plesiomorphic. Our results support the monophyly of only five of the 11 series of *Turnera* and provide a basis

for an updated infrageneric classification of the genus, reflecting phylogenetic relationships, which is being prepared by Rocha et al. (in prep.). Our ancestral state reconstructions also show synapomorphies for most lineages and convergent traits in *Turnera*. Now, it is possible to infer that the ancestor of the clade of Turneraceae, Passifloraceae s.s., and Malesherbiaceae lacked EFNs and was characterized by solitary homostylous flowers, with well developed peduncles and pedicels, and cream petals. The appearance of EFNs, distylous flowers and racemes probably provided greater chances of colonizing new habitats and would have contributed to increase the diversity of these lineages. This study also provides a first phylogenetic context to assess the evolution of ploidy in Turneraceae, previously focused mainly on the *Turnera sidoides* complex and ser. *Turnera*.

The genus *Turnera* is geographically diverse, with lineages ecologically associated/restricted to different phytogeographic domains. For example: ser. *Sessilifoliae* and ser. *Leiocarpae* occur mainly in the Cerrado; ser. *Papilliferae* in the Caatinga; and the new genus *Oxossia* occurs predominantly in the Atlantic forest. Nevertheless, little is known about the distribution and ecological preferences of the Amazonian lineages of *Turnera* (e.g., ser. *Annulares*, ser. *Anomalae*, ser. *Salicifoliae*, and ser. *Stenodictyae*). Representative groups from Amazonia have been assessed for more than two decades (e.g., Arbo, 1997, 2005), but recent collections are few and any inference about their distribution would be hasty; furthermore, obtaining quality DNA of these plants was shown to be difficult. Therefore, studies with more species from Amazonia may provide new insights on the systematics, evolution, and biogeography of *Turnera*.

## 6. Taxonomic implications

Below, we provide an identification key for the American genera of Turneraceae (modified from Arbo, 2007). The new genus *Oxossia* is described along with comments and a list of species with nomenclature changes provided. Finally, an identification key (modified from Arbo, 2000, 2008) for the species of *Oxossia* is presented.

### 6.1. Key to the American genera of Turneraceae

- 1 Indument with porrect-stellate tector trichomes; corona on petals and sepals ..... *Piriqueta*
- 1'. Indument sometimes with stellate tector trichomes, never porrect-stellate tector trichomes; corona absent, rarely a membranous ligule, but then only on petals ..... 2
  - 2 Sepals free from each other or almost so ....
  - ..... 3
  - 2'. Sepals fused to each other, usually by 1/3 of their length ....
  - ..... 4
- 3 Trees, 7–30 m tall. Flowers with petals 6–8(–10) cm long. Fruits 1.5–2 mm wide ..... *Erblichia*
- 3'. Shrubs, ca. 1.1 m tall. Flowers with petals < 6 cm long. Fruits ca. 9 mm wide ..... *Pibiria*
- 4 Plants without glandular trichomes. Flowers homostylous; petals with colleters along the margins; styles divergent at base ....
- ..... *Adenoa*
- 4'. Plants often with glandular trichomes. Flowers heterostylous, rarely homostylous; petals without colleters along the margins; styles parallel at base ..... 4

- 5 Stipules often conspicuous. Petals white with yellow base or, when yellow, pink, or red, the stamens are pilose and only basi-dorsiventrally adnate to the floral tube ..... *Oxossia*
- 5'. Stipules often inconspicuous. Petals usually yellow, when white, the stamens are glabrous and/or with margins adnate to the petal claws, forming nectariferous pockets ..... *Turnera*

*Oxossia* L.Rocha, gen. nov. = *Turnera* ser. *Capitatae* Urb. p.p., Bot. Jahrb. Syst. 25, Beibl., 2: 129. 1883a – Type: *O. capitata* (Cambess.) L.Rocha (= *Turnera capitata* Cambess.).

= *Turnera* ser. *Conciliatae* Arbo, Bonplandia, 17(2): 307. 2008 – Type: *Turnera rubrobracteata* Arbo.

Subshrubs to shrubs, rarely trees, up to 3 m high, with simple tector and microcapitate, sessile-capitate glandular trichomes. Stipules usually conspicuous (up to 9 mm long), persistent. Leaves medium to large (2–21.5 cm long); extrafloral nectaries basilaminar or petiolar, rarely absent. Inflorescences elongated to abbreviated racemes, head-like, spike-like, terminal or lateral, rarely solitary flower, in this case, sometimes gathered at the apex of brachyblasts; peduncle absent or developed, in the latter case, partially to completely adnate to the petiole (epiphyllous flower); bracts often present; prophylls 2, opposite, at the calyx base; pedicel absent or inconspicuous. Flowers heterostylous, usually small; sepals proximally fused by 1/3–1/2(–2/3); lobes narrow-triangular; petals usually white with yellow base, sometimes totally yellow, rarely pink or red; corona absent, rarely a membranous ligule at the apex of the petal claw; stamens pilose, rarely glabrous, filaments free from each other, rarely irregularly connate at different heights above adnation, basi-dorsiventrally adnate to the floral tube, anthers ovate, dorsifixed; ovary pilose, styles pilose, stigma lobed or brush-like. Fruit globose to ovoid; exocarp smooth-warted, granulate, punctate or smooth. Seeds obovoid to pyriform, curved, seed coat (episperm) reticulate or striate-reticulate; reticule areoles usually with point-shaped depressions; epidermis smooth or papillose; chalaza pulvinate, surface concave, exceptionally obtuse with surface not concave; aril lobulate or laciniate, sometimes pilose.

*Oxossia* consists of 15 species, all species (11) previously classified in *Turnera* ser. *Capitatae*, two species from ser. *Microphyllae*, one from ser. *Annulares*, and one from ser. *Conciliatae* (Arbo, 2000, 2008). They are predominantly shrubs from rainforests in the Atlantic forest and Amazon domains, with some species occurring in seasonally dry tropical forests of Caatinga and in campos rupestres (rocky grasslands) of Cerrado (*Oxossia annularis*, *O. calyptrocarpa*, and *O. hebetepetala*). The name of the genus refers to Oxossi, a divinity of African mythology who lives in forests (Barbosa Junior, 2014), like most species of this new genus.

The new genus can be recognized by the usually conspicuous stipules, the small flowers in congested inflorescences, styles and stamens usually pilose, with stamens adnate to the floral tube only basi-dorsiventrally. *Oxossia* can be divided into two morphological groups: one with white petals, yellow towards the base, and the other with yellow, pink, or red petals. In contrast, in the few species of *Turnera* with white petals, the stipules are inconspicuous, the stamens and styles glabrous (ser. *Leiocarpae*), and the stamens are sometimes marginally fused to the petal claw, forming nectariferous pockets (ser. *Anomalae* and ser. *Turnera*). The species of *Oxossia* with yellow, pink, or red petals resemble those of the ser. *Anomalae* and ser. *Leiocarpae*; but in ser. *Anomalae*, the floral structure is different (see the discussion above), and in ser. *Leiocarpae*, the stipules are almost always inconspicuous and the exocarp is smooth.

## 6.2. New combinations in *Oxossia*

*Oxossia albicans* (Urb.) L.Rocha, **comb. nov.** = *Turnera albicans* Urb., Jahrb. Königl. Bot. Gart. Berlin, 2: 135. 1883a – Type: Brazil, Bahia, in sylvis umbrosis prope Ilheos [Ilhéus], Feb 1822, L. Riedel 743 [lectotype: LE; isolectotypes: BR barcode BR0000005420995 (photo!), C, F barcode V0074078F (photo!), G barcode G00357408 (photo!), K barcode K000373154 (photo!), P barcode P00506567 (photo!), P barcode P00715471 (photo!), P barcode P00715472 (photo!), S barcode S04-580 (photo!), W barcode 1888-0000248 (photo!); designated by Arbo, 2000].

*Oxossia annularis* (Urb.) L.Rocha, **comb. nov.** = *Turnera annularis* Urb. var.  $\alpha$ , Jahrb. Königl. Bot. Gart. Berlin, 2: 124. 1883a – Type: Brazil, Rio de Janeiro, Jurujuba, près de la mer, fl jaunes, 19 Oct 1873, A. Glaziou 6812 [lectotype: P barcode P00715474 (photo!); isolectotypes: C, K barcode K000373173 (photo!), K barcode K000373172

(photo!); P barcode P00715475 (photo!), P barcode P00715476 (photo!); B destroyed, F barcode F0BN013565 (photo!); designated by Arbo, 2000].

= *Turnera annularis* var. *conglomerata* Urb., Jahrb. Königl. Bot. Gart. Berlin, 2: 124. 1883a – Type: Brazil, Bahia, prope Cachoeira, J. Casaretto 2074 [lectotype: P barcode P00506573 (photo!); designated by Arbo, 2000]

*Oxossia calyptrocarpa* (Urb.) L.Rocha, **comb. nov.** = *Turnera calyptrocarpa* Urb., Jahrb. Königl. Bot. Gart. Berlin, 2: 128. 1883a – Type: Brazil, Bahia, partie Mérédionale, Pouço d'Areia, Jun 1844, J.S. Blanchet 3863 [lectotype: BR barcode BR0000005420834 (photo!); isolectotypes: BS-ML barcode BS-ML000624777 (photo!), F barcode F0077450F (photo!), K barcode 000,373,167 (photo!), P barcode P00715487 (photo!), P barcode P00715488 (photo!), P barcode P00715489 (photo!); designated by Arbo, 2000].

*Oxossia capitata* (Cambess.) L.Rocha, **comb. nov.** = *Turnera capitata* Cambess. in Fl. Bras. Merid., 2: 215. 1830 – Type: Brazil, Minas Gerais, bords d'un bois près Pouso Alto, A. de Saint Hilaire 562 [lectotype: P barcode P00506569 (photo!); designated by Arbo, 2000].

= *Turnera capitata* Cambess. subsp. *capitata* f. *rufescens* Urb., Jahrb. Königl. Bot. Gart. Berlin, 2: 134. 1883a – Type: Brazil, São Paulo, in fruticetis montosis prope Bananal, Oct 1833, L. Riedel 1402 [lectotype: LE; isolectotypes: K barcode K000373156 (photo!), M barcode M0113131 (photo!), P barcode P00506568 (photo!), P barcode P00715493 (photo!), P barcode P00715492 (photo!); B destroyed, F barcode F0BN013570 (photo!); designated by Arbo, 2000].

*Oxossia dasystyla* (Urb.) L.Rocha, **comb. nov.** = *Turnera dasystyla* Urb., Bot. Jahrb. Syst. 25, Beibl. 40: 10. 1898 – Type: Brazil, Minas Gerais, Barra, Ouro Preto, terreno pedregoso, 1893, F.M. Magalhães-Gomes s.n. [holotype: B destroyed; lectotype: OUPR (EM) (photo!); designated by Arbo, 2000].

*Oxossia hatschbachii* (Arbo) L.Rocha var. *hatschbachii*, **comb. nov.** = *Turnera hatschbachii* Arbo var. *hatschbachii*, Bonplandia, 10(1–4): 27. 2000 – Type: Brazil, Espírito Santo, municipality Domingos Martins, Chapéu, Rio Jucu, Braço Norte, 8 Nov 1993, G. Hatschbach & M. Hatschbach 59,722 [holotype: MBMI; isotype: CVRD, CTES!, MBML, R, SP, SPF, VIES].

*Oxossia hatschbachii* var. *miniata* (Arbo) L.Rocha, **comb. nov.** = *Turnera hatschbachii* var. *miniata* Arbo, Bonplandia, 10(1–4): 29. 2000 – Type: Brazil, Espírito Santo, municipality Domingos Martins, Chapéu, Rio Jucu, Braço Norte, 8 Nov 1993, G. Hatschbach & M. Hatschbach 59,721 [holotype: MBMI; isotype: CTES!].

*Oxossia hebetepetala* (Urb.) L.Rocha, **comb. nov.** = *Turnera hebetepetala* Urb., Jahrb. Königl. Bot. Gart. Berlin, 2: 127. 1883a – Type: Brazil, Piauí, prope Oeiras, Apr 1839, G. Gardner 2062 [lectotype: K barcode K000373170 (photo!); isolectotypes: BS-ML barcode BS-ML000624776 (photo!), FI barcode FI004356 (photo!), G barcode G00357471 (photo!), K barcode K000373171 (photo!); P barcode P00715534 (photo!), P barcode P00715535 (photo!), NY barcode NY00110369 (photo!), US barcode US00114927 (photo!), W; designated by Arbo, 2000].

*Oxossia maracasana* (Arbo) L.Rocha, **comb. nov.** = *Turnera maracasana* Arbo, Bonplandia, 10(1–4): 29. 2000 – Type: Brazil, Bahia, municipality Maracás, Rod. BA-250, Faz. dos Pássaros a 24 km E de Maracás, 4 May 1979, S.A. Mori & T.S. dos Santos 11,774 [holotype: CEPEC!; isotypes: CTES!, MO, NY].

*Oxossia marmorata* (Urb.) L.Rocha, **comb. nov.** = *Turnera marmorata* Urb., Bot. Jahrb. Syst. 25, Beibl., 60: 9. 1898 – Type: Brazil, Bahia, ad Nazareth [Nazaré], s.d., F. Sellow s.n. [holotype: B destroyed, F barcode F0BN013591 (photo!); lectotype: K barcode K000373182 (photo!); designated by Arbo, 2000].

*Oxossia pernambucensis* (Urb.) L.Rocha, **comb. nov.** = *Turnera pernambucensis* Urb., Jahrb. Königl. Bot. Gart. Berlin, 2: 133. 1883a – Type: Brazil, Pernambuco, Catucá (aprox. 48 km a W de Recife), shady woods, Nov 1837, G. Gardner 1154 [lectotype: K barcode K000373158 (photo!); isolectotypes: K barcode K000373157 (photo!), B destroyed, F

barcode F0BN013596 (photo!); designated by Arbo, 2000].

*Oxossia princeps* (Arbo) L.Rocha, comb. nov. = *Turnera princeps* Arbo, Bonplandia, 10(1–4): 35. 2000 – Type: Minas Gerais, Serra do Espinhaço, ca. 22 km E of Diamantina, 15 Mar 1970, H.S. Irwin, S.F. da Fonseca, R. Souza, R.R. dos Santos & J. Ramos 27,623 [holotype: UB!; isotypes: CTES!, NY barcode NY00452420 (photo!)].

= *Turnera capitata* subsp. *intermedia* Urb., Jahrb. Königl. Bot. Gart. Berlin, 2: 135. 1883a – Type: Brazil, without location and date, *Martius Herbarium* without number. [lectotype: BR barcode BR0000005420520 (photo!); designated by Arbo, 2000]. The type material may have been collected by the prince Maximilian A.P. zu Wied-Neuwied (Urban, 1883b; Arbo, 2000).

*Oxossia rubrobracteata* (Arbo) L.Rocha, comb. nov. = *Turnera rubrobracteata* Arbo, Bonplandia, 7(1–4): 90. 1993 – Type: Brazil. Espírito Santo, Rio Pancas, Colatina, 8 Dec 1943, J.G. Kuhlmann 6656 (holotype: RB!).

*Oxossia schomburgkiana* (Urb.) L.Rocha, comb. nov. = *Turnera schomburgkiana* Urb., Jahrb. Königl. Bot. Gart. Berlin, 2: 132. 1883a – Type: Guyana [Venezuela (Steyermark, 1981)], Roraima, 1842–1843, R.H. Schomburgk 624 [lectotype: P barcode P00506571 (photo!); isotypes: BM barcode BM000839154 (photo!), K barcode K000373159 (photo!), G barcode G00357449 (photo!), W barcode 0,074,777 (photo!), W barcode 1889–0017800 (photo!); designated by Arbo, 2000].

*Oxossia spicata* (L.Rocha & Arbo) L.Rocha, comb. nov. = *Turnera spicata* L.Rocha & Arbo, Phytotaxa, 343: 168. 2018 – Type: Brazil, Espírito Santo, Linhares, Reserva da Companhia Vale do Rio Doce, 11 Apr 2006, J. Paula-Souza et al. 5733 (holotype: RB!; isotypes: CTES!, CVRD, ESA!, ICN!, SPF!, VIES).

*Oxossia waltherioides* (Urb.) L.Rocha, comb. nov. = *Turnera waltherioides* Urb., Repert. Spec. Nov. Regni Veg., 13: 158. 1914 – Type: Brazil, Rio Branco [Roraima], Surumu, Serra de Mairary, Sep 1909, E. Ule 8421 (holotype: B, destroyed, F barcode F0BN013611 (photo!); lectotype: K barcode K000373209 (photo!); isotypes: G barcode G00357437 (photo!), L barcode L.2465981 (photo!), U barcode U0006950 (photo!); designated by Arbo, 2000].

### 6.3. Identification key to species of *Oxossia*

1. Plants with sessile-capitate glandular trichomes, conspicuous on both sides of prophylls and exocarp ..... 2
- 2' Plants with microcapitate glandular or only simple tector trichomes on both sides of prophylls and exocarp ..... 5
- 5 2 Flowers in dense and head-like racemes; bracts ovate to obovate. Exocarp smooth ..... *O. annularis*
- 3' Flowers solitary or in brachyblasts; bracts absent. Exocarp granulate ..... 3
- 3 Leaves discolored, obovate, elliptic, rarely ovate, marginally serrate-crenate almost down to the base. Seeds with a point-shaped depression per areole ..... *O. calyptrocarpa*
- 3' Leaves usually concolor, narrow-obovate, marginally dentate, with only 1–4 pairs of teeth at the apical portion. Seeds without point depression ..... *O. hebetepetala*
- 5 Bracts reddish or purple, even when dry. Petals pink. Filaments irregularly connate at different heights above adnation .... *O. rubrobracteata*
- 5' Bracts and petals with other colors. Filaments free from each other ..... 6
- 6 Petals yellow. Inflorescences axillary. Amazon .... 7
- 6' Petals white, rarely yellow (*O. marmorata*) or red (*O. hatschbachii* var. *miniata*). Inflorescences terminal or axillary. Atlantic forest or

Caatinga ..... 8

7. Leaves chartaceous, wide-elliptic to lanceolate, upper surface sparse-pilose, lower surface tomentose. External bracts with slightly pedunculate nectaries. Longitudinal seed coat ridges slightly more prominent than transversal ones ..... *O. schomburgkiana*

7' Leaves coriaceous, ovate, ovate-elliptic or obovate, both surfaces tomentose-velutinous. External bracts with sessile nectaries. Longitudinal seed coat ridges clearly prominent, the transversal ones almost invisible ..... *O. waltherioides*

8. Stipules 1.5–9 mm long, margins usually laciniate to incised. Petals with a ligule between the claw and blade .....

... 9

8' Stipules 0.5–1.5(–2) mm long, margins entire. Petals without ligule (except for a flat ligule in *O. capitata*) .....

12

9. Extrafloral nectaries 0.2–0.3 mm diam., only a pair per leaf, sometimes absent. Calyx 7–9 mm long; corolla 11–14 mm long .... *O. maracasana*

9' Extrafloral nectaries 0.5–1 mm diam., > 1 pair per leaf. Calyx 5–6 mm long; corolla 5.5–8 mm long .....

..... 10

10 Leaves elliptic, obovate to wide-ovovate, both surfaces pilose .... *O. princeps*

10' Leaves lanceolate, upper surface glabrous to subglabrous, lower surface sparse-pilose ..... 11

11. Shrubs to 1.2 m tall; petals white, with a cylindrical ligule; ovary glabrous or subglabrous at base and pilose at apex .... *O. hatschbachii* var. *hatschbachii*

11' Little trees to 3 m tall; petals red, with a flat ligule; ovary pilose .....

..... *O. hatschbachii* var. *miniata*

12. Leaves pilose, sometimes tomentose on the lower surface. Long-styled flowers with styles arched or geniculate at the middle portion ....

..... 13

12' Leaves subglabrous or with tector trichomes at the main veins and margins. Long-styled flowers with styles straight .....

..... 15

13. Leaves slightly serrate along the margins; upper surface glabresent to dense-strigose. Fruit valves without an apical horn-like appendix ..... *O. pernambucensis*

13' Leaves serrate or crenate-serrate along the margins, upper surface dense-pilose. Fruit valves with an apical horn-like appendix ....

..... 14

14. Leaves ovate-oblong, elliptic or lanceolate. Bracts elliptic-lanceolate to linear. Flowers heterostylous; petals with a flat ligule ....

..... *O. capitata*

14' Leaves ovate or ovate-elliptic. Bracts ovate, obovate to lanceolate. Flowers homostylous; petals without ligule ....

..... *O. dasystyla*

15. Prophylls linear. Flowers short-pedunculate, peduncle 1–2.2 mm long. Petals yellow .....

..... *O. marmorata*

15' Prophylls lanceolate, obovate to spatulate. Flowers sessile or peduncles up to 1 mm long. Petals white, yellow towards the base ....

..... 16

16. Plants with microcapitate glandular trichomes. Bracts ovate or lanceolate; prophylls lanceolate. Flowers in abbreviate spike-like racemes .....

..... *O. spicata*

16' Plants without glandular trichomes. Bracts subcircular or wide-ovate; prophylls obovate or spatulate. Flowers in globular head ....

..... *O. albicans*

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## Appendix. Supplementary material

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