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Delving deeper into the phylogenetics of the herbaceous bamboos (Poaceae, Bambusoideae, Olyreae): evaluation of generic boundaries within the *Parodiolyra/Raddiella* clade uncovers a new genus

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The present study aims to expand the knowledge of phylogenetic relationships in Olyrinae, a subtribe of herbaceous bamboos (Poaceae: Bambusoideae: Olyreae). Our focus is on *Parodiolyra* and *Raddiella*, two historically related genera that, with their sister *Diandrolyra*, form one of the four main lineages in the subtribe. Previous phylogenetic analyses suggested that *Parodiolyra* is not monophyletic, but its taxonomic boundaries and its relationship with *Raddiella* remain uncertain due to low sampling. We increased the taxon sampling and sequenced five regions of the nuclear and plastid genomes for this lineage and other representatives of Olyreae. We used maximum parsimony, maximum likelihood, Bayesian inference and coalescence analysis. Our results corroborate the paraphyly of *Parodiolyra*, with *P. micrantha* sister to a clade including the remaining *Parodiolyra* and *Raddiella*. All remaining *Parodiolyra* form a well-supported clade, but *Raddiella* had conflicting resolutions, being either monophyletic or not. Thus, based on phylogenetic and morphological evidence, we here recircumscribe *Parodiolyra*, transferring *P. micrantha* and *P. colombiensis* to the new genus *Taquara* (described here). Regarding *Raddiella*, sampling is still not comprehensive and does not allow a decision on to its taxonomic status to be made at this time. Inclusion of other phreatophytic species may be crucial to resolve the problem of conflicting topologies.

ADDITIONAL KEYWORDS: coalescent analysis – grasses – molecular data – Neotropics – taxonomy – *Taquara*.

INTRODUCTION

Herbaceous bamboos (Olyreae) constitute a monophyletic group in Poaceae subfamily Bambusoideae (BPG, 2012; Oliveira *et al.*, 2014; Kellogg, 2015; Soreng *et al.*, 2017). They currently comprise 22 genera and 123 species almost exclusive to the Neotropics, occurring from Mexico and the Caribbean to northern Argentina and Paraguay (Ferreira *et al.*, 2013; Oliveira *et al.*, 2014; Vorontsova *et al.*, 2016; Clark & Oliveira, 2018). Members of Olyreae mainly inhabit forest edges or understory, but less commonly occur in open, humid areas (Soderstrom, 1984; Judziewicz *et al.*, 1999; Ferreira *et al.*, 2013;

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Oliveira *et al.*, 2014; Clark, Londoño & Ruiz-Sanchez, 2015; Clark & Oliveira, 2018). Brazil has the greatest diversity of Olyreae, especially in the Atlantic Forest, one of the 25 global biodiversity hotspots (Soderstrom, Judziewicz & Clark, 1988; Clark, 1990; Myers *et al.*, 2000; Oliveira, Longhi-Wagner & Jardim, 2011; BFG, 2015).

Olyreae are monoecious and mostly perennial plants with well-developed and shortly pseudopetiolate leaf blades (Judziewicz *et al.*, 1999; BPG, 2012). They differ from woody bamboos by the lack of well-differentiated culm leaves and outer ligules (contraligules) combined with relatively weakly lignified culms, restricted vegetative branching and their predominantly unisexual, one-flowered spikelets (Clark *et al.*, 2015; Kellogg, 2015). Some genera display extensive variation in vegetative characters, and the grouping of spikelets in racemose, paniculate or spiciform synflorescences and synflorescence position along the body of the plant help characterize generic boundaries (Judziewicz *et al.*, 1999; Oliveira *et al.*, 2011, 2014).

Three subtribes are currently accepted in Olyreae: Buergersiochloinae; Olyrinae and Parianinae (Judziewicz & Clark, 2007; Oliveira *et al.*, 2014; Clark *et al.*, 2015; Kellogg, 2015). Buergersiochloinae are monotypic and endemic to New Guinea, whereas the other two are mostly restricted to the Neotropics and comprise the vast majority of the diversity in the tribe, especially concentrated in Olyrinae (18 genera and 88 species) (Oliveira *et al.*, 2014; Clark & Oliveira, 2018).

Several phylogenetic studies have focused on bamboos and included members of Olyreae (e.g. Sungkaew *et al.*, 2009; Triplett & Clark, 2010; Kelchner & BPG, 2013; Wysocki *et al.*, 2015; Saarela *et al.*, 2018), but the most comprehensive phylogenetic tree to date for the tribe is that of Oliveira *et al.* (2014). In that study, four main lineages were recovered in Olyrinae, one composed of the genera *Raddia* Bertol. and *Sucrea* Soderstr., one of *Piresia* Swallen and *Reitzia* Swallen, one of *Arberella* C.E.Calderón & Soderstr., *Cryptochloa* Swallen, *Lithachne* P.Beauv. and *Olyra* L. and one of *Diandrolyra* Stapf, *Parodiolyra* Soderstr. & Zuloaga and *Raddiella* Swallen, which is the main focus of the present work.

Diandrolyra, *Parodiolyra* and *Raddiella* have a connection with *Olyra*, either morphologically or nomenclaturally (Soderstrom & Zuloaga, 1989). *Diandrolyra*, the earliest described among them (Stapf, 1906), includes just three species endemic to the understory of lowland forests in the Brazilian Atlantic Forest. These species are characterized by usually specialized flowering culms, composed of a single leaf with the blade inverted, covering the contracted synflorescence containing both female and male spikelets, the latter with two stamens (Judziewicz *et al.*, 1999; Oliveira & Clark, 2009; Kellogg, 2015). *Raddiella*, described by Swallen (1948), includes eight tiny species, most of them rare, found in savannas or forest margins or among wet rocks near rivers and waterfalls (phreatophytes) from near sea level to 1500 m. This genus is characterized by decumbent and monomorphic culms, unisexual synflorescences and female spikelets with filiform pedicels, three-nerved glumes and smooth, white, indurate anthoecia (Zuloaga & Judziewicz, 1991; Clark *et al.*, 2015). *Parodiolyra*, described by Soderstrom & Zuloaga (1989), includes six species of erect to scandent plants that may reach up to 4 m tall, and are found in forests, or occasionally in savannas, from sea level to 1200–1800 m, from Costa Rica to Bolivia and Brazil (Judziewicz *et al.* 1999, 2000). They are characterized by the presence of firm culms, female spikelets that disarticulate below the glumes, filiform pedicels, inflated internodes between the glumes and a shortened hilum (Judziewicz *et al.*, 1999; Zuloaga & Davidse, 1999; Grande Allende, 2011; BPG, 2012).

Although *Diandrolyra*, *Raddiella* and *Parodiolyra* seem distinctive in general appearance, a close relationship among them had been hypothesized previously by Soderstrom & Zuloaga (1989) based on the presence of female spikelets with filiform pedicels that disarticulate below the glumes, an inflated and conspicuous internode between the glumes and a caryopsis with a shortened hilum. The molecular phylogenetic study of Oliveira *et al.* (2014) corroborated this hypothesis, recovering *Diandrolyra* as monophyletic and sister to the clade composed of *Parodiolyra* + *Raddiella*. These authors also showed that *Parodiolyra* might not be monophyletic, with *P. micrantha* (Kunth) Davidse & Zuloaga as sister to a clade formed by *P. ramosissima* (Trin.) Soderstr. & Zuloaga and *Raddiella esenbeckii* (Steud.) C.E.Calderón & Soderstr. However, these were the only species sampled, and only one plastid (*trnD–trnT*) region and one nuclear (ITS) DNA region were analysed.

Parodiolyra and *Raddiella* are both widely distributed in the Neotropics, mainly due to the ranges of *P. micrantha* and *R. esenbeckii*, respectively. These species, however, are also highly variable in morphology, raising questions about their delimitation, as mentioned by Oliveira *et al.* (2014). The relationship between these two genera was discussed by Zuloaga & Judziewicz (1991), who emphasized that *R. esenbeckii* is more similar to *P. lateralis* (J.Presl ex Nees) Soderstr. & Zuloaga than to its phreatophytic congeners, leading to problems in the delimitation of the two genera. Recently, Grande Allende (2016) expanded the circumscription of *Raddiella* by the inclusion of *Parodiolyra* in its synonymy, making it highly heterogeneous. However, his decision was based

only on morphology, and therefore the evolutionary relationships among these genera and their species remain uncertain.

Thus, the objective of the present work is to provide a better, phylogenetically based circumscription for *Parodiolyra* and *Raddiella*, based on the following questions. (1) Are *Parodiolyra* and *Raddiella* monophyletic genera? (2) Are there supported relationships in and between *Parodiolyra* and *Raddiella*? (3) What is the correct phylogenetic placement of *Parodiolyra micrantha*? (4) What are the taxonomic implications of the molecular analyses herein presented? To answer these questions, we have increased the taxon sampling and the number of DNA regions analysed for the clade composed on these genera and tested the topologies of the resulting phylogenetic trees, with an emphasis on testing the monophyly of both *Parodiolyra* and *Raddiella*. These results allow us to make more confident taxonomic decisions regarding some generic boundaries and provide a more stable classification for the group.

MATERIAL AND METHODS

Taxon sampling

Fourteen genera and 42 species currently accepted for Olyreae were sampled (following BPG, 2012; Vorontsova *et al.*, 2016; Clark & Oliveira, 2018), including multiple accessions for some taxa of interest. Species (number sampled/total number in the genus) of *Eremitis* Döll (4/5), *Pariana* Aubl. (3/27), *Parianella* Hollowell, F.M.Ferreira & R.P.Oliveira (2/2) (subtribe Parianinae) and *Arberella* (1/7), *Cryptochloa* (2/9), *Diandrolyra* (2/3), *Lithachne* (2/4), *Olyra* (4/25), *Parodiolyra* (4/6), *Piresia* (2/5), *Raddia* (9/9), *Raddiella* (3/8) and *Sucrea* (3/3) (subtribe Olyrinae) were selected as ingroup taxa (Table 1). The New Guinean *Buergersiochloa bambusoides* Pilg. (Buergersiochloinae) was chosen as the outgroup.

Most samples were already available from previous studies done by our bamboo research team (Oliveira, 2001; Oliveira *et al.*, 2014; Carvalho *et al.*, unpubl. data; Ferreira *et al.*, 2019). New samples, especially of *Parodiolyra* and *Raddiella*, were obtained either through field work or from herbarium specimens (Table 1). Specimen acquisition was performed following the procedures described by Bridson & Forman (1998) and Soderstrom & Young (1983), including preservation of leaves in silica gel for DNA extraction (Chase & Hills, 1991).

DNA extraction, amplification and sequencing

Samples dehydrated in silica gel were extracted using the 2× CTAB protocol (Doyle & Doyle, 1987), modified for microtubes. For herbarium material, we used the extraction kits DNeasy Plant Mini Kit (QIAGEN, GmbH, Hilden, Germany) and ReliaPrep gDNA Tissue Miniprep System (Promega, Madison, WI, USA), following the manufacturer's protocols. All samples are stored in the DNA bank of the Plant Molecular Systematics Laboratory (LAMOL) of the State University of Feira de Santana, Bahia, Brazil.

The regions *trnD–trnT*, *trnS–trnG*, *rpl32–trnL* and *ndhF* from the plastid genome and ITS1–5.8S–ITS2 (ITS) of the nuclear genome were amplified via PCR (Table 2). These markers were selected because they were found to be informative for phylogenetic reconstruction in bamboos (Clark, Zhang & Wendel, 1995; Ferreira, 2012; Carvalho, 2013; Oliveira *et al.*, 2014). PCR reactions were performed using the TopTaq Master Mix Kit (QIAGEN, GmbH, Hilden, Germany) following the manufacturer's protocol with an adjustment for a final volume of 10 µL. ITS reactions also included 0.2 µL of bovine serum albumin 0.3%, 2 µL of betaine 5 M and 0.2 µL of dimethyl sulphoxide 99.5%. Primers used for amplification and sequencing and PCR conditions for each region are presented in Table 2.

PCR products were purified using the enzymes exonuclease I and shrimp alkaline phosphatase (EXOSAP kit, GE Healthcare) or PEG 20% (polyethylene glycol; Paithankar & Prasad, 1991) and sequenced in both directions using the Big Dye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems, Austin, TX, USA) according to the following protocol: a hot start with 3 min of initial denaturation at 96 ºC, 30 cycles of 96 ºC denaturation for 15 s, 50 ºC annealing for 10 s and 60 ºC extension for 4 min. Sequenced products were cleaned using isopropanol 80% and ethanol 70%, and analysed on a 3130xl Genetic Analyzer (Applied Biosystems/HITACHI, Tokyo, Japan).

Phylogenetic analysis

Raw sequence reads were edited using the Staden Package v.2.0.0b10 released (Staden, Beal & Bonfield, 1999) or Geneious Pro v.4.8.4 (Biomatters, Auckland, New Zealand) and assembled in individual matrices for each region, which were first aligned using the GUIDANCE Web Server (Penn *et al.*, 2010), using the algorithm MAFFT and then manually checked. The data sets were analysed individually and in combination using maximum parsimony (MP), Bayesian Inference (BI) and maximum likelihood (ML) (Table 3). A multispecies coalescence analysis was also carried out. Gaps were considered as missing data.

MP analyses were performed in PAUP* 4.0b10a (Swofford, 2002) with Fitch parsimony as the optimality criterion (Fitch, 1971). The heuristic search was conducted using the TBR (tree bisection-reconnection) algorithm, with 1000 replications

Table 1. Samples used in the present study, with vouchers and accession numbers for the ITS, *trnD–trnT*, *trnS–trnG*, *rpl32–trnL* and *ndhF* sequences from GenBank. (--) indicates missing data, (**) indicates herbarium material and italicized accession numbers indicates new sequences generated in this study

Species	VOUCHER	ITS	*trnD–trnT*	*trnS–trnG*	*rpl32–trnL*	*ndhF*
Outgroup						
Buergersiochloinae						
Buergersiochloa bambusoides Pilg.	*Dransfield 1365* (K)	KC990734	FJ643988	KX027403	KY612930	----------
		----------	----------	----------	----------	AF182341.1
Ingroup						
Parianinae						
Eremitis afimbriata F.M.Ferreira & R.P.Oliveira	*Ferreira 2196* (HUEFS)	KX016075	KX016043	*MK175382*	KY612894	*MK175271*
Eremitis linearifolia Hollowell, F.M.Ferreira & R.P.Oliveira	*Ferreira 2185* (HUEFS)	KX016085	KX016050	----------	KY612904	*MK175272*
Eremitis magnifica F.M.Ferreira & R.P.Oliveira	*Ferreira 2158* (HUEFS)	KX016086	KX016051	----------	KY612905	*MK175273*
Eremitis robusta Hollowell, F.M.Ferreira & R.P.Oliveira	*Ferreira 2215* (HUEFS)	KX016093	KX016056	----------	KY612912	----------
Pariana nervata Swallen	*Oliveira 1876* (HUEFS)	KX016099	KX016060	*MK175385*	KY612919	*MK175278*
Pariana pallida Swallen	*Oliveira 1194* (HUEFS)	----------	FJ644017	*MK175386*	KY612920	*MK175279*
Pariana vulgaris Tutin	*Oliveira 1844* (HUEFS)	KY674523	KY659797	*MK175387*	*MK175320*	*MK175280*
Parianella carvalhoi (R.P.Oliveira & Longhi-Wagner) F.M.Ferreira & R.P.Oliveira	*Mota 298* (HUEFS)	KX016105	KX016066	*MK175388*	KY612925	*MK175281*
Parianella lanceolata (Trin.) F.M.Ferreira & R.P.Oliveira	*Oliveira 681* (HUEFS)	KC990729	KC990763	KX027433	KY612927	*MK175282*
Olyrinae						
Arberella bahiensis Soderstr.& Zuloaga	*Jardim s.n.* (HUEFS)	KC990700	KC990735	MK175377	*MK175309*	----------
Cryptochloa capillata (Trin.) Soderstr.	*Oliveira 969* (HUEFS)	KC990710	KC990745	----------	----------	----------
	Silva 359 (HUEFS)	----------	----------	*MK175378*	*MK175310*	*MK175266*
Cryptochloa decumbens Soderstr. & Zuloaga	*Sánchez-Ken 664* (MO)	*MK175245*	*MK175358*	MK175379	*MK175311*	*MK175267*
Diandrolyra bicolor Stapf	*Oliveira 850* (HUEFS)	KC990727	KC990761	MK175381	*MK175313*	*MK175269*
Diandrolyra bicolor	*Oliveira 2278* (HUEFS)	*MK175246*	*MK175359*	*MK175380*	*MK175312*	*MK175268*
Diandrolyra tatianae Soderstr. & Zuloaga	*Oliveira 726* (HUEFS)	KC990728	KC990762	KX027406	*MK175314*	*MK175270*
Lithachne horizontalis Chase	*Viana 5202* (BHCB)	KC990706	KC990741	MK175383	*MK175315*	*MK175274*
Lithachne pauciflora (Sw.) P.Beauv.	*Oliveira 970* (HUEFS)	KC990707	----------	KX027407	*MK175316*	*MK175275*
	Clark 1297 (ISC)	----------	KC990741	----------	----------	----------
Olyra bahiensis R.P.Oliveira & Longhi-Wagner	*Oliveira 977* (HUEFS)	KC990705	KC990740	MK175384	*MK175317*	*MK175276*
Olyra glaberrima Raddi	*Verveloet 2206* (HUEFS)	KC990702	KC990737	KX027408	*MK175318*	*MK175277*
Olyra humilis Nees	*Longhi-Wagner 8001* (HUEFS)	KC990701	KC990736	KX027409	----------	----------
Olyra latifolia L.	*Oliveira 667* (HUEFS)	KC990704	KC990739	KX027410	*MK175319*	----------
	Londoño & Clark 911 (ISC)	----------	----------	----------	----------	U21971.1
Parodiolyra lateralis (J.Presl ex Nees) Soderstr. & Zuloaga	*Londoño & Clark 898* (US)	----------	*MK175360*	*MK175390*	*MK175322*	*MK175284*
Parodiolyra lateralis	*Cardoso 3362* (HUEFS)	----------	----------	*MK175389*	*MK175321*	*MK175283*
Parodiolyra luetzelburgii (Pilg.) Soderstr. & Zuloaga	*Oliveira 2330* (HUEFS)	----------	----------	----------	*MK175323*	*MK175285*
Parodiolyra luetzelburgii	*Oliveira 2335* (HUEFS)	----------	----------	----------	*MK175324*	*MK175286*
Parodiolyra micrantha (Kunth) Davidse & Zuloaga	*Oliveira 650* (HUEFS)	KC990713	KC990748	KX027411	*MK175330*	*MK175291*
Parodiolyra micrantha	*Oliveira 939* (HUEFS)	*MK175250*	*MK175366*	*MK175393*	*MK175331*	*MK175292*
Parodiolyra micrantha	*Oliveira 2258* (HUEFS)	*MK175249*	*MK175365*	*MK175392*	*MK175329*	*MK175290*

Table 1. *Continued*

Species	VOUCHER	ITS	*trnD–trnT*	*trnS–trnG*	*rpl32–trnL*	*ndhF*
Parodiolyra micrantha	*Oliveira 2249* (HUEFS)	*MK175248*	*MK175364*	*MK175391*	*MK175328*	*MK175289*
Parodiolyra micrantha	*Zanatta 13* (HUEFS)	*MK175247*	*MK175361*	----------	*MK175325*	*MK175287*
Parodiolyra micrantha	*Oliveira 2326* (HUEFS)	----------	*MK175362*	----------	*MK175326*	----------
Parodiolyra micrantha	*Oliveira 2336* (HUEFS)	----------	*MK175363*	----------	*MK175327*	*MK175288*
Parodiolyra ramosissima (Trin.) Soderstr. & Zuloaga	*Oliveira 688* (HUEFS)	KC990714	KC990749	MK175396	*MK175334*	*MK175295*
Parodiolyra ramosissima	*Oliveira 2252* (HUEFS)	*MK175252*	*MK175368*	*MK175395*	*MK175333*	*MK175294*
Parodiolyra ramosissima	*Silva 426* (HUEFS)	*MK175251*	*MK175367*	*MK175394*	*MK175332*	*MK175293*
Piresia goeldii Swallen	*Oliveira 1205* (HUEFS)	KC990708	KC990743	KX027413	*MK175335*	----------
Piresia sympodica (Döll) Swallen	*Oliveira 1195* (HUEFS)	KC990709	KC990744	KX027417	*MK175336*	----------
Raddia angustifolia Soderstr. & Zuloaga	*Oliveira 725* (HUEFS)	KC990715	KC990750	MK175397	*MK175337*	----------
Raddia brasiliensis Bertol.	*Oliveira 972* (HUEFS)	KC990716	KC990751	MK175398	----------	----------
Raddia distichophylla (Schrad. ex Nees) Chase	*Oliveira 601* (HUEFS)	KC990717	KC990752	MK175399	*MK175338*	----------
	Clark 1306 (ISC)	----------	----------	----------	----------	U22007.1
Raddia guianensis (Brongn.) Hitchc.	*Oliveira 911* (HUEFS)	KC990718	----------	MK175400	*MK175339*	----------
	Oliveira 993 (HUEFS)	----------	KC990753	----------	----------	----------
Raddia lancifolia R.P.Oliveira & Longhi-Wagner	*Oliveira 980* (HUEFS)	KC990719	KC990754	MK175401	*MK175340*	----------
Raddia megaphylla R.P.Oliveira & Longhi-Wagner	*Oliveira 981* (HUEFS)	KC990720	KC990755	MK175402	*MK175341*	----------
Raddia portoi Kuhlm.	*Oliveira 1042* (HUEFS)	KC990721	KC990751	MK175403	*MK175342*	----------
Raddia soderstromii R.P.Oliveira, L.G.Clark & Judz.	*Oliveira 722* (HUEFS)	KC990722	----------	KX027427	*MK175343*	----------
	Oliveira 993 (HUEFS)	----------	KC990757	----------	----------	----------
Raddia stolonifera R.P.Oliveira & Longhi-Wagner	*Oliveira 1078* (HUEFS)	*MK175253*	KC990758	MK175404	*MK175344*	----------
Raddiella esenbeckii (Steud.) C.E.Calderón & Soderstr.	*Oliveira 664* (HUEFS)	*MK175258*	KC990747	KX027428	*MK175352*	*MK175303*
Raddiella esenbeckii	*Longhi-Wagner s.n.* (HUEFS)	----------	*MK175372*	*MK175408*	*MK175348*	*MK175299*
Raddiella esenbeckii	*Silva 1441* (HUEFS)	----------	*MK175373*	*MK175409*	*MK175350*	*MK175301*
Raddiella esenbeckii	*Oliveira 1181* (HUEFS)	*MK175257*	*MK175374*	*MK175410*	*MK175351*	*MK175302*
Raddiella esenbeckii	*Silva 748* (HUEFS)	*MK175254*	*MK175369*	*MK175405*	*MK175345*	*MK175296*
Raddiella esenbeckii **	*Irwin 15566* (NY)	----------	----------	----------	*MK175349*	*MK175300*
Raddiella esenbeckii	*Silva 924* (HUEFS)	*MK175255*	*MK175370*	*MK175406*	*MK175346*	*MK175297*
Raddiella esenbeckii	*Silva 940* (HUEFS)	*MK175256*	*MK175371*	*MK175407*	*MK175347*	*MK175298*
Raddiella malmeana (Ekman) Swallen	*Silva1404* (HUEFS)	*MK175259*	KC990746	*MK175411*	*MK175353*	*MK175304*
*Raddiella malmeana***	*Londoño 317* (NY)	*MK175260*	----------	----------	*MK175354*	----------
Raddiella minima Judz. & Zuloaga	*Viana 2712* (INPA)	*MK175262*	*MK175376*	*MK175413*	----------	*MK175306*
Raddiella minima	*Viana 2634* (INPA)	*MK175261*	*MK175375*	*MK175412*	----------	*MK175305*
Sucrea maculata Soderstr.	*Oliveira 851* (HUEFS)	*MK175263*	----------	MK175414	*MK175355*	----------
	Clark & Zhang 1345 (ISC)	----------	FJ644061	----------	----------	AF182343.1
		----------	----------	----------	----------	----------
Sucrea monophylla Soderstr.	*Oliveira1072* (HUEFS)	*MK175264*	KC990759	KX027430	*MK175356*	*MK175307*
Sucrea sampaiana (Hitchc.) Soderstr.	*Oliveira 991* (HUEFS)	*MK175265*	KC990760	MK175415	*MK175357*	*MK175308*

Table 2. Summary of the DNA regions used: primer sequences, PCR amplification conditions and models used for each partition in Bayesian inference. PCR conditions for ITS and *trnD–trnT* follow Oliveira *et al.* (2014) and Carvalho (2013), for *ndhF* and *trnS–trnG* follow Silva *et al.* (2015) and for *rpl32–trnL* follow Carvalho (2013) and Ferreira *et al.* (2019)

Primer	Sequence	Reference	PCR conditions	Partitions from each data set	Pb	Models used to Bayesian Inference
ITS 92	AAG GTT TCC GTA GGT GAA C	Desfeaux *et al.*, 1996	1 cycle of initial denaturing: 94 °C for 3 min; 28 amplification cycles of denaturing: 94°C for 1 min; primer annealing: 50 °C for 1 min and chain extension: 72 °C for 7 min; 1 cycle of final extension: 72 °C for 7 min.	ITS 1	*282*	GTR+G
ITS 4	TCC TCC GCT TAT TGA TAT GC	White *et al.*, 1990		5.8 S	*164*	K80+I+G
				ITS 2	*271*	GTR+I+G
trnD	ACC AAT TGA ACT ACA ATC CC	Demesure, Sodzi & Petit, 1995	1 cycle of initial denaturing: 94 °C for 1 min; 30 amplification cycles of denaturing: 94°C for 30 s; primer annealing: 52 °C for 40 s and chain extension: 72 °C for 1 min and 10 s; 1 cycle of final extension: 72 °C for 5 min.	*trnD–trnT*	*1628*	GTR+G
trnT	CCC TTT TAA CTC AGT GGT A	Demesure *et al.*, 1995				
trnS	AGA TAG GGA TTC GAA CCC TCG GT	Shaw *et al.*, 2005	1 cycle of initial denaturing: 94 °C for 1 min; 30 amplification cycles of denaturing: 94°C for 30 s; annealing 52 °C a 40 s and chain extension: 72 °C a 1 min 10 s; 1 cycle of final extension: 72 °C for 5 min.	tRNA–Ser	405	GTR+I
trnG	GTA GCG GGA ATC GAA CCC GCA TC	Shaw *et al.*, 2005		*psbZ*	*189*	HKY+I
				psbZ–trnG	*338*	GTR+G
rpl32	CAG TTC CAA AAA AAC GTA CTT C	Shaw *et al.*, 2007	1 cycle of initial denaturing: 80 °C for 5 min; 30 amplification cycles of denaturing: 94°C for 1 min; primer annealing: 50 °C for 1 min and chain extension: 65 °C for 4 min; 1 cycle of final extension: 65 °C for 5 min.	*rpl32*: Codon 1	*54*	F81+G
				rpl32: Codon 2	*54*	HKY
trnL	CTG CTT CCT AAG AGC AGC GT	Shaw *et al.*, 2007		*rpl32*: Codon 3	*54*	GTR
				rpl32–trnL	*950*	GTR+G
972F	GTC TCA ATT GGG TTA TAT GAT G	Olmstead & Sweere (1994)	1 cycle of initial denaturing: 94 °C for 1 min; 35 amplification cycles of denaturing: 94°C for 30 s; primer annealing: 53 °C for 40 s and chain extension: 72 °C for 50 s; 1 cycle of final extension: 72 °C for 5 min.	*ndhF:* Codon 1	*234*	GTR+I+G
1660R	ATC CAA TGA ACA AAG TAA AAA	Aliscioni *et al.*, 2003		*ndhF:* Codon 2	*234*	GTR+G
				ndhF: Codon 3	*234*	GTR+I

Table 3. Summary of the phylogenetic analyses performed, based on four plastid and one nuclear DNA regions. Legend: *N* – number of samples analysed; Matrix – aligned matrix size; PIC – potentially informative character numbers for parsimony; % PIC – percentage of potentially informative characters for parsimony; NMPT – number of most-parsimonious trees; CI – consistency index and RI – retention index. Support values are provided for the clades, bootstrap for MP, bootstrap for ML and posterior probability for BI. — indicates an unrecovered relationship in the analysis

DNA Regions	*N*	Matrix	PIC / %PIC	NMPT	MP score	CI	RI	Olyrinae	*Taquara micrantha*	*Parodiolyra*	*Parodiolyra* + *R. malmeana*	*R. malmeana* + (*R. esenbeckii* + *R. minima*)
ITS	53	717	283 / 39.5	579	1045	0.56	0.80	64 / 73 / 0.82	100 / 100 / 0.99	100 / 100 / 1.0	— / — / —	— / — / —
rpl32–trnL	58	1112	185 / 16.6	390	390	0.79	0.94	86 / 92 / 1.0	99 / 100 / 1.0	0.93 / 99 / 1.0	— / — / —	73 / 97 / 0.88
Plastid (3) combined	61	3262	401 / 12.3	10 000	849	0.79	0.92	83 / 85 / 0.99	91 / 99 / 0.99	84 / 100 / 0.99	93/ 99 / 1.0	— / — / —

and random taxa addition, saving up to 15 trees per replication, with an upper limit of 10 000 trees. A second round of TBR swapping was performed on the resulting trees, keeping the upper limit of 10 000 trees. Statistical support was generated using non-parametric bootstrapping (Felsenstein, 1985) with 2000 replications (Hedges, 1992; Müller, 2005), simple taxon-addition and TBR, saving 15 trees per replicate.

ML analyses were conducted using RAxML v.8.2.8 (Stamatakis, 2006) on the CIPRES Science Gateway v.3.3 (Miller, Pfeiffer & Schwartz, 2010), under the model GTR + Γ, with the option '-f a' (search for the best-scoring ML tree and a rapid bootstrap analysis) and 1000 bootstrap replicates (Stamatakis, Hoover & Rougemont, 2008). Only bootstrap values ≥ 70% were considered as significant for MP and ML (70–79% weak, 80–89% moderate and 90–100% strong support).

For the BI analyses, models for each partition (spacers, coding and non-coding genes) were chosen using the Akaike information criterion (Akaike, 1974) in MrModeltest v.2.3 (Nylander, 2004) (Table 2). Two parallel simultaneous runs were performed using the Metropolis-coupled MCMC algorithm with four random-initiated chains (Huelsenbeck *et al.*, 2001) for 10 000 000 generations, sampling trees every 1000 generations. The trees produced in both runs were graphically analysed using Tracer v.1.5 (Rambaut & Drummond, 2009), and then the initial 2500 trees of each run were discarded as burn-in. The remaining trees were summarized in a majority consensus tree with posterior probabilities (PP) as branch support estimates. Only values of PP ≥ 0.95 were considered as significant (Erixon *et al.*, 2003). Trees were edited using ITOL (Interactive Tree of Life) (Letunic & Bork, 2016) and CorelDraw (Corel Corporation).

To reconcile conflicts among the estimated ML trees, we inferred a coalescent-based species tree using ASTRAL III (Zhang *et al.*, 2018). Independent ML trees for each DNA region were input into ASTRAL III to produce a species tree. Support values for the branches of the species tree were calculated with a multi-locus resampling procedure to estimate local posterior probabilities (LPP). Phylogenetic incongruence was assessed by comparing the bootstrap support values across clades according to Cardoso *et al.* (2013).

Alternative tree topology tests

The monophyly of *Raddiella* and *Parodiolyra* was tested with the non-parametric test of Shimodaira–Hasegawa (SH), using a likelihood criterion (Shimodaira & Hasegawa, 1999), under the model GTR + Γ and 1000 bootstrap replicates (Stamatakis *et al.*, 2008). The trees were generated from each marker separately, and then the constrained topologies from each genus were compared with the topology obtained

from the ML analyses. The test was conducted with PAUP, using 1000 bootstrap replicates.

Taxonomy

Morphological descriptions, identification keys, data about distribution and habitat, protologue information and photographs of the living plants are based on data from the literature (Soderstrom & Zuloaga, 1989; Zuloaga & Judziewicz, 1991; Zuloaga & Davidse, 1999; Judziewicz & Sepsenwol, 2007; Oliveira & Clark, 2009; Grande Allende, 2011), field work carried out by our bamboo research team, analyses of herbarium specimens from CEPEC, HUEFS, INPA, NY, UB and US (acronyms according to Thiers, 2019) and the online databases Tropicos (www.tropicos.org), International Plant Names Index (www.ipni.org) and World Checklist of Selected Plant Families (www.kew.org/wcsp). Distribution maps were generated using ArcMap v.10.1 (ESRI, 2012).

RESULTS

Data sets

We used a total of 266 sequences from plastid and nuclear genomes, of which 155 were newly generated for the present study (49 of *rpl32–trnL*, 19 of *trnD–trnT*, 23 of *trnS–trnG*, 43 of *ndhF* and 21 of ITS; Table 1). The matrices comprised 5091 characters of which 717 belong to ITS, 1628 to *trnD–trnT*, 1112 to *rpl32–trnL*, 932 to *trnS–trnG* and 702 to *ndhF* (Table 3). For *rpl32–trnL*, 12 characters were considered as ambiguous (522–533) and were excluded (Table 2). Topologies inferred from the ML and BI analyses were congruent with MP, recovering clades with significant statistical support (Fig. 1). The individual *trnD–trnT*, *trnS–trnG* and *ndhF* topologies were congruent with each other, so these were combined into a single partition. However, the *rpl32–trnL* topology was incongruent with the other plastid markers, so it was analysed separately. The ITS topology was similar to the *rpl32–trnL* topology, but it was incongruent with the combined plastid topology, so it was also analysed separately.

The matrix combining *trnD–trnT*, *trnS–trnG* and *ndhF* data resulted in 3262 characters, in which 2644 were constant, 217 variable and 401 potentially informative for parsimony, reaching the limit of 10 000 most-parsimonious trees with 894 steps [consistency index (CI) = 0.80; retention index (RI) = 0.92] (Table 3). Of the 1100 characters for the *rpl32–trnL* marker, 840 were constant, 75 variable and 185 potentially informative for parsimony. Heuristic searches resulted in an upper limit of 10 000 most-parsimonious trees with 390 steps each for *rpl32–trnL* (CI = 0.79; RI = 0.94) (Table 3).

Individually, *rpl32–trnL* demonstrated the highest percentage of potentially informative characters [% potentially informative characters (PIC)], with 16.6% PIC, followed by *ndhF* (13.2%), *trnD–trnT* (12.5%) and *trnS–trnG* (11.4%) (Table 3). The ITS matrix (ITS1–5.8S–ITS2) resulted in 717 characters, from which 359 were constant, 75 variable and 283 potentially informative for parsimony with 39.5% PIC (Table 3). Heuristic searches found 579 most-parsimonious trees with 1045 steps (CI = 0.56; RI = 0.80) (Table 3).

The results obtained from the SH test, performed for each marker separately, could not reject a monophyletic *Raddiella* (ITS, $P = 0.312$; *trnD–trnT*, $P = 0.339$; *trnS–trnG*, $P = 0.230$; *rpl32–trnL*, $P = 0.499$ and *ndhF*, $P = 0.103$). ITS ($P = 0.358$), *trnS–trnG* ($P = 0.05$) and *ndhF* ($P = 0.063$) did not support the monophyly of *Parodiolyra*.

Combined three-marker plastid data analysis

The combined analysis of the three congruent plastid markers recovered a clade including *Parianella*, *Eremitis* and *Pariana* with strong support (MPBS 100/MLBS 100/PP 1.0), corresponding to Parianinae (Fig. 1). In this clade, *Parianella* [*P. carvalhoi* (R.P.Oliveira & Longhi-Wagner) F.M.Ferreira & R.P.Oliveira + *P. lanceolata* (Trin.) F.M.Ferreira & R.P.Oliveira (100/100/1.0)] emerged as sister to *Pariana* + *Eremitis* with strong support (95/93/1.0) (Fig. 1).

Species of Olyrinae were recovered in a moderately supported clade (83/85/0.99), composed of two main clades (Fig. 1). In the first clade, *Piresia goeldii* Swallen + *P. sympodica* (Döll) Swallen (100/100/1.0) were recovered as sister to the clade composed of *Olyra*, *Cryptochloa*, *Lithachne* and *Arberella* + *Sucrea* and *Raddia* (95/99/1.0) (Fig. 1). Only *Cryptochloa* [*C. capillata* (Trin.) Soderstr. + *C. decumbens* Soderstr. & Zuloaga (100/100/1.0)] and *Lithachne* [*L. pauciflora* (Sw.) P.Beauv. + *L. horizontalis* Chase (100/100/1.0)] were recovered as monophyletic (Fig. 1). In *Olyra*, three main relationships were resolved: (1) *O. latifolia* L. as sister to the clade formed by *Cryptochloa* spp. (76/84/0.99); (2) *O. bahiensis* R.P.Oliveira & Longhi-Wagner as sister to *Lithachne* (100/100/1.0) and (3) *O. glaberrima* Raddi + *O. humilis* Nees (99/100/1.0) (Fig. 1). The only sample of *Arberella* (*A. bahiensis* Soderstr. & Zuloaga) emerged as sister to the *Olyra* spp. described as lineage 3 (53/54/–) (Fig. 1). The clade formed by *Olyra* and related genera is sister (61/68/0.95) to the strongly supported clade including *Sucrea* and *Raddia* (98/100/1.0) (Fig. 1). *Sucrea sampaiana* (Hitchc.) Soderstr. emerged as sister to the other *Sucrea* spp. and the relationship of *S. maculata*

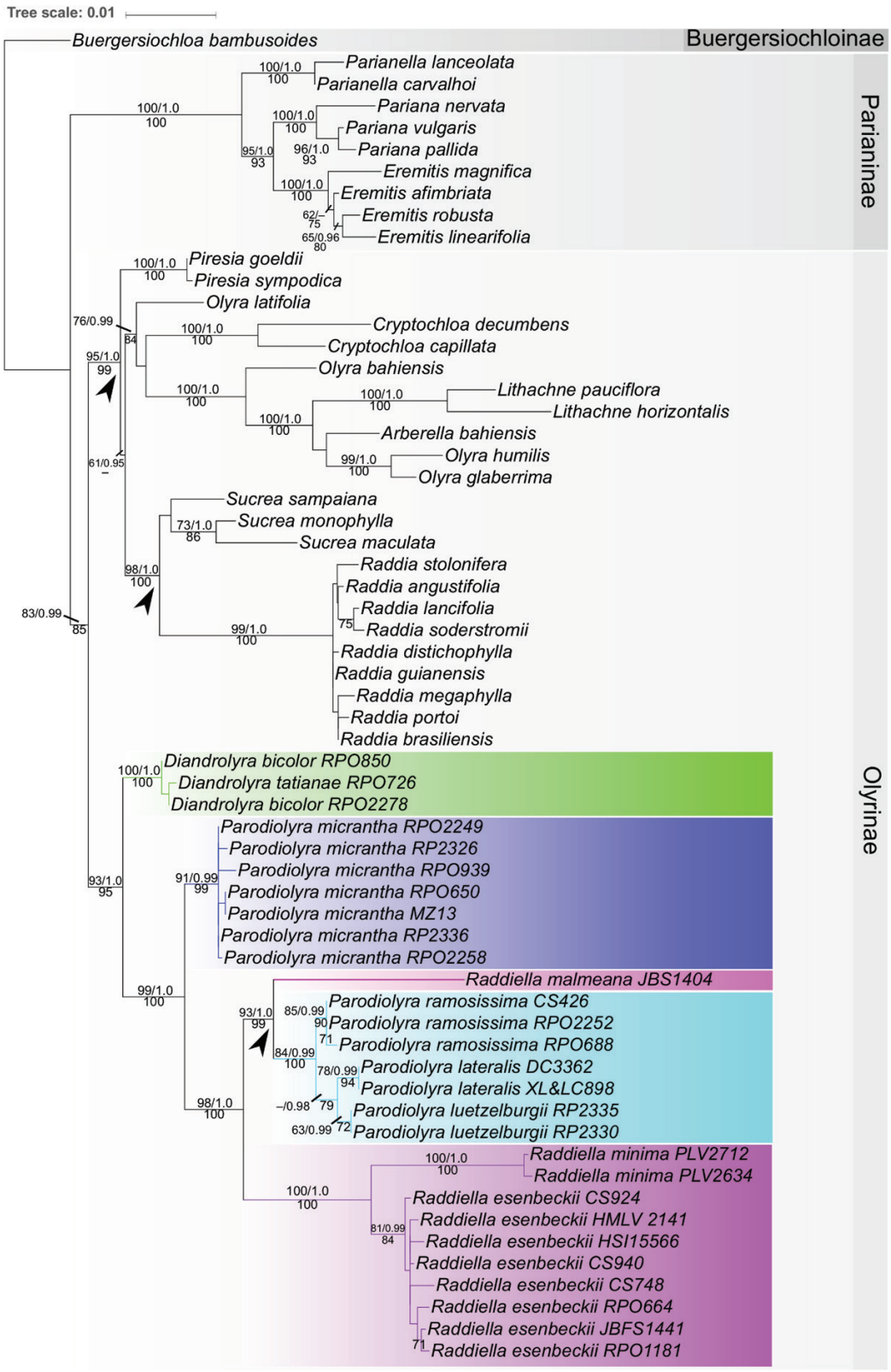

Figure 1. Plastid combined tree (*trnD–trnT*, *trnS–trnG* and *ndhF*) obtained using maximum likelihood. The numbers below the branches indicate bootstrap support (values ≥ 70%; 1000 replications), numbers above the branches indicate the

Soderstr. + *S. monophylla* Soderstr. was also recovered with support (73/86/1.0) (Fig. 1). The nine *Raddia* spp. formed a clade with strong support (99/100/1.0) (Fig. 1).

The other clade in Olyrinae, composed of *Diandrolyra*, *Parodiolyra* and *Raddiella*, was recovered with strong support (93/95/1.0) (Fig. 1). *Diandrolyra* spp. composed the clade sister to all the other species (100/100/1.0), and multiple samples of *P. micrantha* also emerged in a well-supported clade (91/99/0.99), which was sister to the clade formed by *Raddiella* and the other *Parodiolyra* spp. (98/100/1.0) (Fig. 1). The clade formed by *R. esenbeckii* + *R. minima* Judz. & Zuloaga (100/100/1.0) was recovered as sister to *R. malmeana* (Ekman) Swallen (–/–/1.0) + [*P. ramosissima* + (*P. luetzelburgii* (Pilg.) Soderstr. & Zuloaga + *P. lateralis*) (84/100/0.99)] (93/99/1.0) (Fig. 1).

Topology incongruence

ITS and *rpl32–trnL* each recovered the same relationships found in the combined plastid analyses, except for three clades. First, *Sucrea sampaiana* formed a polytomy with *Piresia-Olyra-Cryptochloa-Lithachne-Arberella* and *Sucrea-Raddia* in the *rpl32–trnL* topology; in the ITS analysis *S. sampaiana* was recovered as sister to the *Sucrea-Raddia* clade (MPBS –/ MLBS 49/PP 0.99). Second, the *Piresia* clade was recovered as sister to the clade composed of *Olyra* and related species (64/75/0.96). The third exception is with the samples of *Raddiella malmeana* (99/100/1.0), which emerged in a clade with the other species of *Raddiella* (73/97/–) in the *rpl32–trnL* analysis (Fig. 2C) or as sister (–/41/0.80) without support to the ((*Parodiolyra ramosissima* + (*Raddiella esenbeckii* + *R. minima*)) (99/100/1.0; 58/57/0.98) clade in the ITS analysis (Fig. 2A).

The multispecies coalescence tree was informed by the independent trees from each of the five loci. A summary diagram of the species tree focused on the *Parodiolyra* and *Raddiella* clade is provided in Fig. 3, and the full coalescent tree with local posterior probability branch support is available in Supplementary Material. The topology of the recovered species tree is most similar to the *trnD–*trnT, *trnS–*trnG and *ndhF* ML trees. *Parodiolyra* and *Raddiella*, as sampled here, were not monophyletic in the coalescent tree. *Parodiolyra micrantha* was a well-supported clade (LPP 1.39) sister to a clade containing the other sampled species of *Raddiella* and *Parodiolyra* (LPP 1.39). In this well-supported sister clade (LPP 1.39), *R. esenbeckii* and *R. minima* were both monophyletic and well supported (both LPP 1.20); *R. malmeana* received only weak support (LPP 0.69). *Pariodiolyra* spp. were also recovered as monophyletic, but with *P. lateralis* and *P. luetzelburgii* having weaker support (both LPP 0.69) than *P. ramosissima* (LPP 1.20). *Raddiella malmeana* formed a poorly supported sister relationship with these remaining *Pariodiolyra* spp. (LPP 0.29), and that clade was sister to the rest of *Raddiella*.

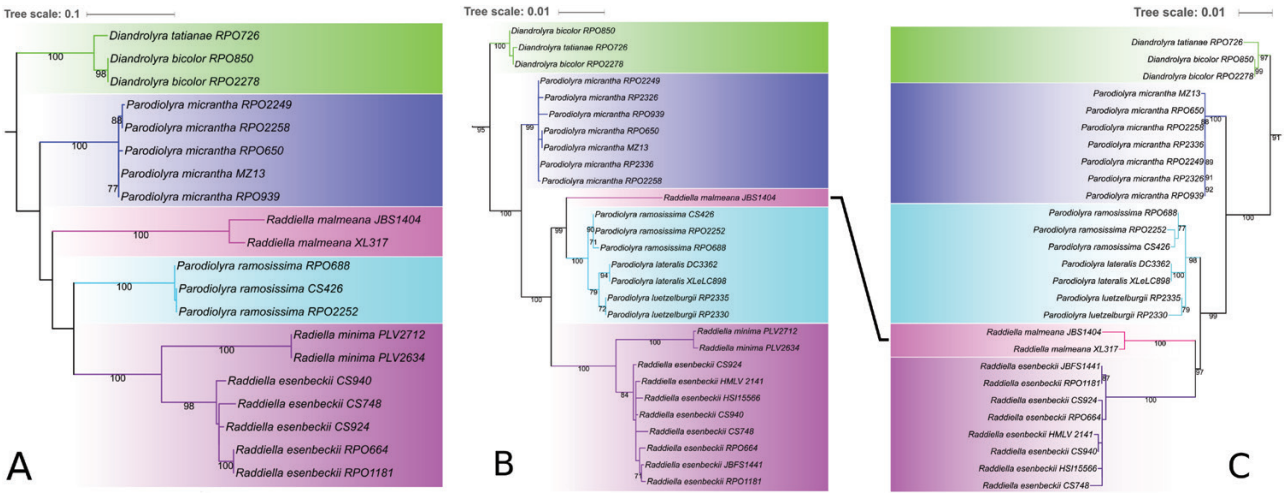

Figure 2. Trees from the maximum likelihood analysis for the individual markers or set of markers. A, ITS. B, *trnD–trnT*, *trnS–trnG* and *ndhF* combined. C, *rpl32–trnL*. Numbers below the branches indicate bootstrap support (%; 1000 replications).

Bayesian posterior probability (values ≥ 0.95) and maximum parsimony bootstrap support (values ≥ 70%). Arrows indicate incongruent clades in the ITS and *rpl32–trnL* analyses.

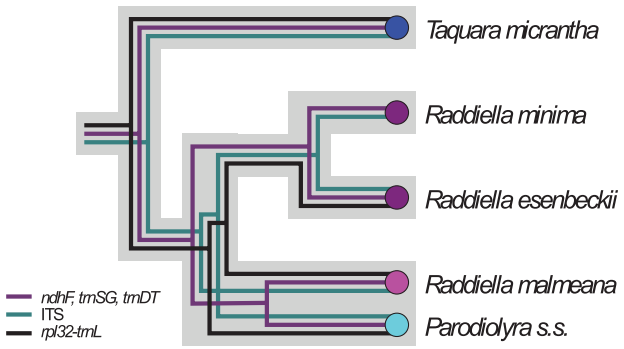

Figure 3. Summary diagram of the species tree (grey) inferred under a multispecies coalescent model from gene trees inferred from maximum likelihood for *ndhF*, *trnS–trnG*, *trnD–trnT* (same topology; purple line), internal transcribed spacer (ITS; green line) and *rpl32–trnL* (blue line).

DISCUSSION

Molecular evolution of the regions used

The considerable level of molecular variation found between plastid and nuclear markers is related to an abundance of homoplasy in the ITS markers, especially the spacers ITS1 and ITS2, indicated by the low CI and RI values. In addition, ITS shows a higher percentage of PIC for parsimony than those found in previous studies involving herbaceous bamboos [17.8% (Ferreira, 2012); 37.8% (Carvalho, 2013); 38.2% (Oliveira *et al.*, 2014)] and other groups of Poaceae [e.g. Pooideae, 37.4% PIC (Hsiao *et al.*, 1995); Panicoideae, 29.6% (López & Morrone, 2012); Chloridoideae, 26% (Siqueiros-Delgado *et al.*, 2013)], reflecting different evolutionary rates between different lineages of the family.

Plastid markers were more conservative than ITS, but high numbers of PICs were found when compared to the variation in tropical woody bamboos such as *Chusquea* Kunth (Fisher *et al.*, 2009; Fisher, Clark & Kelchner, 2014; Vidal *et al.*, unpubl. data). On the other hand, the plastid markers showed similar variability to previous phylogenetic analyses of Olyrinae (Oliveira *et al.*, 2014) and Parianinae (Ferreira, 2012). Additionally, many indels (insertions and deletions) were found, inhibiting the establishment of homologies in the alignment, except in *ndhF*, which is a coding region (gene) expected to be less variable and to contain few to no indels, despite the presence of high evolutionary rates (Olmstead & Sweere, 1994; Olmstead & Reeves, 1995; Scotland *et al.*, 1995). Regarding the other markers, *rpl32–trnL* had the most informative characters but also incongruent positions for *Sucrea sampaiana*, *Piresia* and *Raddiella malmeana*.

Phylogenetic relationships in Olyreae focusing on Olyrinae

Our data presented confirmed the results of previous phylogenetic studies involving herbaceous bamboos (Ferreira, 2012; Carvalho, 2013; Kelchner & BPG, 2013; Oliveira *et al.*, 2014) that recovered Olyrinae and Parianinae as monophyletic. Although the relationships among the main groups in Olyrinae were similar to previous studies, we increased sampling in the subtribe and improved the statistical support for some clades. The most significant change occurred in the clade including *Raddia* and *Sucrea*, which previously showed low resolution and no significant statistical support (Oliveira *et al.*, 2014). Our analysis also unambiguously resolved *Sucrea* as non-monophyletic, suggesting the need for more detailed investigation, which is in progress by Oliveira *et al.* (Reinterpreting the phylogenetic position, systematics and distribution of the Raddia-Sucrea lineage (Poaceae, Olyrinae), with a new monotypic and endangered herbaceous bamboo genus from Brazil, unpubl. data).

Another update in comparison to previous studies refers to the genus *Cryptochloa*, sampling of which in previous phylogenetic analyses was restricted to *C. capillata* (Trin.) Soderstr. (Carvalho, 2013; Oliveira *et al.*, 2014). In the current study we increased its sampling with the addition of *C. dressleri* Soderstr., indicating for the first time that the genus is probably monophyletic. Although the diversity of *Cryptochloa* is not high (seven or eight species), the genus displays an interesting biogeographic pattern, represented by a disjunction in which the majority of species occur in Central America and northern and western South America, with only one species occurring in the Atlantic Forest of Brazil (Judziewicz *et al.*, 1999). However, complementary studies on systematics and evolution of *Cryptochloa* are in progress and will require the inclusion of other species, including the type species, to further elucidate its internal relationships.

The *Diandrolyra-Parodiolyra-Raddiella* clade

In agreement with the results of Oliveira *et al.* (2014), the clade within Olyrinae comprising *Diandrolyra*, *Parodiolyra* and *Raddiella* was recovered. Therefore, it showed higher statistical support in our analyses in comparison to Oliveira *et al.* (2014), which can be explained by the increase in sampling for *Parodiolyra* and *Raddiella* or the inclusion of more molecular markers.

Diandrolyra was historically considered to be related to *Piresia* (Soderstrom & Calderón, 1974; Clayton & Renvoize, 1986) due to the presence of synflorescences produced on dimorphic culms. Oliveira *et al.* (2014) recovered this relationship based

on a combined ITS + *trnD–trnT* dataset, but with no significant support. However, Carvalho (2013) used greater sampling in *Piresia* and *Reitzia*, and was able to show that these two genera compose a strongly supported lineage in Olyrinae, with many shared morphological characters (Carvalho & Oliveira, 2014) and did not exhibit a direct relationship to the *Diandrolyra-Parodiolyra-Raddiella* clade.

As discussed by Oliveira *et al.* (2014), synflorescences produced on dimorphic and commonly decumbent culms occur in several genera of Olyreae. In Olyrinae, this condition has been reported in *Piresia*, *Diandrolyra*, *Cryptochloa*, *Piresiella* Judz., Zuloaga & Morrone, *Mniochloa* Chase and some *Olyra* spp. In Parianinae, dimorphic culms occur in *Eremitis* and in some species of *Pariana*, but in *Parianella* only monomorphic culms are known thus far (Ferreira *et al.*, 2019). Considering that this character is present in many but not all lineages of the tribe, there are two possible explanations: (1) the character represents a symplesiomorphy of the tribe, being lost or modified in diverse lineages; or (2) the character evolved independently in different lineages.

Representatives of *Diandrolyra-Parodiolyra-Raddiella* are heterogeneous in their general morphological characters. However, they share a shortened hilum, in contrast to other Olyrinae (with the hilum typically extending the length of the caryopsis), female spikelets that disarticulate below the glumes, inflated internodes between the glumes and filiform pedicels (Soderstrom & Zuloaga, 1989). These characters are possible synapomorphies of this clade, but ancestral state reconstruction analysis, as recently performed for Parianinae by Ferreira *et al.* (2019), is necessary to test these characters.

Diandrolyra, here represented by two of its three species (*D. bicolor* Stapf and *D. tatianae* Soderstr. & Zuloaga), was recovered with high support values in all our analyses. It differs from *Parodiolyra* and *Raddiella* in vegetative aspects and synflorescence structure, which is racemose and usually develops on differentiated culms, with a single leaf protecting and hiding the synflorescence (Soderstrom & Calderón, 1974). Female and male spikelets are slightly dimorphic, and the male spikelets possess only two stamens (Stapf, 1906; Soderstrom & Zuloaga, 1985). Despite having only three described species, there are several putative new species in this genus the delimitation of which requires more investigation (Oliveira & Clark, 2009).

On the other hand, *Parodiolyra* and *Raddiella* are morphologically similar to each other, possessing synflorescences produced on non-differentiated culms with completely developed leaves, differing especially by the presence of unisexual synflorescences in *Raddiella* and bisexual ones in *Parodiolyra* (Judziewicz *et al.*, 1999). Our data indicate that *Parodiolyra* is paraphyletic, with *P. micrantha* arising as a sister lineage of the clade including the other species of *Parodiolyra* + *Raddiella*. This relationship agrees with the results of Oliveira *et al.* (2014) and is bolstered by greater taxon sampling and more markers. In the present work, the other *Parodiolyra* spp. constitute a well-supported clade, including the type species, *P. ramosissima*. *Raddiella* was recovered as paraphyletic in most gene trees, but was monophyletic in the *rpl32–trnL* tree (Fig. 2C), leaving its circumscription inconclusive.

Uncertainties about the circumscription of *Raddiella*

Only three *Raddiella* spp. were included in this study (*R. esenbeckii*, *R. malmeana* and *R. minima*), two from dry environments and only one (*R. malmeana*) being a phreatophyte. The further addition of other phreatophyte species in our analyses would be crucial, but there is a scarcity of knowledge about the distributions of these species, some of which are only known from type material. They are difficult to collect because they grow in remote parts of the Amazon region (Zuloaga & Judziewicz, 1991; Cardoso *et al.*, 2017), and our attempts to obtain quality DNA from herbarium samples were not successful.

Raddiella esenbeckii and *R. minima* were recovered as sister groups in all analyses, but *R. malmeana* was recovered as their sister only in the *rpl32–trnL* analysis. Despite this, the alternative hypothesis for the monophyly of *Raddiella* in the SH test was rejected for that marker. The branches in each of these lineages are long (Figs 1, 2), indicating accumulation of mutations. Thus, it is possible that the position of *R. malmeana* was the result of long-branch attraction due to an excess of homoplasy in the *rpl32–trnL* matrix. This type of systematic error tends to happen when two lineages with long branches separated by a short internode evolve identical bases by chance, which are interpreted as synapomorphic (Bergsten, 2005), which seems to be the case for *R. malmeana*. Additionally, in contrast to Oliveira *et al.* (2014), in which *R. malmeana* was recovered as a poorly supported part of the *Raddia-Sucrea* lineage, we found no relationship between *Raddiella* and that lineage.

Raddiella is identified by the reduced size of its plants, including the smallest species (*R. vanessae* Judz.) known in Bambusoideae (Soderstrom, 1984; Judziewicz & Sepsenwol, 2007). *Raddiella* spp. possess numerous and well-developed axillary synflorescences (Zuloaga & Judziewicz, 1991) and male and female spikelets arising from different synflorescences (Soderstrom & Zuloaga, 1989) (Fig. 4). Some species are obligatory phreatophytes, growing

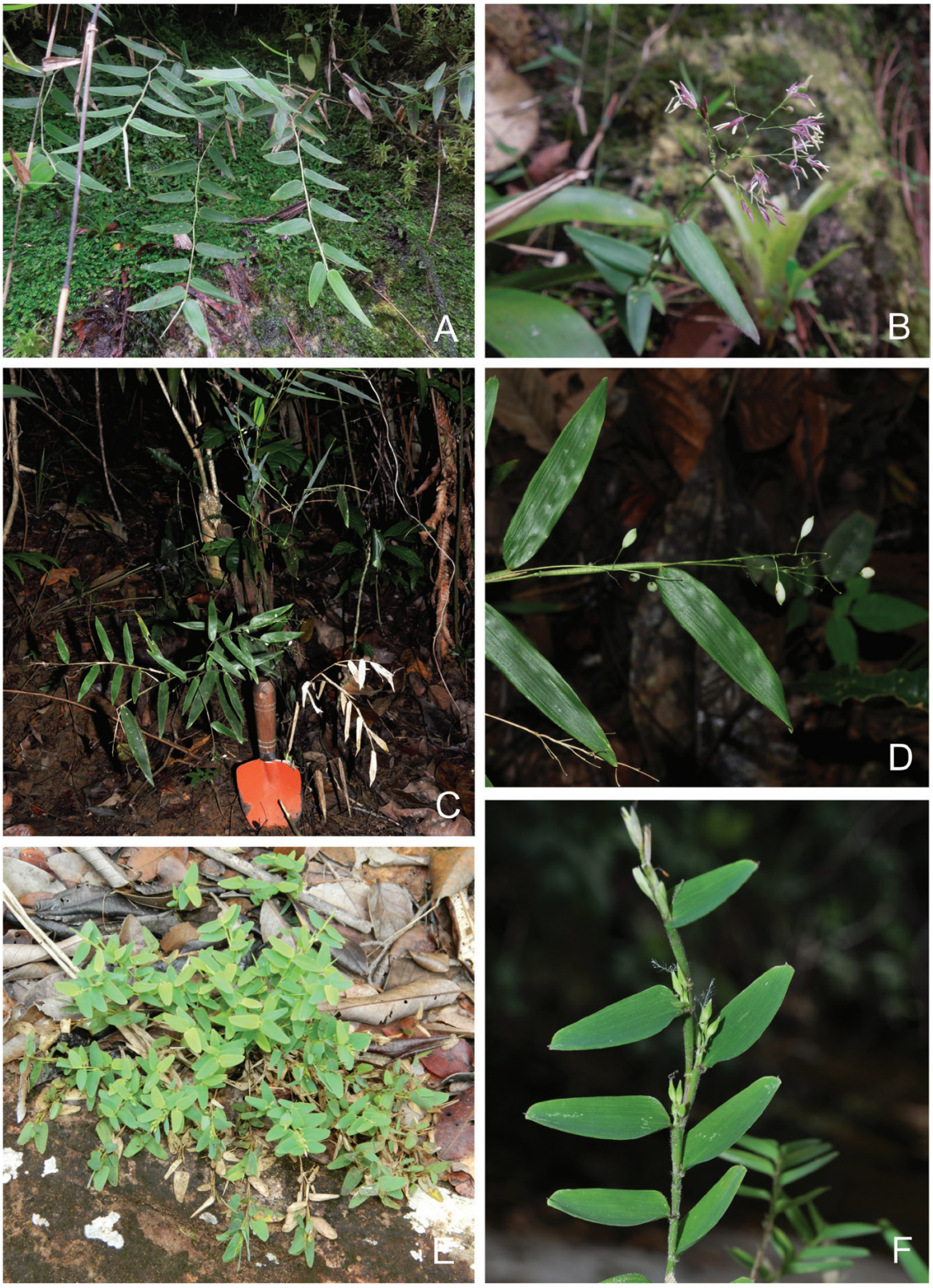

Figure 4. Habit and detail of inflorescences in *Parodiolyra* and *Raddiella*. A, B, *Parodiolyra lateralis*; C, D, *Parodiolyra ramosissima*; E, F, *Raddiella esenbeckii*. Photographs by D. Cardoso (A–B) and C. Silva (C–F).

on humid rocks and at the base of waterfalls (Zuloaga & Judziewicz, 1991), except *R. esenbeckii*, *R. minima* and *R. vanessae*, which inhabit dry savannas and cerrados (Fig. 5). These are the only species in the genus to exhibit nyctinasty or 'sleep movements' (Zuloaga & Judziewicz, 1991; Judziewicz & Sepsenwol, 2007), even though this mechanism is common in several other genera in Olyreae (Judziewicz *et al.*, 1999; Oliveira, 2006). Nyctinasty is characterized by rhythmic movements in which the leaf blades fold during the night or under water stress (Kerbauy, 2004), and functions in protection, water economy and maximizing photosynthesis in adverse conditions (Rodrigues, 2006). Thus, the presence of this character in *Raddiella* spp. seems to be related to their habitat and the consequent need to reduce water loss in dry environments.

The *R. minima* + *R. esenbeckii* clade, strongly supported in this study, is characterized by firm, strongly asymmetrical leaf blades (Zuloaga & Judziewicz, 1991), contrasting with the phreatophyte species, which possess ovate-triangular leaf blades that are membranous and slightly asymmetrical, with a truncate base and acuminate apex (Zuloaga & Judziewicz, 1991). In addition, the male spikelets are borne on terminal, whereas female spikelets are on axillary synflorescences (Zuloaga & Judziewicz, 1991), as is the case in *R. malmeana*. The monophyly of *Raddiella* is difficult to discern from our analyses. Morphologically, *R. malmeana* possesses the diagnostic characteristics for the genus, despite the differences from the other species sampled. Molecularly, the *rpl32–trnL* analysis places *R. malmeana* with *Parodiolyra*, but it does not seem to share morphological similarities with

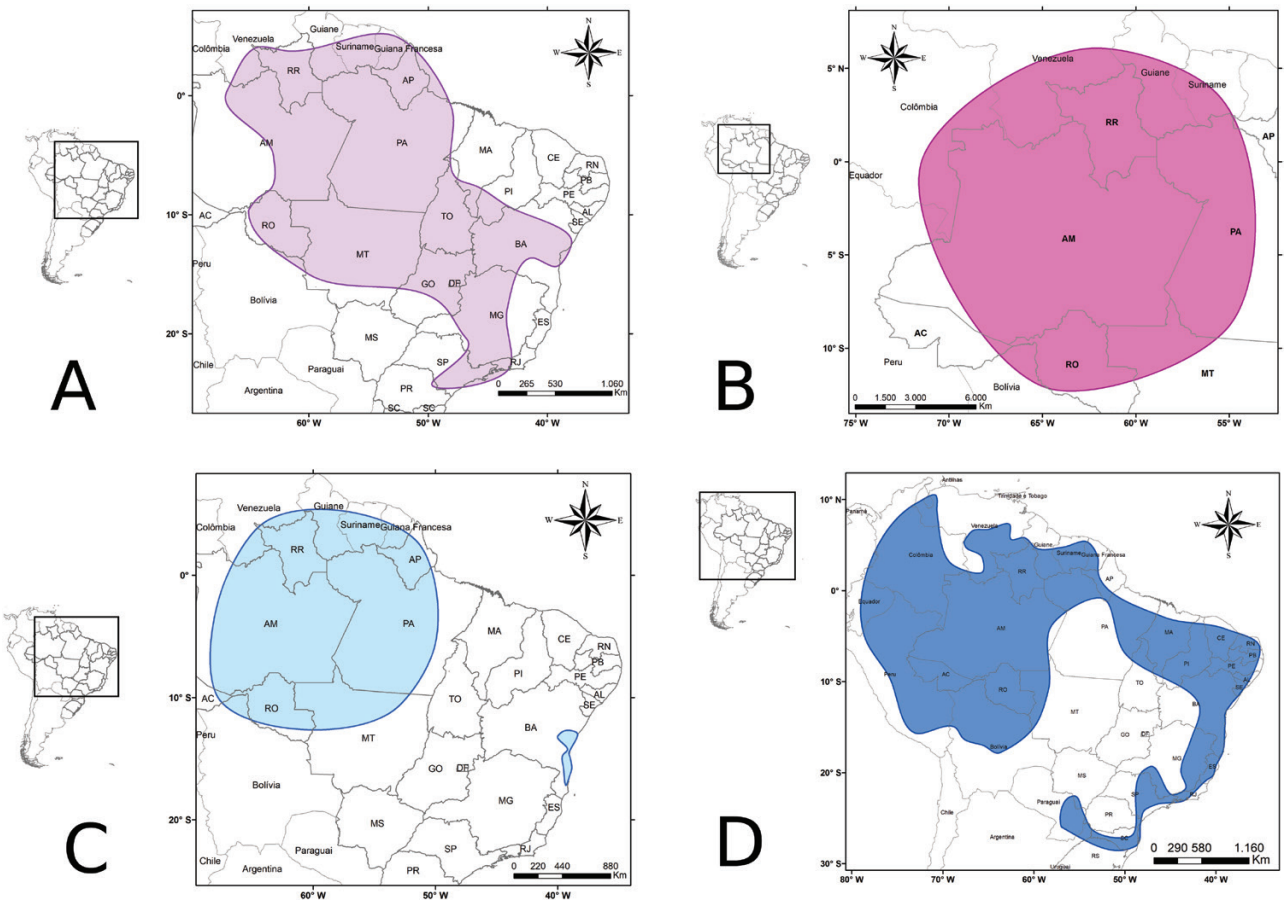

Figure 5. Known geographical distribution of the species belonging to the lineages under study. (Acronyms of the states of Brazil: Acre, AC; Alagoas, AL; Amapá, AP; Amazonas, AM; Bahia, BA; Ceará, CE; Distrito Federal, DF; Espírito Santo, ES; Goiás, GO; Maranhão, MA; Mato Grosso, MT; Mato Grosso do Sul, MS; Minas Gerais, MG; Pará, PA; Paraíba, PB; Paraná, 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). A, Distribution of *Raddiella* spp. occurring in savannas and forests. B, Distribution of phreatophyte *Raddiella* spp. C, Distribution of *Parodiolyra s.s.* D, Distribution of *Taquara*, including *T. micrantha* and *T. colombiensis*.

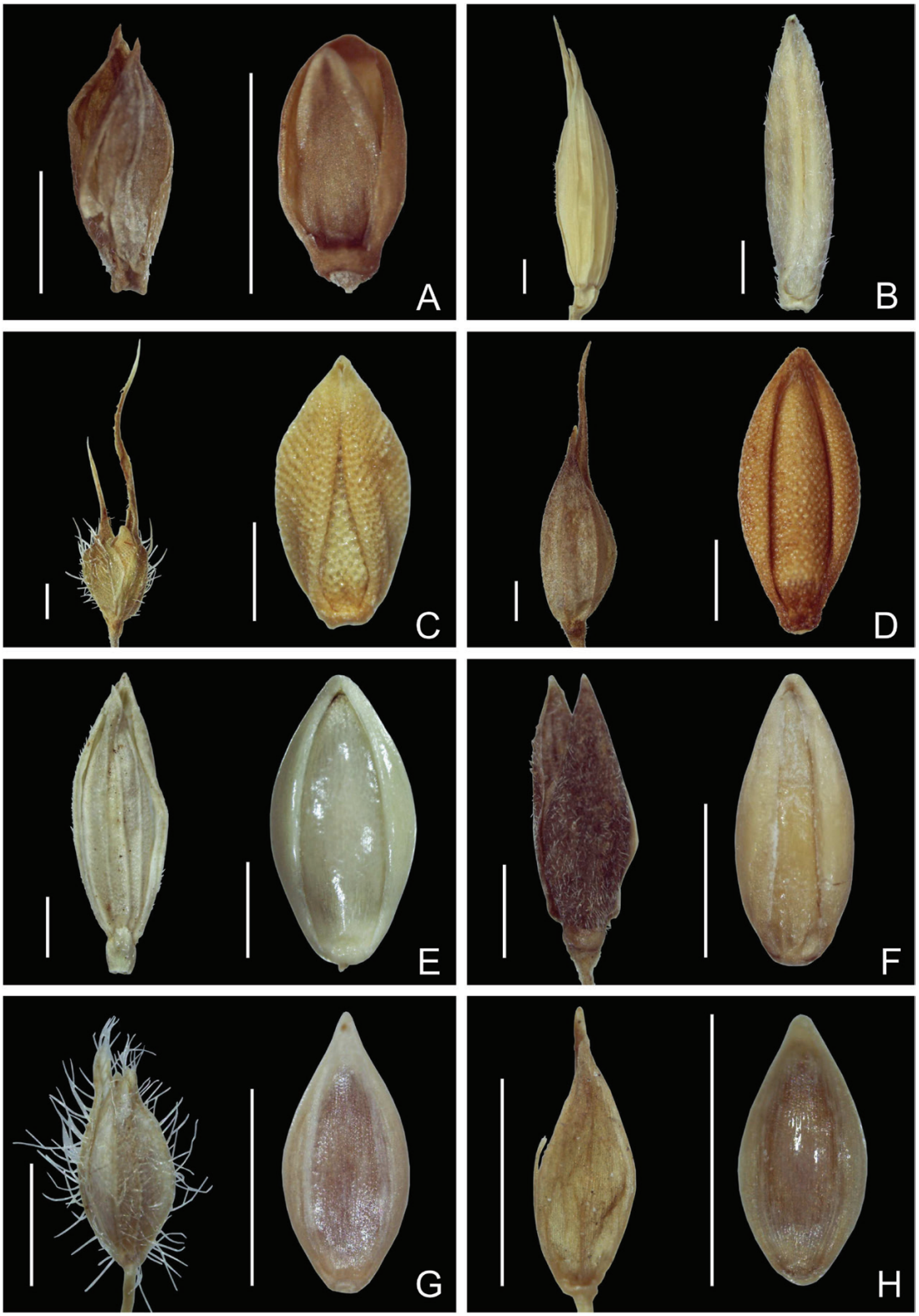

Figure 6. Comparison of female spikelets and the female anthoecium of the analysed species of *Parodiolyra* and *Raddiella*. A, *Parodiolyra lateralis* (*Cardoso 3362*). B, *P. luetzelburgii* (*Oliveira 2335*). C, *P. micrantha* (*Queiroz et al. 9429*). D, *P. micrantha* (*Oliveira 2326*); E, *P. ramosissima* (*Silva 426*). F, *Raddiella esenbeckii* (*Longhi-Wagner 9451*). G, *R. malmeana* (*Silva 1404*). H, *R. minima* (*Viana 2712*).

that genus. Clearly, the circumscription of *Raddiella* will require inclusion of additional species to sort it out. In addition, the use of additional conservative markers (e.g. *rbcL*) may be needed in order to reconstruct the relationships given the elevated amount of homoplasy observed in the non-coding plastid markers.

Paraphyly of *Parodiolyra* and its taxonomic implications

The paraphyly of *Parodiolyra* was suggested for the first time by Oliveira *et al.* (2014), based only on *P. micrantha* and *P. ramosissima*, and is confirmed in the present work, following the inclusion of *P. lateralis* and *P. luetzelburgii*. The latter two species are morphologically similar and overlap in their distribution (both occur in the northern portion of South America), whereas *P. ramosissima* is endemic to Bahia (Soderstrom & Zuloaga, 1989) (Figs 4, 5). *Parodiolyra lateralis*, *P. luetzelburgii*, *P. ramosissima* and *P. aratitiyopensis* J.R.Grande possess morphological affinities, mainly in the ornamentation of the female anthoecia (smooth or with rounded pits only at the apex of lemma and palea) (Fig. 6). *Parodiolyra aratitiyopensis* is known only from the Venezuelan Amazon (Grande Allende, 2011), and was not sampled in this study. Additionally, *P. lateralis*, *P. luetzelburgii* and *P. ramosissima* appear to share zoochoric dispersal syndromes. The first two species produce sticky secretions from micro-trichomes at the apex of the female lemma that facilitate external dispersal. The third species has shiny, glabrous lemmas, suggesting internal dispersal by animals via ingestion (Davidse, 1987; Judziewicz *et al.*, 1999).

Originally described as part of *Olyra*, *P. micrantha* was always considered atypical for the genus, due to the presence of female spikelets disarticulating below the glumes, conspicuous internodes between the glumes and filiform pedicels (Soderstrom & Zuloaga, 1989) (Figs 6, 7). Even after its transfer to *Parodiolyra* (Zuloaga & Davidse, 1999), this species remained somewhat anomalous because of its much longer leaves and synflorescences with numerous male and female spikelets (Judziewicz *et al.*, 1999). The species is most similar to *P. colombiensis* Davidse & Zuloaga, because these are the only two species with a completely foveolate anthoecia (Zuloaga & Davidse, 1999) (Fig. 6).

The foveolate female anthoecia has been noted in different genera of Olyreae, with the depth and distribution of the depressions varying. This character is conspicuous in *Parodiolyra micrantha* and *P. colombiensis* (Zuloaga & Davidse, 1999) and in some *Olyra* spp., e.g. *O. filiformis* Trin., *O. longifolia* Kunth, *O. ecaudata* Trin. and *O. fasciculata* Trin. (Soderstrom & Zuloaga, 1989). In *Raddia* and *Sucrea* (Oliveira, 2006) and some *Raddiella* spp. (Zuloaga & Judziewicz, 1991), however, the anthoecia are only slightly foveolate. Thus, the extent to which this character, which also seems to have evolved independently, occurs in other genera of Olyrinae needs to be better investigated.

Many bamboos exhibit specialized mechanisms for fruit and seed dispersal, with adaptations reflected in the presence of specialized synflorescences and spikelets (Davidse, 1987). Vasconcelos *et al.* (2005) observed that granivorous birds are associated with the fruiting events of 'taquaras' in the Espinhaço Range. After analysing the crop content of an individual of *Tiaris fuliginosus* (Thraupidae), the authors found caryopses of *P. micrantha*, and other non-identified grasses. This bird is partially migratory (Sigrist, 2013) and its distribution overlaps the distribution of *P. micrantha*, suggesting a possible animal-plant relationship in the dispersal of the species. In this way, the wide distribution of *P. micrantha* in the Neotropical region may be attributable to the efficiency of its dispersal mechanisms and the behaviour of the dispersal agent.

Taxonomic implications

Based on the phylogenetic information presented here, the circumscription of *Parodiolyra* is confirmed, being composed of four species (*P. lateralis*, *P. luetzelburgii*, *P. ramosissima* and *P. aratityopensis*). Additionally, we propose transferring *Parodiolyra micrantha* and *P. colombiensis* to the new genus *Taquara* (Fig. 7), which is sister to the *Raddiella-Parodiolyra* clade (Fig. 8) and shares the characters discussed above, but differs by the characters indicated below.

KEY TO THE GENERA OF THE DIANDROLYRA, PARODIOLYRA, RADDIELLA AND TAQUARA CLADE

1. Synflorescences produced on dimorphic culms ..... *Diandrolyra*
1'. Synflorescences produced on monomorphic culms.
  2. Female and male spikelets in separate synflorescences ..... *Raddiella*
  2'. Female and male spikelets in the same synflorescences.
    3. Female anthoecia with small pits (foveolate) only at the apex of lemma and/or palea ..... *Parodiolyra*
    3'. Female anthoecia completely covered with small pits (completely foveolate) ..... *Taquara*

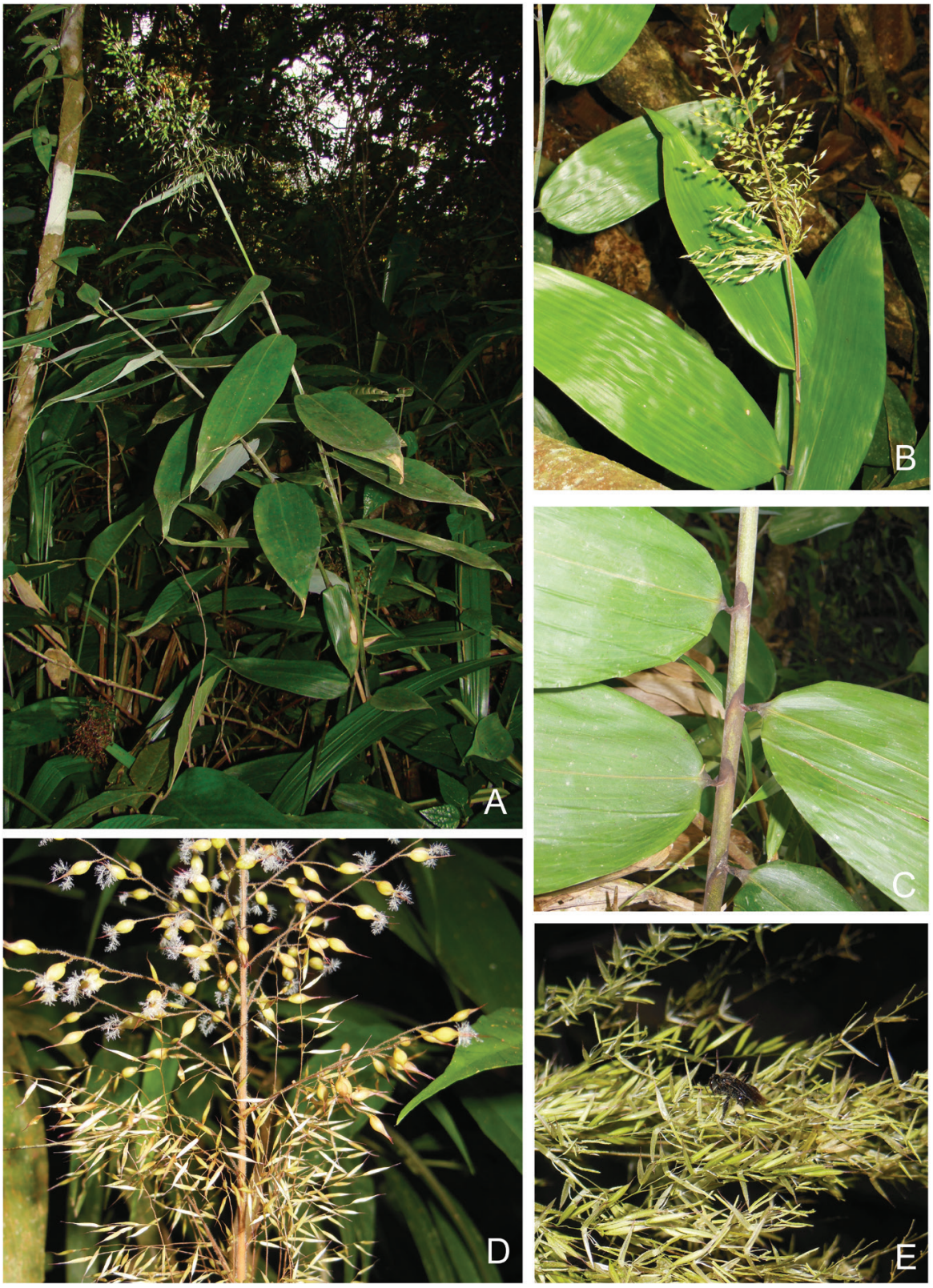

Figure 7. *Taquara micrantha* (≡ *Parodiolyra micrantha*). A, Habit. B, Inflorescence location on the culm. C, Detail of the leaves in the stem. D, Detail of the arrangement of the female (upper portion) and male (lower portion) spikelets in the inflorescence. E, Floral visitor registration. Photographs by Reyjane Patrícia de Oliveira.

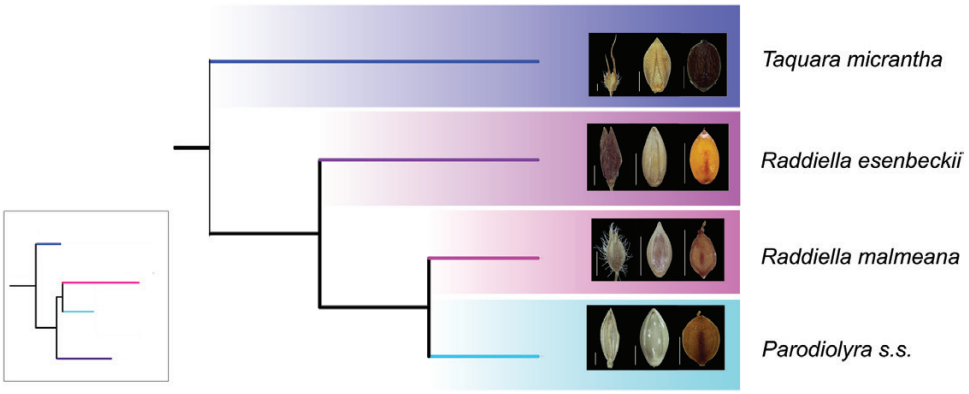

Figure 8. Summary of recovered relationships and detail of the female spikelets, female anthoecia (florets) and hilum.

Taquara I.L.C.Oliveira & R.P.Oliveira, **gen. nov.** ≡ *Parodiolyra micrantha*. Type: *Olyra micrantha* Kunth [≡ *Taquara micrantha* (Kunth) I.L.C.Oliveira & R.P.Oliveira].

Taquara differs from other genera of Olyreae by having usually terminal panicles with male spikelets in the lower portion and female spikelets above, and female anthoecia entirely foveolate (covered in small pits).

Perennial. Culms erect, ramified at the upper nodes, sometimes leaning on surrounding vegetation; internodes cylindrical, hollow and glabrous; nodes compressed, dark, glabrous to pubescent. Leaf sheaths striate or not, brownish or straminous, glabrous to densely pubescent; auricles present or absent at the apex; ligules membranous-ciliate, small or conspicuous; blades oblong-lanceolate or ovate-lanceolate, apex acuminate, base symmetric or asymmetric, truncate or subcordate, margins ciliate to scabrous or glabrous, midnerve prominent or not. Synflorescences paniculate, terminal, lax, open or diffuse, with male spikelets in the lower portion and female spikelets above; axillary synflorescences present or absent; rachis scaberulous to hispid; pedicels filiform, not thickened. Female spikelets oval to elliptical, aristate to acuminate, with an internode between the glumes present or absent, disarticulating below the glumes; lower glume scabrous or hispid, three- to five-nerved; upper glume scabrous or hispid, three- to five-nerved; anthoecia (florets) ovoid or ellipsoid, foveolate over the entire surface, lemma five-nerved, pilose or glabrous. Male spikelets fusiform to lanceolate; lemma acuminate or aristate, scabrous; palea scabrous, two-nerved.

This new genus is named based on the common name of herbaceous bamboos in Brazil ('taquaras' or 'taquarinhas'). It includes only two species, one widely distributed in the Neotropical region and the other restricted to the Araracuara region of Colombia. They are found along forest edges and in the understory or in sandy paramos, respectively.

Taquara colombiensis (Davidse & Zuloaga) I.L.C.Oliveira & R.P.Oliveira, comb. nov. based on *Parodiolyra colombiensis* Davidse & Zuloaga. Novon 9(4): 587, f. 1–2. 1999. TYPE: Colombia. Caquetá: Região de Araracuara, arredores da pista aérea, *D. Restrepo* & *A. Matapi* 467 (holotype, COAH-017796; isotypes, COAH-020068, MO-05102566).

Distribution and habitat: Known only from the type material collected in south-western Colombia in sandy paramos (Zuloaga & Davidse, 1999) (Fig. 5).

Taquara micrantha (Kunth) I.L.C.Oliveira & R.P.Oliveira, comb. nov. based on *Olyra micrantha* Kunth. Humboldt, Bonpland & Kunth, Nov. Gen. Sp.1:199. 1816 [≡ *Parodiolyra micrantha* (Kunth) Davidse & Zuloaga. Novon 9(4): 590. 1999]. TYPE: Venezuela. Amazonas: Maypures do Rio Orinoco, *Humboldt* and *Bonpland s.n.* (holotype: P; isotype: US-2877940 (fragment ex P)).

Distribution and habitat: Widely distributed in South America, from eastern Colombia and Venezuela to the Atlantic Coast of Brazil and the eastern Andes along forest edges and in the interior of forests (Soderstrom & Zuloaga, 1989) (Fig. 7).

KEY TO THE SPECIES OF *TAQUARA*

1. Leaf blades oblong-lanceolate, base symmetrical, subcordate, adaxially glabrous; female and male spikelets aristate ..... *T. micrantha*
1'. Leaf blades ovate-lanceolate, base asymmetrical, truncate, adaxially pilose; female and male spikelets acuminate ..... *T. colombiensis*

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