

ORIGINAL ARTICLE

# Disentangling a big genus: unwinding Ipomoeae s.l. (Convolvulaceae) using an Angiosperms353-guided classical phylogenetic approach

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- **Background** Taxonomic studies of big plant genera are invariably complex due to their high species diversity. Big genera with tropical species representation exhibit higher taxon descriptions, since tropical and subtropical regions contribute immensely to species diversity. *Ipomoea* is an example of a large genus, with over 800 species distributed mostly in tropical and subtropical regions and fewer occurring in temperate regions. It is polyphyletic, nesting nine other genera, which collectively form tribe Ipomoeae. *Ipomoea* has a long history of taxonomic and nomenclatural confusion, mainly due to a lack of clear morphological delimitation. Phylogenetic studies have greatly contributed to the clarification of taxa within Ipomoeae. However, sampling biases overlooking Asian and African taxa representation means that these results are still insufficient for advanced generic classification of the group.
- **Scope** To improve the understanding of phylogenetic relationships within Ipomoeae, with a focus on the contribution of newly generated phylogenomic data from 17 African taxa.
- **Methods** This study, for the first time, employed the target enrichment strategy with the universal Angiosperms353 probe set. We utilized a single-locus (ITS) constrained-phylogenetic analysis approach for Ipomoeae, guided by a phylogenomic-generated phylogeny.
- **Key Results** The Angiosperms353 tree resolved with strong support and corroborated the monophyly of Ipomoeae as well as the polyphyly of *Ipomoea*. Internal branches of the constrained phylogenetic tree exhibited stronger statistical support than in the unconstrained phylogeny. Conflicting gene trees were also observed across the Angiosperms353 phylogeny despite the observed strong support.
- **Conclusions** This study emphasizes the need for infrageneric divisions in *Ipomoea* and a subtribal classification of tribe Ipomoeae. We also advocate the utilization of phylogenomic data for phylogenetic inference and delimitation of Ipomoeae. Nuclear molecular data and a multi-species coalescent approach could prove useful in classification of Ipomoeae, hence increased taxon sampling is recommended to fully understand the tribe.

**Key words:** Convolvulaceae, big plant genera, herbarium, *Ipomoea*, morning glories, sweet potato, taxonomy, Angiosperms353.

## INTRODUCTION

Since the 18th century, taxonomic and evolutionary studies of big genera have been a central focus of botanical research (Stevens, 1997; Frodin, 2004; Fertig, 2015; Moonlight *et al.*,

2024). Previous studies on big genera focused mainly on addressing what the upper taxon limits were in big genera (Stevens, 1997) and the subdivisions of large genera into smaller, more stable and predictable clades (Stevens, 1997; Humphreys and Linder, 2009). Intrinsicly, members of large

genera have no biological features in common and large genera are only characterized by their size. Ideally, the recognition of genera, regardless of their sizes, is based on monophyly (Backlund and Bremer, 1998; Humphreys and Linder, 2009). However, for several large genera, like *Ipomoea* (Stefanović *et al.*, 2002, 2003; Eserman *et al.*, 2014; Simões *et al.*, 2022), monophyly has not yet been established.

A 'good' genus is stable and predictive, and genera that have been recognized based on monophyly observe these two features. However, for a genus to be taxonomically useful it should be diagnosable and of manageable size (Humphreys and Linder, 2009). Comprehensive studies of large genera that endeavour to narrow taxonomic circumscriptions require considerable resources, time and expertise. Revising these genera requires assessing hundreds of thousands of specimens, in addition to comprehensive knowledge of the species and the morphological diversity they encompass. Geographically focused studies (e.g. Wood *et al.*, 2020) are more manageable but rarely capture the full diversity within big genera (Moonlight *et al.*, 2018; Ardi *et al.*, 2022; Muñoz-Rodríguez *et al.*, 2023; Souza *et al.*, 2023). As a result, newly described species are often placed in larger, more broadly circumscribed genera, rather than assigned to smaller, morphologically well-defined ones. Despite these challenges, the total number of big genera (genera with more than 500 species) has increased to as many as 86, due to new taxon descriptions, which suggests active research in these groups (Moonlight *et al.*, 2024).

Big genera have often been considered impenetrable and impossible to study (Miller *et al.*, 2014). This challenge is further compounded when high species diversity results from rapid radiations, as evolutionary processes such as introgression, hybridization and incomplete lineage sorting can obscure morphological patterns. Over half of the big genera are found in the tropics, while 31 % primarily occur in the temperate zones, the remainder occurring both in the tropics and temperate zones (Moonlight *et al.*, 2024). Tropical genera are less understood than their temperate counterparts (Fertig, 2015). Yet, tropical and subtropical regions contribute immensely to the species diversity in the world, with Africa contributing ~45 000 plants to the world's plant checklist (Linder, 2014). The slow rate of taxonomic studies in these regions is partly due to the inaccessibility of geographical areas, mostly due to isolation and harsh conditions, which have contributed to the slow updating of floristic inventories (Sosef *et al.*, 2017).

Moreover, most of the type specimens collected from tropical regions are not housed in their countries of origin and as a result local researchers are forced to travel abroad to study type specimens (Figueiredo and Smith, 2010). This challenge, however, has been overcome with the digital access to type collections through virtual taxonomic databases such as GBIF (<https://www.gbif.org/>), Tropicos (<https://www.tropicos.org/home>), JSTOR (<https://www.jstor.org/>), WFO (<https://www.worldfloraonline.org/>) etc. However, some of the largest herbaria in the world are yet to be fully digitized and made available online, e.g. Kew Herbarium, with ~7 million specimens, and Missouri Botanical Garden, with >7.5 million specimens. Additionally, fewer smaller herbaria have the resources to make their specimens digitally accessible, particularly small herbaria in the Global South, although studies have demonstrated the high value of these small herbaria for plant science and conservation (Delves *et al.*, 2024). All these factors have

hindered studies in large genera with species concentrated in tropical and subtropical regions, as in the case of *Ipomoea*.

Recently, molecular data have been widely used to investigate the nature and composition of genera (Humphreys and Linder, 2009). However, such studies have been met with uncertainties mainly due to incomplete taxon sampling, which results in poorly supported taxon groups. This drawback has formed the basis for lumping of taxa to form large genera instead of defining smaller clades with distinct features that are strongly supported. Recent studies have incorporated phylogenomics, to understand phylogenetic relationships in different plant groups (Leebens-Mack *et al.*, 2019; Baker *et al.*, 2022; Fonseca *et al.*, 2024; Helmstetter *et al.*, 2025; Musker *et al.*, 2025). Phylogenomic datasets include many genes, providing sufficient data to improve the support for phylogenetic relationships. However, this technique is relatively costly compared with Sanger sequencing of single gene regions. Even with the development of bait kits for specific plant groups, the main challenge remains how to sample taxa in a way that yields useful and unambiguous results while still staying within budget, especially when working with large genera.

*Ipomoea* is a great example of a big genus (Muñoz-Rodríguez *et al.*, 2023). It is the largest genus in Convolvulaceae (morning glories) and one of the largest genera worldwide (Muñoz-Rodríguez *et al.*, 2019; Eserman *et al.*, 2020; Wood *et al.*, 2020; Simões *et al.*, 2022, 2024a). It is ubiquitous and consists of over 600 species (800 species, depending on its circumscription) distributed mostly in tropical and subtropical regions, with fewer species occurring in the temperate regions (Eserman *et al.*, 2020; Wood *et al.*, 2020; Simões *et al.*, 2022, 2024a). Tropical Africa single-handedly contributes ~30 % of the total recorded *Ipomoea* species worldwide, with 25 % being distributed in East Africa alone (GBIF, 2025; POWO, 2025). Economically, like most big genera, it contains important species, i.e. sweet potato, morning glories and bindweeds (Simões *et al.*, 2024a). It belongs to a monophyletic tribe, Ipomoeae s.l. (Wilkin, 1999; Manos *et al.*, 2001; Stefanović *et al.*, 2002, 2003; Eserman *et al.*, 2014; Simões *et al.*, 2022, 2024a), which consists of ten genera in total (Table 1); *Ipomoea*, *Argyreia*, *Stictocardia*, *Turbina*, *Astipomoea*, *Rivea*, *Lepistemon*, *Lepistemonopsis*, *Paralepistemon* and *Muigaia* (Ngima *et al.*, 2025) (Wilkin, 1999; Manos *et al.*, 2001; Stefanović *et al.*, 2002, 2003; Eserman *et al.*, 2014; Simões *et al.*, 2022, 2024a, Sumanon *et al.*, 2025). Ipomoeae is characterized by the presence of spiny (echinate) pollen, a potential reason for the increased reproductive success in this diverse tribe (Simões *et al.*, 2022, 2024a). Recognition of the remaining nine genera makes *Ipomoea* polyphyletic, with only a few of the proposed infrageneric subdivisions of *Ipomoea* being monophyletic (Miller *et al.*, 1999; Manos *et al.*, 2001; Stefanović *et al.*, 2002, 2003). These infrageneric subdivisions were proposed before molecular data and digital information were more commonly available, and are therefore highly skewed towards the geographical region of specialism of the author and the herbarium collections they had available for study. Thus, neither the current generic delimitation in Ipomoeae nor the infrageneric divisions available by region deal satisfactorily with the polyphyletic nature of *Ipomoea* or its infrageneric morphological variation.

As with other big genera, uncertainties exist in *Ipomoea* delimitation. *Ipomoea* has a long history of taxonomic and nomenclatural muddles, mainly due to lack of distinct morphological features, its polyphyletic nature (Eserman *et al.*, 2020) and convergent evolution of morphological characters used to circumscribe species (Simões *et al.*, 2024a). An integrative, global

TABLE 1. Current circumscribed genera in tribe Ipomoeae with accepted number of taxa and geographic distribution.

Genus	Number of species	Geographical distribution	Sampled in this study	References
<i>Argyreia</i>	142	Asia, Africa (Madagascar)	Yes	Simões <i>et al.</i> (2024b); Sumanon <i>et al.</i> (2025)
<i>Astripomoea</i>	12	Africa	Yes	Simões <i>et al.</i> (2024b)
<i>Ipomoea</i>	615	Africa, Australia, Asia, America	Yes	Simões <i>et al.</i> (2024a)
<i>Lepistemon</i>	7	Africa, Asia, Australia	Yes	Wilkin (1999); Staples (2007a)
<i>Lepistemonopsis</i>	1	Africa	Yes	Wilkin (1999); Staples (2007a)
<i>Muigaia</i>	7	Africa, Asia, Australia	Yes	Ngima <i>et al.</i> (2025)
<i>Paralepistemon</i>	2	Africa	No	Wilkin (1999); POWO (2025)
<i>Rivea</i>	3	Asia	Yes	POWO (2025); Sumanon <i>et al.</i> (2025)
<i>Stictocardia</i>	12	Africa, Asia, Australia	Yes	Simões <i>et al.</i> (2024b)
<i>Turbina</i>	20	America	Yes	Simões <i>et al.</i> (2024b)

approach to the classification of the genus and the tribe has been slow to develop and implement, while some authors have preferred to treat tribe Ipomoeae as equivalent to genus *Ipomoea*, to guarantee the monophyly of the genus and steer clear of the challenges of integrating the molecular and morphological data into a more adequate generic and infrageneric delimitation. Previous studies have proposed solutions to infrageneric revisions within Ipomoeae, namely (1) lumping, i.e. retaining the traditional *Ipomoea* in the broad sense as the only genus in the tribe and reassigning the other nine genera to *Ipomoea*, affecting >200 species currently (Wilkin, 1999; Muñoz-Rodríguez *et al.*, 2019, 2023), or (2) splitting, i.e. separating the traditional genus *Ipomoea* into individual genera (Eserman *et al.*, 2020; Staples *et al.*, 2021; Rattanakrajang *et al.*, 2022), which would result in a higher number of genera (nine and counting) and would require name changes depending on where generic boundaries are drawn (Stefanović *et al.*, 2003). Regardless of which opinion is chosen, increased taxon sampling in phylogenetic analyses and improved understanding of morphological characters, as advocated by Manos *et al.* (2001), are essential for a conclusive, phylogeny-based revision of the tribe.

This study, for the first time, employed the target enrichment strategy with the universal Angiosperms353 probe set (Johnson *et al.*, 2019; Baker *et al.*, 2022) to study the phylogenetics of tribe Ipomoeae, with a focus on the contribution and position of African *Ipomoea* taxa in the tribe. Phylogenomic data provide better support than single-locus data and can be used to constrain a single-gene phylogenetic tree for better resolution. This study aimed to (1) test the monophyly of the two major clades of the tribe Ipomoeae, (2) identify the position of African clades and document their contribution to the systematics of Ipomoeae, and (3) identify clades and genera within the tribe that still require in-depth taxonomic and phylogenetic work to achieve better classification. The study utilized a single-locus internal transcribed spacer (ITS) region-constrained phylogenetic analysis approach to Ipomoeae, guided by a well-supported phylogenomic-generated tree.

## MATERIALS AND METHODS

### Taxon sampling

Samples for this study were obtained from Meise Botanic Garden (BR), Muséum national d'Histoire naturelle (P),

Royal Botanic Garden, Kew (K), Atlanta Botanical Garden Conservation DNA biorepository, and during fieldwork that was conducted in Kenya in 2022. Voucher specimens were deposited at the East Africa Herbarium (EA). This study employed both Angiosperms353 (A353) and ITS gene regions, capitalizing on existing available datasets from previous studies (Muñoz-Rodríguez *et al.*, 2023; Zuntini *et al.*, 2024) complemented by newly generated sequences from this study.

A total of 57 taxa, including the outgroups (Table 2; Supplementary Data File S1) were sampled for the A353 dataset, of which 45 were newly generated, and the rest added from the Plant and Fungal Trees of Life (PAFTOL) project (Zuntini *et al.*, 2024). The A353 dataset included representatives from nine out of the ten genera belonging to Ipomoeae, i.e. *Ipomoea* (40/615 species), *Lepistemon* (2/7 species), *Lepistemonopsis* (1/1 species), *Turbina* (2/20 species), *Stictocardia* (2/12 species), *Argyreia* (6/142 species), *Astripomoea* (2/12 species) and *Muigaia* (2/7 species). Only *Rivea* was not represented in the phylogenomic analysis. The A353 dataset included novel data for 17 African taxa, of which one is endemic to Madagascar, three are restricted to East Africa and 13 are widespread in tropical and subtropical Africa (Table 2). The ITS dataset consisted of 830 accessions, including the outgroups, mostly derived from Muñoz-Rodríguez *et al.* (2019) and Simões *et al.* (2015). The ITS dataset included 41 novel sequences (Table 3) representing 36 African taxa, including 28 species and 8 varieties. Of the 36 taxa sampled, 24 are restricted to, or mainly distributed in, Eastern Africa, 4 are endemic to Madagascar and 7 are widespread across tropical and subtropical regions of the Eastern Hemisphere (Africa, Asia and Australia).

Genera *Daustinia*, *Decalobanthus* and *Merremia*, from the tribe Merremieae, were used as outgroups since Ipomoeae is nested within Merremieae (Simões *et al.*, 2022). As the taxonomic composition of the ITS dataset was far more comprehensive than the A353 dataset, they were not analysed together. However, the A353 phylogenomic analyses provided well-resolved relationships in clades, unlike the ITS tree, hence the topology of the A353 was used to constrain the analyses of the ITS dataset. The A353 phylogenomic analyses and two ITS trees (A353-constrained and -unconstrained) are presented and discussed in this study.

### DNA extraction, library preparation and sequencing

DNA extraction for both the ITS and A353 dataset was conducted using the CTAB protocol (Doyle and Doyle, 1987;

TABLE 2. Novel sequences of African taxa introduced in this study and their geographical distribution.

Species	ITS	A353	Geographical distribution
<i>Argyreia androyensis</i>	x		Madagascar
<i>Argyreia onilahiensis</i>		x	Madagascar
<i>Astripomoea lachnosperma</i>		x	Tropical and subtropical Africa
<i>Astripomoea malvacea</i>		x	Tropical and subtropical Africa
<i>Ipomoea abyssinica</i>	x		Ethiopia
<i>Ipomoea carnea</i> subsp. <i>fistulosa</i>	x		Tropical and subtropical regions
<i>Ipomoea crassipes</i> var. <i>hewittiioides</i>	x		Angola, Cape Provinces, DR Congo, Ethiopia, Tanzania
<i>Ipomoea crepidiformis</i>	x		Congo, DR Congo, Ethiopia, Kenya, Malawi, Somalia, Tanzania, Uganda, Zambia, Zimbabwe
<i>Ipomoea crepidiformis</i> var. <i>microcephala</i>	x		Congo, DR Congo, Ethiopia, Kenya, Somalia, Tanzania, Zambia
<i>Ipomoea darainensis</i>	x		Madagascar
<i>Ipomoea fulvicaulis</i>	x		Angola, Botswana, Burundi, Chad, DR Congo, Ethiopia, Kenya, Malawi, Mozambique, Sudan – South Sudan, Tanzania, Uganda, Zambia, Zimbabwe
<i>Ipomoea fulvicaulis</i> var. <i>asperifolia</i>	x		Angola, DR Congo, Malawi, Mozambique, Tanzania, Zambia, Zimbabwe
<i>Ipomoea heterotricha</i>		x	Tropical and subtropical Africa
<i>Ipomoea hildebrandtii</i>	x	x	DR Congo, Ethiopia, Kenya, Rwanda, Tanzania, Uganda
<i>Ipomoea involucrata</i>	x		Tropical and subtropical Africa
<i>Ipomoea involucrata</i> var. <i>burtii</i>	x		Tanzania, Zambia
<i>Ipomoea involucrata</i> var. <i>operosa</i>	x		Mozambique, Malawi, Tanzania, Zambia
<i>Ipomoea irwiniae</i>	x		Kenya, Tanzania
<i>Ipomoea jaegeri</i>	x		Ethiopia, Kenya, Tanzania
<i>Ipomoea keraudreniae</i>	x		Madagascar
<i>Ipomoea kituiensis</i>	x		Ethiopia, Kenya, Malawi, Tanzania, Zambia, Zimbabwe
<i>Ipomoea lapathifolia</i>	x		Botswana, Burundi, Cape Provinces, DR Congo, Eswatini, Kenya, Malawi, Mozambique, Nigeria, Tanzania, Uganda, South Africa (Northern Provinces), Zambia, Zimbabwe
<i>Ipomoea longituba</i>	x	x	Kenya, Tanzania, Uganda
<i>Ipomoea mombassana</i>	x	x	Kenya, Sudan-South Sudan, Tanzania
<i>Ipomoea obscura</i>	x	x	Tropics and subtropical Africa, Asia and Australia
<i>Ipomoea ochracea</i>	x		Tropics and subtropical Africa, Asia and Australia
<i>Ipomoea oenotherae</i>	x		Botswana, Eritrea, Ethiopia, South Africa (Free State, Northern Provinces), Kenya, Malawi, Namibia, Rwanda, Somalia, Tanzania, Uganda, Zambia, Zimbabwe
<i>Ipomoea pes-tigridis</i>	x	x	Tropics and subtropical Africa, Asia and Australia
<i>Ipomoea pes-tigridis</i> var. <i>longibracteata</i>	x		Kenya, Tanzania
<i>Ipomoea pileata</i>	x	x	Tropics and subtropical Africa and Asia
<i>Ipomoea prismatosyphon</i>	x	x	West, Central and East Africa
<i>Ipomoea pseudomarginata</i>	x		Madagascar
<i>Ipomoea rubens</i>		x	Native to Tropical and subtropics of the Eastern Hemisphere; introduced in Tropical America
<i>Ipomoea shirambensis</i>	x		Botswana, DR Congo, Malawi, Mozambique, South Africa (Northern Provinces), Tanzania, Zambia, Zimbabwe
<i>Ipomoea triflora</i>	x		Kenya, Saudi Arabia, Somalia, Yemen
<i>Ipomoea trinervia</i>	x		Malawi, Tanzania
<i>Ipomoea tuberculata</i> var. <i>odontosepala</i>	x		Tanzania, Zambia
<i>Ipomoea wightii</i>	x	x	Tropical Africa and Indian subcontinent
<i>Lepistemonopsis volkensii</i>		x	Ethiopia, Kenya, Tanzania

Table 2. Continued

Species	ITS	A353	Geographical distribution
<i>Muigaia coptica</i>	x	x	Africa, Madagascar and Indian subcontinent
<i>Muigaia palmatisecta</i>	x	x	East Africa (Kenya, Mozambique, Tanzania and Uganda); Madagascar; India (Andhra Pradesh, Tamil Nadu); Sri Lanka; introduced in Thailand
<i>Turbina bracteata</i>	x		Madagascar
<i>Turbina stenosphon</i>		x	Cape Provinces, DR Congo, Kenya, Madagascar, Malawi, Mozambique, Northern Provinces, Sudan-South Sudan, Tanzania, Uganda, Zambia, Zimbabwe

The x denotes the type of data present for the study.

Doyle, 1991) modified to adapt to Convolvulaceae (Simões *et al.*, 2024a). The total genomic DNA for each sample was quantified and assessed using a 1.5× agarose gel and Qubit 3.0 fluorometer (ThermoFisher Scientific, Waltham, MA, USA). Samples with  $\geq 500$  bp ( $18 \text{ ng } \mu\text{L}^{-1}$ ) were considered slightly fragmented, while those with  $< 500$  bp ( $18 \text{ ng } \mu\text{L}^{-1}$ ) were considered highly fragmented.

For the ITS sequences, primers *AB101* and *AB102* (Carine *et al.*, 2004) and *ITS4* and *ITS5* (White *et al.*, 1990) were used in a 1:2 ratio to amplify the entire ITS region, i.e. ITS1–ITS2, from slightly fragmented DNA. In the cases of highly fragmented DNA, internal primers were used. Primers *ITS2* and *ITS5* (White *et al.*, 1990) were used to amplify the ITS1 region, while *ITS3* and *ITS4* (White *et al.*, 1990) primers were used to amplify the ITS2 region. Asymmetrical PCR parameters (Baldwin, 1992) were implemented. An exonuclease–calf intestine phosphatase combination was used to clean the amplicons. The amplicons were then duplicated, and a single-direction primer was added to each before being sent for sequencing at Macrogen (Geumcheon, Republic of Korea).

For the A353 sequences, 26  $\mu\text{L}$  of the total extracted genomic DNA was used per sample. To minimize the impact of intra-sample differences in fragment length, sizes ranging from 200 to 350 bp were selected to maximize sequencing capacity and data quality. Dual-indexed libraries with Dual Index Primers Set 1, NEBNext Multiplex Oligos for Illumina (New England BioLabs, Ipswich, MA, USA) were prepared using the DNA NEBNext<sup>®</sup> Ultra<sup>™</sup> II FS DNA Library Prep Kit (New England BioLabs). The quality and quantity of each library were determined using a Qubit dsDNA HS Assay Kit (Thermo Fisher Scientific, Waltham, US) and an Agilent 2100 Bioanalyzer. Libraries were pooled and hybridized using the myBaits Expert Predesigned Panel (Arbor Biosciences, Ann Arbor, MI, USA) Angiosperms353 v.1 (catalogue no. 308196) (Johnson *et al.*, 2019) following the manufacturer’s protocol (<http://www.arborbiosci.com/mybaits-manual>). Libraries were hybridized at 65 °C for up to 32 h in a Hybex Microsample Incubator (Scigene, Sunnyvale, CA, USA). Enriched products were amplified, and PCR products were cleaned using the QIAquick PCR purification kit (Qiagen, Manchester, UK). Enriched library pools were then multiplexed and sequenced on an Illumina MiSeq (Illumina, San Diego, CA, USA) with v3 reagent chemistry (2 × 300-bp paired-end reads) at Macrogen (Geumcheon, Republic of Korea).

#### Sequence annotation, contig assembly and multiple sequence alignment

The ITS sequences were annotated using Geneious (Kearse *et al.*, 2012). A total of 41 new ITS sequences were generated for this study (Table 3). The sequence alignment (with a total of 1237 accessions) from Muñoz-Rodríguez *et al.* (2019) was merged with the newly generated sequences and sequences from Simões *et al.* (2015). To reduce computational workload, only taxa belonging to Ipomoeae were kept. The supermatrix was realigned using the L-INS-I strategy in MAFFT v.7 (Katoh *et al.*, 2002; Katoh and Standley, 2013) with 1000 maximum iterations and auto-adjustment options. Gaps were removed using Phyutility (Smith and Dunn, 2008) with default parameters. To identify and remove outliers from the sequence alignment, Spruceup (Borowiec, 2019) was employed using default parameters. The alignment was visualized and manually edited using AliView v.1.27 (Larsson, 2014) and sequences with  $< 200$  bp were removed. The final ITS datasets had a total of 830 accessions.

HybPiper v.1.2 (Johnson *et al.*, 2016) was used with default settings to process the raw sequence data. Reads were mapped to targets (A353 target file) using BWA v.0.7.5a (Li and Durbin, 2009), and successfully mapped reads were assembled into contigs using SPAdes v.3.11.1 (Bankevich *et al.*, 2012). Exonerate (Slater and Birney, 2005) was used to align contigs to their associated target exon sequence. If contigs were found to be overlapping (Johnson *et al.*, 2016), they were combined into ‘supercontigs’ that contained both target (exon) and off-target (intron) sequence data. Paralogues were filtered and retrieved using the HybPiper paralog-retriever option and sequences with paralogues were removed. Extracted A353 supercontigs from the individual taxa were aligned individually using the L-INS-I strategy in MAFFT v.7 (Katoh *et al.*, 2002; Katoh and Standley, 2013) with 1000 maximum iterations and auto-adjustment options. Gaps were removed using Phyutility (Smith and Dunn, 2008) with default parameters and trimAl v.1.2 (Capella-Gutiérrez *et al.*, 2009) was used to trim the ends using default parameters. To identify and remove outliers from the sequence alignment, Spruceup (Borowiec, 2019) was employed using default parameters on each gene region. The multiple sequence alignments were visualized and manually adjusted using AliView v.1.27 (Larsson, 2014) where necessary.

TABLE 3. Voucher specimens and GenBank accession numbers of the newly generated ITS sequences employed in this study.

Species	Collector	Collection number	Herbarium deposited	GenBank accession number
<i>Argyreia androyensis</i>	Humbert, H.	20 345	P	PV084877.1
<i>Ipomoea abyssinica</i>	Quartin-Dillon, R. & Petit, A.		P	PV084900.1
<i>Muigaia coptica</i>	Sangai, G.W.	953	BR	PV084896.1
<i>Muigaia palmatisecta</i>	Faulkner, H.	3384	BR	PV084895.1
<i>Ipomoea carnea</i> subsp. <i>fistulosa</i>	Massawe, G.	86	P	PV084906.1
<i>Ipomoea crassipes</i> var. <i>hewittioides</i>	Redhead, E. & Taylor, P.G	8496	BR	PV084867
<i>Ipomoea crepidiformis</i>	Wilson, J.	389	BR	PV084863
<i>Ipomoea crepidiformis</i>	Bidgood, S.	4099	P	PV084864
<i>Ipomoea crepidiformis</i> var. <i>crepidiformis</i>	Kibuwa, S.P.	1072	BR	PV084865
<i>Ipomoea crepidiformis</i> var. <i>microcephala</i>	Kokwaro, J.O.	3011	BR	PV084866
<i>Ipomoea darainensis</i>	Ranirison, P.	725	P	PV084899.1
<i>Ipomoea fulvicaulis</i> var. <i>asperifolia</i>	Jacques-Felix, H.	4461	P	PV084856
<i>Ipomoea fulvicaulis</i> var. <i>fulvicaulis</i>	Raynal, J.	13 090	P	PV084857
<i>Ipomoea hildebrandtii</i> var. <i>hildebrandtii</i>	Kagame, S.P.	11	EA	PV084862
<i>Ipomoea involucrata</i> var. <i>burtii</i>	Greenway, P.J. and Polhill, R.M.	11 425	BR	PV084873
<i>Ipomoea involucrata</i> var. <i>involucrata</i>	A.D.	117	P	PV084874
<i>Ipomoea involucrata</i> var. <i>operosa</i>	Milne-Redhead, E. and Taylor, P.G	11 114	BR	PV084875
<i>Ipomoea irwiniae</i>	Polhill, R.M. and Kibuwa, S.P.	872	BR	PV084909.1
<i>Ipomoea jaegeri</i>	Kagame, S.P.	19	EA	PV084897.1
<i>Ipomoea keraudreniae</i>	Andriamihajarivo, T. and Rakotoarinony, F.	1191	P	PV084918.1
<i>Ipomoea kituiensis</i>	Jaeger, P.M.L.	6892	P	PV084870
<i>Ipomoea lapathifolia</i>	Faulkner, H.	3649	BR	PV084907.1
<i>Ipomoea longituba</i>	Kagame, S.P.	20	EA	PV084910.1
<i>Ipomoea mombassana</i>	Kagame, S.P.	31	EA	PV084910.1
<i>Ipomoea obscura</i>	Polhill, R.M. and Kibuwa, S.P.	1977	BR	PV084884
<i>Ipomoea obscura</i> var. <i>fragilis</i>	Robson, N.K.B.	1568	BR	PV084885
<i>Ipomoea obscura</i> var. <i>sagittifolia</i>	Richards, H.M.	19 820	BR	PV084886
<i>Ipomoea ochracea</i>	Starzenski, A.	20	BR	PV084888
<i>Ipomoea ochracea</i>	Drummond, R.B. and Hemsley, J.H.	4079	BR	PV084889
<i>Ipomoea oenotherae</i>	de Wilde, J.J.F.E	6424	BR	PV084914.1
<i>Ipomoea pes-tigridis</i>	Napier, E.R.	6248	BR	PV084894
<i>Ipomoea pes-tigridis</i> var. <i>longibracteata</i>	Polhill, R.M. and Kibuwa, S.P.	1326	BR	PV084893
<i>Ipomoea pileata</i>	Taylor, C.M.	8305	P	PV084872
<i>Ipomoea prismatosyphon</i>	Bullock, A.	1949	BR	PV084911.1
<i>Ipomoea pseudomarginata</i>	Humbert, H.	25 872	P	PV084861
<i>Ipomoea shirambensis</i>	Milne-Redhead, E. and Taylor, P.G	7365	BR	PV084876
<i>Ipomoea triflora</i>	Gillett, J.B.	13 431	BR	PV084855
<i>Ipomoea trinervia</i>	Lovett, J.C.	4449	P	PV084890
<i>Ipomoea tuberculata</i> var. <i>odontosepala</i>	Polhill, R.M. and Kibuwa, S.P.	2032	BR	PV084891
<i>Ipomoea wightii</i>	Lovett, J.C.	3414	P	PV084860
<i>Turbina bracteata</i>	Decary, R.	3448	P	PV084859

### Phylogenetic inference

Both the ITS and A353 datasets were analysed using maximum likelihood (ML). The A353 tree was generated first and subsequently used to constrain the ITS analysis.

Considering that different gene regions have different evolutionary rates, the A353 supercontig multiple sequence alignments were each subjected to ML analysis independently. Evolutionary models for each gene region were estimated using

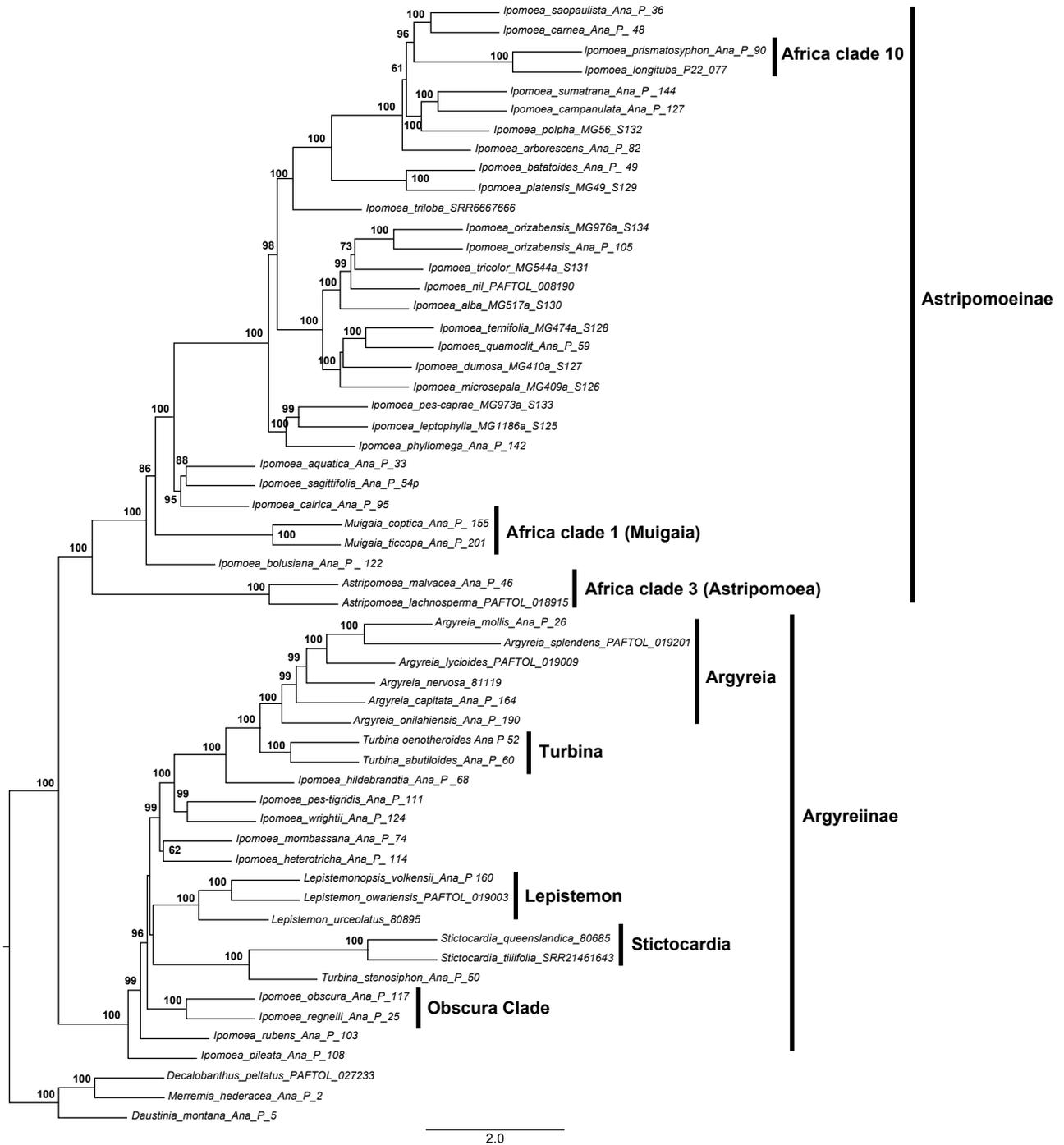


Fig. 1. Coalescent species phylogenomic tree of tribe Ipomoeae. The species tree was generated from the Angiosperms353 gene trees. Only branch labels >60% are shown. The scale bar represents nucleotide substitution per site (branch length).

ModelFinder (Kalyanamoorthy *et al.*, 2017) embedded within IQ-Tree multicore version v.1.6.12 (Minh *et al.*, 2020) and based on the Akaike information criterion (AIC). The best evolutionary models were selected for each gene region and ML analysis was conducted in IQ-TREE multicore v.1.6.12 (Minh *et al.*, 2020) using the UltraFast bootstrapping method (Hoang *et al.*, 2018) to generate gene trees. The resulting gene trees were used to generate a consensus multispecies coalescent

(MSC) species tree using weighted (w)ASTRAL v.1.22.3.7 (Zhang and Mirarab, 2022) with default parameters. This approach was implemented to curb the uncertainty caused with long terminal branches as well as missing taxa by reducing the impact of quartets with low support or long terminal branches (or both) (Zhang and Mirarab, 2022). The generated consensus species tree (Fig. 1) was visualized using FigTree (Rambaut, 2010) and was used to constrain the ITS tree analysis.

The final ITS dataset was subjected to ML analysis. Evolutionary models were estimated using ModelFinder (Kalyaanamoorthy *et al.*, 2017) embedded within IQ-TREE multicore version v.1.6.12 (Minh *et al.*, 2020) based on the AIC. SYM + R5 was selected as the best evolutionary model. A constrained ML analysis was conducted in IQ-TREE multicore v.1.6.12 (Minh *et al.*, 2020) using the UltraFast bootstrapping option (Hoang *et al.*, 2018) with the selected model and a constraint file. The generated tree (Figs 2 and 3) was visualized using FigTree (Rambaut, 2010). For comparison reasons, an unconstrained ML analysis was also run in IQ-TREE using a similar evolutionary model. The scale bar represents nucleotide substitution per site (branch length).

#### Gene tree discordance inference

We explored gene tree discordance in two ways. (1) To predict and summarize biological variations and discordance among the gene trees with respect to the MSC species tree (Mirarab *et al.*, 2014; Lanfear and Hahn, 2024), quartet concordance factors (qCFs) were generated using wASTRAL (Zhang and Mirarab, 2022) and mean discordance statistics calculated and visualized using the Quaint tool (<https://github.com/ethanbaldwin/quaint>). (2) To evaluate the numbers of gene trees that are concordant, or discordant or uninformative (i.e. the gene tree low support values at that particular branch) with the species tree topology at each branch, the phyparts tool (Smith *et al.*, 2015) was employed, and the resulting output was visualized on the wASTRAL MSC species tree topology (Fig. 4) using phypartspiecharts.py tool ([github.com/mossmatters/phyloscripts](https://github.com/mossmatters/phyloscripts)).

## RESULTS

#### A353-constrained ITS tree versus unconstrained ITS tree

Both the A353 (Fig. 1) and constrained ITS (Figs 2 and 3, Supplementary File S2) trees corroborated the monophyletic status of tribe Ipomoeae. Both trees included representatives of Ipomoeae genera, with the A353 tree missing *Rivea* (Fig. 1). *Paralepistemon* was the only unsampled genus in this study. The ITS-constrained tree (Figs 2 and 3) was resolved with lower support along the backbone (Bootstrap (BS) < 70) than for more shallow nodes. This was different from the A353 tree, which had strong support (BS > 80) both along the backbone and along shallow nodes (Fig. 1). This signalled the significant contribution of more data (gene regions) in the resolution of more recent divergences. There was a distinct separation of the Argyreiinae and Astripomoeinae (Fig. 1), corroborating previous studies (Stefanović *et al.*, 2003; Eserman *et al.*, 2014, 2020; Wood *et al.*, 2020; Sumanon *et al.*, 2025). This study also indicated the presence of the African grades within Astripomoeinae.

#### General topology and higher-level relationships

The unconstrained ITS tree (Supplementary File S3) resulted in poorly resolved and supported topologies, in most part incongruent with previous studies. For this reason, results of this study are discussed based on A353 (Fig. 1) and

A353-constrained ITS phylogenetic trees (Figs 2 and 3). Tribe Ipomoeae is resolved into two sister clades (BS = 100): Argyreiinae and Astripomoeinae. This relationship has been recovered in previous studies. However, the exact composition of each of the clades has been unstable depending on the data utilized and taxon sampling. The unsettled position of genus *Astripomoea*, either in Argyreiinae or Astripomoeinae, is key for fixing the generic delimitation of each of these clades. This study demonstrates with strong support, and corroborating previous studies showing that:

- (1) Argyreiinae and Astripomoeinae are two sister clades (BS = 100);
- (2) Argyreiinae is composed of mainly genera and species native to the Eastern Hemisphere (tropical and subtropical Africa, Asia and Australia), namely *Argyreia*, *Stictocardia*, *Turbina* (*pro parte*), *Lepistemon*, *Lepistemonopsis* and several species of *Ipomoea* of uncertain generic placement;
- (3) Astripomoeinae comprises mostly *Ipomoea* species from the Western Hemisphere, albeit with representatives of African, Asian and Australian taxa, and two Eastern Hemisphere endemic genera, namely *Astripomoea* and *Muigaia* (Ngima *et al.*, 2025);
- (4) *Astripomoea* is positioned within the Astripomoeinae clade (BS = 100).

#### Argyreiinae clade

Argyreiinae is maximally supported in both A353 and constrained ITS trees, leaving no doubt about its current delimitation. This supports the possibility of recognizing it as a subtribe, separate from Astripomoeinae. Simões *et al.* (2024a) stated the likelihood of *Argyreia*, *Lepistemon*, *Lepistemonopsis* and several species of *Ipomoea* in this clade sharing pollen with tetra- to hexagonal areas, which could potentially be a valuable palynological synapomorphy for Argyreiinae.

*Lepistemonopsis* is nested within *Lepistemon* (Figs 1 and 2), which corroborates Wilkin (1999). The two genera are nested within *Stictocardia* in the constrained ITS tree (Fig. 2), but in the A353 tree (Fig. 1) they form a sister clade to *Stictocardia* and *Turbina*, albeit with low support. The two genera share unique pollen morphology, with narrow and elongated (wide) ektexinous columellae, which are not found elsewhere in Ipomoeae (Wilkin, 1999). Wilkin (1999) suggested the sinking of monotypic genus *Lepistemonopsis* into *Lepistemon*, a suggestion that has been supported by this study. *Lepistemonopsis* closely resembles *Lepistemon* as it shares the filament base scales feature but is characterized by its campanulate, five-lobed corolla and an indehiscent (tardily dehiscent) four-seeded fruit (Wilkin, 1999; Staples, 2007a). *Lepistemon*, on the other hand, is easily recognizable by the sub-umbellate, many-flowered head-like inflorescence, which is almost sessile in the leaf axils (Wilkin, 1999; Staples, 2007a). Despite these unique individual features, the development of the lower filament into a curved scale and its uniquely shaped urceolate corolla has kept the two genera separated from *Ipomoea* (Staples, 2007a). This study sampled three of its seven accepted species; *Lepistemon binectarifer*, *L. urceolatus* and *L. owariense*.

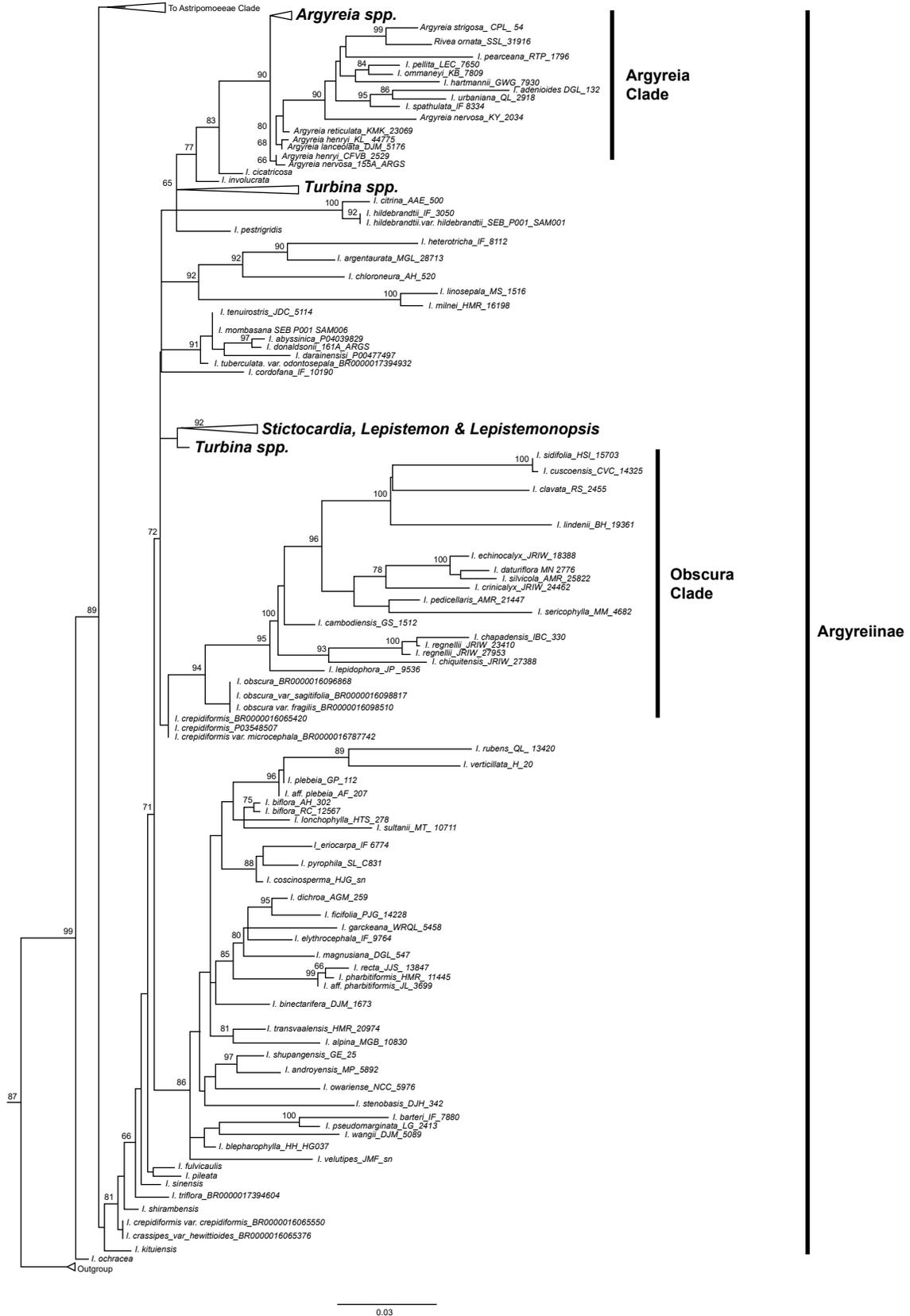


FIG. 2. Constrained ITS phylogenetic tree of subtribe Argyreinae. Only branch labels >60 % are shown. The scale bar represents nucleotide substitution per site (branch length).

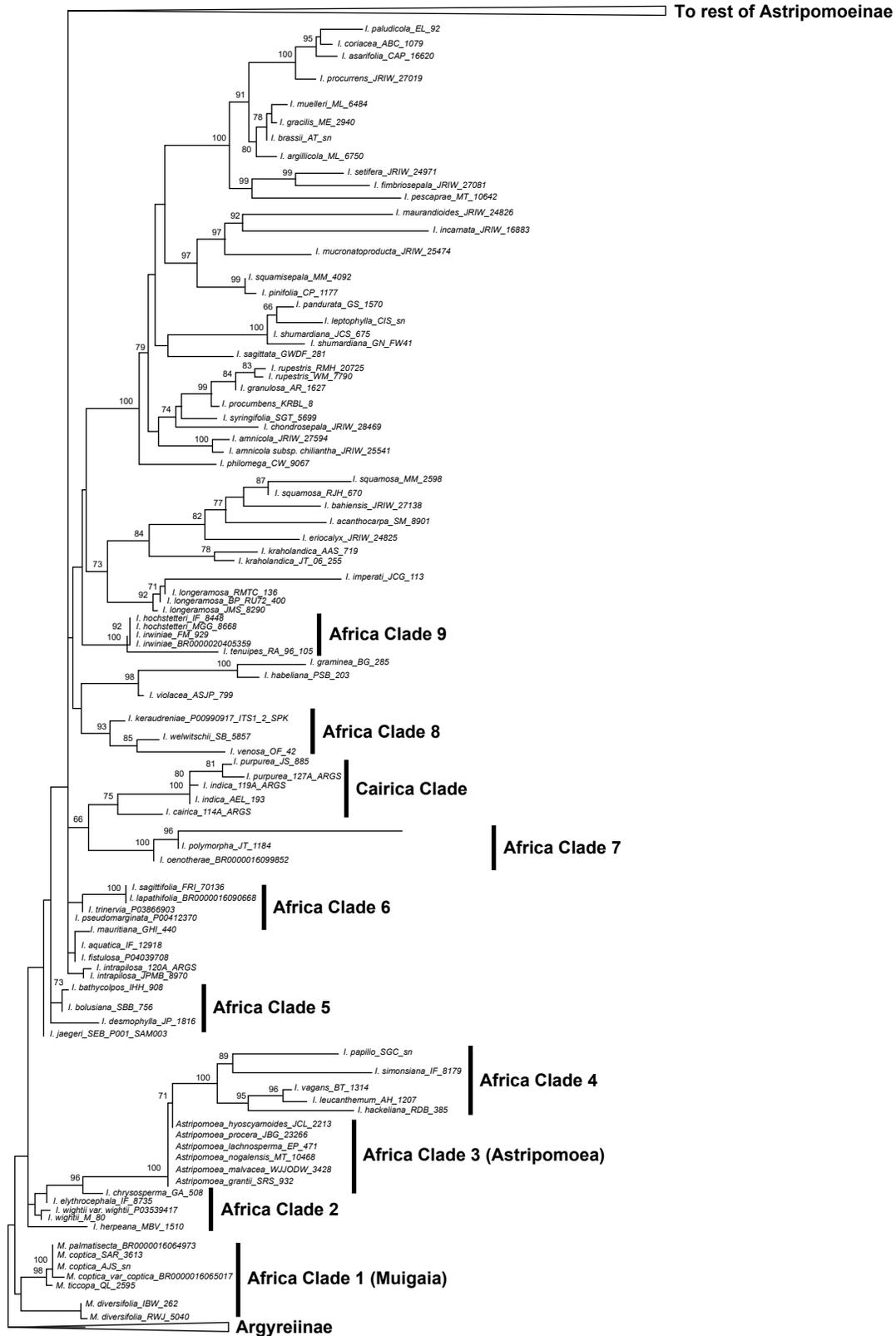


Fig. 3. Constrained ITS phylogenetic tree of subtribe Astripomoeinae with African clades included. Only branch labels >60 % are shown. The scale bar represents nucleotide substitution per site (branch length).

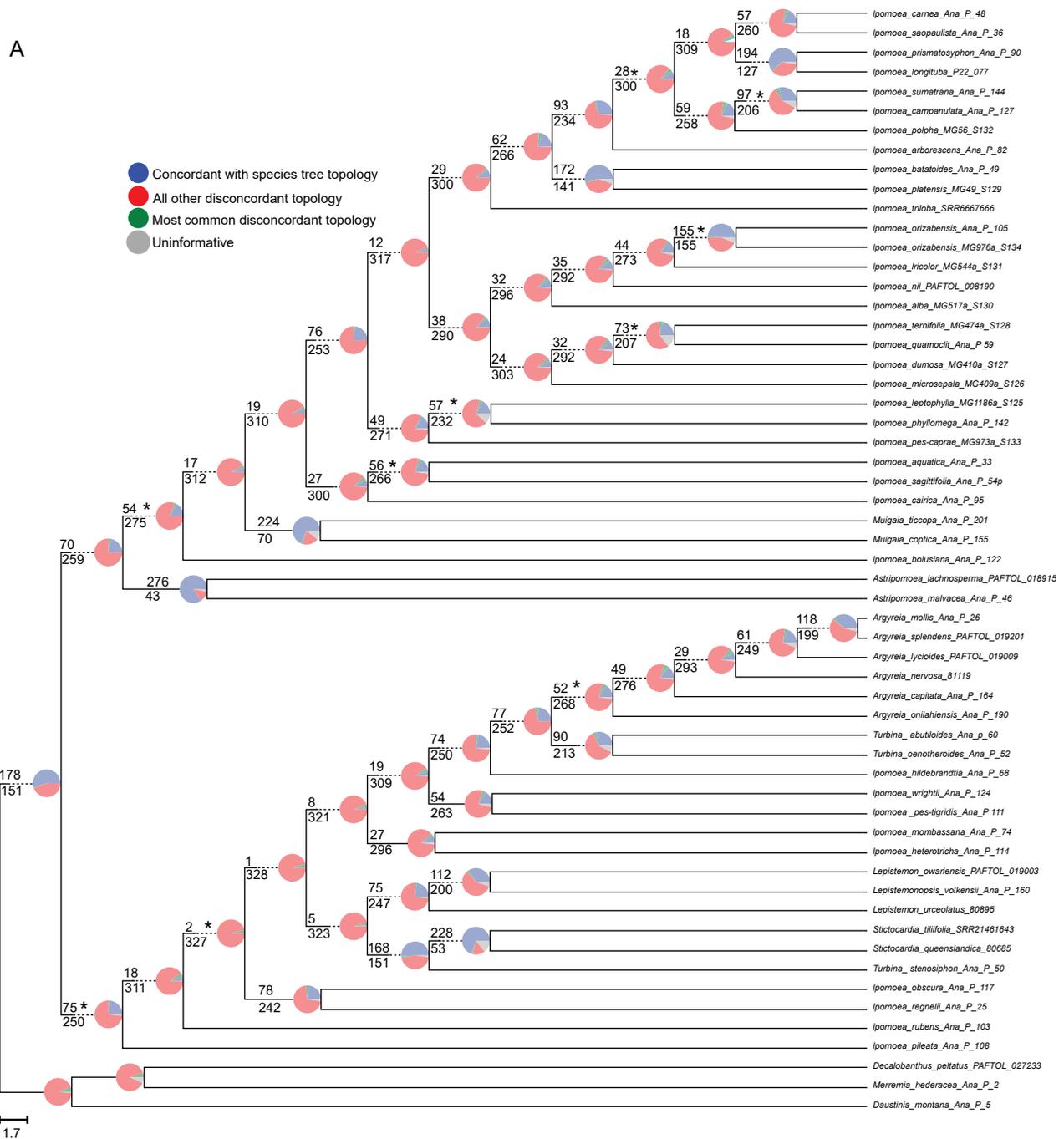


FIG. 4. (A) Gene tree discordance visualized on the ASTRAL species tree. Asterisks (\*) indicate nodes with significant qCF differences between the alternative resolutions around each node as inferred by wASTRAL. The pie charts at each node represent the number of gene trees that fall into one of four categories: concordant with the species tree (blue), discordant with the species tree but the most common alternative (green), all other alternatives (red), and uninformative (grey). The number above each branch is the number of gene trees concordant with the species tree topology at that node (blue slice). The number below each branch is the number of informative discordant topologies at that node (green + red slices). A high green proportion means there is a dominant alternative topology that should be considered. A very small sliver of blue is indicative of low overall support for the resolution around each node in the topology. (B) Visualization of discordance ( $D$ ) statistics generated from the Quint tool using qCF from wASTRAL. The scale bar represent nucleotide substitution per site (branch length).

*Stictocardia* is here resolved as sister to *Turbina*, and the clade that includes both *Turbina* and *Stictocardia* is sister to *Lepistemon* and *Lepistemonopsis*, in both the A353 and ITS phylogenies (Figs 1 and 2). *Stictocardia* is distributed in tropical Africa and tropical Asia and the Pacific and comprises 13

species (Simões *et al.*, 2024a, b). It is characterized by accrescent sepals, indehiscent or tardily dehiscent fruit with four-lobed septum and a four-lobed loculicidal spongy endocarp and absence of solitary latex cells (Austin and Demissew, 1997; Manos *et al.*, 2001; Johnson, 2004). It has a distinct

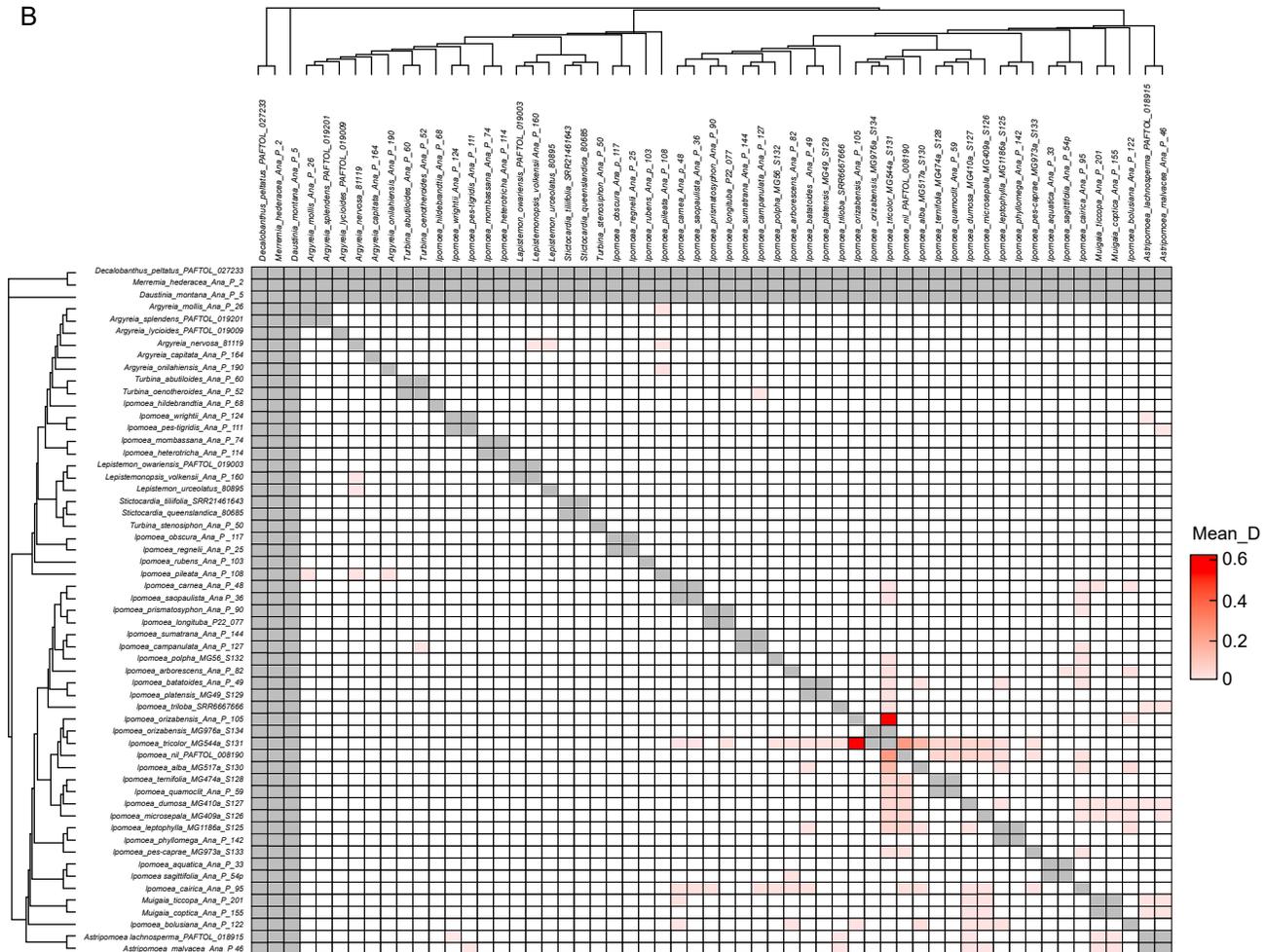


Fig. 4. Continued

endocarp with ‘pockets’ that hold seeds until they are dispersed (Austin and Demissew, 1997; Austin and Eich, 2001). It is also easily distinguished by the presence of black dots (peltate glandular trichomes) (Olaranont *et al.*, 2018), especially on the abaxial side of the leaves (Fang and Staples, 1995; Austin and Demissew, 1997; Austin and Eich, 2001). The application of phytochemistry studies on the glandular trichomes would also be key in further understanding this genus. This study supports re-instatement of this genus as an independent genus by Simões *et al.* (2024b) as it stands out independently from its close Palaeotropical relatives, i.e. *Turbina*, *Argyreia*, *Astripomoea*, and *Lepistemonopsis*.

*Turbina* was resolved as polyphyletic (Figs 1 and 2), a result that corroborated Manos *et al.* (2001) and Simões *et al.* (2024b). It comprises 20 species and is the only genus in the Argyreiinae to have both Palaeotropical and Neotropical distribution (Simões *et al.*, 2024b). The genus is morphologically cohesive with a good synapomorphy trait: a pyramidal chartaceous fruit, indehiscent or faintly four-valved, with a long persisting style (Austin and Staples, 1983, 1991; Wilkin, 1999; Simões *et al.*, 2024b), which solely distinguishes it from *Ipomoea*. This genus was reinstated by Simões *et al.* (2024b) and has the potential to

be segregated into smaller genera and/or for some of its species being reassigned to other genera. For instance, *Turbina stenosi-phon* is resolved as sister to *Stictocardia* and it is possible that it would better be placed in this genus, based on molecular and morphological evidence. Hence, increased taxonomic sampling is needed in this genus. Also, the employment of phytochemical components in this group can also be utilized to further classify and understand the group as ergot alkaloids have been reported in this genus (Austin and Eich, 2001).

*Argyreia* was resolved as paraphyletic, corroborating previous studies (Staples and Traiperm, 2017; Lawand and Shimpale, 2024; Yadav *et al.*, 2024; Simões *et al.*, 2024b; Sumanon *et al.*, 2025) (Fig. 2) with two major clades, one nesting *Rivea* and some species of *Ipomoea*, the other one comprising three Malagasy (*Argyreia androyensis*, *A. onilahiensis* and *A. vahibora*) and Asian *Argyreia* species (Sumanon *et al.*, 2025). *Argyreia* is regarded as the largest (Manos *et al.*, 2001) and the most diverse and species-rich genus among tropical Asian Convolvulaceae (Staples and Traiperm, 2017; Lawand and Shimpale, 2024), with a total of 142 accepted species (Lawand and Shimpale, 2024; Yadav *et al.*, 2024; Simões *et al.*, 2024b; Sumanon *et al.*, 2025). It is distinguished from

*Ipomoea* on the basis of variably pigmented indehiscent fruit with a fleshy to leathery pericarp (Meeuse, 1957; Manos *et al.*, 2001) and pubescent corolla (Wilkin, 1999), including remarkable silvery pubescence on the abaxial surface of leaves (but not universally present) (Lawand and Shimpale, 2024; Sumanon *et al.*, 2025). Some species, e.g. *Argyreia cuneata*, have only a very thin fleshy pericarp, which is also observed in two African species, *Ipomoea urbaniana* and *I. zanzibarica*, previously reported to be closely related to *Argyreia* (Wilkin, 1999). Additionally, they also share large persistent, foliaceous bracts and a shrubby habit with the four-locular species of *Argyreia* (Wilkin, 1999). In this study, *I. urbaniana* was resolved in this group (as previously suggested by Wilkin, 1999) (Fig. 2), which corroborated its strong relationship with *Argyreia*. Other species of *Ipomoea* also nested within *Argyreia* included: *I. adenioides*, *I. spathulata* (featuring yellowish spreading pubescence and a funnel-shaped, white cream or yellow corolla with a purple centre), *I. pellita* (characterized by leaves being densely covered on both surfaces with silvery-white hairs and a funnel-shaped rose-magenta corolla), *I. ommanneyi* (shares features with *I. pellita* and both are native in Southern Africa) and *I. hartmannii*. These are also characterized by dense pubescent leaves with white (or pale mauve) purple-centred, densely pubescent corollas. While the *Argyreia*–*Rivea* clade is supported morphologically based on indehiscent and leathery fruit, it does suggest a morphologically diverse group of taxa based on fruit locule number and septum thickness (Manos *et al.*, 2001). The A353 results also support the inclusion of *Blinkworthia* (*B. lycioides* = *A. lycioides*) in *Argyreia* (Rattanakrjang *et al.*, 2018, 2022) as it is strongly supported/nested within *Argyreia*.

*Rivea* is strongly supported within *Argyreia* (Fig. 1), corroborating results by Manos *et al.* (2001). This genus, originally considered of doubtful placement and delimitation within *Argyreinae* (Manos *et al.*, 2001), can be morphologically characterized by its large nocturnal and fragrant flowers, with a tubular–salverform, white corolla, two stigmas that are longer and wide, and a hard walled, four-locular (a feature in *Argyreia* and *I. urbaniana*), leathery indehiscent or tardily dehiscent fruit that breaks irregularly, but almost a dry fruit which resembles that of *Argyreia* species like *A. cuneata* (van Ooststroom, 1943; Wilkin, 1999). Additionally, the genus has leaf blades that are silvery pubescent beneath, and with a pair of prominent dark glands at the apex of the petiole, with seeds embedded in a spongy matrix that dries like cork inside the hard-shelled, woody, nut-like fruit (Staples, 2007b). The three accepted species of *Rivea* have corollas suggesting they are moth-pollinated, which supports van Ooststroom's (1943) thoughts that they were possibly *Argyreia* species that had adapted to that mode of pollination. Additionally, the characteristic is also observed in *I. adenioides*, an African endemic species occurring in Southern Africa and a sister to another African endemic species, *I. urbaniana*. The two are homotypic synonyms of *R. adenioides* and *R. urbaniana*, respectively. *Ipomoea adenioides* has a long salver-shaped, white or pink corolla with a deep magenta inside, up to 11 cm long; *I. urbaniana* on the other hand has a narrowly funnel-shaped, rose or purple corolla, up to 7 cm long. Both species are characterized by a yellowish indumentum, a characteristic that is shared across *Argyreia*.

Even though a more detailed morphological study is needed to further understand the *Argyreia*–*Rivea* clade, this study

suggests a targeted re-circumscription of this group is necessary, either (1) to subsume *Rivea* (Sumanon *et al.*, 2025) and the African-endemic *Ipomoea* in *Argyreia*, hence making the group monophyletic, or (2) to reinstate/synonymize the *Ipomoea* species in this group to *Rivea*, hence making the group paraphyletic.

The Obscura clade (Figs 1 and 2) is another important clade worth mentioning. This clade was again strongly supported (Eserman *et al.*, 2014), now with more taxa. In a broad sense, this clade consists mostly of Neotropical species except *Ipomoea cambodiensis* (South-East Asia endemic) and *I. obscura* itself, which occurs in tropical and subtropical regions of Africa and Asia. From a geographic perspective, this clade is peculiar in that it has a mostly Neotropical distribution, within a clade that is mostly Palaeotropical (*Argyreinae*), although this is also observed in *Turbina*, a genus within *Argyreinae* that also has Neotropical representatives. Considering that the type species of the genus *Ipomoea* is absent from the *Argyreinae* clade, rendering the genus paraphyletic in the current systematic arrangement, the species of *Ipomoea* present in *Argyreinae* are considered of yet doubtful generic placement. It is possible that the Obscura clade would warrant generic recognition, but in-depth taxonomic studies would be ideal to fully understand this clade.

#### *Astripomoeinae* clade

This clade is maximally supported and may be recognized as a subtribe, although no morphological synapomorphies have yet been identified for this group. This clade comprises three genera, as mentioned before. *Muigaia* (**Africa Clade 1**) is a strongly supported clade which corroborates Ngima *et al.* (2025). In the ITS constrained tree, it is resolved as sister to the rest of the *Astripomoeinae* (Fig. 3), whereas in the A353 analyses it is nested within it, with two other African lineages (*Astripomoea* and *Ipomoea bolusiana*) being more external. This genus is strictly Palaeotropical and characterized by its markedly angular stems, irregularly dissected (deeply palmate lobes) leaves, leaf-like stipules at the base of the petiole and a tri-globose stigma with six-valved capsules (Ngima *et al.*, 2025). It consists of seven species that occur in tropical Africa, Madagascar, India, South-East Asia and Australia (Ngima *et al.*, 2025).

**Africa Clade 2 (*wightii* complex)** comprises *Ipomoea chrysoesperma*, *I. elythrocephala* and *I. wightii*. All these taxa are East African-endemic except *I. wightii*, which is distributed across tropical Africa. Our study cements the treatment of *I. elythrocephala* as a member of the *I. wightii* complex (Verdcourt, 1963). This clade is characterized by their palmately dissected (three-lobed) leaves. *Astripomoea* (**Africa Clade 3**) resolves within *Astripomoeinae* with strong support (Fig. 1). It is an African-endemic genus (Simões *et al.*, 2024a, b) characterized by its distinct erect habit with densely stellate pubescence, oblong stigmas and a solanaceous corolla (Wilkin, 1999; Manos *et al.*, 2001). It forms a sister to **Africa Clade 4**, which comprises *I. papilio* (East/Southern Africa), *I. simonsiana* (East/Southern Africa and Madagascar), *I. vagans* (North Tropical Africa), *I. leucanthemum* (Central/Southern Africa) and *I. hackeliana* (Central/Southern Africa).

**Africa Clade 5** comprises *Ipomoea bathycolpos*, *I. bolusiana* (South Africa and Madagascar) and *I. desmophylla* (Madagascar). Even though this clade is poorly supported,

they all share a similar geographical range. Both *I. bolusiana* and *I. bathycolpos* have tuberous rootstock, with the latter being woodier. **Africa Clade 6** consists of *I. trinervia* (endemic to Malawi, Tanzania), *I. sagittifolia* (tropical and subtropical Africa and Asia), *I. pseudomarginata* (Madagascar) and *I. lapa-thifolia* (East, Central and Southern Africa). **Africa Clade 7** comprises *I. oenotherae* (East and Southern Africa), *I. polymorpha* (Africa, Asia and Australia) and *I. kotschyana* (Africa). *Ipomoea oenotherae* has seed features that resemble those of *I. polymorpha* and is also characterized by the presence of an edible storage root consumed mainly by the Maasai community in Kenya (Maundu *et al.*, 1999; S.P. Kagame, pers. comm.).

**Africa Clade 8** includes *Ipomoea venosa* (East Africa and Madagascar), *I. welwitschii* (Africa) and *I. keraudreniae* (Madagascar). *Ipomoea welwitschii* is characterized by its tuberous rootstock (almost as large as a cricket ball) and flowers immense when leafless (Verdcourt, 1963). It is widespread across tropical Africa (Verdcourt, 1963). **Africa Clade 9** comprises *I. tenuipes* (Africa and Indian subcontinent), *I. irwiniae* (East Africa) and *I. hochstetteri* (Africa and Indian subcontinent). They form a clade with a strong support value. They have a native range distribution in tropical Africa, with *I. irwiniae* native to Kenya and Tanzania. The other two are palaeotrophs with distribution in tropical Asia.

**Africa Clade 10 (*longituba*–*marmorata* complex)** comprises *Ipomoea prismatosyphon*, *I. paolii*, *I. pohlii*, *I. marmorata*, *I. gigantea*, *I. longibracteolata*, *I. queirozii*, *I. verbascoidea*, *I. albivenia*, *I. bullata*, *I. macrosiphon*, *I. macrocalyx*, *I. grantii*, *I. lapidosa*, *I. bakeri*, *I. longituba* and *I. alterniflora*. This clade encompasses the *I. longituba*–*marmorata* complex first mentioned by Verdcourt (1961), a species complex of mainly sweet-scented night-flowering flowers, (sub-)shrubs or lianas with salver-shaped corollas with a frilly-edged limb, which initially included *I. lapidosa*, *I. paolii*, *I. marmorata* and *I. longituba* (Verdcourt, 1961), all producing edible storage roots (apart from *I. paolii*, e.g. no record of tuberous rootstock) and endemic to east Africa (POWO, 2025). The current species complex comprises mainly East African endemics featuring the aforementioned floral morphology and presence of edible storage roots. The other eight species within this clade are all African endemics except for *I. alterniflora*, *I. longibracteolata*, *I. queirozii* and *I. gigantea*, which are endemic in North America (e.g. *I. alterniflora*, endemic to Cuba) and South America (Wood and Scotland, 2017; POWO, 2025).

#### Discordance in *Ipomoeae*

Phylogenomic datasets typically yield strong support when evaluated using metrics such as bootstrapping and posterior probability (Sayyari and Mirarab, 2016). Nodes that are maximally supported may still have evidence of conflicting signals among gene trees, which can be further explored by summarizing support for each bipartition across many gene trees (Overson *et al.*, 2023). Gene tree conflicts were observed across the *Ipomoea* phylogeny despite the high support values. Gene tree conflicts were demonstrated in ten different nodes/clades (Fig. 4) using qCFs in wASTRAL, with the highest conflicting signals observed at the crown nodes of *Argyreinae* and *Astripomoeinae* (excluding *Astripomoea* and *Muigaia*). Surprisingly, the clades *Ipomoeae*, *Astripomoea* and *Muigaia*

were strongly supported as the majority of the trees were congruent with the species tree, thus further supporting the monophyly of the tribe and the position of *Astripomoea* in *Astripomoeinae*. Most of the clades with high conflicting signals are characterized by their widespread distribution, presence of storage roots and their Eastern Hemisphere (tropical) distribution. These conflicting signals predicted through qCFs are the result of processes such as incomplete lineage sorting, gene introgression and/or horizontal gene transfer (Lanfear and Hahn, 2024).

#### DISCUSSION

Large genera present major obstacles for plant taxonomy, and unresolved phylogenetic trees and unresolved classifications can have negative impacts on related fields such as evolutionary biology (Moonlight *et al.*, 2018). Taxonomic studies in large genera have proven challenging, leading many researchers to focus instead on smaller genera within diverse plant families (Simões *et al.*, 2015; Wood *et al.*, 2015; Simões and Staples, 2017; Nepomuceno *et al.*, 2025). Others have pursued geographically focused taxonomic studies (Wood *et al.*, 2020; Souza *et al.*, 2023), primarily targeting Neotropical and other Western Hemisphere taxa. One of the main challenges hindering efforts to resolve taxonomic complexities in large genera is the continued dependence on traditional morphological methods for delimitation of genera. While these techniques have historically underpinned taxonomy, they lack statistical rigor and are susceptible to subjective bias, leading to inconsistencies in interpreting character homologies among researchers (Scotland *et al.*, 2003). Such limitations have slowed taxonomic progress in different plant families. Therefore, to fully resolve the taxonomic muddles within large genera, recourse needs to be taken. With advancement in technology, there is a need to employ other recent techniques to complement morphological and molecular data already acquired to further push taxon delimitation. The use of phylogenomic data to generate well-supported ‘backbone’ trees, as seen here, would be useful. With such a backbone tree, researchers can constrain their improved taxon-sampled single-gene phylogenetic trees using the well-supported phylogenomic trees that are generated. However, the issue of how to sample taxa for phylogenomic analysis remains unresolved.

The solution to addressing the taxonomy of large genera, *Ipomoea* in particular, remains in subdivision into smaller, stable, predictive, diagnosable and workable-sized groups that are easily memorized and taxonomically palatable. Wilkin’s (1999) proposition of lumping all the segregated genera of *Ipomoeae* into broader *Ipomoea* came as a result of unsupported distinct genera recognition; however, with the advent of sequencing technology, molecular data proved otherwise (Stefanović *et al.*, 2003; Eserman *et al.*, 2014; Muñoz-Rodríguez *et al.*, 2019). Based on molecular data, the tribe clearly splits into two maximally supported major clades, as seen in this study and other corroborating previous studies (Stefanović *et al.*, 2003; Eserman *et al.*, 2014; Muñoz-Rodríguez *et al.*, 2019, 2023; Wood *et al.*, 2020; Simões *et al.*, 2022, 2024a; Sumanon *et al.*, 2025), and they have the potential to be recognized as subtribes. This, in part, forms the basis for subdivision of the taxa in the tribe into smaller clades, with a possibility of generic delimitation. The

inclusion and increased sampling of African taxa brings new insight to the systematic study of the tribe. Additionally, the polyphyletic nature of *Ipomoea* provides a good basis for the genus to be sampled adequately and broken down into smaller genera, especially now that the type specimen of *Ipomoea* has been changed (Appelquist, 2023). With the increase in taxon sampling, the segregated clades are now well supported and form potential candidates for future generic delimitation.

Submerging all the taxa into one big genus will be akin to burying our heads in the sand and assuming the taxonomic impediments within the tribe. Acknowledging the position of a big genus taxonomically and working on the smaller clades based on their morphology, molecular data and other techniques will result in the circumscription of new genera (as seen in Ngima *et al.*, 2025). Currently, it is feasible to study big genera not only due to new methods and data types but also due to the advent of global collaborations (Moonlight *et al.*, 2024), especially with scientists and students from tropical regions. No longer are single taxonomists (or a few individuals) developing hypotheses of new taxa or the criteria for delimiting them (as discussed in Stevens, 1997), but synthesis and consensus are common (Moonlight *et al.*, 2024). At present taxonomists are more connected than in the past and have been collaborating more across continents to revise and reclassify big genera (Joppa *et al.*, 2011; Fertig, 2015).

### Conclusions

With the increase in engagement of taxonomists and students with African Convolvulaceae, more studies focusing on African *Ipomoea* species would result in possible re-circumscription and better understanding of the genus. The transfer of the type specimen of *Ipomoea* to *Astripomoeinae* has given more freedom to taxonomists, especially from Africa, to work on native *Ipomoea* clades and conduct possible re-circumscription of the genus. Our study acknowledges the diversity and ambiguity of Ipomoeae. The clear separation of Ipomoeae into *Astripomoeinae* and *Argyreinae* reflects the exclusive biodiversity in the geographical origins of each clade, including the synapomorphy characteristics and generic delimitations within them. This study supports the subdivision of large genera into smaller diagnosable clades. We encourage the use of phylogenomic data in taxon delimitation in big genera as this will result in the treatment of taxa in their proper groupings and gives support to the molecular phylogenetic placements of such taxa.

### SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following. **File S1:** complete ITS dataset with voucher information employed in the study. **File S2:** constrained complete phylogenetic tree of tribe Ipomoeae. **File S3:** unconstrained complete phylogenetic tree of tribe Ipomoeae. **File S4:** methodology.

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### AUTHOR CONTRIBUTIONS

S.P.K., A.W.T.M., L.W.C. and A.R.G.S. initiated the study, conceptualized the paper and wrote the manuscript. A.R.G.S. and P.R. taxonomically verified, sampled and prepared the Angiosperms353 libraries for 35 samples, which L.A.E. curated, quality-certified and aligned. S.P.K. conducted the A353 phylogenomic analysis with support of L.A.E. and J.H.L.M. P.A. assisted with extraction, library preparation and sequencing of additional specimens. V.K., S.W. and P.C.M. helped S.P.K. with the fieldwork studies in Kenya. All authors commented on, contributed to and approved the final version.

### CONFLICT OF INTEREST

The authors declare no conflict of interest.

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