Peeling Back the Layers: the Complex Dynamics Shaping the Evolution of the Ledebouriinae (Scilloideae, Asparagaceae)

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Abstract—The Ledebouriinae (Scilloideae, Asparagaceae) are a widespread group of bulbous geophytes found predominantly throughout seasonal climates in sub-Saharan Africa, with a handful of taxa in Madagascar, the Middle East, India and Sri Lanka. An understanding of the phylogenetic relationships within the group have been historically difficult to reconstruct, however. Here, we provide the first phylogenomic perspective into the Ledebouriinae. We use this renewed phylogenetic framework to hypothesize historical factors that have resulted in the topology recovered. Using the Angiosperms353 targeted enrichment probe set, we consistently

recovered four major clades (i.e. two *Ledebouria* clades, *Drimiopsis*, and *Resnova*). The two *Ledebouria* clades closely align with geography, either consisting almost entirely of sub-Saharan African taxa (*Ledebouria* Clade A), or East African and non-African taxa (*Ledebouria* Clade B). Our results also suggest that the Ledebouriinae underwent a rapid radiation leading to rampant incomplete lineage sorting. [Asparagaceae; *Drimiopsis*; geophytes; *Ledebouria*; monocots; *Resnova*; Scilloideae.]

Africa houses an enormous diversity of plants found across a range of habitats from tropical rainforests to arid landscapes (Linder 2014; Couvreur et al. 2020). Although seemingly distinct from one another, many habitats have intertwined evolutionary histories. For instance, the historical expansion of semi-arid and arid landscapes repeatedly separated western/central and eastern tropical forests, resulting in increased speciation and endemicity (Couvreur et al. 2008). Numerous additional historical phenomena have resulted in a unique, modern-day assemblage of flora and fauna on the continent. As research on Africa's biota has increased, so too has an appreciation for the contributions and influences of African lineages in shaping the floras of adjacent biomes (Zhou et al. 2011; Buerki et al. 2012; Gostel et al. 2015). Still, there remain numerous, understudied African organisms that have the potential to either support established hypotheses regarding evolution within Africa (e.g., the Rand Flora [Pokorny et al. 2015], the "arid track" [Balinsky 1962]), or showcase their own distinct patterns.

Geophytes offer unique insights into the evolution of seasonal or disturbance-prone habitats as these plants are especially adept at surviving such conditions due to belowground bud and resource placement (Rees 1989). Structures commonly associated with geophytism include bulbs, corms, stem tubers and rhizomes. The hyacinths (Scilloideae, Asparagaceae; formerly

Hyacinthaceae; APG IV ([he Angiosperm Phylogeny Group 2016]) consist of approximately 1,000 bulbous geophytes found throughout seasonal climates in Africa, as well as Madagascar, Europe, the Middle East, India, Sri Lanka, and South America (Speta 1998). Many clades within the Scilloideae have received varying degrees of phylogenetic and systematic attention (e.g., Ledebouriinae, Massonieae, Ornithogaloideae; (Pfosser et al. 2003; Lebatha et al. 2006; Martínez-Azorín et al. 2011); among many others), but phylogenomic applications are almost nonexistent (Steele et al. 2012). To showcase the value of focusing attention on understudied groups such as this, we investigate the phylogenomic space of one of its subclades—the Ledebouriinae—the evolutionary relationships of which have been historically difficult to reconstruct.

The Ledebouriinae are widespread across sub-Saharan Africa, found predominantly within the "arid track" (Balinsky 1962), with just a handful of taxa in Madagascar, Yemen, India and Sri Lanka (Fig. 1a; Venter 1993; Giranje and Nandikar 2016). The current center of diversity is the Limpopo, Mpumalanga and KwaZulu-Natal regions of South Africa (Venter 1993), with a secondary center in East Africa (Lebatha 2004; Lebatha et al. 2006). Taxonomically, the group currently consists of *Ledebouria* Roth with two sections: *Drimiopsis* (Lindl. & Paxton) J.C. Manning & Goldblatt and *Resnova* (Van der Merwe) J.C. Manning & Goldblatt (Manning et al. 2003; Manning and Goldblatt 2012; Manning 2020). However, taxonomic concepts still vary and a lack of consistency in the hypotheses generated by phylogenetic studies has resulted in disagreements regarding the nature of the Ledebouriinae and whether this group includes one or more distinct entities (Manning et al. 2003; Lebatha et al. 2006). Historically, *Ledebouria* and *Drimiopsis* Lindl. & Paxton were classified as separate taxa, and *Drimiopsis* enjoyed its own identity for some time (Lebatha et al. 2006; Müller-Doblies and Müller-Doblies 2008; Goldblatt

et al. 2012). The status of *Resnova* van der Merwe, on the other hand, has always been in question (Manning et al. 2003; Lebatha et al. 2006; Goldblatt et al. 2012; Manning 2020). There are currently 53 *Ledebouria*, 16 *Drimiopsis*, and five *Resnova* species accepted (The Plant List 2013), with the majority of systematic work occurring in South Africa (Venter 1993). Thus far, difficulties in reconstructing the phylogenetic history of the Ledebouriinae have stemmed from morphological homoplasy (Lebatha et al. 2006), the use of a small number of molecular markers with low information content (Manning et al. 2003), the lack of robust phylogenetic methods (Pfosser et al. 2003; Wetschnig et al. 2007), and the inclusion of a small fraction of the taxonomic and geographic diversity of the group. These limitations constrain our ability to detect confounding factors that have likely impacted the evolutionary history of the Ledebouriinae, which may be why it has been difficult to confidently reconstruct it.

The widespread distribution of the Ledebouriinae holds complementary promise for highlighting intricate details of evolution within and outside of Africa. Based on the results from previous studies (Ali et al. 2012; Buerki et al. 2012), the Ledebouriinae may have originated during a time (i.e. within the last 30 My) when African was undergoing major climatic and geological shifts (increasing seasonality and aridity, mountain building, etc.) (Partridge and Maud 1987; Jacobs 2004; Bobe 2006). Being geophytes and probably well-suited to withstand these changes, the Ledebouriinae may have undergone a rapid radiation in response to open niche space. Therefore, to recover a well-supported phylogenetic hypothesis for the group, the use of a large, genomic dataset consisting of rapidly evolving markers is likely needed. Unfortunately, the Ledebouriinae still lack the necessary genomic resources to develop a custom probe set. However, broadly applicable targeted-capture kits (e.g., Angiosperms353; Johnson et

al. 2019) have been instrumental in bringing complex groups like the Ledebouriinae to the phylogenomic playing field (Dodsworth et al. 2019).

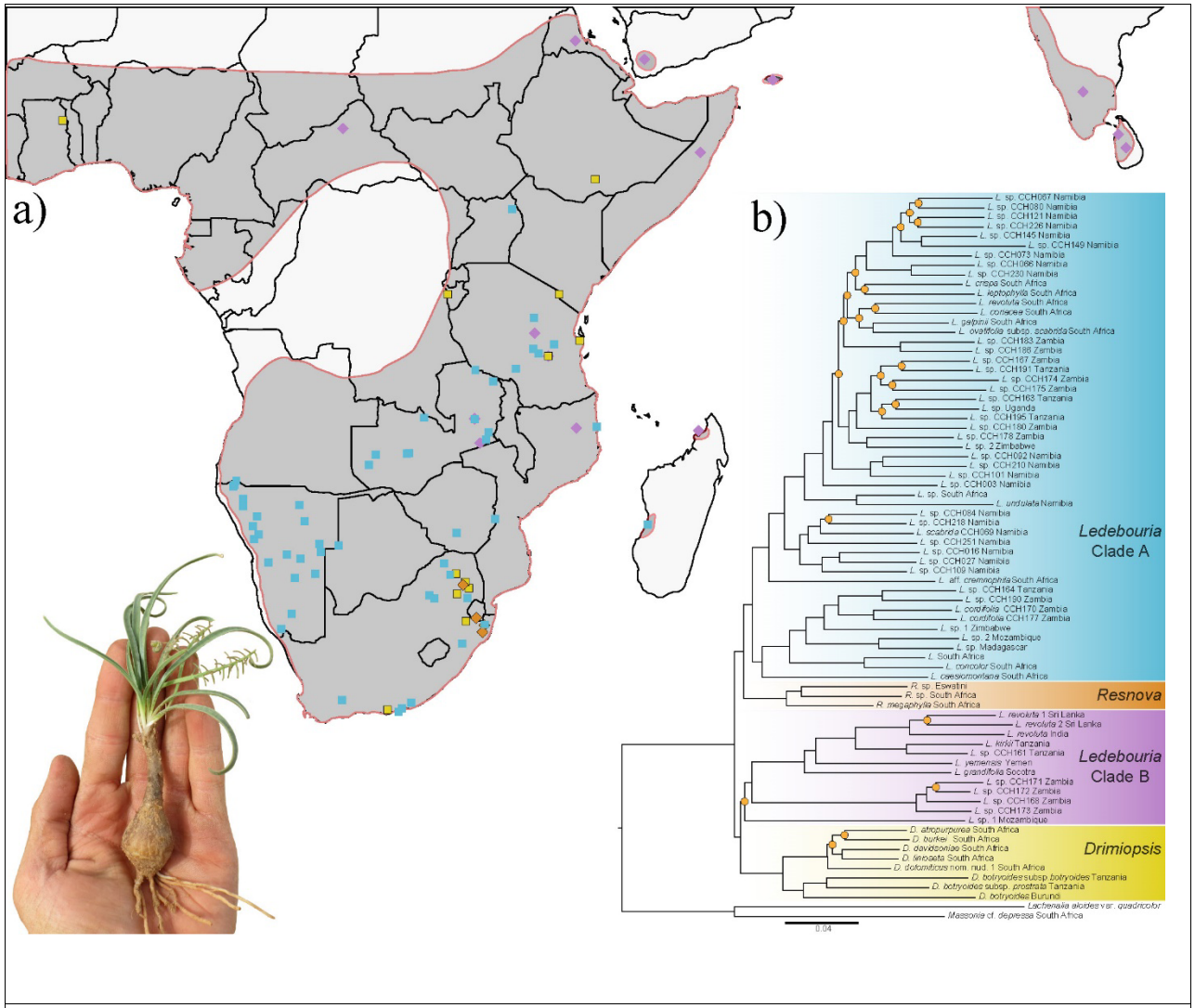

Figure 1. a) Distribution of all samples included in this study (full dataset) overlaid on the general distribution of the Ledebouriinae (dark gray polygon). Shapes and colors correspond to clades shown in (b): *Ledebouria* Clade A (blue squares), *Ledebouria* clade B (purple diamonds), *Resnova* (outlined orange diamonds), *Drimiopsis* (outlined yellow squares). b) Maximum likelihood phylogenetic reconstruction of the Taxa70 dataset with the four major clades labeled. Orange circles indicate nodes with SH-aLRT and ultrafast bootstrap values *below* 80 and 95,

respectively.

Here, we apply a HybSeq/targeted enrichment approach using the Angiosperms353 probe set, which has been effective in uncovering relationships at both deep and shallow scales (Larridon et al. 2019). The use of this probe set circumvents the lack of genomic resources that plagues the Ledebouriinae and allows future studies to leverage our dataset, which will enable continual refinement of the phylogenetic understanding of this group, as well as the Scilloideae. We include samples from across the distribution of the group using both field-collected and museum-based specimens to investigate the historical evolution of the Ledebouriinae and its putative lineages within (i.e. *Ledebouria*, *Drimiopsis* and *Resnova*).

MATERIALS AND METHODS

Taxon Sampling and Sequence Assembly

Plants of Ledebouriinae were collected from the field in 2012 (Namibia), 2014 (Namibia), and 2017 (Tanzania, Zambia, and Namibia). Leaves of each sample were dried in silica gel for DNA extractions. Herbarium material from four institutions (Missouri Botanical Gardens, Uppsala's Evolutionsmuseet Botanik, Sweden Museum of Natural History, and The Royal Botanic Gardens, Kew, DNA Bank, https://www.kew.org/data/dnaBank/) were also included. Additionally, silica-dried leaf material from specimens with known provenance were generously donated from private collections. Our final dataset included 94 Ledebouriinae samples from across the distribution of the group as well as two outgroup taxa (*Massonia* cf. *depressa* Houtt. and *Lachenalia aloides* var. *quadricolor* (Jacq.) Engl.). See Supplementary Table 1 for the specimen list with associated collection and locality information. Targeted capture was performed using the Angiosperms353 probe set on an Illumina HiSeq 2000 followed

by sequence assembly and alignment. See Supplementary Methods for an expanded explanation of methodology.

Phylogenetic Analyses

We analyzed both the full supercontig dataset as well as a subset of our dataset. The full dataset included all samples regardless of missing data. The second dataset included taxa with less than 70% missing data in the supermatrix alignment (i.e. <= 70% gaps/ambiguities; referred to as Taxa70). Maximum likelihood phylogenetic reconstruction was performed using IQ-Tree v2.0-rc1 (Minh et al. 2018). We quantified discordance and concordance using 1) gene concordance factors (gCF; percentage of genes supporting the input topology) and site concordance factors (sCF; percentage of sites informative for a branch) as implemented in IQ-Tree v2.0-rc1, and 2) Quartet Sampling (QS), which provides unique and more revealing information pertaining to discordance often prevalent in phylogenomic datasets (Pease et al. 2018). To obtain a species tree while also accounting for potential instances of incomplete lineage sorting, we used ASTRAL III v5.6.2 (Zhang et al. 2018) as well as singular value decomposition quartet species-tree estimation (SVDQuartets) (Chifman and Kubatko 2014).

RESULTS

Raw reads from all the samples included in our study have been submitted to the SRA (BioProject ID: *pending acceptance*). All supermatrix alignment files with corresponding partition files as well as output files for each analysis are available on Digital Dryad (*pending acceptance*). See Supplementary Results for a more detailed reporting of our results.

Excluding the full dataset, which included samples with a lot of missing data, each major clade received overall high support using SH-aLRT, ultrafast bootstrap (UFBoot), and local posterior priority (LPP) (Table 1, Fig. 2, Supplementary Figs. 1 – 4). This resulted in a

paraphyletic *Ledebouria*, with each *Ledebouria* clade sister to either *Resnova* or *Drimiopsis* (Fig. 2). However, two results warrant attention. First, in the full dataset, we found a paraphyletic *Resnova* (Supplementary Fig. 1) and recovered low LPP for *Resnova* (Supplementary Fig. 2). After the removal one herbarium sample found in only four alignments (i.e. *Resnova lachenalioides*, which was a sample that consistently jumped around potentially due to missing data [compare Supplementary Figs. 1, 2, 9]), we found increased support for a monophyletic *Resnova* across all measures (Table 1, Fig. 2, Supplementary Figs. 3, 4, 11). Second, *Drimiopsis* + *Ledebouria* Clade B recovered overall high support except in the full dataset (Table 1, Supplementary Figs. 1, 2). Using all samples, we found low support for *Ledebouria* Clade B in terms of the placement of *Ledebouria* sp. 1 Mozambique (Fig. 2, Table 1, Supplementary Figs. 1, 2). The subclade sister to this sample shows higher but still low support in the full dataset (Fig. 2, Supplementary Figs. 1, 2). In the Taxa70 dataset, we find stronger support for *Ledebouria* Clade B + *Drimiopsis* (Supplementary Figs. 3, 4). Support increases further for *Ledebouria* Clade B + *Drimiopsis* as well as *Ledebouria* Clade B after the removal of *Ledebouria* sp. 1 Mozambique (Table 1, Supplementary Figs. 5 ,6).

	Dataset	*Ledebouria* Clade A + *Resnova*	*Ledebouria* Clade A	*Resnova*	*Ledebouria* Clade B + *Drimiopsis*	*Ledebouria* Clade B	*Drimiopsis*
UFBoot	Full	97	90	100	93	76	100
	Taxa70	100	100	100	95	70	100
	L. sp. 1 Moz removed	100	100	100	100	97.2	100
SH-aLRT	Full	100	97.7	100	98.9	15.9	100
	Taxa70	100	99	100	99.6	14.3	100
	L. sp. 1 Moz removed	100	98.8	100	100	100	100
LPP	Full	1	0.97	0.34	0.91	0.62	1
	Taxa 70	1	0.95	1	0.96	0.74	1
	L. sp. 1 Moz removed	1	0.93	1	0.98	1	1
gCF	Full	3.67	2.56	44.2	3.57	2.78	26.8
	Taxa70	4.67	2.56	46.6	4.87	3.47	32.7
	L. sp. 1 Moz removed	5.67	2.56	47	4.55	16	34
sCF	Full	38.8	34.3	59.7	32.4	36.1	44.8
	Taxa70	40	37.7	65.1	34.3	36.5	55.5
	L. sp. 1 Moz removed	39.5	38	64.3	33.9	38.5	54.1
QC	Full	0.035	0.031	0.32	0.019	-0.017	0.37
	Taxa70	-0.0045	0.025	0.33	0.0081	0.031	0.27
	L. sp. 1 Moz removed	0.05	0.023	0.39	0.047	0.026	0.33
QD	Full	0.81	0.76	0.95	0.92	0.77	0.47
	Taxa70	0.88	0.83	0.77	0.86	0.85	0.55
	L. sp. 1 Moz removed	0.74	1	0.92	0.86	0.98	0.43
QI	Full	0.34	0.41	0.54	0.3	0.33	0.48
	Taxa70	0.33	0.38	0.58	0.31	0.31	0.5
	L. sp. 1 Moz removed	0.34	0.39	0.57	0.27	0.32	0.55

Table 1. Support value measures, gene concordance factor (gCF), site concordance factor (sCF), and quartet sampling measures for the four major clades recovered. Full shows values for the full dataset, Taxa70 reports values for the Taxa70 dataset, and *L*. sp. 1 Moz removed shows values when *Ledebouria* sp. 1 Mozambique is removed from the analyses. Support measures are ultrafast bootstrap (UFBoot), SH-like approximate likelihood ratio test (SH-aLRT), and local posterior probability (LPP). Support measures are those recovered using the GENESITE partition resampling measure in IQ-Tree. Gene concordance factor (gCF) is expressed as the percentage of genes that support a given topology, site concordance factor (sCF) is expressed as the number of sites informative for a branch. Quartet sampling measures include quartet concordance (QC), quartet differential (QD), and quartet informativeness (QI). See Supplementary Methods or Pease et al. (2018) for a detailed explanation of these measures.

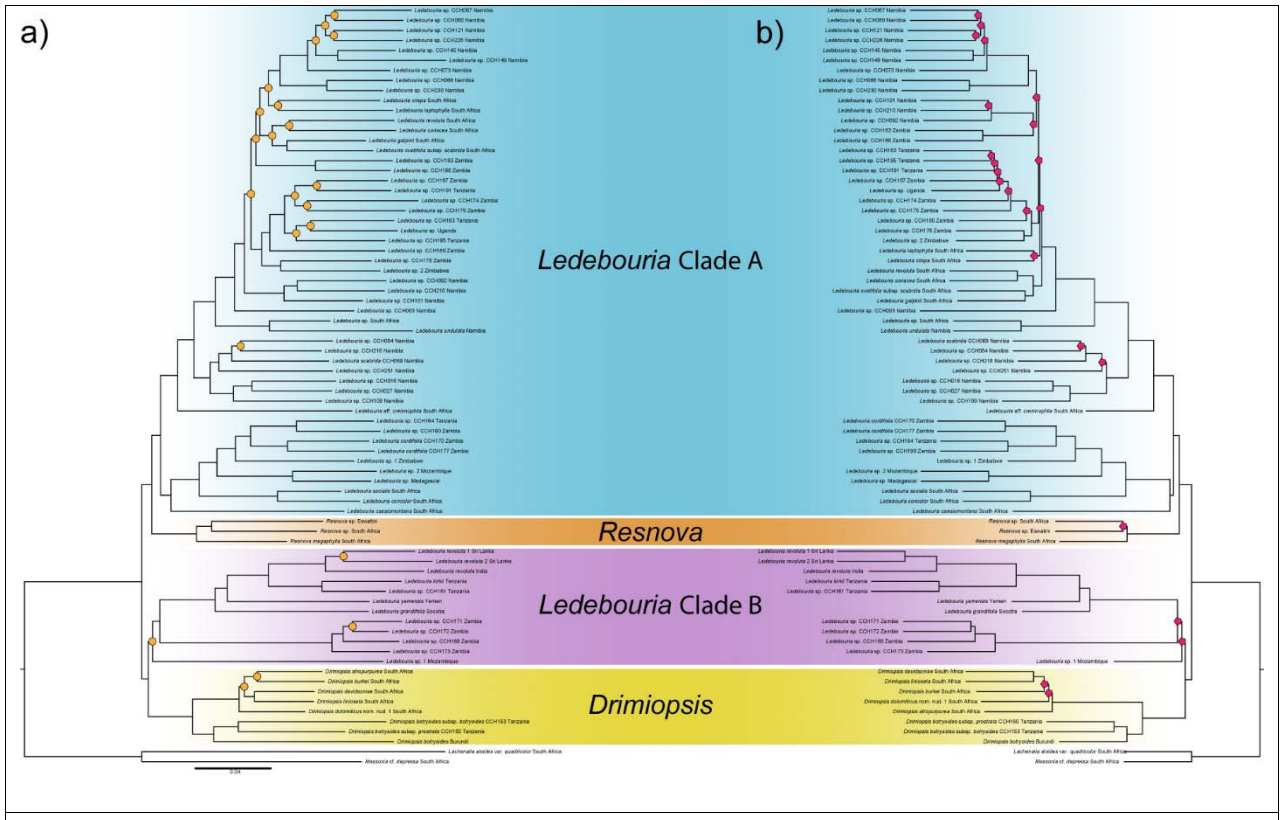

Figure 2. Phylogenetic reconstruction of the Taxa70 datasets using maximum likelihood as implemented in IQ-Tree (a), and species tree estimation as implemented in ASTRAL III (b). a) Orange circles indicate nodes with SH-aLRT and ultrafast bootstrap values below 80 and 95, respectively. b) Pink polygons indicate nodes with local posterior probability (LPP) below .95. Note, the same four major clades are recovered in both, with differences in relationships of subclades and tips between the two analyses, particularly within *Ledebouria* Clade A.

We found relatively low gene (gCF) and site (sCF) concordance factors for many nodes in both the full and Taxa70 datasets (Table 1; Supplementary Figs. 1, 3). Quartet concordance values were mostly positive for the four major clades, indicating overall concordance (Table 1; Supplementary Figs. 7, 8). Quartet differential (QD) indicated low proportions of an alternative evolutionary history (i.e. values nearer to 1) (Table 1; Supplementary Figs. 7, 8). Quartet

informativeness (QI) indicated low informativeness of the quartets for the topology, reflecting the results of sCF (Table 1; Supplementary Figs. 7, 8).

For both the full dataset and Taxa70 dataset, SVDQuartets returned the same overall results as IQ-Tree and ASTRAL with a few notable exceptions (Supplementary Figs. 9, 11). Low bootstrap values were found across the full dataset phylogeny, and *Resnova lachenalioides* was placed within *Ledebouria* Clade B (Supplementary Fig. 9, 10). In both datasets, *Ledebouria* sp. 1 Mozambique was placed sister to the remaining Ledebouriinae (Supplemental Figs. 9, 11). Additionally, one *Drimiopsis botryoides* subsp. *botryoides* was nested within *Ledebouria* Clade A (Supplemental Fig. 9, 11). The Taxa70 SVDQuartet bootstrap tree placed *Drimiopsis* as sister to *Resnova* + *Ledebouria* Clade A, but with the lowest bootstrap support of all the nodes (Supplemental Fig. 12).

DISCUSSION

We provide the first phylogenomic insights into the Ledebouriinae. Four major clades were recovered: *Ledebouria* Clade A, *Resnova*, *Drimiopsis*, and *Ledebouria* Clade B (Figs. 1b, 2, Supplementary Figs. 1 – 6). The low number of informative genes coupled with coalescence and concordance analyses suggest that incomplete lineage sorting due to rapid radiations and/or hybridization may have played significant roles in the group's evolutionary history. Past phylogenetic studies of the Ledebouriinae have recovered conflicting signal or low resolution along the backbone of the group (Manning et al. 2003; Pfosser et al. 2003; Lebatha et al. 2006; Wetschnig et al. 2007; Pfosser 2012). The focus of these studies has largely been on whether *Drimiopsis* and *Resnova* constitute two distinct taxa or are deeply nested within *Ledebouria* (Manning et al. 2003; Lebatha et al. 2006; Manning and Goldblatt 2012). Our findings suggest that delimitation of *Drimiopsis* and *Resnova* has been a misguided focus since both have easily

distinguishing characteristics, such as tepal shape, stamen positioning, and non-stipitate ovaries (Lebatha 2004; Lebatha et al. 2006). Perhaps a more appropriate goal is to uncover diversity within *Ledebouria*, and we suggest attention should now shift to delimiting and interpreting the history of its two independent lineages. Reconfiguring both the broad- and fine-scale taxonomy of the Ledebouriinae is beyond the scope of this work, but our results lead us to question the status of *Ledebouria* sensu Manning (2003).

The current geographic distribution of the Ledebouriinae is reflected within the phylogeny and provides clues as to potential historical factors that have shaped their evolution. *Ledebouria* Clade A includes sub-Saharan African samples in addition to a Malagasy lineage (Fig. 1; Supplementary Fig. 1). *Ledebouria* Clade B includes its own Malagasy lineage as well as samples from eastern parts of Africa, the Horn of Africa, Yemen, Socotra, India, and Sri Lanka (Fig. 1; Supplementary Fig. 1). African Apocynaceae and Rutaceae show similar distributions (Thiv et al. 2011; Bruyns et al. 2014), where clades consist of Eastern/Horn of African and/or non-Africa clades, and other clades have only sub-Saharan African taxa. Similar patterns within African can also be seen in ungulate distributions (Lorenzen et al. 2012). Our findings suggest that the two *Ledebouria* clades may have dispersed and radiated across Africa at different times, each with an independent dispersal to Madagascar. Interestingly, the two *Ledebouria* clades overlap geographically in eastern Africa, a highly heterogenous landscape due to recent changes in climate and geology (Linder et al. 2012; Linder 2014, 2017). This area now serves as a melting pot, center of diversity, area of endemism, and biogeographical hub for many different African lineages (Lebatha 2004; Zhou et al. 2011; Lorenzen et al. 2012; Dagallier et al. 2020), and any number of climatic or geological factors that shaped eastern Africa may have also contributed to the two distinct *Ledebouria* clades we recovered. Similar environmental

influences may have also influenced the current diversity and distribution of *Drimiopsis*, which, based on our limited sampling, consist of two clades: a South African clade, and an East African clade (Fig. 1). The two *Drimiopsis* clades are also distinguishable by morphological and ploidy characteristics (Stedje and Nordal 1987; Lebatha 2004), but increased sampling is needed to fully understand the history of this group.

Ledebouriinae taxa are continually being described (Hankey et al. 2014; Cumming 2018; Hankey 2020), which suggests that much remains to be uncovered about their diversity. This is exemplified by *Ledebouria* sp. 1 Mozambique, whose placement has low support in the IQ-Tree and ASTRAL trees (Fig. 2), has different placement in the IQ-Tree and SVDQuartet trees (Fig. 2a, Supplementary Figs. 9 – 10), has the lowest quartet fidelity value (rogueness) of all the tips (Taxa70 dataset; Supplementary Fig. 13), and exhibits unique morphological characteristics compared to currently known Ledebouriinae (e.g., pointed seeds). Whether this sample represents a distinct lineage remains to be understood. Increasing *Ledebouria* samples from Central and Western Africa as well as significantly improving sampling of *Resnova* and *Drimiopsis* will be necessary to fully capture the intricate details of the group's evolutionary history. For example, SVDQuartets consistently, albeit with low support, placed the Eastern African *Drimiopsis botryoides* subsp. *botryoides* within *Ledebouria* Clade A, and East African *Drimiopsis* are known polyploids (Stedje and Nordal 1987). Perhaps this is due to an ancient hybridization with a *Ledebouria* ancestor; however, more extensive sampling is needed to test further hypotheses regarding any ancestral hybridization within the Ledebouriinae.

Our results showcase the value of extending the phylogenomic repertoire to groups with unexplored potential. Our use of the Angiosperms353 probe set was vital for uncovering this Ledebouriinae phylogeny, but a custom probe set may prove more informative. Quartet

sampling, gCF and sCF values suggest that gene tree conflict and incomplete lineage sorting are prevalent throughout the phylogeny (Table 1), and short branches are common suggesting rapid radiation(s) (Fig. 2). One clade that may particularly benefit from more detailed study using a custom probe set is a subclade within *Ledebouria* Clade A that consistently returned low support (Fig. 2), and which contains many samples from southern Africa (Namibia, Zambia, and South Africa). Similarly to East Africa, southern Africa has also undergone drastic changes in habitat, geology, and climate within the past 30 million years (e.g., savanna expansion, aridification of southwest Africa, and rise of the Great Escarpment) (Burke and Gunnell 2008; Hoetzel et al. 2013; Linder 2014). The role that these and other factors may have played in obscuring the evolutionary history of this, and other clades present an exciting opportunity for further study.

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SUPPLEMENTARY TABLES

Supplementary Table 1. List of specimens used in this study. Specimens include only those returned after adjusting for sequences coverage and removing sequences with paralogy warnings.

SUPPLEMENTARY FIGURES

Supplementary Figure 1. Maximum likelihood phylogenetic reconstruction using IQ-Tree of the full dataset. Branch labels show SH-aLRT support value/Ultrafast bootstrap support value/gene concordance factor/site concordance factor. Strong support is branches with SH-aLRT and UFBoot values above 80 and 95, respectively.

Supplementary Figure 2. Species tree estimation of the full dataset inferred from ASTRAL. Branch labels indicate local posterior probability (LPP) support values.

Supplementary Figure 3. Maximum likelihood phylogenetic reconstruction using IQ-Tree of the Taxa70 dataset. Branch labels show SH-aLRT support value/Ultrafast bootstrap support value/gene concordance factor/site concordance factor. Strong support is branches with SH-aLRT and UFBoot values above 80 and 95, respectively.

Supplementary Figure 4. Species tree estimation of the Taxa70 dataset inferred from ASTRAL. Branch labels indicate local posterior probability (LPP) support values.

Supplementary Figure 5. Maximum likelihood phylogenetic reconstruction using IQ-Tree of the Taxa70 dataset with *Ledebouria* sp. 1 Mozambique removed from the analysis. Branch labels show SH-aLRT support value/Ultrafast bootstrap support value/gene concordance factor/site concordance factor. Strong support is branches with SH-aLRT and UFBoot values above 80 and 95, respectively.

Supplementary Figure 6. Species tree estimation of the Taxa70 dataset with *Ledebouria* sp. 1 Mozambique removed inferred from ASTRAL. Branch labels indicate local posterior probability (LPP) support values.

Supplementary Figure 7. Maximum likelihood phylogeny with quartet sampling values drawn on branches using the full dataset. Values on branches are quartet concordance (QC)/quartet differential (QD)/quartet informativeness (QI).

Supplementary Figure 8. Maximum likelihood phylogeny with quartet sampling values drawn on branches using the Taxa70 dataset. Values on branches are quartet concordance (QC)/quartet differential (QD)/quartet informativeness (QI).

Supplementary Figure 9. Species tree estimation of the full dataset using singular value decomposition quartet species-tree estimation (SVDQuartets). Phylogeny was reconstructed using an exhaustive search.

Supplementary Figure 10. Species tree estimation of the full dataset using singular value decomposition quartet species-tree estimation (SVDQuartets). Phylogeny was reconstructed using an exhaustive search. Branch labels indicate bootstrap support from 100 bootstrap replicates.

Supplementary Figure 11. Species tree estimation of the Taxa70 dataset using singular value decomposition quartet species-tree estimation (SVDQuartets).

Supplementary Figure 12. Species tree estimation of the Taxa70 dataset using singular value decomposition quartet species-tree estimation (SVDQuartets). Phylogeny was reconstructed using an exhaustive search. Branch labels indicate bootstrap support from 100 bootstrap replicates.

Supplementary Figure 13. Maximum likelihood phylogeny showing quartet fidelity (QF) values for each of the samples in the Taxa70 dataset. Values represent a measure of taxon “rogueness”, that is, a measure of how much a tip jumps around a phylogeny.