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36

37

38 **Abstract**

39 Aim

40 Within sub-Saharan Africa, plants inhabiting more seasonal and arid landscapes showcase
41 unique distributional patterns that hint at fascinating evolutionary histories. Research on plants in
42 these habitats have highlighted a complex interplay between climate and orogenic activities.
43 However, despite a steady improvement in our understanding of evolution within these diverse
44 and widespread habitats, many taxa within these regions remain understudied. The
45 Ledebouriinae (Scilloideae, Asparagaceae) are widespread throughout sub-Saharan Africa, and
46 can also be found in Madagascar, the Middle East, India, and Sri Lanka. Unfortunately, this
47 widespread distribution coupled with taxonomic uncertainties have made uncovering the
48 evolutionary history of the Ledebouriinae very difficult. Here, using the most comprehensive
49 sampling of the lineage to date, we investigate the timing and historical biogeography of these
50 bulbous monocots within and outside of Africa.

51 Location

52 Sub-Saharan Africa, Madagascar, Asia

53 Taxon

54 Ledebouriinae (Scilloideae, Asparagaceae)

55 Methods

56 We infer age estimates of major clades and subclades using penalized likelihood as implemented
57 in treePL. Capitalizing on our broad geographic sampling and using BioGeoBEARS, we then

58 reconstruct ancestral ranges across the phylogeny to investigate the role vicariance and dispersal
59 have played in the biogeographic history of the lineage.

60 Results

61 Our results suggest that the *Ledebouriinae* originated within the past ~30 myr in southeastern
62 sub-Saharan Africa, with the major subclades arising soon thereafter. Vicariance likely led to the
63 current distribution of *Ledebouria* in Asia, not long-distance dispersal as previously
64 hypothesized. The two *Ledebouria* overlap in eastern Africa, but have divergent biogeographical
65 histories, divided into mostly northern and southern clades, yet each has an independent dispersal
66 to Madagascar. A similar north-south split is seen in *Drimiopsis*. The predominantly sub-Saharan
67 African *Ledebouria* clade has a complex biogeographic history, with a rapid radiation estimated
68 ~14 mya, likely driven by drastic climate change and mountain building in southern Africa.

69 Main conclusions

70 The expansion of seasonal and arid landscapes in sub-Saharan Africa coupled with mountain
71 building likely spurred the radiation of the *Ledebouriinae* as well as several subclades.
72 Fragmentation, due to Miocene-driven aridification, of a once widespread distribution led to the
73 current distribution in Asia.

74 **Keywords** Africa, *Drimiopsis*, geophytes, *Ledebouria*, *Resnova*, Scilloideae

75

76 **1 INTRODUCTION**

77 Modern-day Africa is dominated by arid and semi-arid landscapes that contain a diversity
78 of habitats from deserts, woodlands and savannas, to name a few (Bobe, 2006; Linder, 2014). In
79 sub-Saharan Africa, these drier ecosystems collectively form a fairly continuous sickle-shaped
80 corridor that connects the floras of southwestern, northeastern and western Africa, and that skirts
81 around the wet tropics of central and western Africa (Balinsky, 1962; Bellstedt et al., 2012;
82 Jürgens, 1997) (Figure 1). The recent onset of aridity in Africa (i.e., approximately from the
83 Mid-Eocene onwards) is hypothesized to have been caused by the synergistic activities of rapid
84 global cooling, tectonic events (e.g., Eastern African rift) and oceanic upwelling (i.e., Benguela
85 current) that altered precipitation patterns across the continent (Bobe, 2006; Couvreur et al.,
86 2021; Hagen et al., 2021; Linder, 2017; Senut et al., 2009; Sepulchre et al., 2006). These changes
87 had immense impacts on the evolutionary trajectories of countless lineages on the African
88 continent. For example, in the early Eocene, equatorial Africa was largely covered by tropical
89 forests, but aridification repeatedly fragmented and reduced these habitats over time (Couvreur,
90 2015; Couvreur et al., 2008; Hagen et al., 2021). Evidence from plant fossils and phylogenetic
91 studies suggest that lineages with past widespread distributions across the continent, as well as
92 between eastern Africa and southern Asia, are now disjunct as a result of recent aridification (Ali
93 et al., 2013; Jacobs et al., 1999; Pokorny et al., 2015; Sanmartín et al., 2010; Zhou et al., 2011).
94 Conversely, dry and more seasonal climates have been linked to the diversification and dispersal
95 of lineages both in and out of Africa. Today, a diversity of taxa can be found in abundance
96 within the more arid regions of Africa as well as surrounding areas with similar climates (e.g.,
97 Arabian Peninsula) (Bruyns et al., 2014; Coe & Skinner, 1993; Jürgens, 1997; Lorenzen et al.,
98 2012; Nylinder et al., 2016). Therefore, it is imperative we gain a broad understanding of the

99 historical evolution of diverse lineages across different landscapes, habitats, and biomes in order
100 to continually refine our understanding of the past and future changes of biodiversity within
101 Africa.

102 Geophytes, herbaceous plants with renewal buds located belowground on structures such
103 as bulbs, corms, and stem tubers, are ubiquitous components of seasonal or disturbance-prone
104 habitats, and are phylogenetically diverse (Howard et al., 2019; Pausas et al., 2018; Tribble et al.,
105 2021). Within Africa, geophytes are major components of the Greater Cape Floristic Region and
106 the Mediterranean Basin (Buerki et al., 2012; Procheş et al., 2006). Although geophytes are
107 predominant elements of these two areas, the geophytic habit is widespread throughout sub-
108 Saharan Africa, particularly within seasonal or disturbance-prone (e.g., fire) habitats (Esler et al.,
109 1999; Kornas, 1985). Studies have reported that many African geophytes' origins coincide with
110 the onset of increased seasonality and/or aridity within the continent (i.e., since the Eocene), with
111 the majority of diversity evolving in response to the relatively more drastic climatic changes
112 since the Oligocene/Miocene (Ali et al., 2012, 2013; Buerki et al., 2012; del Hoyo et al., 2009;
113 Procheş et al., 2006). At a broad scale, therefore, geophytic lineages make excellent candidates
114 for understanding recent evolutionary and biogeographic dynamics within seasonal and arid
115 climates.

116 Scilloideae (Asparagaceae) are a bulbous geophyte lineage widespread both within and
117 outside of Africa (Speta, 1998a). This monocotyledonous clade consist of 1,000+ taxa found
118 throughout seasonal climates in Africa as well as Madagascar, Europe, the Middle East, and
119 Asia, with a single lineage found in South America (i.e., *Oziroe* Raf.; (Giranje & Nandikar,
120 2016; Speta, 1998b). Although only a handful of studies have investigated the historical
121 biogeography of the Scilloideae and its subclades, so far, all have pointed to sub-Saharan Africa

122 as the origin for the majority of the group (excluding *Oziroë* in South America), followed by a
123 complex history within and outside of the continent (Ali et al., 2012, 2013; Buerki et al., 2012;
124 Pfosser, 2012). However, most inferences have been made using a broad view of each groups'
125 distribution (i.e., in biogeographical studies sub-Saharan Africa has been subdivided into one to
126 three areas) (Ali et al., 2012, 2013; Buerki et al., 2012; Pfosser, 2012). Focusing on widespread
127 groups within the Scilloideae using a more detailed approach to the regionalization of Africa as
128 well as a greater taxon sampling, may provide refined insights into the biogeographical processes
129 that have impacted the dispersal of plants across and out of Africa.

130 The Ledebouriinae are an ideal group to study because they are widespread within sub-
131 Saharan Africa, with a handful of taxa found in Madagascar, Socotra, Yemen, India, and Sri
132 Lanka (Giranjé & Nandikar, 2016; Venter, 1993) (Figure 1). This distribution is unique within
133 Scilloideae since many sympatric lineages with Ledebouriinae are also found in northern Africa
134 (Pfosser, 2012; Speta, 1998a), but the Ledebouriinae are absent from the Scilloideae-rich
135 Mediterranean Basin (Venter, 2008) (Figure 1). In sub-Saharan Africa, the Ledebouriinae are
136 predominantly found within more seasonal landscapes, with highest diversity in the Limpopo,
137 Mpumalanga, and KwaZulu-Natal regions of South Africa (Venter, 1993), yet some occurrences
138 are documented from more wet, tropical regions (Figure 1). Much diversity within the
139 Ledebouriinae, however, remains undescribed to science (Howard, 2014; Howard et al., 2022).
140 Additionally, an expanded phylogenomic analysis of the group suggests that a complex
141 biogeographical history awaits to be thoroughly examined (Howard et al., 2022). Previous dating
142 analyses have estimated the origin of the Ledebouriinae sometime within the last 25 myr in sub-
143 Saharan Africa (Ali et al., 2012; Buerki et al., 2012). However, this clade was not the focus of
144 study and therefore, taxon sampling was low. Additionally, results were unable to provide fine-

145 scale biogeographical patterns since sub-Saharan Africa was considered and analyzed as one
146 large area. A more detailed categorization of the various regions in the continent would provide a
147 better understanding of the biogeographical history of the group. For example, Ali et al. (2012)
148 found that Malagasy and Indian *Ledebouria* were sister to one another, which led the authors to
149 invoke long-distance dispersals from Madagascar to India. However, as stated by the authors,
150 Ledebouriinae samples from eastern, western, and northern sub-Saharan Africa were absent,
151 limiting confidence in these conclusions (Ali et al., 2012). Furthermore, the phylogenetic
152 reconstructions of Pfosser et al. (2012) suggested two independent dispersal events to
153 Madagascar, but low phylogenetic resolution diminished confidence in this hypothesis. A recent
154 phylogenomic analysis of the Ledebouriinae provided the framework to suggest (without testing)
155 multiple dispersals to Madagascar, and a potential migration out of Africa via the Arabian
156 Peninsula into India (Howard et al., 2022).

157 The widespread distribution of the Ledebouriinae provides us with the opportunity to
158 refine our understanding of evolution and biogeography within Africa, potentially during a time
159 of extensive climatic, geologic, and habitat change on the continent. Here, we investigate the
160 timing and historical dispersal of the Ledebouriinae both within and out of Africa. We ask: 1)
161 Which region within Africa acted as the putative origin of the group, and 2) What roles have
162 dispersal and vicariance played in the evolutionary history of the Ledebouriinae, if any? Our
163 specific focus on these questions and the use of an increased sampling of the Ledebouriinae
164 allow for a more thorough investigation into the evolutionary history of the group and improve
165 our knowledge on patterns and processes within Africa.

166 **2 METHODS**

167 2.1 Phylogenetic analysis

168 Ledebouriinae samples were obtained from the field, private collections, and herbarium
169 vouchers (Howard et al., 2022). DNA extractions were performed using a modified CTAB
170 protocol, followed by high throughput sequencing on an Illumina HiSeq using the
171 Angiosperms353 universal probe set (Johnson et al., 2019). Raw reads were cleaned using
172 SECAPR (Andermann et al., 2018), sequences were pulled using hybpiper (Johnson et al., 2016)
173 and aligned using MAFFT v.7 (Katoh & Standley, 2013). See Howard et al. (2022) for more
174 details on Ledebouriinae sequence acquisition and analysis as well as data used.

175 We incorporated outgroup taxa from the Plant and Fungal Tree of Life project (Baker et
176 al., 2022) and the 1KP dataset (Matasci et al., 2014). Exons were only available for the outgroup
177 taxa included to estimate divergence times using fossils and secondary calibration points.
178 Phylogenetic reconstruction including the Ledebouriinae plus outgroups was performed on a
179 concatenated, partitioned supermatrix of exons with 10% gappy/ambiguous sites removed using
180 phyx (Brown et al., 2017). This matrix was analyzed using IQ-Tree v.2-rc1 (Nguyen et al., 2015)
181 with 1000 ultrafast bootstraps (Nguyen et al., 2015) with 1000 ultrafast bootstraps, a best-fit
182 partitioning scheme using the greedy algorithm of PartitionFinder (Lanfear et al., 2012), and a
183 relaxed clustering percentage of 10 (Lanfear et al., 2014), followed by phylogenetic
184 reconstruction (-m TESTMERGE). However, the exon-only dataset returned low support for
185 many nodes within the Ledebouriinae. Therefore, we reran the IQ-Tree analysis with a
186 topological constraint tree (-g) that was previously built from a supercontig (i.e., exons + introns)
187 dataset of the Ledebouriinae (Howard et al., 2022).

188 2.2 Time calibration

189 We incorporated eight outgroup fossil calibration points, each with a minimum age
190 specified in Iles et al. (2015) (Table S1). A secondary calibration point at the crown node of
191 monocots was inferred between 131–135 mya based on previous analyses (Givnish et al., 2018;
192 Magallón et al., 2015).

193 Given the size of the dataset, we used penalized likelihood as implemented in treePL
194 (Smith & O’Meara, 2012) for time calibration. To incorporate uncertainty around age estimation,
195 we took a multi-tiered approach (see <https://github.com/sunray1/treepL>) similar to previous
196 studies estimating divergence times using large phylogenetic datasets (Embets et al., 2020; Li et
197 al., 2019; Magallón et al., 2015). We generated 100 bootstrap replicates of our original exon
198 supermatrix alignment using RAxML v.8.2.0 (f -j option) (Stamatakis, 2014). A maximum
199 likelihood tree for each replicate with a corresponding partition file was then reconstructed using
200 a topological constraint (i.e., the phylogeny from the IQ-Tree analysis) to ensure consistent
201 calibration point placement, and a GTRGAMMA model of evolution. The resulting 100 “best
202 trees” were rooted on *Acorus gramineus* using phyx (Brown et al., 2017). In Step 1, each
203 replicate tree had a priming step completed with a random seed number and the thorough
204 command invoked. Step 2 was performed three independent times to assess convergence on the
205 best smoothing parameter for each individual tree. Step 2 also included the individual outputs
206 from each tree’s previous priming step (e.g., optad, moredetail, etc.) as well as the cross-
207 validation (CV) steps, which were set to cvstart=10000, cvstop=.000000000000001,
208 cvmultstep=0.09. Lastly, Step 3 summarized each individual tree’s CV output to determine and
209 scale each tree using the appropriate smoothing parameter. The 100 ultrametric phylogenies were

210 summarized using TreeAnnotator v.1.10.4 (Bouckaert et al., 2014) to obtain a maximum clade
211 credibility tree with 95% confidence intervals around each node and median node heights.

212 2.3 Biogeographical analysis

213 The biogeographical regionalization of Linder et al. (2012) was used for categorizing the
214 location of each sub-Saharan African Ledebouriinae accession. The exact distribution of
215 populations/taxa represented by many field-collected individuals (i.e., collections made by C.C.
216 Howard) remains to be fully assessed since they are undescribed species and/or are only known
217 from one locality. Additionally, many described species are currently known as occurring in
218 small geographic ranges or even single mountain tops (Lebatha, 2004; Venter, 2008).
219 Consequently, most samples were assigned only to known areas of occurrence. Accessions found
220 outside of Africa were coded according to their respective areas of occurrence: Madagascar,
221 Yemen, Socotra, or Sri Lanka). Another reason we coded each taxon using this approach is
222 exemplified by *Ledebouria revoluta*, reported from the Cape Region of South Africa to Sri
223 Lanka (Mwafongo et al., 2017; Venter, 1993). This widespread taxon likely represents a species
224 complex with a wide range of morphological variation (Brita Stedje, 1998), and therefore, often
225 this name is associated with individuals whose species identification is difficult (Mwafongo et
226 al., 2017). Consequently, and not surprisingly, *L. revoluta* is an ambiguous entity as evidenced
227 by its polyphyly within the Ledebouriinae (Howard et al., 2022). In total, 14 geographic regions
228 were used to categorize all terminals. To estimate ancestral ranges, we compared the maximum
229 likelihood implementations of three biogeographical models, DEC, DIVA-like, and BAYAREA-
230 like as implemented in BioGeoBEARS (Matzke, 2013a, 2013b, 2014) in R (R Core Team,
231 2016). We used log-likelihood and AICc values to determine the best model between the three.
232 Given the debate surrounding the use of models with the +j parameter (Matzke, 2022; Ree &

233 Sanmartín, 2018), we decided to not include them and, additionally, their implementation tends
234 to infer a high number of jump dispersals, which are unlikely biological scenarios for the
235 majority of the Ledebouriinae (see Discussion).

236 2.3.1 Biogeographical uncertainty

237 Within a subclade of *Ledebouria* Clade A, phylogenetic relationships are poorly
238 supported (Figure 2, node a) (Howard et al., 2022). However, given the potential rapid radiation
239 along the backbone of this group, we wanted to explore the biogeography of this clade since it
240 may contain an interesting history. To compensate for the uncertainty, we incorporated
241 topological and branch depth variability into our biogeographical analysis by using a random
242 sampling of trees from the posterior of a Bayesian analysis for the subclade of interest
243 (Ceccarelli et al., 2019; Magalhaes et al., 2021). To begin, we reduced our total alignment to the
244 most clock-like genes using SortaDate (Smith et al., 2018). This was done due to failure to reach
245 convergence when using the entire alignment (data not shown). We kept genes that were at least
246 10% concordant (bipartition >0.1), had a tree length greater than 7.24, and had root-to-tip
247 variation of less than 0.009. Cutoff values for the latter two were determined using the median
248 values for all gene trees, as previously reported (Pillon et al., 2021). Of the remaining
249 alignments, we included only taxa within the subclade of interest (Figure 2b) and removed
250 duplicate Ledebouriinae outgroup taxa as well as those putatively duplicate within the
251 Ledebouriinae ingroup (indicated by * in Figure 2). Each gene was then aligned using MAFFT
252 (Kato & Standley, 2013) invoking the --auto option. Sites with 5% gaps/ambiguity were
253 removed using phyx (Brown et al., 2017). Due to failure to reach convergence using a
254 partitioned, concatenated alignment in BEAST v1.10.4 (Drummond & Rambaut, 2007), we
255 instead input an unpartitioned, concatenated alignment using a GTR+GAMMA model of

256 substitution, a speciation birth-death prior, and a lognormal distribution with an offset 17.1,
257 mean 1.0, stdev 1.0 (95% range 17.24–19.88) on the root node of the subclade. This initial value
258 was chosen based on the treePL divergence time estimates for this node. We ran an MCMC
259 chain of 300k generations sampling every 10k generations. Convergence was assessed using
260 Tracer v1.7.1 (Rambaut et al., 2018) to ensure all ESS values were above 200. We removed 50%
261 of trees as burnin and used the remaining trees in the analysis. We randomly sampled 100 trees
262 after burnin, and performed a DIVA-like analysis (i.e., the best model) on each tree followed by
263 stochastic mapping using BioGeoBEARS (Matzke, 2013a). Trees were summarized to obtain an
264 average number of biogeographical events within and between each region included in the
265 analysis. Scripts for running the analysis can be found on github
266 (https://github.com/ivanlfm/BGB_BSM_multiple_trees). The rationale for incorporating
267 phylogenetic uncertainty was developed by Ceccarelli et al. (2019) and Magalhaes et al. (2021).

268 **3 RESULTS**

269 3.1 Phylogenetic relationships and age estimates

270 We recovered a polyphyletic *Ledebouria*, and a monophyletic *Drimiopsis* and *Resnova*,
271 which is congruent with a recent study (Howard et al., 2022). However, shallow-level
272 relationships differed compared to Howard et al. (2022), particularly within the *Ledebouria*
273 clades, and especially within *Ledebouria* Clade A. This is due to using a topological constraint (-
274 g), which searches tree parameter space, over using a fixed topology (-te) which does not
275 perform a tree search (see <http://www.iqtree.org/doc/Command-Reference>). Given differences in
276 the inputs between Howard et al. (2022) and our exons-only datasets, we preferred a topological
277 constraint allowing for a tree search over forcing a fixed topology.

278 Within a penalized likelihood framework, the Scilloideae originated approximately 52.0
279 my (95% HPD 51.2 – 54.5) (Figure 2; Table 1). We recovered a median crown age estimate for
280 the Ledebouriinae of 28.0 myr (95% HPD 26.1–28.3), with age estimates of the four major
281 Ledebouriinae clades soon thereafter. The split between *Drimiopsis* and *Ledebouria* Clade B was
282 estimated at 27.1 mya (95% HPD 25.2–27.5). The crown of *Drimiopsis* was dated to 22.1 mya
283 (95% HPD 20.5–23.5), and *Ledebouria* Clade B was dated at 26.1 mya (95% HPD 24.0–26.5).
284 The split between *Resnova* and *Ledebouria* Clade A occurred at 26.3 mya (95% HPD 23.7–
285 25.2). The *Resnova* crown was dated at 17.9 mya (95% HPD 16.6–18.5), and *Ledebouria* Clade
286 A was estimated at 25.0 mya (95% HPD 23.0–25.4) (Table 1).

287 3.2 Biogeography

288 The DIVA-like model produced the most likely ancestral range estimates among the
289 models (LnL -220.54) (Table 2). The regions Natal+Zambeian were reconstructed as the
290 ancestral range for the Ledebouriinae ($p = .53$) and *Drimiopsis* ($p = .84$), while Zambeian was
291 reconstructed for *Drimiopsis* + *Ledebouria* Clade B ($p = .95$) and *Ledebouria* Clade B ($p = .98$).
292 Within *Ledebouria* Clade B, the model favors a widespread distribution of Yemen+Zambeian
293 ($p = .55$) followed by subsequent reconstructions containing various combinations of Zambeian
294 and other regions, or Zambeian alone (Figures 3 and S2). Within *Ledebouria* Clade B we also
295 recover one of the two dispersals of the Ledebouriinae to Madagascar (Figure 3).

296 The Kalahari+Natal regions were recovered as the ancestral range for *Resnova* +
297 *Ledebouria* Clade A ($p = .42$), whereas the Natal region was recovered for *Resnova* ($p = .99$),
298 and Kalahari for *Ledebouria* Clade A ($p = .51$) (Figures 3 and S2). Within *Ledebouria* Clade A,
299 we find an additional dispersal to Madagascar (Figure 3). Additionally, in summarizing the 10
300 biogeographic stochastic reconstructions (see section 2.3.1), we recovered a steady rise in the

301 number of lineages in the Zambezian and Kalahari regions from ~15 myr onwards in a subclade
302 of *Ledebouria* Clade A (Figure 3b). Additionally, despite some differences in topology between
303 these results and those of Howard et al. (2022), both studies overall share clades that largely
304 reflect geography. We recover two subclades of mostly Namibian taxa, a subclade containing
305 mostly South African taxa, and a subclade containing a mixture of Zambian, Tanzanian, and
306 Zimbabwean taxa (Figures 2 and 3).

307 **4 DISCUSSION**

308 4.1 Broad biogeographical patterns

309 Here, we present the best and most comprehensive sampling of the Ledebouriinae to date
310 (representing ~30% of described Ledebouriinae taxa (POWO, 2019) plus numerous undescribed
311 taxa) which has provided greater insights into the historical biogeography of this widespread,
312 bulbous lineage than previously uncovered. Our results suggest a rapid radiation along the
313 backbone of the Ledebouriinae, estimated between ~28–26 mya (Figure 2; Table 1) in
314 southeastern, sub-Saharan Africa (Figures 3, S1, S2). This region corresponds somewhat to the
315 current center of diversity of the Ledebouriinae, which is at the intersection of the Natal-
316 Kalahari-Zambezian biogeographical regions (Lebatha, 2004; Manning, 2020; Venter, 1993).
317 The four major subclades (*Ledebouria* Clade A, *Ledebouria* Clade B, *Resnova*, and *Drimiopsis*)
318 originated in neighboring regions to one another soon thereafter (Table 1; Figure 3). During this
319 timeframe in Africa, major shifts in climate and habitat composition have been inferred at both
320 local and continental scales, and at shallow and deep phylogenetic scales (Couvreur et al., 2021;
321 Gizaw et al., 2021; Hagen et al., 2021; Kandziora et al., 2022; Pokorny et al., 2015). From the
322 Eocene-Oligocene transition, global cooling promoted the expansion of seasonal and arid
323 climates as well as savanna, grassland, and fire-prone habitats in Africa, with greater increases

324 during the Miocene (Senut et al., 2009; Sepulchre et al., 2006). Furthermore, the Great
325 Escarpment underwent renewed uplift in the early Miocene, which increased habitat
326 heterogeneity that was coupled with an intensification of global cooling and aridification that
327 collectively led to lineage radiation and dispersal in many African taxa (Cowling et al., 2009;
328 Galley et al., 2007; Neumann & Bamford, 2015; Partridge & Maud, 1987). Being bulbous
329 geophytes, the *Ledebouriinae* may have been “pre-adapted” for these climatic and environmental
330 changes, and therefore diversified in response (Howard et al., 2020). Overall, our biogeographic
331 reconstructions and divergence time estimations lead us to hypothesize that the expansion of
332 seasonal habitats and extensive orogenic activity in southern, sub-Saharan Africa spurred the
333 radiation of the *Ledebouriinae* and promoted additional radiations and dispersals over time.

334 4.2 A tale of two *Ledebouria*

335 We estimate that the two *Ledebouria* lineages originated at slightly different times
336 (Figure 2; Table 1) in neighboring regions (i.e., Kalahari vs Zambezi), which lead to
337 subsequent divergent biogeographic histories (Figure 3). In general, the two *Ledebouria* overlap
338 in eastern Africa with a geographical divide between southern and northern sub-Saharan Africa
339 (Figure 2) (Howard et al., 2022). The divergent evolutionary histories and current overlapping
340 distribution of the two *Ledebouria* may have been influenced by the expansion and contraction
341 of wet, tropical, forested habitats in eastern Africa that repeatedly split a historically more
342 widespread distribution (Couvreur, 2015; Couvreur et al., 2021). These past habitat fluctuations
343 have created a mosaic of climates and vegetation types in eastern Africa, and have influenced the
344 evolutionary trajectory of countless lineages (Dagallier et al., 2020; Lorenzen et al., 2012). Other
345 lineages adapted to seasonal and arid habitats share similar distributions with the two *Ledebouria*
346 (Grace et al., 2015; Jürgens, 1997). For example, the two lineages overlap geographically with

347 that of stapeliads (Ceropegieae, Apocynaceae)—*Ledebouria* Clade B overlaps with the Northern
348 grade, whereas *Ledebouria* Clade A overlaps with the Pan-African clade (see Fig. 3 in Bruyns et
349 al. (2014)). We also find two dispersals of *Ledebouria* to Madagascar (Figure 3), which had been
350 previously hypothesized (Pfosser, 2012). Madagascar and mainland Africa have been separated
351 since at least the Paleocene (Couvreur et al., 2021), which suggests long distance dispersal from
352 Africa to Madagascar led to the origin of *Ledebouria* on the island.

353 4.2.1 The Voyage of *Ledebouria* Out of Africa, or *Ledebouria* Clade B

354 Previous studies invoked long distance dispersal from Madagascar to India to explain the
355 distribution of *Ledebouria* in Asia (Ali et al., 2012); however, we find little support for this
356 hypothesis. Reconstructions place the ancestral area of *Ledebouria* Clade B in the Zambezian
357 region followed by migration into other regions, such as Yemen and India, between ~20–15 mya
358 (Figures 2 and 3). During this time, the Arabian Peninsula and Socotra were connected or in
359 close proximity with mainland Africa (Edgell, 2006; Fleitmann et al., 2004; Jacobs, 2004; Rögl,
360 1999), which would have allowed overland dispersal to these regions. Pollen and wood fossils
361 indicate historical widespread distributions between eastern Africa and south Asia of other
362 closely related taxa (Bonnefille, 2010; Morgan et al., 1994). Additionally, fossils indicate that
363 forested habitats were present in the Arabian Peninsula during the Eocene and Oligocene, that
364 later gave way to more open, xeric, grassland habitats in the Miocene (Jacobs et al., 1999;
365 Whybrow & McClure, 1980). The modern-day equivalents of these conditions are commonly
366 inhabited by *Ledebouria* (Venter, 1993). Given the historical environments present in Africa and
367 south Asia during the Late Oligocene/Early Miocene, the ancestor of *Ledebouria yemenensis* +
368 *L. nossibeensis* likely had a widespread distribution that was fragmented as aridification
369 increased during the Miocene. Additionally, vicariance likely promoted allopatric speciation of

370 Socotran *Ledebouria* as the islands drifted away from mainland Africa over time. Vicariance has
371 been invoked for other lineages with hypothesized widespread historical ranges between Africa,
372 the Arabian Peninsula, Socotra, and/or southern Asia, including *Isodon* (Lamiaceae) (Yu et al.,
373 2014), *Aganope* (Fabaceae) (Sirichamorn et al., 2014), *Searsia* (Anacardiaceae) (Yang et al.,
374 2016), *Smilax* (Smilacaceae) (Chen et al., 2014), and several reptiles (Main et al., 2022; Smíd et
375 al., 2013; Tamar et al., 2016), many of which have similar age estimates and distributions as
376 *Ledebouria* Clade B. In other groups, such as the Urgineoideae (Asparagaceae) (Ali et al., 2013)
377 and *Uvaria* (Annonaceae) (Zhou et al., 2011), dispersals from Africa to south Asia by way of the
378 Arabian Peninsula have been hypothesized. Furthermore, *Ledebouria* seed has limited dispersal
379 capacity, which occurs primarily via sheet water flow (i.e., travels only short distances and is
380 rainfall dependent) (Venter, 1993). In years of limited rainfall and/or in flat terrains, seeds and
381 seedlings can be found surrounding the parent plant (CCH, pers. obs.), and the ephemeral nature
382 of the seeds in some taxa warrants germination soon after ripening (CCH and TSH, pers. obs.).
383 Thus, our age estimates and biogeographical reconstructions as well as the limited dispersal
384 ability of *Ledebouria* lead us to hypothesize that Clade B dispersed out of Africa to south Asia
385 via overland migration through the Arabian Peninsula. This historical, widespread distribution
386 was then fragmented by Miocene-driven aridification. Today, *L. yemenensis*, the only
387 *Ledebouria* currently recorded from the Arabian Peninsula, likely represents a relic of this
388 once widespread distribution as it is endemic to the cooler, higher elevation of the Yemeni
389 Highlands surrounded by arid lowlands.

390 4.2.2 Within Africa—*Ledebouria* Clade A

391 Our results suggest that *Ledebouria* Clade A originated slightly later and in a more
392 southerly region than that of *Ledebouria* Clade B (Table 1; Figures 2 and 3). Based on our

393 dataset, *Ledebouria* Clade A arose ~25–23 mya and remained predominantly within sub-
394 equatorial Africa (Figures 2 and 3). Despite the low resolution within some areas of Clade A
395 (Howard et al., 2022), we recovered multiple subclades that reflect geographic affinity (Figure
396 2). For example, we see a subclade of mixed geographic composition (i.e., *L. caesiomontana* + *L.*
397 sp. 12 CCH190) (node c, Figure 2) that suggests a widespread distribution between the Kalahari
398 and Zambebian regions that diverged and lead to *in situ* speciation in the Zambebian region
399 followed by a dispersal to Madagascar (Figure 3). We recovered an additional subclade of
400 predominantly Zambebian taxa (i.e., *L. sp. 37* CCH169 + *L. sp. 24* Uganda) (subclade in node a,
401 Figure 2) with evidence of a dispersal to the Sudanian region (i.e., *L. sp. 24* Uganda).
402 Furthermore, two subclades of predominantly Namibian taxa (i.e., *L. sp. 14* CCH109 + *L. sp. 18*
403 CCH218 (node b, Figure 2), and *L. sp. 7* CCH066 + *L. sp. 32* CCH145 (subclade in node a,
404 Figure 2)) suggest multiple dispersals to the region followed by *in situ* speciation (Figure 3).
405 Lastly, a subclade of mostly South African taxa (i.e., *L. galpinii* + *L. coriacea*) (subclade in node
406 a, Figure 2) was recovered (Figure 3). Overall, our results suggest that within a relatively short
407 time frame (~20–15 mya), a complex history of dispersals followed by *in situ* speciation events
408 occurred within *Ledebouria* Clade A in southern Africa (Figure 3; Table S2).

409 From the Miocene onwards, complex interactions between mountain uplift and climate
410 change have promoted diversification across lineages within southern Africa (García-Aloy et al.,
411 2017; Maswanganye et al., 2017; Neumann & Bamford, 2015; Nielsen et al., 2018). *Ledebouria*
412 Clade A may have originated in southeastern Africa then dispersed and diversified as the region
413 grew more heterogeneous and arid. For example, we found an instance of potentially rapid
414 radiation within *Ledebouria* Clade A between 20–17 mya (Figure 3b), which corresponds to a
415 clade with consistently poor phylogenetic resolution (Howard et al., 2022). This subclade

416 contains taxa from across southern sub-Saharan Africa with geographic signals within (i.e.,
417 clades of South African, Namibian, and Zambian taxa) (Figures 2 and 3). It is possible that the
418 Middle Miocene Climatic Optimum or Middle Miocene Climate Transition (Zachos et al., 2001)
419 coupled with renewed uplift of the Great Escarpment spurred this radiation, and we see a steady
420 rise in lineage accumulation from ~20–15 mya (Figure 3b). During the Middle Miocene, the
421 vegetation of South Africa was likely tropical, which gave way to more xerophytic shrubland by
422 Late Miocene due to a global cooling climate (Pound et al., 2012). This time period is associated
423 with diversification in the Crassulaceae (Lu et al., 2022) and also the expansion of C4
424 grasslands/savannas at a global scale (Bobe, 2006; Senut et al., 2009). Current biogeographical
425 patterns of *Aloe* suggest dispersal from southern Africa to East Africa as seasonality and
426 aridification increased across the continent within the past ~16 my (Grace et al., 2015).
427 *Monsonia* (Geraniaceae) share similar distributional patterns as *Ledebouria* Clade A with
428 multiple lineages comprised of mainly southwestern or southeastern taxa (i.e., southern African
429 split between eastern and western clades), which radiated within the past ~20–15 myr (García-
430 Aloy et al., 2017). Overall, we find a fascinating, albeit more complicated, evolutionary history
431 of *Ledebouria* Clade A within southern sub-Saharan Africa that remains to be fully resolved.

432 4.3 Limited, but intriguing insights into *Drimiopsis*

433 Based on our limited sampling of *Drimiopsis*, we find additional evidence for a southern
434 and northern sub-Saharan African divide (Figures 2 and 3), which is also seen in ungulates
435 (Lorenzen et al., 2012), *Lycaon pictus* (Canidae) (Marsden et al., 2012), *Encephalartos*
436 (Cycadaceae) (Mankga et al., 2020), and *Agama* (Reptilia) (Leaché et al., 2014). The
437 eastern/northern sub-Saharan African *Drimiopsis* arose ~19–17 mya (Figure 2), during a time of
438 increased mountain building in the region (~17 and ~13.5 mya; (Wichura et al., 2015) that was

439 followed by a shift towards a more arid climate (Bonnefille, 2010; Linder, 2017; Morgan et al.,
440 1994; Senut et al., 2009). Several East African *Drimiopsis* have overall more succulent leaves
441 compared to their southern African relatives (Lebatha, 2004), which may have been selected for
442 as eastern Africa experienced greater aridification compared to the southeast. Additionally, East
443 African *Drimiopsis* are known polyploids (Lebatha, 2004; B Stedje & Nordal, 1987), which may
444 have further spurred evolution in this region since polyploidy may provide an advantage in
445 particular environmental conditions (e.g., aridity) (Manzaneda et al., 2012; Sonnleitner et al.,
446 2010). In contrast, South African *Drimiopsis* occur in moist and shady habitats, and are not
447 found in the drier portions of southwestern Africa (Lebatha, 2004). Given the estimated age of
448 South African *Drimiopsis* (~13.6 mya) (Figure 2), uplift of the Great Escarpment may have
449 increased aridity in southwest Africa (Bobe, 2006; Partridge & Maud, 1987) that hindered
450 *Drimiopsis* establishment in this region, but at the same time promoted diversification in
451 southeastern Africa leading to its high diversity in the area (Lebatha, 2004). However, far greater
452 sampling of *Drimiopsis* from its entire distribution is needed to test hypotheses regarding their
453 evolutionary history. Ideally, an expanded phylogenetic framework would be coupled with
454 ploidal inferences, anatomical studies, and experimental manipulations to fully assess the
455 relationship between historical biogeography and morphological evolution.

456 4.4 Where to sample next?

457 Our taxon sampling heavily consisted of southern, sub-Saharan African taxa (Figure 1),
458 and largely excluded *Resnova*. Therefore, increased sampling of *Resnova* as well as *Ledebouria*
459 and *Drimiopsis* from western, central, and northern Africa will provide further insights into the
460 biogeographical history of the Ledebourinae. For example, *Ledebouria* occurs in northern
461 Angola (Gregory Jongsma, pers. obs.) and Gabon (Figure 1). This leads us to wonder whether a

462 continuous distribution was once present along the central/western coast of Africa, or if the
463 Central African tropical forests have consistently obstructed Ledebouriinae dispersal within the
464 coastal, wet tropics. Furthermore, a *Ledebouria* accession from Uganda is nested within
465 *Ledebouria* Clade A, which suggests that by increasing sampling from northern/western Africa
466 we may uncover additional biogeographic events. Lastly, multiple, morphologically distinct
467 *Ledebouria* taxa are recorded from Socotra and surrounding islands (Miller & Alexander, 2010),
468 and India (Giranje & Nandikar, 2016). Incorporating these into future phylogenetic studies may
469 highlight further dispersals, or bolster support for allopatric speciation/vicariance as a major
470 evolutionary process leading to the current distribution of the group outside of Africa.

471 **5 CONCLUSION**

472 The Ledebouriinae are a widespread, bulbous lineage of monocots that remain poorly
473 understood taxonomically due to a high degree of phenotypic plasticity and significant under
474 collection of specimens. Our study provides a pivotal first step towards refining our
475 understanding of historical evolution and biodiversity within this fascinating lineage. The results
476 of our analyses highlight the complex biogeographic history of the Ledebouriinae within and
477 outside of sub-Saharan Africa. We find that the Ledebouriinae evolved within the past ~30 myr,
478 which suggests the group radiated in response to increasing climatic seasonality and orogenic
479 activity since. We find evidence that vicariance led to the current distribution of *Ledebouria* in
480 Asia and Socotra, with overland dispersal out of Africa into Asia likely occurring via the Arabian
481 Peninsula. We also find evidence of two independent dispersals to Madagascar. Within Africa,
482 we find evidence of a northern and southern sub-Saharan division between the two *Ledebouria*
483 lineages and within *Drimiopsis*. We also uncover a complex history of dispersals and *in situ*
484 speciation events within southern Africa in *Ledebouria* Clade A, a clade that warrants improved

485 phylogenetic resolution to further elucidate the processes affecting its current distribution. In
486 conclusion, our study shows the value of increasing research focus on understudied lineages
487 inhabiting seasonal and arid habitats.

488 **Tables**

489 **Table 1.** Comparison of median age estimates and associated uncertainty (95% highest
490 probability density (HPD)) for each major Ledebouriinae clade using penalized likelihood as
491 implemented in treePL.

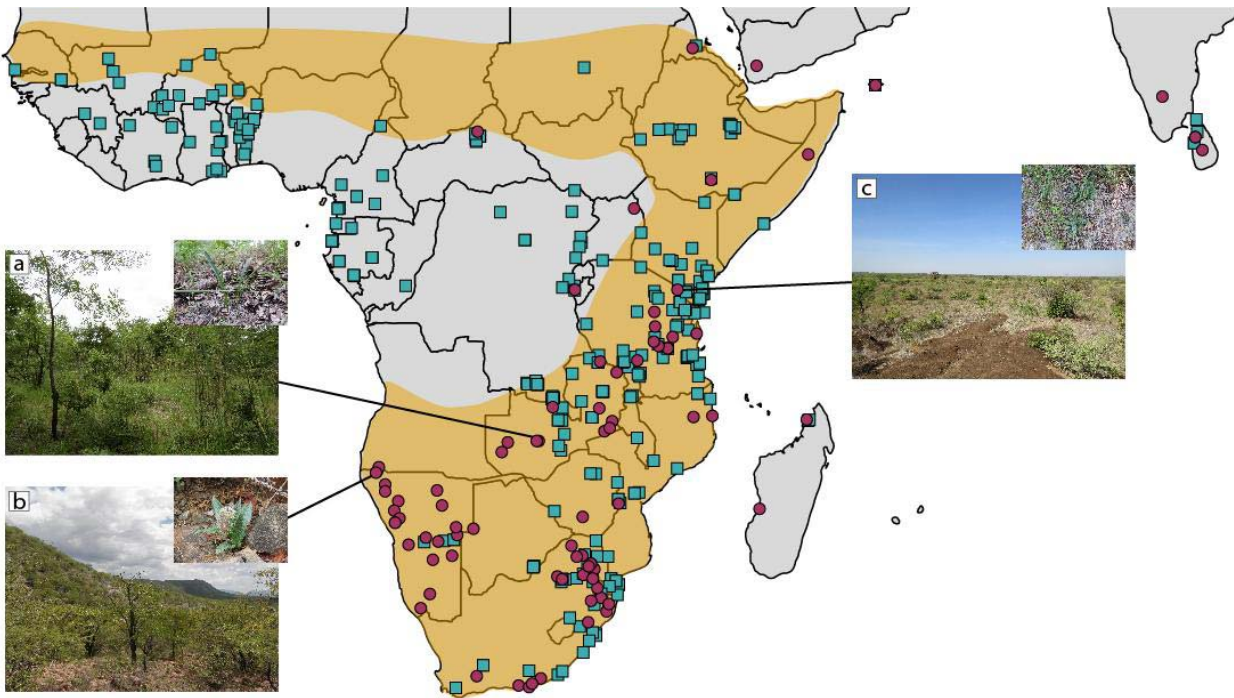
Clade	median estimate	95% HPD
Scilloideae	52.2	51.2 – 54.5
Ledebouriinae	28.0	26.1 – 28.3
<i>Ledebouria</i> Clade A	25.0	23.0 – 25.4
<i>Resnova</i>	17.9	16.6 – 18.5
Clade A + <i>Resnova</i>	26.3	24.5 – 26.7
<i>Drimiopsis</i>	22.1	20.5 – 23.5
<i>Ledebouria</i> Clade B	26.1	24.0 – 26.5
Clade B + <i>Drimiopsis</i>	27.1	25.2 – 27.5

492

493 **Table 2.** Statistical outputs for each model from BioGeoBEARS. log-likelihood (LnL); rate of
494 dispersal (d); rate of extinction (e); Akaike's Information Criterion (AIC)

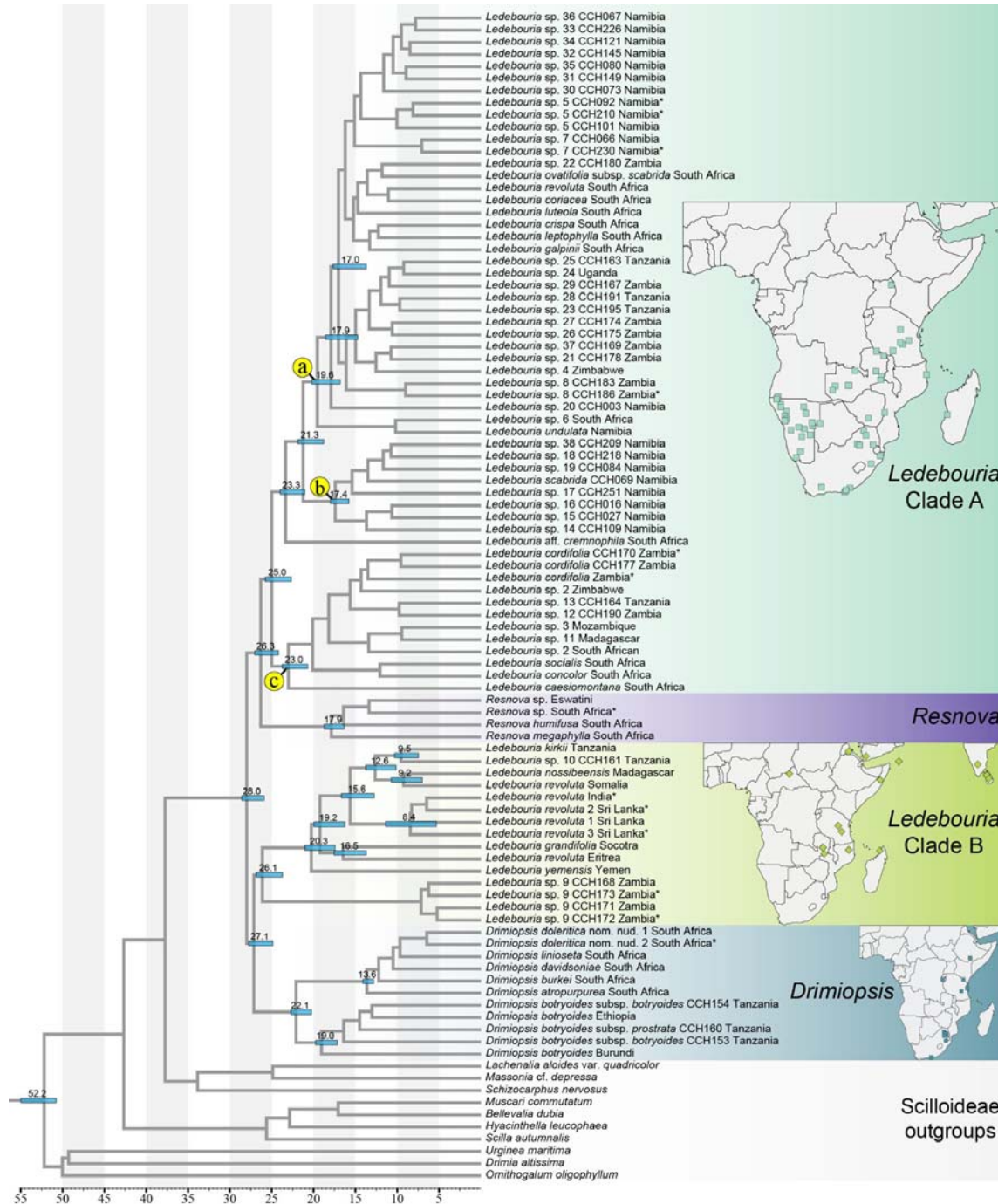
Model	LnL	Number of parameters	d	e	j	AIC
DEC	-267.1	2	0.01	0.01	0	538.4
DIVA-like	-220.5	2	0.0027	0.009	0	445.2
BAYAREA-like	-232.8	2	0.0036	0.04	0	469.8

495 **Figures**

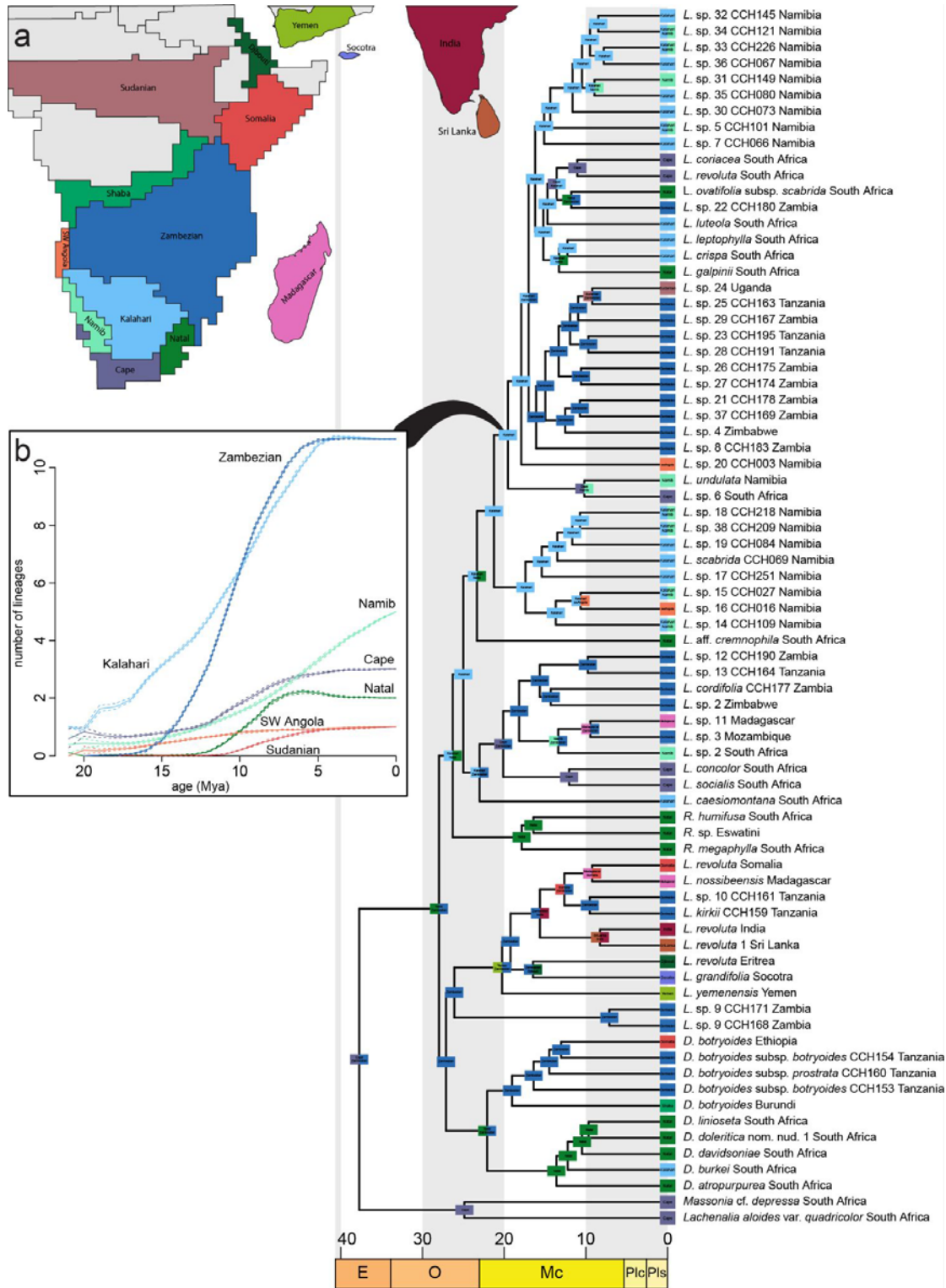


496

497 **Figure 1.** General distribution of the seasonal and arid ecosystems of sub-Saharan Africa (light
498 orange polygon) underlain by the distribution of the Ledebouriinae displayed using GBIF
499 specimen occurrence data (teal squares; GBIF.org (22 March 2022) GBIF Occurrence Download
500 <https://doi.org/10.15468/dl.xmccae>). Collection localities of samples used in this study are
501 denoted with maroon circles. Examples of habitats and associated Ledebouriinae taxa are
502 displayed in the images. a) *Ledebouria* sp. 8 CCH186, b) *Ledebouria* sp. 15 CCH027, c)
503 *Drimiopsis botryoides* subsp. *botryoides* CCH153. See Figure 2 for phylogenetic placement of
504 these example taxa. General distribution of seasonal landscapes adapted from Balinsky (1962),
505 Jürgens (1997), and Bellstedt et al. (2012).



506 **Figure 2.** Divergence times within the Ledebouriinae as estimated using penalized likelihood in
 507 treePL. For each clade, collection localities are overlaid on a map of Africa, Madagascar, and
 508 Asia to aid with discussions of geographical patterns. Clades labeled with a, b, and c in yellow
 509 are clades discussed within the manuscript. Numbers above blue bars denote median age
 510 estimates. Blue bars denote 95% highest posterior density (95% HPD). * indicate samples
 511 excluded from subsequent biogeographical analyses. Not all nodes are annotated with estimated
 512 divergences times for illustrative simplicity. For a fully annotated phylogeny, see Figure S1.



514 **Figure 3.** Biogeographical reconstruction using the DIVA-like model as implemented in
515 BioGeoBEARS and plotted using RevGadgets. a) Regionalization scheme used in the
516 classification of taxa for analysis. b) Summary of 10 stochastic mappings from a posterior
517 distribution of trees including only taxa from the indicated clade (solid black line). For pie chart
518 probabilities at each node, see Figure S2.

519

520 **Data Availability**

521 Raw reads from PAFTOL are available in ENA (accession PRJEB35285) and assembled reads
522 from www.treeoflife.kew.org. Raw reads of the Ledebouriinae are available from the SRA
523 (accession PRJNA721471). Alignments, species trees, biogeography inputs/outputs are all
524 available on Dryad (*doi: currently in process*) (but try <https://doi.org/10.5061/dryad.r4xgxd2gw>).

525 **Biosketch**

526 Cody Coyotee Howard is an Assistant Professor at Oklahoma State University broadly interested
527 in geophyte evolution and biogeography, and he has a particular fascination with bulbous plants.
528 The Ledebouriinae represent one bulbous lineage that has captivated him for years, and these
529 plants will continue to do so for many more.

530 Author contributions: Conceptualization CCH, TSH, NC; Formal analysis, CCH and ARZ;
531 Investigation, CCH and ARZ; Resources, TSH, LN, DC, LN, PM, ARZ, NC; Writing —
532 Original Draft, CCH and NC; Writing — Review & Editing, all authors; Visualization, CCH;
533 Funding acquisition, CCH and NC.

534 **Supporting information**

535 **Table S1.** Fossil and secondary calibration points used in the penalized likelihood (treePL)
536 analysis. With the exception of monocots, all calibrations were set as minimum values in the
537 analysis.

node	minimum calibration	source
Zingiberaceae	72.1	Iles et al., 2015
Typhaceae	51.66	Iles, et al. 2015
Cyperaceae	47.0	Iles, et al. 2015
Amaryllidaceae	48.88	Pigg et al., 2018
Coryphoideae	83.6	Iles, et al. 2015
Agavoideae	14.5	Iles, et al. 2015
Xanthorrhoeaceae	38.0	Iles, et al. 2015
Goodyerinae	15.0	Iles, et al. 2015
Monocots	131 – 135	Magallón et al., 2015

538

539 **Table S2.** Top ten most common transition types found in a subclade of *Ledebouria* Clade A

540 (Figure 3b) using stochastic mapping of biogeographic events.

starting_range	ending_range	average_n_events	SD	transition_type
K	K	23.432	2.121	in situ speciation
Z	Z	19.252	1.297	in situ speciation
K	KN	3.393	0.517	dispersal
T	T	2.764	2.089	in situ speciation

C	C	1.29	1.912	in situ speciation
KZ	K	1.09	0.307	vicariance or subset sympatry or extinction
KZ	Z	1.09	0.307	vicariance or subset sympatry or extinction
K	KZ	1.029	0.215	dispersal
CK	C	0.912	0.703	vicariance or subset sympatry or extinction

541

542 **Figure S1.** Full dated phylogeny with 95% highest posterior density plots shown.

543 **Figure S2.** Biogeographical reconstruction using the DIVA-like model with nodes showing the
544 probable range for each region at that node.

545

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