Combing Africa: Preliminary attempts at untangling the historical evolution of the Ledebouriinae (Scilloideae, Asparagaceae)

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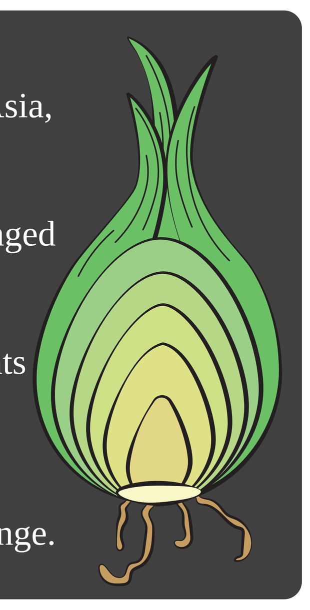
What are the Scilloideae?

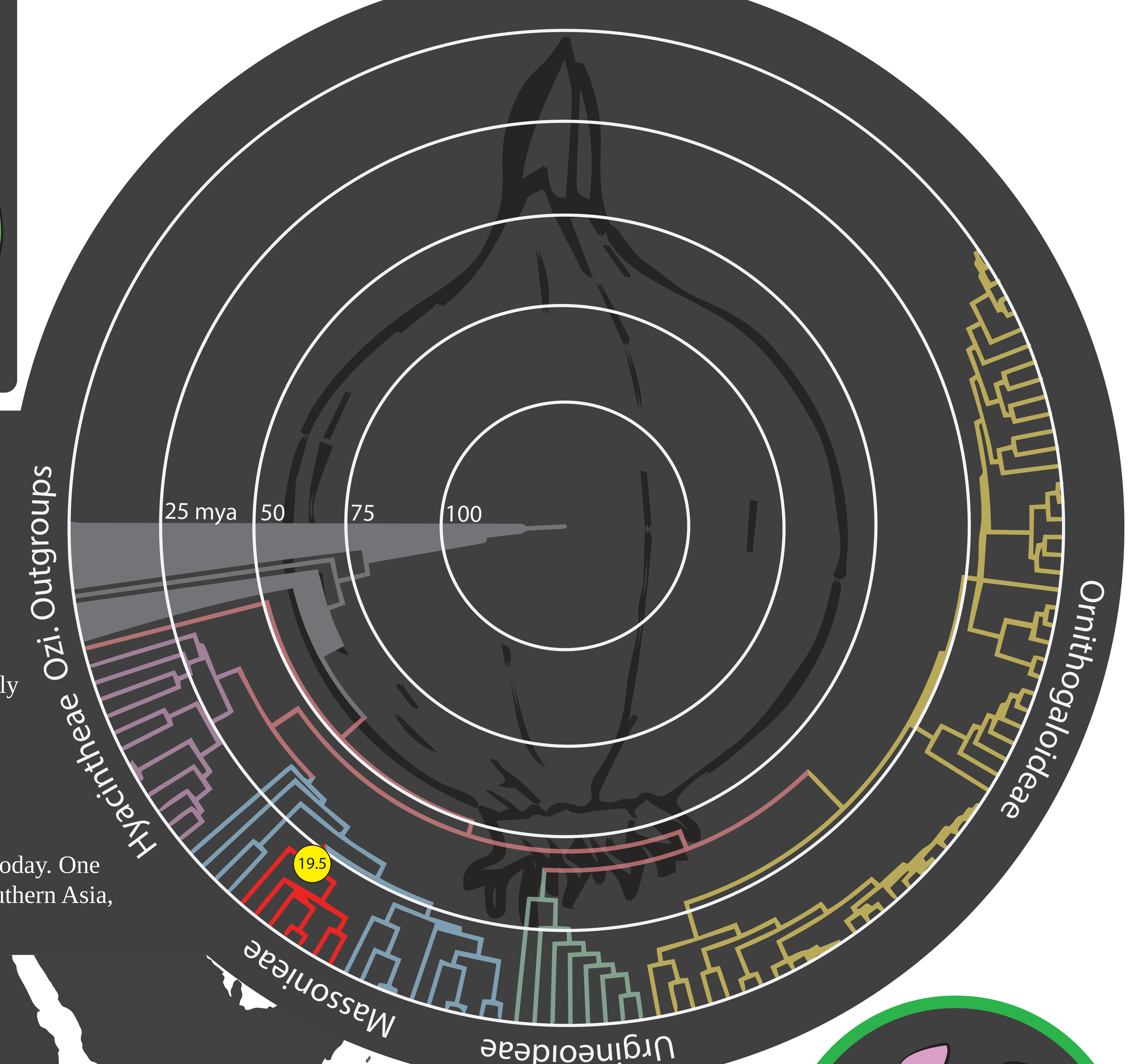
The Scilloideae are a group of bulbous monocots that are found throughout arid, alpine, or seasonal climates in Africa, Europe and Asia, with one group found in South America.

Bulbs, which have a reduced stem with modified leaves used for food storage, are especially adapted to life in climates with a prolonged dry season.

This adaptation has independently evolved multiple times across the plant tree of life, and by studying the evolution of bulbous plants we can better understand the evolution of the arid habitats they occupy.

Research on clades within the Scilloideae will not only increase our understanding of its overall diversity, but will also enhance our ability to investigate this group's dispersal history throughout these harsh climates, and their potential response to future climate change.





The Historical Evolution of the Scilloideae

Attempts at dating the origin of the Scilloideae have recovered conflicting results [1 - 3], due to a combination of lack of fossils, taxon sampling, and different analytical approaches.

The Eocene origins recovered from our dating analysis (see right) coincide with the steady cooling trend that followed the Eocene Climatic Optimum, which occurred roughly 50 mya [4]. This suggests that the ancestors of present-day Scilloideae potentially evolved in response to the onset of cooler, drier conditions that were taking hold across the globe.

Our results suggest that the diversification of the Scilloideae increased with this cooling trend and major clades evolved around 25 mya, which is roughly when the Earth began experiencing overall increased aridification and many of the modern-day arid to semi-arid habitats began to form..

The ability of this group to endure unfavorable conditions would have allowed them to survive, and even thrive during this period of aridification. Additionally, their ability to take full advantage of favorable climatic conditions would have only hastened their dispersal and diversification.

Within the Scilloideae are a number of fascinating clades that show promise for revealing the historic climatic events that have shaped the taxa we see today. One of these groups, the Ledebouriinae, has a widespread distribution throughout arid to semi-arid habitats in Africa, the Arabian Peninsula, and parts of southern Asia, and it may highlight the complex interplay that has occurred between climate and topography throughout its current distribution.

Evolutionary uncertainties within the Ledebouriinae

The Ledebouriinae, consisting of *Ledebouria*, *Drimiopsis* and *Resnova*, are found throughout dry climates in Africa, the Arabian Peninsula, and Asia (Fig. 1).

Traditionally, the Ledebouriinae have been distinguished by subtle differences in floral and bulb morphology (Fig. 2), consequently species identification can be difficult, and has led to historical taxonomic confusion.

Morphological phylogenetic analyses corroborate the historical classification of the Ledebouriinae [5], whereas molecular data supports an expanded classification of *Ledebouria* [6].

However, low support along the backbone of this clade hinders our ability to confidently infer the evolutionary relationships and history of this group, and plastid data have proven insufficient for this task (data not shown).

Regardless of species relationships, the Ledebouriinae are estimated to have evolved during a time (~19.5 mya) when the Earth was experiencing increased aridification, and modern-day arid to semi-arid habitats were beginning to form.

Uncovering the evolutionary history of this group will enhance our understanding of the expansion of the arid climate that this group now inhabits, and the adaptations acquired by this group in order to cope with a dry environment. With this information, we can then begin to predict how this group, as well as associated taxa, will respond to future aridification of this region.

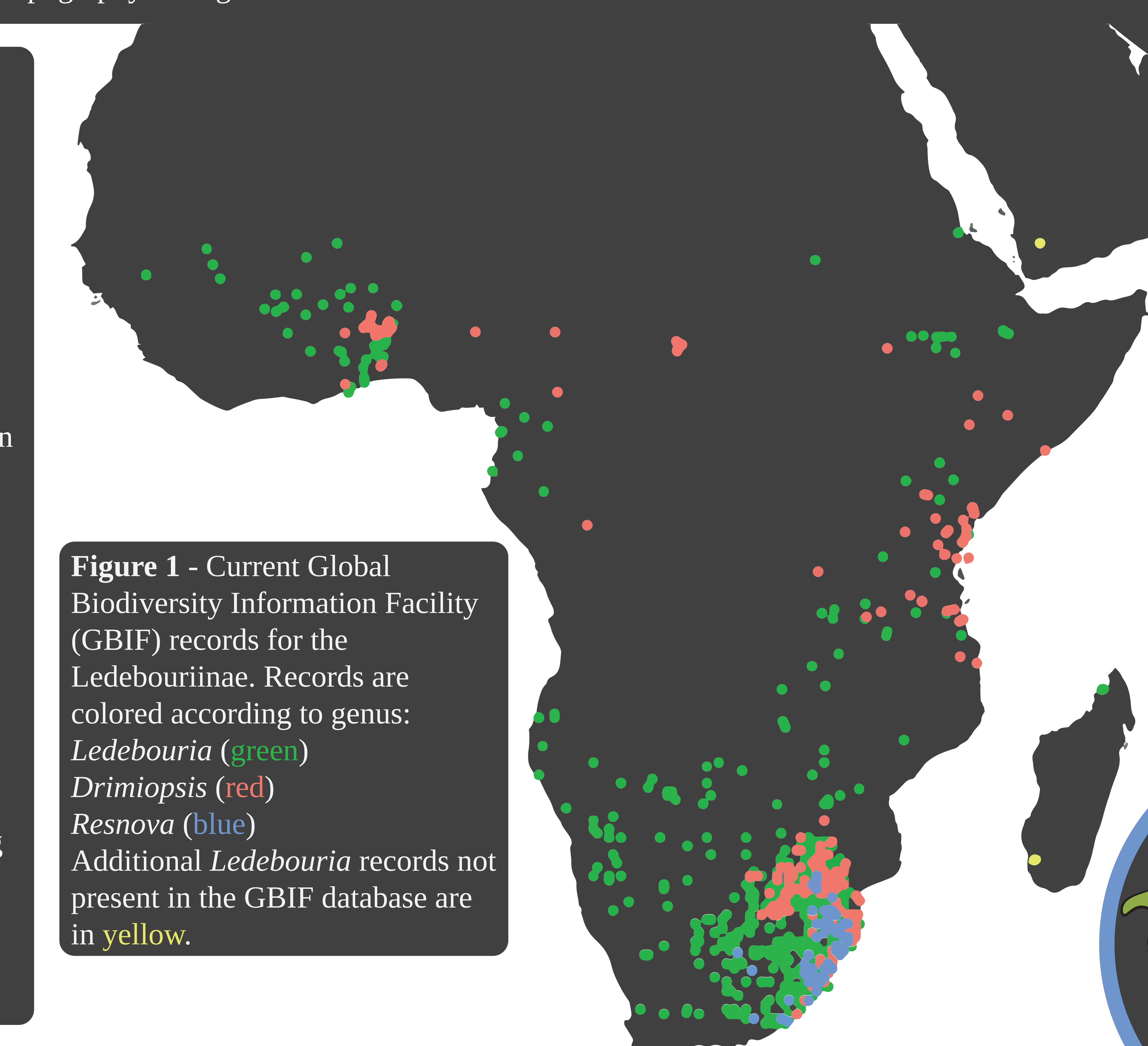


Figure 1 - Current Global Biodiversity Information Facility (GBIF) records for the Ledebouriinae. Records are colored according to genus: *Ledebouria* (green) *Drimiopsis* (red) *Resnova* (blue) Additional *Ledebouria* records not present in the GBIF database are in yellow.

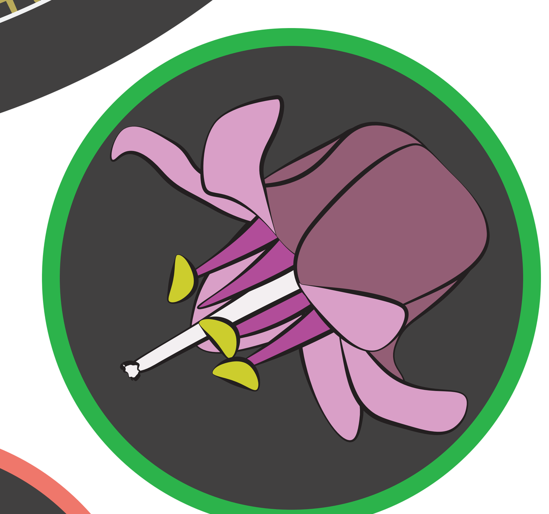


Figure 2 - Floral morphologies commonly used to distinguish between *Ledebouria* (green), *Drimiopsis* (red), and *Resnova* (blue). *Drimiopsis* and *Resnova* illustrations adapted from [9].

What's next for the Ledebouriinae?

Regions of interest to focus future collecting/sampling efforts include:

Eastern Africa – a proposed secondary center of diversity of the Ledebouriinae;

India – important for investigating the historical biogeography of *Ledebouria*, which is the only taxon of this group to have dispersed out of Africa;

Western Africa – a sampling void for the Ledebouriinae, which hinders our ability to investigate this group's dispersal across Africa.

With these samples in hand, we will then use RNAseq to aid in the selection of hundreds of single-copy nuclear loci, which will help uncover the historical evolution of this group.

Luckily, bulbs transport easily and living collections will allow for a more thorough investigations into cryptic morphological details that may help corroborate our molecular phylogenetic results and highlight potential adaptive strategies utilized by the Ledebouriinae (e.g., leaf maculation, chemical defenses).

Our understanding about the diversity of this group continues to grow and further research will only reveal more species. For example, over 150 collections of *Ledebouria* from Namibia have produced at least four new species (Fig. 3, unpublished data), and increased the total number of known species in this country.

Figure 3 - Namibian species of *Ledebouria* currently being characterized for proper species description.

Methods

Sequences for the plastid regions *trnL-F*, *rbcL*, *matK*, and *trnC-ycf6* were downloaded from GenBank for members of the Scilloideae, as well as outgroup taxa to allow calibration by using available fossils.

A concatenated dataset containing taxa that had three of the four genes of interest was analyzed with BEAST, using four fossil calibrations for the Asparagales [7]. All calibrations had a log normal distribution with a standard deviation of two, except for the node leading to Apsaragales which was given a normal distribution centered on 110 Ma (range 106 – 118) [8].

Which questions do we want to answer?

Are *Ledebouria*, *Drimiopsis*, and *Resnova* monophyletic, or does the current expanded classification of *Ledebouria* accurately reflect the phylogenetic relationships within this group?

The Mediterranean basin is a hotspot of diversity for the Scilloideae, but why are *Ledebouria* not found here? What might have hindered their dispersal into this region?

Sympatric populations of all three taxa are commonly encountered in eastern South Africa. Has hybridization played a role in the history of this group? Are *Drimiopsis* and *Resnova* of hybrid origin?

The Ledebouriinae are sister to a group of predominantly winter-growing taxa found in southwest Africa. Did the Ledebouriinae originate in southwest Africa in response to the formation of the dry climate in this region?

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