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Abstract:

The evolutionary and biogeographical history of the Mulberry family (Moraceae) is only beginning to be understood and virtually nothing is known about *Dorstenia*. DNA sequence data was used to reconstruct the first *Dorstenia* phylogeny. Phylogenetic analysis of samples showed that the genus *Dorstenia* is monophyletic, the sectional classification does not convey evolutionary history, and that the genus originated in the Old World during the Eocene, then migrated via the boreotropical North Atlantic Landbridge to the New World with a subsequent return migration back to the Old World.



Figure 1. On the left: the inflorescence of *Dorstenia foetida*, center: *D. foetida*, and on the right: inflorescence of *D. hildibrandtii*

Introduction:

The genus *Dorstenia*, is the second largest genus in the family Moraceae (fig and mulberry family), and is the only genus within Moraceae that is equally distributed on both sides of the Atlantic Ocean, in Africa and South America. The 105 species of *Dorstenia* display unique diversity. *Dorstenia* has been divided into nine different sections based on habit and morphological characteristics, which do not represent evolutionary inferences on the genus (Berg 1999). *Dorstenia* can be distinguished from the every other genus in Moraceae by the predominance of herbaceous species, which make up ninety percent of the genus. The rest of the family is woody. Although both woody and herbaceous species are represented in *Dorstenia*, the woody species are exclusive to the Old World habitats in Africa. Not only does the uniqueness of this genus warrant its study, but also the concern that many species are threatened by extinction or may all ready be extinct, and the fact that virtually nothing is known about its basic biology and reproduction.

Post-Gondwanian Orgins of *Dorstenia*?

The restriction of *Dorstenia* to African and South American tropical climates has led scientists to hypothesize that the genus originated on Gondwana before the continents separated, approximately 105 mya (McLoughin 2001). Recent phylogenetic studies of Moraceae revealed a much younger divergence time for the family, 89.1 million years ago and 35-18.4 mya for the genus (Zeraga et. al. 2005). This suggests that *Dorstenia* evolved after the break up of Gondwana and that it crossed the Atlantic by means of either long distance dispersal or migration, accounting for its distribution in both South America and Africa. However, Zeraga et. Al. (2005) only included two New World *Dorstenia* species and was, thus, not able to determine where the genus evolved.

Objectives:

- Test the monophyly of *Dorstenia*
- Examine *Dorstenia* sectional classification from an evolutionary perspective
- Use molecular data for the first time to reconstruct *Dorstenia* phylogeny
- Estimate the time and place of *Dorstenia*'s origins to test a post-Gondwana versus Gondwanan origin hypothesis and its subsequent dispersal and migration

Methods:

DNA was extracted from 83 herbarium specimens of *Dorstenia* using a CTAB protocol. The nuclear ribosomal ITS region was amplified, cleaned, and sequenced on the CEQ 8000 Genetic Analysis System. Due to the old age and degradation of herbarium samples, only fourteen samples were successfully sequenced and aligned using Se-al. The oldest specimen was from 1931. Phylogenetic analyses included maximum likelihood and maximum parsimony criterion and bootstrap support as implemented in PAUP 4.0 (Swofford 2002). The phylogeny was dated using penalized likelihood as executed in r8s (Sanderson 2003). Date estimates were made by calibrating the divergence of *Morus* from *Artocarpus* at a minimum age of 55 mya based on *Morus* fossils from the early Eocene (Collinson 1989).

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Results:

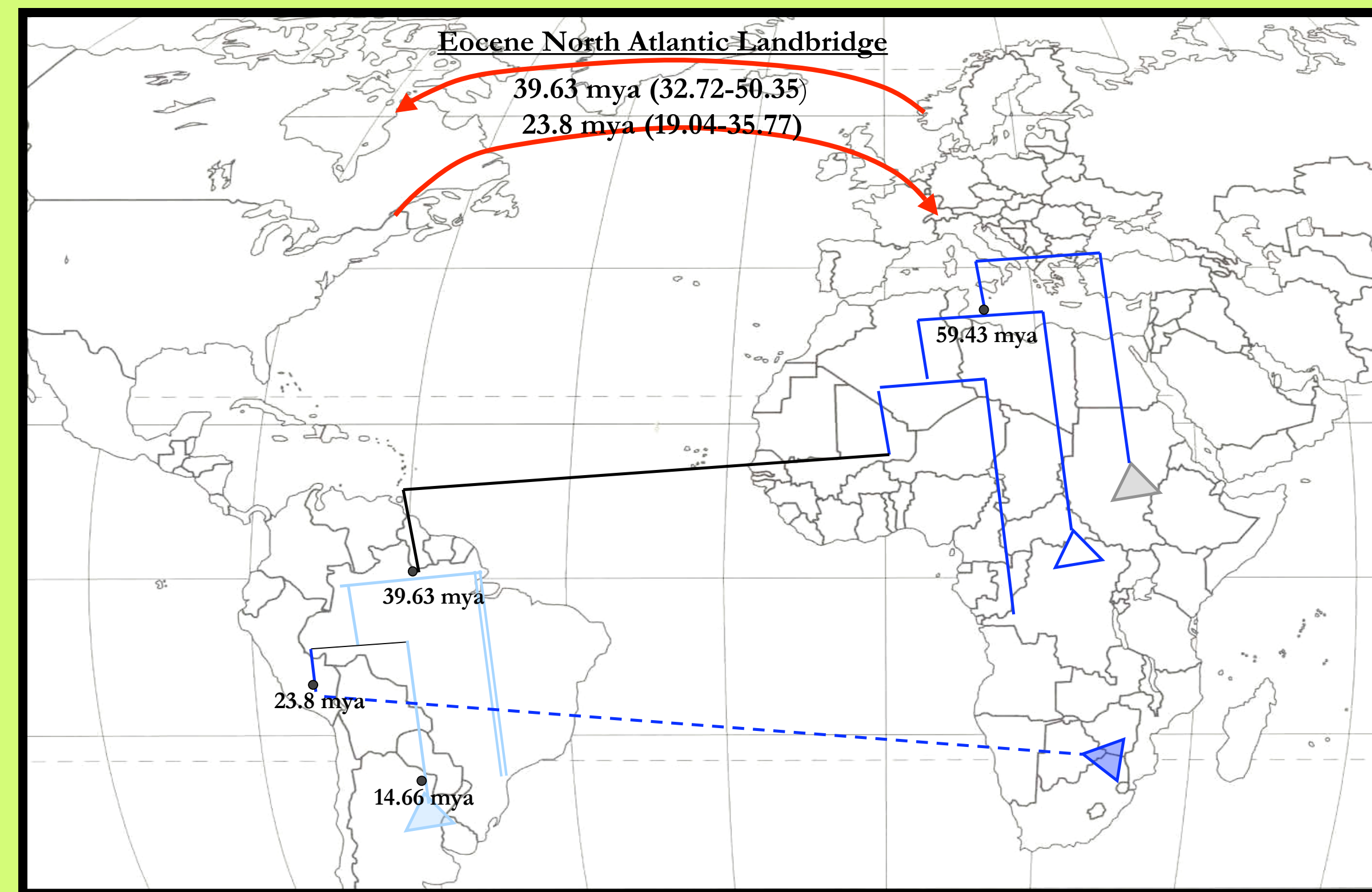


Figure 2. *Dorstenia* phylogeny in the New and Old World, *Dorstenia*'s migration across the Atlantic, and the Eocene North Atlantic Landbridge,

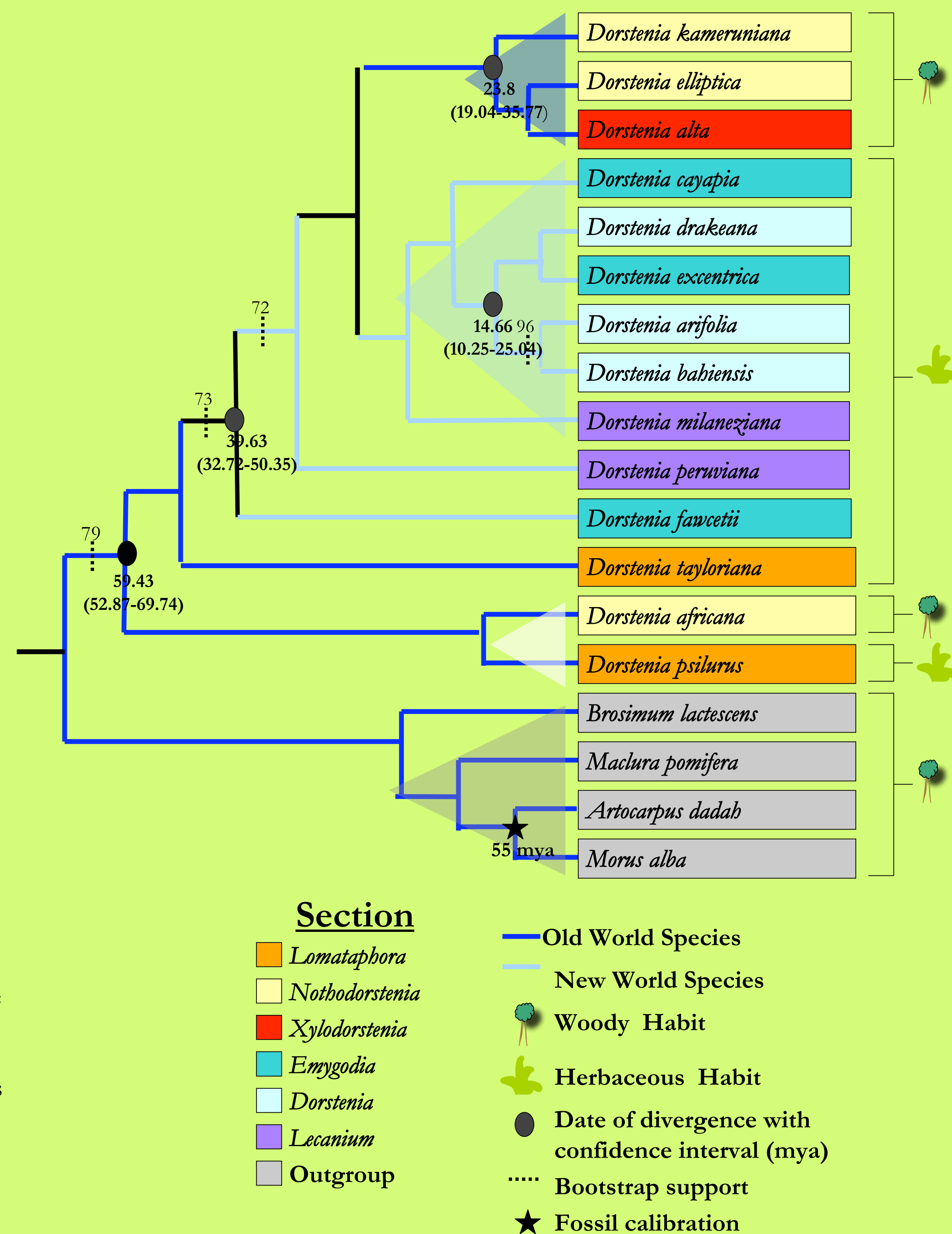


Figure 3. Maximum likelihood (ML) with bootstrap values 50% indicated on branches. Section, habit, and divergence dates are also indicated. Analyses generated one most parsimonious tree and two ML trees. Minimal conflict existed between trees within section *Dorstenia*.

Discussion:

Monophyletic or Polyphyletic? **Monophyletic**

The molecular phylogenetic reconstruction presented in this study indicates that *Dorstenia* is indeed monophyletic and represents a natural lineage (Fig. 3). Confirming *Dorstenia*'s monophyly lays an important foundation for future studies of the genus. However, the sectional classification of Berg and Hijman (1999) is polyphyletic. This calls for re-evaluation of the evolutionary integrity of the sections, but more complete taxon sampling is necessary before this can be accomplished.

Gondwanan or Post-Gondwanan Orgins? **Post-Gondwanan**

In order for *Dorstenia* to have Gondwanan origins, the genus must have evolved over 105 mya, the last time Africa and South America were connected. The present study, calculated the origin of *Dorstenia* dated at 59.43 (52.87–69.74) mya, establishing the origins of *Dorstenia* to be post-Gondwanan.

Old World or New World Origins? **Old World**

With the post-Gondwanan origins of *Dorstenia* established, the question remains: on which continent did the genus originate? The phylogenetic reconstruction indicates that Old World species diverged first at 59.43 (52.87–69.74) mya, and the New World species divergence date was 39.63 (32.72–50.35) mya. This suggests that *Dorstenia* originated in the Old World and then crossed the Atlantic to South America where the New World species evolved.

Across the Atlantic! How did *Dorstenia* do it? **The Eocene North Atlantic Landbridge**

One possible route for *Dorstenia*'s Atlantic crossing was via long distance, trans-oceanic seed dispersal. However, upon closer examination this method seems unlikely considering that *Dorstenia* does not possess the mechanisms for long or even mid distance dispersal. (Berg 1999). Ruling out this method, the most probable and best supported means for *Dorstenia*'s Atlantic crossing is via long distance land migration.

The time at which the New World species diverged, 39.63 (32.72–50.35) mya, coincides not only with the presence of the North Atlantic Land Bridge, during the Eocene, but also with a time period when Northern latitudes possessed warmer, more tropical climates (Tiffney 1985). It seems most probable that during the Eocene, which lasted from 35 to 55 mya, *Dorstenia* migrated from Africa to the tropical northern latitudes, crossed the Atlantic via the North Atlantic Land Bridge and then migrated southward through scattered islands that brought North America and South America in close proximity.

A Return Trip!

Subsequently, another lineage migrated back to Africa while this boreotropical land route still existed. The phylogenetic reconstruction shows a second lineage of Old World species that were derived 23.80 (19.04–35.77) mya, which falling within the Eocene. This suggests a second migration across the Atlantic, from the New World to the Old.

Woody vs. Herbaceous

Dorstenia is the only genus within Moraceae that includes herbaceous species. The woody species within the genus are exclusive to the Old World. Previous studies (Zeraga et. al. 2005) suggested that Moraceae family originated in the Old World, thus, the fact that woody species are exclusive to the Old World lends further support to the hypothesis that *Dorstenia* originated in Africa.

Admittedly, our findings are based on minimum age estimates that could change as new fossils are accumulated. Nonetheless, the available evidence points to an Old World origin followed by migration.

Further Research:

Dorstenia's phylogeny is far from complete. Future work aims to reconstruct a complete *Dorstenia* phylogeny. With more complete taxon sampling and additional genes, *Dorstenia*'s biogeography can be further elucidated..



Figure 4. Representatives of the genus *Dorstenia*

Works Cited:

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