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Phylogenetic Comparative Method illuminates Macroevolutionary origin of the Amaryllidaceae Umbel

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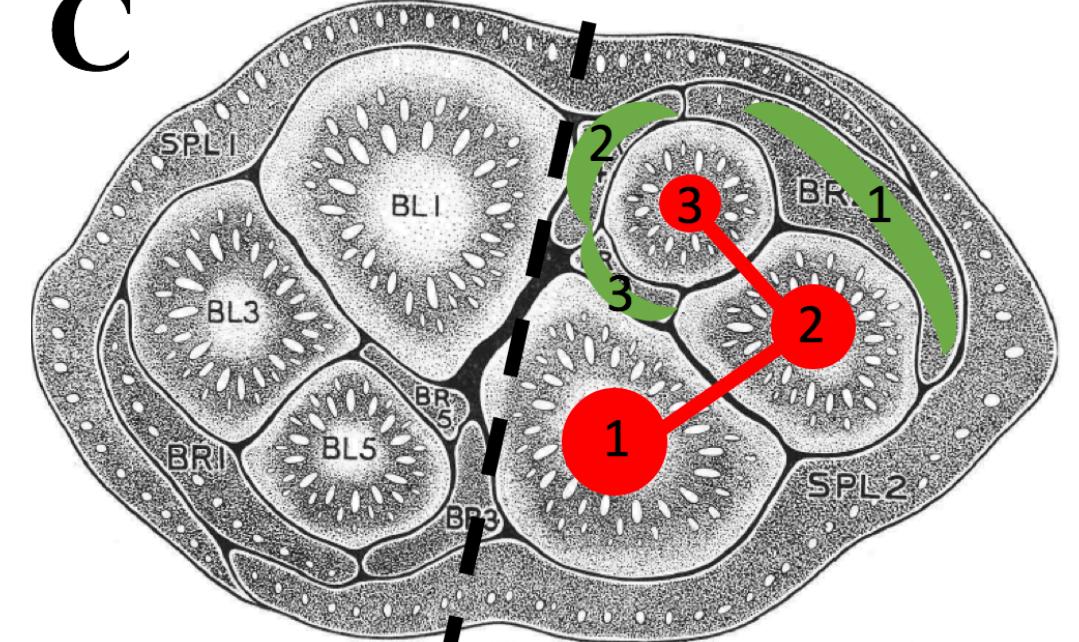
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The placement of the flowers along the axis of a plant is an important feature of the life history of a plant. While Inflorescence architecture has been topologically described and simulations have predicted a diversity of architectures, most studies are ahistorical - lacking a phylogenetic framework to understand biological diversity. This has inhibited our understanding of the phenotypic evolution of inflorescence morphology through time. In order to investigate the macroevolutionary origins of inflorescence architectural diversity, we assess an inflorescence type not predicted by many contemporary models: the Amaryllidaceae umbel. Umbels are traditionally described as all flowers arising from a single point. Multiple evolutionary hypotheses explain the evolutionary origin of the Amaryllidaceae umbel, with the ancestral form being either (1) a cymose lateral branch, (2) a dichasial branch or (3) a racemose branch. In order to address the trajectory of inflorescence evolution that gave rise to the Amaryllidaceae umbel, we use a comparative phylogenetic framework to test models of phenotypic evolution and infer ancestral states. Descriptions of adult inflorescence morphology at the generic-level were obtained from members of Amaryllidaceae, Asparagaceae and Asphodelaceae. A molecular phylogeny containing members of all three clades was inferred based on published sequence data. Competing evolutionary hypotheses were formalized as Continuous-Time Markov Models and tested in a Bayesian framework. This study provides insights into the evolutionary mode of inflorescence architectural diversity and complements current model-based simulation approaches by explicitly accounting for phylogeny.

Introduction

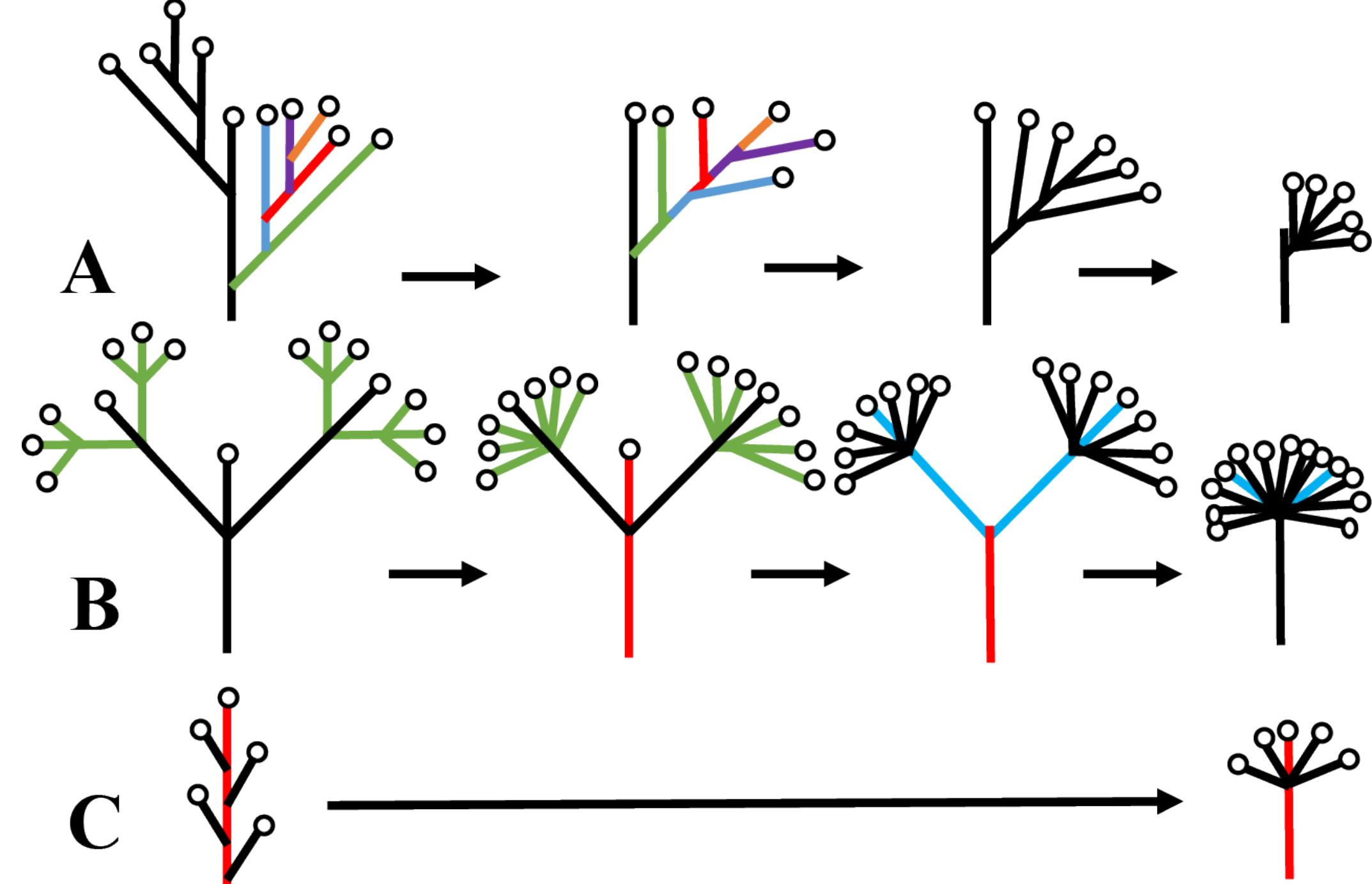


The Amaryllidaceae Inflorescence
Umbels are classically described as all flowers arising from a single point (A - *Hippeastrum*). However studies of early inflorescence development show complex organization within the inflorescence meristem (B - idealized model of architecture). The Amaryllidaceae inflorescence has been classified as a bostryx (C - Idealized bostryx superimposed on early inflorescence cross section of *Hippeastrum*¹)



Hypothesis of Amaryllidaceae Inflorescence Evolution

Idealized hypothesis of umbel evolution **A**) cyme origin², only right branch is shown after first step. **B**) dichasial origin³ **C**) Raceme origin⁴. Morphological changes are highlighted by color of branches.



Goal

Goal: Using a phylogenetic framework test estimate mode of inflorescence morphological evolution and assess degree of homology vs. homoplasy in inflorescence morphology.

SUPERMATRIX Constructor (SUMAC)⁵

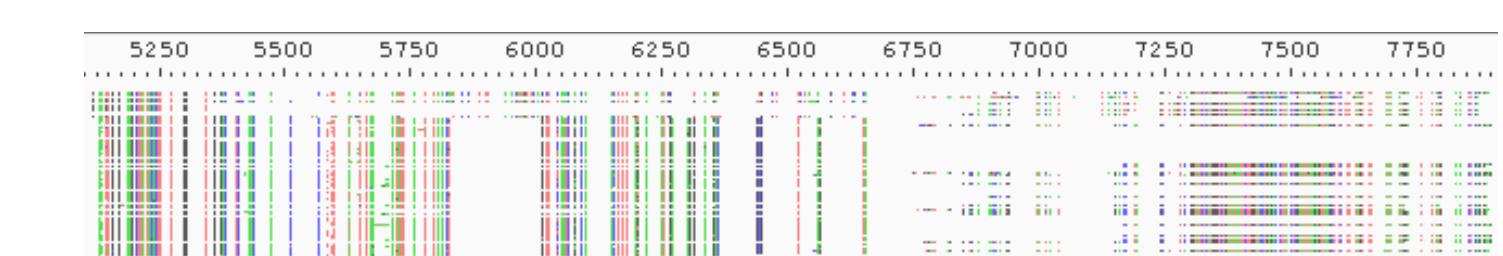
Maximum Likelihood (RAxML)

Time Calibration

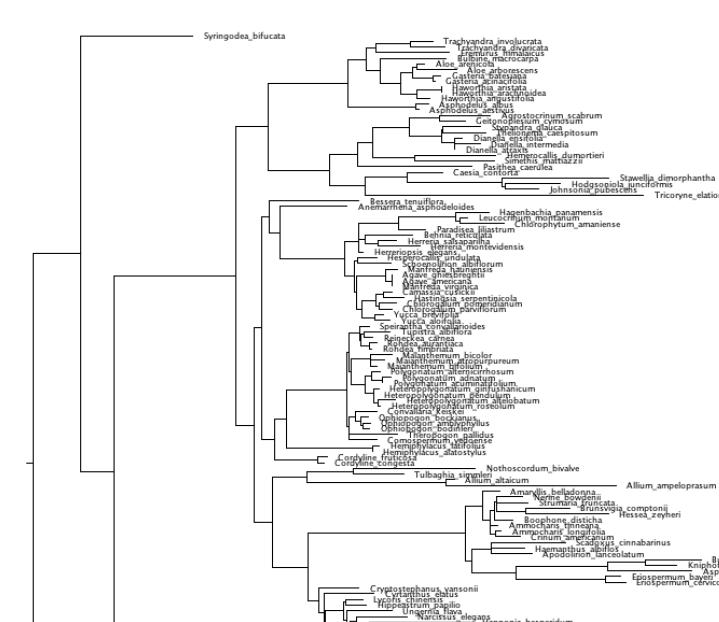
Inflorescence Morphology Data

Transition Rate Estimation and Ancestral State Reconstruction

Methods



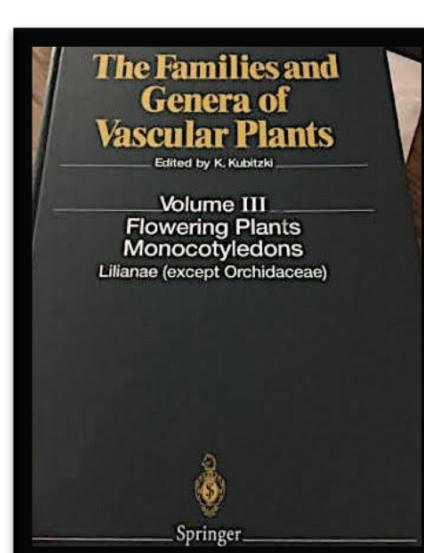
1) Mine GeneBank with SUMAC for sequence to generate a genera level phylogeny of Amaryllidaceae, Asparagaceae, Asphodelaceae



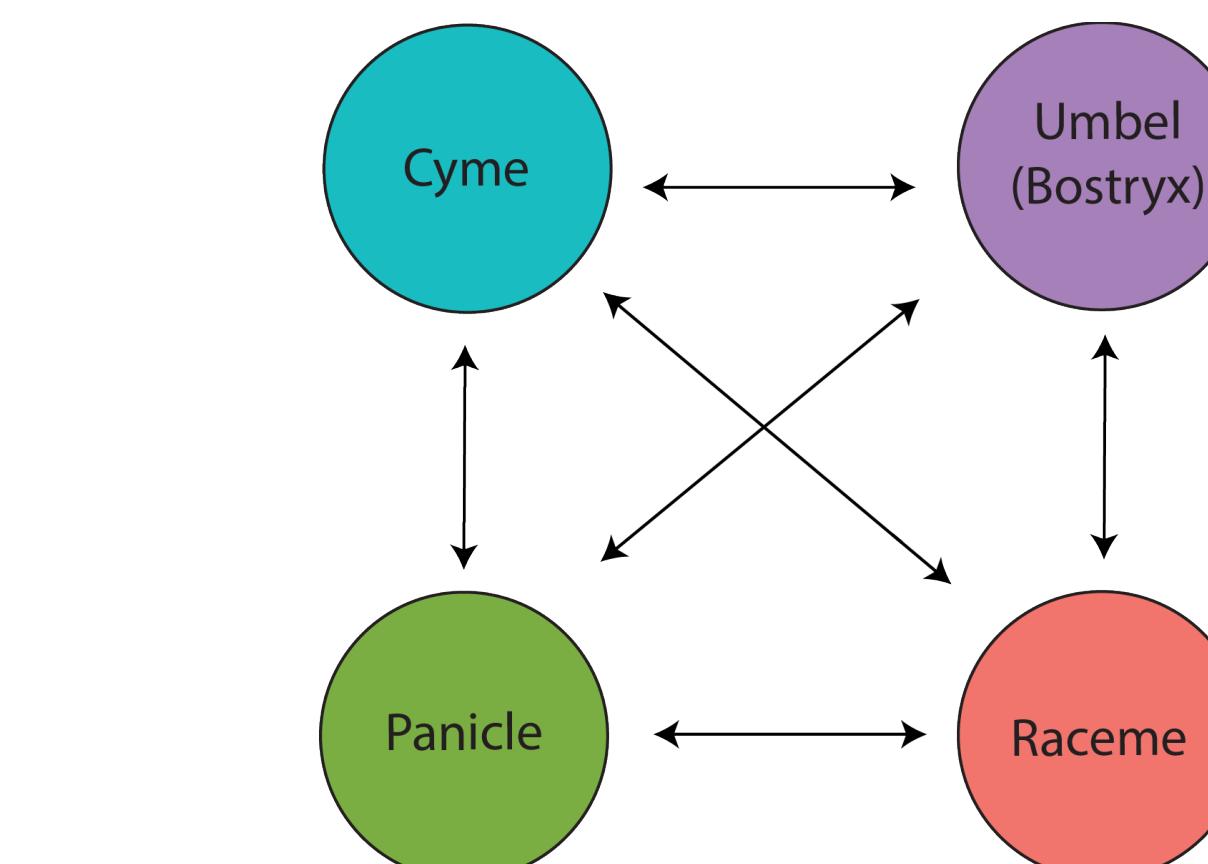
2) Infer phylogeny in Maximum likelihood framework.

Placement	Fossil	Age
Cordyline	<i>Paracordyline kerguelensis</i>	22–26
Yucca	<i>Prototucca shadishii</i>	14.5–16.2
Hemerocallidoideae	<i>Dianellophyllum eocenicum</i>	38.0–47.8

3) Estimate Divergence Time by Penalized Least Square with three fossil calibrations⁶

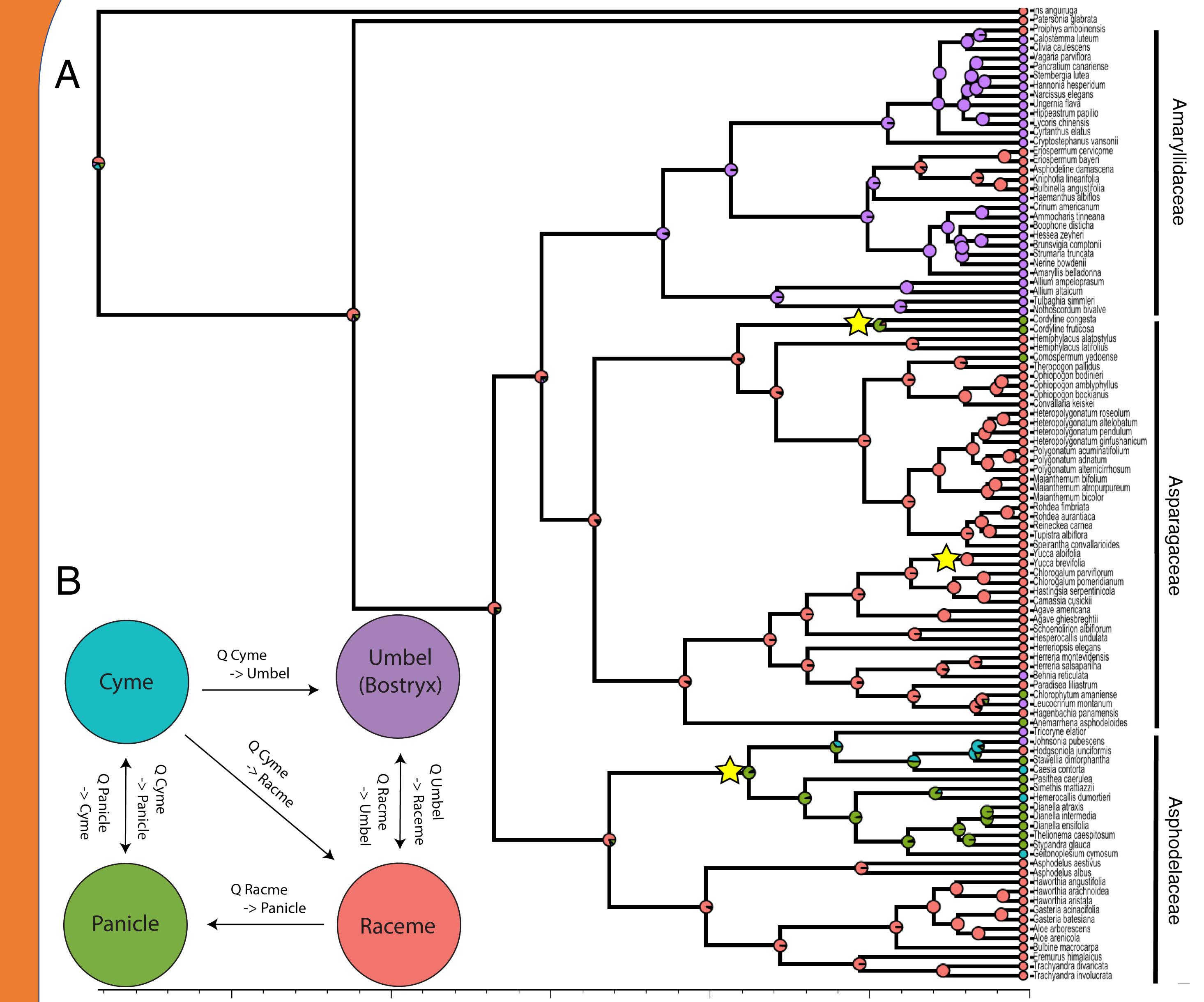


4) Inflorescence morphology data obtain primarily from genera level descriptions in Kubitzki⁷



5) Continues time Markov Model 'all rates different.' States based on Kubitzki terminology.

Results



Inflorescence Marginal Likelihood Ancestral State under Mk Model

A) Phylogeny with ancestral state reconstructions at nodes. Stars indicate fossil calibration points. B) Mk model shows estimation of transition rates parameters in Mk model.

Summary

- Phylogenetic and Divergence Time Inference:** Major family and tribe relationships and divergence time supports previous work
- Ancestral State Reconstruction:** Multiple origins of both umbellate and raceme inflorescences. Umbel/ Bostryx have multiple times. Umbellate inflorescence structure have racemes and cymes origin. However evidence from development (Fig. 1) indicates this could be due to convergence.

Future Directions

- Inflorescence classification can be confusing and incorrectly described. Rescore inflorescence based on additional source and using different classification scheme.
- In order to take account uncertainty in tree topology, divergence time, and morphological model use an entirely Bayesian framework.

1. Blaauw 1931

2. Bravis & Bravis *Anna. Sci. Nat.* (1837)

3. Qu et al. 2014

4. Stebbins *Flora* (1973)

Reference

5. Freyman *Evo. Bio.* 2015

6. Illes et al. *Bot. Linnean Soc.* 2015

7. Kubitzki 1996

Acknowledgment
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