A Phylogenetic and Geographic Analysis of Leaflet Anatomy in *Zamia* (Cycadales: Zamiaceae)

Rosemary A. E. Glos\(^1\), Shayla Salzman\(^1\), Michael Calonje\(^2\), Andrew P. Vovides\(^3\), Chelsea D. Specht\(^1\)

\(^1\)School of Integrative Plant Science and Liberty Hyde Bailey Hortorium, Cornell University, Ithaca, New York; \(^2\)Montgomery Botanical Center, Coral Gables, Florida; \(^3\)Instituto de Ecología, Xalapa, Veracruz, Mexico

**Premise**

Cycads in the genus *Zamia* (81 spp.) display a high level of morphological convergence that has historically frustrated efforts to elucidate fine-scale species relationships. As such, these relationships have only recently been resolved through phylogenetic analyses of DNA-based character data. However, it remains unknown whether leaflet anatomical variation corresponds to phylogeny and geography, as has been investigated in other major cycad genera. This project presents a broad comparative survey of leaflet anatomy across 20 *Zamia* species with the goals of defining diagnostic characters and understanding character evolution.

**Significance**

Cycads are among the most ancient lineages of extant seed-bearing plants and are the most threatened plant order on Earth, with circa 75% of the 355 accepted species threatened with extinction. The knowledge obtained through this project improves our understanding of micromorphological character evolution, anatomical diversity, and phylogenetic relationships within the second-largest cycad genus. With this information, we may better understand phenotypic evolution and facilitate the identification, classification, and conservation of these highly vulnerable plants.

**Methods**

Plant material was sampled from the living collections at Montgomery Botanical Center and Fairchild Tropical Botanical Garden. Leaflets from 20 *Zamia* species covering all major clades and spanning the geographic distribution of the genus were chosen for sectioning. Transverse and longitudinal preparations were stained to elucidate structures, observed under light microscopy, and scored for a range of anatomical characters. Selected characters were analyzed in the context of published phylogenetic relationships and geographic distributions.

**Key Findings**

*Zamia* leaflet anatomy shows widespread anatomical variation within a consistent core bauplan. Most anatomical characters have a high degree of homology consistent with variation seen in gross leaflet morphology. A newly reported mesophyll cell type with thick walls and conspicuous pitting ("flat tire" cells) may prove diagnostic for the clade consisting of species from South America and the Isthmus of Panama plus *Zamia soconusensis*.

**Next Steps**

The incongruence between anatomy and phylogeny indicates that we must look elsewhere to enhance our understanding of the distribution of anatomical traits in *Zamia*. Future studies comparing specific anatomical characters to habitat or climatic variables may reveal patterns not apparent in the phylogeny. Additional analysis is also required to determine the composition, function, and distribution of the sclereid-like "flat tire" cells across the entire genus.

**Acknowledgments**

We thank the Cornell College of Agricultural and Life Sciences (CALS) Alumni Association and the Dextra Undergraduate Research Endowment Fund; P. Barry Tomlinson; Patrick Griffith and the entire Montgomery Botanical Center staff; Chad Husby and Yisl Santamarina; Alejandra Gandolfo and Jennifer Sitkow; Dennis Stevenson; Melissa Whitakes, and members of the Specht Lab at Cornell University.

**Full text and references:**

---

**Leaflet anatomy in the cycad genus *Zamia* displays striking variation within a consistent core bauplan.**

**Most of the anatomical characters examined are not phylogenetically informative, but the presence of sclereid-like cells may prove diagnostic for one clade.**