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Phylogenetics and the evolution of major structural characters in the giant genus *Euphorbia* L. (Euphorbiaceae)

James W. Horn [a], Benjamin W. van Ee [b], Jeffery J. Morawetz [c], Ricarda Riina [d,e], Victor W. Steinmann [f], Paul E. Berry [d], Kenneth J. Wurdack [a,*]

[a] *Department of Botany, Smithsonian Institution, NMNH MRC-166, P.O. Box 37012, Washington, DC 20013-7012, USA*
[b] *Black Hills State University Herbarium, 1200 University St., Spearfish, SD 57799, USA*
[c] *Rancho Santa Ana Botanic Garden, 1500 North College Ave., Claremont, CA 91711-3157, USA*
[d] *Department of Ecology and Evolutionary Biology, and University of Michigan Herbarium, 3600 Varsity Dr., Ann Arbor, MI 48108-2287, USA*
[e] *Real Jardín Botánico, CSIC, Plaza de Murillo 2, 28014 Madrid, Spain*
[f] *Instituto de Ecología, A.C., Centro Regional del Bajío, A.P. 386, 61600 Pátzcuaro, Michoacán, Mexico*

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ABSTRACT

Euphorbia is among the largest genera of angiosperms, with about 2000 species that are renowned for their remarkably diverse growth forms. To clarify phylogenetic relationships in the genus, we used maximum likelihood, Bayesian, and parsimony analyses of DNA sequence data from 10 markers representing all three plant genomes, averaging more than 16 kbp for each accession. Taxon sampling included 176 representatives from Euphorbioideae (including 161 of *Euphorbia*). Analyses of these data robustly resolve a backbone topology of four major, subgeneric clades—*Esula*, *Rhizanthium*, *Euphorbia*, and *Chamaesyce*—that are successively sister lineages. Ancestral state reconstructions of six reproductive and growth form characters indicate that the earliest *Euphorbia* species were likely woody, non-succulent plants with helically arranged leaves and 5-glanded cyathia in terminal inflorescences. The highly modified growth forms and reproductive features in *Euphorbia* have independent origins within the subgeneric clades. Examples of extreme parallelism in trait evolution include at least 14 origins of xeromorphic growth forms and at least 13 origins of seed caruncles. The evolution of growth form and inflorescence position are significantly correlated, and a pathway of evolutionary transitions is supported that has implications for the evolution of *Euphorbia* xerophytes of large stature. Such xerophytes total more than 400 species and are dominants of vegetation types throughout much of arid Africa and Madagascar.

1. Introduction

Euphorbia L. sensu lato (Euphorbiaceae), with close to 2000 currently recognized species and a nearly global distribution, is among the largest of the "giant genera" of flowering plants (Govaerts et al., 2000; Frodin, 2004). Unlike most other large angiosperm clades recognized as genera, species richness in *Euphorbia* is coupled with remarkable structural variability (Figs. 1 and 2). The combination of these attributes distinguishes the genus as a promising group in which to investigate fundamental evolutionary questions about the origin of morphological novelty and diversification. An understanding of the evolution of reproductive and vegetative traits that encompass the most striking structural variants for which *Euphorbia* is renowned is necessary to achieve this goal. Hence, our primary objective in presenting a new phylogenetic hypothesis of *Euphorbia* is to use it as framework for a series of evolutionary analyses that illuminate the origin and evolution of the kaleidoscopic structural diversity within the entire clade. We discuss the biological significance of these results, and comment on their possible significance to the diversification of *Euphorbia*. Although we do not explicitly test the effect of trait origin on diversification, our results provide a reasonable basis with which to develop two such hypotheses, which will be addressed in future studies.

Variation in reproductive traits within *Euphorbia* mostly involves characteristics of the inflorescences and the seeds. *Euphorbia* has a specialized inflorescence type, the cyathium (Fig. 1a), that mimics a flower by clustering reduced male and female flowers within a cup-shaped involucre formed from the bracts associated with groups of male flowers (Hoppe and Uhlarz, 1982; Prenner and Rudall, 2007; Prenner et al., 2008). The cyathium has been invoked as the key innovation that drove the spectacular diversification of the clade, because its origin supposedly enabled a shift from wind pollination in close relatives with catkin-like inflorescences to insect pollination (Croizat, 1937;

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* Corresponding author.
E-mail address: wurdackk@si.edu (K.J. Wurdack).

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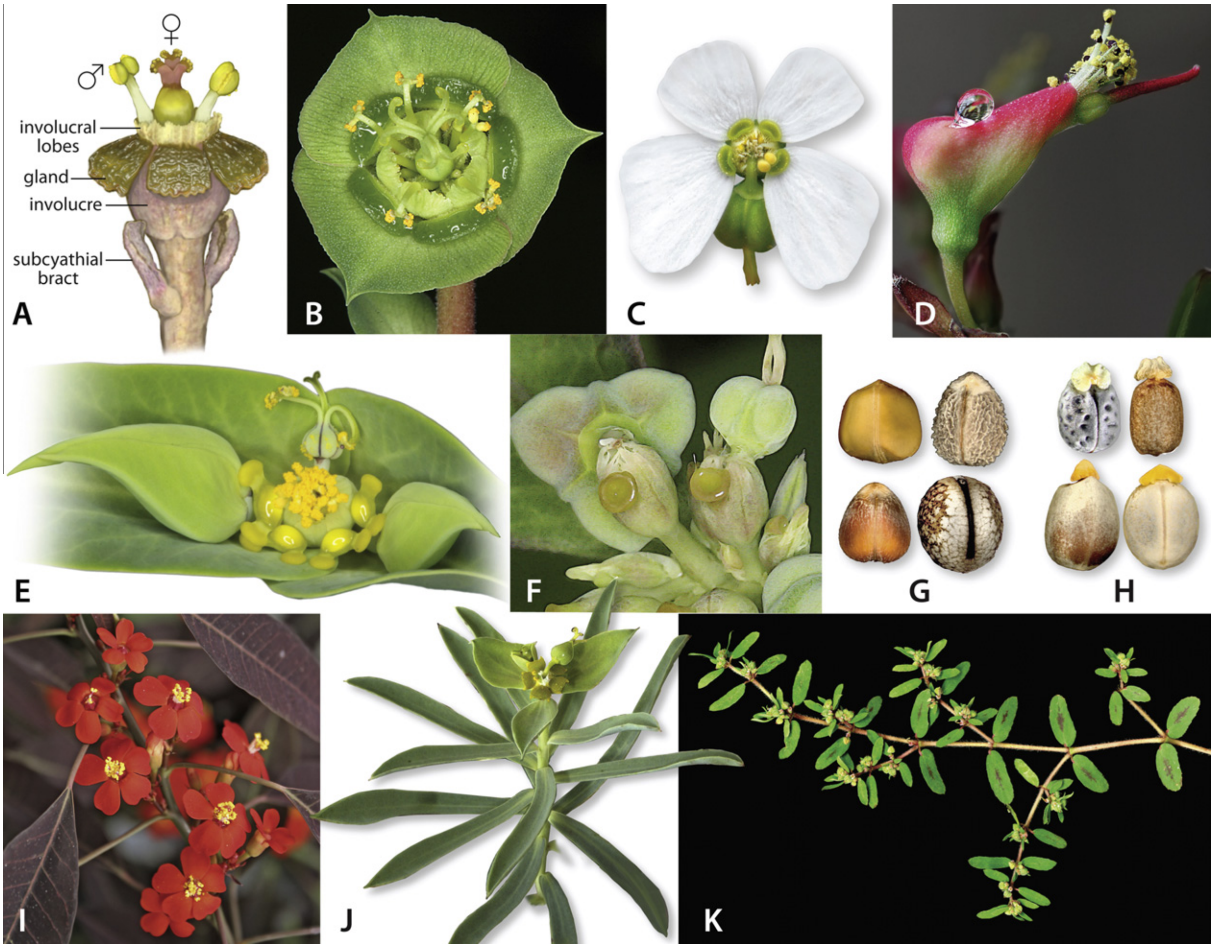

Fig. 1. Cyathial, seed, and leaf position characters in *Euphorbia*. (A) Cyathium of *E. fasciculata* (Clade A), with main features labeled. (B) Top view of cyathium of *E. clava* (Clade A), with five dark green unappendaged glands and three lighter green subtending bracts or cyathophylls. (C) Cyathium of *E. tamanduana* (Clade D; sect. *Anisophyllum*), with four green glands each bearing a large white petaloid appendage. (D) Cyathium of *E. tithymaloides* subsp. *padifolia* (Clade C; sect. *Crepidaria*), showing bilateral symmetry and nectar drop emerging from hidden involucral glands. (E) Dichasium of *E. lathyris* (Clade B) showing a central, open cyathium flanked by two unopened cymes and with two open subcyathial bracts behind it. The cyathium has four elliptic glands each with two knob-like appendages. (F) Two cyathia of *E. heterophylla* (Clade D; sect. *Poinsettia*), showing a single cupulate gland on the edge of each involucre. (G) Ecarunculate seeds (clockwise from upper left; not to scale, all clade A except third): *E. dregeana*, *E. clandestina*, *E. breviarticulata* (Clade C), *E. bubalina*. (H) Carunculate seeds (clockwise from upper left; not to scale): *E. commutata* (Clade B), *E. nicaeensis* (Clade B), *E. espinosa* (ventral and dorsal views, Clade D). (I) Alternate leaves and terminal cyathium of *E. minuta* (Clade B). (J) Alternate leaves and axillary cyathia of *E. fulgens* (Clade D; sect. *Alectoroctonum*). (K) Opposite leaves of *E. maculata* (Clade D; sect. *Anisophyllum*). Credits: A. Moller and K. Elliot (A), P. Berry (B, E, I, J), R. Riina (C, F), N. Cacho (D), B. Wagner and K. Elliot (G, H), K. Wurdack (K).

Webster, 1967). The principal structures involved in attracting pollinators in most *Euphorbia* species are a series of nectary glands positioned at the rim of the cyathial involucre (Fig. 1a). Differences in the merosity of this whorl of glands are readily characterizable among species, and modifications in gland number can confer either positional or constitutional bilateral symmetry to orient pollinators. The cyathial glands often bear appendages, which despite their uniform early ontogeny (Hoppe, 1985) are diverse in shape and size at maturity. These appendages can further enhance the attractive function of the glands by increasing their visibility. Cyathia of several *Euphorbia* species have gland appendages with a showy, petaloid appearance, and can superficially appear almost indistinguishable from a typical eudicot flower (Fig. 1i). Among the many seed traits that vary in *Euphorbia*, the presence or absence of a caruncle that functions as an elaiosome is significant because of its potential role in mediating secondary ant dispersal and in its prior use in *Euphorbia* classification.

The broad array of growth forms within *Euphorbia* has been well documented, but corresponding ideas and knowledge about the origin and evolution of these varied growth forms is limited. Habit in *Euphorbia* ranges from small, annual herbs to large trees, but the genus is best known for its great diversity of xeromorphic growth forms that are marked by the presence of tremendous variability in stem succulence (White et al., 1941; Rauh, 1995, 1998). A plant architectural perspective also reflects these perceptions of considerable structural variability. The synoptic survey of Hallé et al. (1978), building on Cremers' (1977) analysis of Madagascan species, established that species of *Euphorbia* conform to 12 of the 23 recognized architectural models, which is more than any other genus of seed plants.

The four main molecular phylogenetic studies of *Euphorbia* to date have addressed the overall phylogeny of the genus, with a major point of consensus being the recognition of four subgeneric clades: *Rhizanthium*, *Esula*, *Euphorbia*, and *Chamaesyce* (Steinmann and Porter, 2002; Bruyns et al., 2006; Park and Jansen, 2007; Zimmermann et al., 2010). Subgenus *Rhizanthium* (Clade A of Steinmann and Porter, 2002; around 200 spp.) has a primarily African distribution, with most of the species comprising a southern African radiation of xerophytes that are physiognomically diverse. Subgenus *Esula* (Clade B; around 500 spp.) contains predominantly herbaceous species distributed in the temperate Northern Hemisphere, especially from the eastern Mediterranean through central