

# Origin of the cyathium-bearing Euphorbieae (Euphorbiaceae): phylogenetic study based on morphological characters

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**Abstract.** A cladistic analysis of the subfamily Euphorbioideae was undertaken to elucidate the origin of the cyathium-bearing Euphorbieae and to provide hypotheses about evolutionary relationships within the subfamily. Twenty-one species representing most of the genera within the study group and three outgroup taxa from the subfamilies Acalyphoideae and Crotonoideae were selected for parsimony analysis. An unweighted parsimony analysis of 24 morphological characters resulted in five equally parsimonious trees with consistency indices of 0.67 and tree lengths of 39 steps. The strict consensus tree supported monophyly of the cyathium-bearing Euphorbieae. The sister group relationships of cyathium bearing Euphorbieae with *Maprounea* (subtribe Hippomaninae) were supported weakly, and the origin of cyathium is possibly in Hippomaneae, or in the common ancestor of Euphorbieae and remaining taxa of Euphorbioideae plus Acalyphoideae. Within the tribe Euphorbieae, both subtribes Euphorbiinae and Neoguilauminiinae are monophyletic, but the African endemic subtribe Anthosteminae is unresolved. The resulting trees support the monophyly of the tribe Stomatocalyceae while the tribe Hippomaneae does not consistently form a clade.

**Keywords:** Cyathium; Euphorbieae; Phylogeny.

## Introduction

In a recent classification of subfamily Euphorbioideae Boiss., Webster (1975, 1994b) recognized six tribes: Stomatocalyceae (Muell. Arg.) Webster, Hippomaneae A. Juss. ex Spach, Pachystromateae (Pax & Hoffm.) Pax, Hureae Dumortier and Euphorbieae Blume. Among these the cyathium-bearing taxa are restricted to the tribe Euphorbieae. Compared to Webster's system, Pax (1924) recognized only two closely related tribes: Hippomaneae and Euphorbieae, and one remotely related tribe, Gelonieae (Muell. Arg.) Pax, on his phyletic tree. However, Gelonieae, corresponding in part to Webster's tribe Stomatocalyceae, was indicated as closely related to tribe Manihoteae (Muell. Arg.) Pax of the subfamily Crotonoideae Pax in Pax's system.

The highly specialized inflorescence—cyathium—of Euphorbieae, is characterized by a central female flower and four or five lateral groups of male flowers within the involucre. Although the unique cyathium in Euphorbieae has been considered evidence of a natural group, the origin and nature of this character have been interpreted diversely (Jussieu, 1824; Mueller, 1866; Haber, 1925; Croizat, 1937, 1942; Gilbert, 1994).

Croizat (1937, 1938) pointed out a strong resemblance between Euphorbieae and Hippomaneae except with regard

to the position of a female flower. Accordingly, the *Euphorbia*-like cyathium results from the alteration of floral axis and the condensation of the axis of male flower in Hippomaneae. This interpretation is also supported by Pax (1924), whose idea of relationships in Euphorbiaceae indicates that Hippomaneae is most closely related to Euphorbieae.

A recent hypothesis, however, does not support the traditional relationships (Pax, 1924; Croizat, 1937, 1938) but rather suggests origin of the cyathium-bearing Euphorbieae from Crotonoideae (Gilbert, 1994). Within the Crotonoideae, *Jatropha*-like species with a primary female flower and lateral male flowers are considered ancestors of Euphorbieae (Gilbert, 1994). Croizat (1942) and Hurusawa (1954) on the other hand insisted that the cyathium of Euphorbieae should be derived from the pseudanthium of *Dalechampia* Plumier ex L. in Acalyphoideae Ascherson via *Pedilanthus* Necker ex Poiteau, but several authors disputed the *Dalechampia* origin of Euphorbieae (Venkata Rao, 1971; Webster and Webster, 1972; Webster, 1994a).

Pollen morphology indicates that *Euphorbia* is similar to *Stillingia* Garden ex L. and *Sapium* P. Browne of Hippomaneae in having an even margo and a similar sculpturing pattern, but its pollen clearly differs from that of Crotonoideae and Acalyphoideae (e.g. *Dalechampia*) (Webster and Webster, 1972; Webster and Rupert, 1973; Park, 1997). The pollen grains of Crotonoideae are mostly inaperturate with triangular supracteal elements completely absent in Euphorbieae (Park and Lee, 1988; Nowicke, 1994; Webster, 1994b).

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Tribe Euphorbieae, the largest tribe within the Euphorbioideae, is divided into three subtribes: Anthosteminae (Baillon) Webster, Neoguillaumininae Croizat and Euphorbiinae Hurusawa (Webster, 1975, 1994b). Most traditional hypotheses have placed the Anthosteminae as a basal lineage within the tribe (Pax, 1924; Croizat, 1937). According to the phyletic tree of Croizat (1937), the Australian endemic *Calycopeplus* Planchon in Neoguillaumininae is to be regarded as the group most closely related to Euphorbiinae. The Euphorbiinae is the largest and systematically most problematic subtribe of the Euphorbioideae, members of which are recognized by a true cyathium, which lacks the calyx of male and female flowers. Most of the taxonomic problems surrounding Euphorbiinae are due to its large size, a profusion of intergrading and overlapping characters (Sherff, 1940), and classifications made on the base of local flora without comprehensive phylogenetic studies within the complete ranges of the group (Gilbert, 1994; Webster, 1994b; Park, 1996).

The objectives of the present study were: 1) to investigate the origin of the cyathium-bearing taxa within subfamily Euphorbioideae; 2) to investigate the phylogenetic relationships within tribe Euphorbieae; and 3) to evaluate Webster's (1994b) recent classification and tribal circumscriptions within the Euphorbioideae.

## Materials and Methods

Twenty-one genera in the subfamily Euphorbioideae as recently circumscribed by Webster (1994b) were included in the analysis (Table 1). Ingroup monophyly of Euphorbioideae, as compared to sister groups Crotonoideae and Acalyphoideae, is supported by a number of apomorphic characters such as whitish latex, simple trichomes, apetalous flowers, lack of a disk, absence of vascular bundles in the inner integument, and perforate-reticulate pollen exine (Webster, 1994b; Tokuoka and Tobe, 1995). Based on the relationships of the Euphorbiaceae (Levin and Simpson, 1994), three species from the Crotonoideae and Acalyphoideae were selected as outgroups for rooting the resulting trees. Taxonomic hypotheses based on morphology (Levin and Simpson, 1994), serology (Jensen et al., 1994), anatomy (Rudall, 1987, 1994), and molecular data (Wurdack and Chase, 1999) strongly supported close relationships among the three subfamilies within Euphorbiaceae.

Morphological characters were obtained by examining herbarium specimens and living materials. Twenty-four characters from 24 terminal taxa were coded (Tables 2, 3). Phylogenetic analyses were conducted on an Apple Macintosh 8600/250 with 80 MBRAM available, using PAUP Version 4.0d65 (Swofford, 1999) under the assump-

**Table 1.** Euphorbioideae taxa, their representative species and voucher information for which morphological data obtained in this study. The classification (system) based on Webster (1994b).

Ingroup	
<b>Subfamily Euphorbioideae</b>	
<b>Tribe Euphorbieae</b>	
<i>Anthostema aubryanum</i> Baill.	J. Lowe 1825 (K)
<i>Dichostemma glaucescens</i> Pierre	A. J. M. Leeuwenberg 9823 (K)
<i>Neoguillauminia cleopatra</i> Croizat	H. S. McKee 39509 (K)
<i>Elaeophorbium drupifera</i> (Thop.) Staff	M. Hakki 28 (K)
<i>Calycopeplus oligandrus</i> P. I. Forst.	A. R. Bean 9089 (BRI)
<i>Cubantheus linearifolius</i> (Gnsef.) Mill.	E. L. Ekman 4742 (K)
<i>Pedilanthus tithymaloides</i> (Millsp.) Dressler	G. N. Batianoff 940725 (OKL)
<i>Synadenium arborescens</i> Hk. f.	L. J. M. Wood 8492 (E)
<i>Monadenium laeve</i> Stapf	J. Pawek 11030 (K)
<i>Euphorbia corollata</i> L.	K. Park 51 (KNUH)
<i>Euphorbia ebracteolata</i> Hayata	K. Park 101 (KNUH)
<i>Euphorbia supina</i> Raf.	K. Park 10 (SKK)
<b>Tribe Hureae</b>	
<i>Hura crepitans</i> L.	D. N. Smith & V. Garcia 13869 (OKL)
<b>Tribe Hippomaneae</b>	
<i>Maprounea brasiliensis</i> St.-Hil.	L. O. Williams 8047 (K)
<i>Sebastiania brasiliensis</i> Spreng.	K. Balkwill et al. 3043 (E)
<i>Excoecaria buaaci</i> (Pax) Pax	H. H. Schmidt 1283 (K)
<i>Sapium japonicum</i> Pax et Hoffm.	K. Park 201 (KNUH)
<i>Stillingia treculiana</i> I. M. Johnston	D. Seigler & T. Lockwood 9009 (OKL)
<i>Omalthus populneus</i> (Geisel.) Pax	
<b>Tribe Stomatocalyceae</b>	
<i>Hamilcoa zenkeri</i> (Pax) Prain	G. Zenker 4130 (E)
<i>Pimelodendron anboinicum</i> Hassk.	Y. Lelean & P. E. Stevens 51280 (E)
Outgroup	
<b>Subfamily Crotonoideae</b>	
<i>Croton monanthogynus</i> Michaux	T. B. Croat 69684 (OKL)
<i>Jatropha variabilis</i> A. Radcliffe-Smith	
<b>Subfamily Acalyphoideae</b>	
<i>Acalypha australis</i> L.	K. Park 202 (KNUH)

**Table 2.** Characters and character states used in cladistic analysis of Euphorbioideae.

1. Succulent stems: 0 = absent; 1 = present.
2. Male inflorescences: 0 = elongated; 1 = condensed.
3. Staminate calyx: 0 = present; 1 = absent.
4. Stamen number: 0 = >8; 1 = 1-7.
5. Pistilate calyx: 0 = present; 1 = absent.
6. Pistilate flower: 0 = basal; 1 = apical.
7. Style: 0 = undivided; 1 = divided.
8. Stigma: 0 = thin (tapered); 1 = thick (capitate).
9. Staminate flower articulation: 0 = absent; 1 = present.
10. Pistilate flower pedicel: 0 = absent; 1 = present.
11. Gland position: 0 = absent; 1 = base of male bracts; 2 = around the male inflorescences.
12. Glands: 0 = separated; 1 = continuous.
13. Gland appendages: 0 = absent; 1 = present.
14. Pollen colpus margins: 0 = absent; 1 = present with smooth margin.
15. Pollen tectum: 0 = reticulate or microreticulate; 1 = foveolate.
16. Seed: 0 = smooth; 1 = tuberculate or wrinkled.
17. Latex color: 0 = red; 1 = yellow; 2 = white.
18. Sexuality: 0 = monoecious; 1 = dioecious.
19. Petiolar glands at the base of leaf blade: 0 = absent; 1 = present.
20. Ovary: 0 = 2-3 locular; 1 = > 3.
21. Bracts: 0 = free; 1 = connate.
22. Petaloid bracts: 0 = absent; 1 = present.
23. Capsule trichomes: 0 = present; 1 = absent.
24. Staminate petals: 0 = present; 1 = absent.

tions of Fitch parsimony (Fitch, 1971). The matrix was analysed using 1,000 random taxon addition sequences followed by the efficient “tree bisection reconnection” (TBR) branch swapping algorithm. The characters were then reweighted using the successive approximations weighting method proposed by Farris (1969). Weights were applied according to the rescaled consistency index, and the procedure was repeated until a stable result was obtained. In order to further evaluate the stability of different branches in the obtained trees, a Bremer support analysis (Bremer, 1988; Källersjö et al., 1992; Bremer, 1994) was performed, making use of the computer program “Autodecay PPC 4.01” (Eriksson, 1998) in combination with PAUP in the generalized manner described by Bremer (1994). Furthermore, bootstrap- (Felsenstein, 1985) and jackknife-analyses (Farris et al., 1996) excluding 37% and 50%, respectively, of the characters were also performed using PAUP with settings analogous to those described above.

**Results**

The first step of the analysis, with unweighted characters, yielded five equally parsimonious trees with a length of 39 steps, a consistency index (CI; Kluge and Farris, 1969) of 0.67 and retention index (RI; Farris, 1989) of 0.90. The strict consensus tree is shown in Figure 1. After successive approximations reweighting a stable result of 18 equally parsimonious trees with a length of 22.84 steps, CI = 0.75 and RI = 0.94 was obtained, the strict consensus of which is shown in Figure 2.

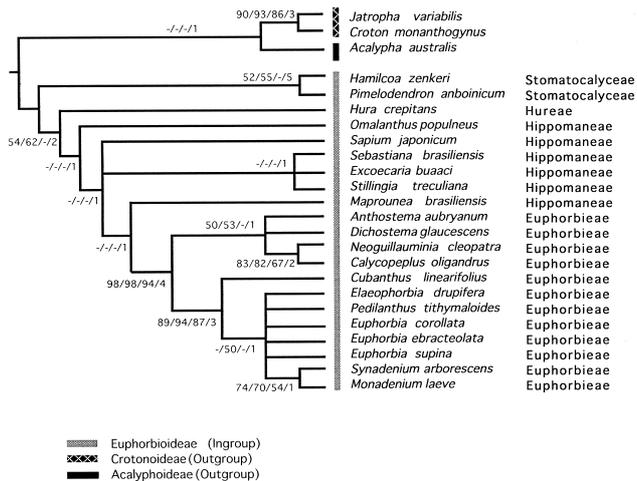
The topologies obtained from the analyses before and after the successive reweighting procedure differ on several points, the main one of which is the identification of two major lineages within the Euphorbioideae, one of which includes the outgroup of Acalyphoideae in the latter. These lineages largely correspond to the well supported tribe Euphorbieae on one hand, and to an assembly of other tribes—albeit weakly supported—on the other hand.

In the lineage consisting of several tribes, moderate support is found for a monophyletic Stomatocalyceae, and weak but unambiguous support for the tribe Hippomaneae. In the unweighted analysis, however, the tribe Stomatocalyceae was indicated as the most basal tribe of the subfamily Euphorbioideae, and the tribe Hippomaneae as being paraphyletic with respect to Euphorbieae.

Within the tribe Euphorbieae, both subtribes Euphorbiinae and Neoguilaumiinae are retrieved as monophyletic, and strongly supported by relatively high supporting values within the studied group, but the

**Table 3.** Data matrix of character states used in the cladistic analysis. “?” designates missing states. The classification based on Webster (1994b).

Taxon	Characters
	0000000011111111122222
	123456789012345678901234
<b>Ingroup</b>	
<b>Subfamily Euphorbioideae</b>	
<b>Tribe Euphorbieae</b>	
<i>Anthostema aubryanum</i>	010101111110011020001011
<i>Dichostemma glaucescens</i>	010101111110011020001011
<i>Neoguilauminia cleopatra</i>	011101111110011020001111
<i>Elaeophorbia drupifera</i>	11111111120010020001011
<i>Calycopeplus oligandrus</i>	011101111110011020001111
<i>Cubanthus linearifolius</i>	11011111120010?20001011
<i>Pedilanthus tithymaloides</i>	11111111120110020001011
<i>Synadenium arborescens</i>	11111111121010120001011
<i>Monadenium laeve</i>	11111111121010120001011
<i>Euphorbia corollata</i>	11111111120110020001011
<i>Euphorbia ebracteolata</i>	11111111120010020001011
<i>Euphorbia supina</i>	11111111120110120001001
<b>Tribe Hureae</b>	
<i>Hura crepitans</i>	0100000010?0100?0110011
<b>Tribe Hippomaneae</b>	
<i>Maprounea brasiliensis</i>	010100000110010020100011
<i>Sebastiania brasiliensis</i>	000100000010010020100011
<i>Excoecaria buaaci</i>	000100000010010020000011
<i>Sapium japonicum</i>	000100000110010020100011
<i>Stillingia treculiana</i>	?00100000010010020100011
<i>Omalanthus populneus</i>	0000000001100???20100011
<b>Tribe Stomatocalyceae</b>	
<i>Hamilcoa zenkeri</i>	0000?000?0?001011000011
<i>Pimelodendron anboinicum</i>	00000?00010?000011010011
<b>Outgroup</b>	
<b>Subfamily Crotonoideae</b>	
<i>Croton monanthogynus</i>	00000011010?001000000000
<i>Jatropha variabilis</i>	00000111010?001000000000
<b>Subfamily Acalyphoideae</b>	
<i>Acalypha australis</i>	0000000000?0000?0000001



**Figure 1.** Strict consensus tree of six equally most-parsimonious cladograms obtained from phylogenetic analysis of unweighted morphological data (length = 39; CI = 0.67; RI = 0.90). Numbers appearing on the branches indicate, in order, [bootstrap / jackknife with 37% deletion / jackknife with 50% deletion / Bremer support].

paleotropical subtribe Anthosteminae was unresolved (Figures 1 and 2). In the unweighted analysis the genus *Cubanthus* (Boiss.) Millsp. is placed as a sister group of the remaining taxa within the subtribe Euphorbiinae, albeit weakly supported. In the weighted analysis *Cubanthus* is unresolved with regards to Euphorbiinae.

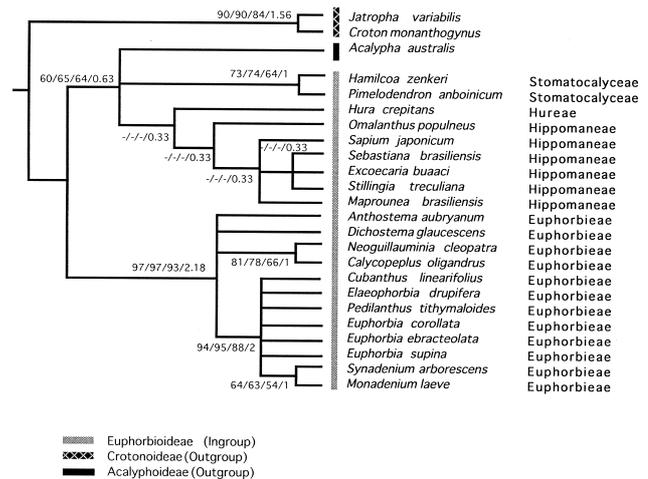
## Discussion

### Phylogeny and Classification

The resulting topology from the analysis largely corresponds to the tribal classification of Euphorbioideae proposed by Webster (1994b).

The monophyly of Euphorbieae, the cyathium-bearing group, is particularly well supported by a number of characters. Branch support values for the clade are substantial in all of the measures. Within the Euphorbieae, three subtribes are recently recognized (Webster, 1975, 1994b): subtribe Anthosteminae, including *Anthostema* and *Dichostemma*, subtribe Neoguillaumininae, containing *Neoguillauminia* and *Calycopeplus*, and subtribe Euphorbiinae including the remaining genera. However, the delimitation of these three subtribes is controversial. Croizat (1937) separated *Dichostemma* from Anthosteminae, and placed it within the subtribe Neoguillaumininae. In the present analysis our results did not show the monophyly of Anthosteminae, as proposed by Webster (1975, 1994b). Neither do they support the separation of *Dichostemma* and *Anthostema* (Croizat, 1937). However, our analyses recovered the Neoguillaumininae and Euphorbiinae clades, as proposed by Webster (1975, 1994b).

The consensus trees of both analyses well support the monophyly of the Stomatocalyceae. However, the rela-



**Figure 2.** Strict consensus tree of 18 equally most parsimonious cladograms obtained from successive approximations reweighted analysis of morphological data (length = 22.84; CI = 0.75; RI = 0.94). Numbers appearing on the branches indicate, in order, [bootstrap / jackknife with 37% deletion / jackknife with 50% deletion / Bremer support].

tionships between Stomatocalyceae and other genera of the Euphorbioideae were equivocal because the tribe was grouped together with Acalyphoideae in the weighted analysis, or as the sister group of all other Euphorbioideae. A previous phylogenetic analysis of Malesian Hippomaneae, *Pimelodendron* Hassk. of Stomatocalyceae always segregated from the tribe Hippomaneae and suggested its divergence within the Euphorbioideae (Esser et al., 1997). A recent molecular phylogenetic study (Wurdack and Chase, 1999) suggests that Webster's subfamily Euphorbioideae is not monophyletic and that Stomatocalyceae is excluded from the subfamily. Although previous pollen studies (Punt, 1987; Nowicke, 1994) indicated the naturalness of subfamily Euphorbioideae, pollen characters such as without marginate colpi (character 13), and rugulate sculpturing pattern (character 12) in the tribe Stomatocalyceae suggest a closer relationship with the subfamily Acalyphoideae (Gillespie, 1994), or at least an exclusion from Euphorbioideae (Pax and Hoffmann, 1931). Its habit, colored latex, and oily endosperm (Webster, 1994b) require additional comparison to taxa outside of Euphorbioideae such as Acalyphoideae to determine whether Stomatocalycinae may be part of the tribe Omphaleae or Plukenetiae in Acalyphoideae. A more global parsimony analysis including most of Acalyphoideae and Crotonoideae is required to test the monophyly of Webster's subfamily Euphorbioideae.

In the weighted analysis, the New World tribe Hureae is the sister group of Hippomaneae and supports the classification system suggested by Webster (1994b). The two tribes share a presence of glands at the blade base and two other parallel characters. This supports the opinion of Pax (1924) who combined them into a single tribe Hippomaninae, and placed them as sister groups to each other.

### *The Origin of the Cyathium-Bearing Group*

In the unweighted analysis, the cyathium-bearing Euphorbieae forms a monophyletic group. It is, albeit weakly supported, nested within Hippomaneae, which is characterized by bisexual inflorescences with basal pistillate and central staminate flowers and inclinate flowers (Esser et al., 1997). The analyses both provide some support for the view that Euphorbieae seems to be evolved from a common ancestor to *Maprounea* of Hippomaneae rather than from a *Jatropha*-like ancestor within the subfamily Crotonoideae (Gilbert, 1994). Furthermore, this interpretation does not contradict the previous hypothesis of Webster and Rupert (1973) on the basis of pollen morphology; they suggested that the Euphorbieae are derived from an ancestral form within the Hippomaneae.

In Hippomaneae, the male inflorescence shows two different types of modification: globose spikes and elongate spikes. The elongate spikes of male inflorescence occur in most of the species in Hippomaneae, while the condensed male inflorescence, characteristic of Euphorbieae, is only found in *Maprounea* of Hippomaneae. Also, insertion of the glands between the clusters of male flowers is well known in two basal clades, Anthosteminae and Neoguillauminiinae of the Euphorbieae, and it only occurs in *Maprounea* within Hippomaneae. Croizat (1938) suggested that the structure of the inflorescence in the Euphorbieae is not fundamentally different from that of the Hippomaneae, except for the position of the axes, because the cyathium of Euphorbieae has resulted from the condensation of the male axis of Hippomaneae. Gilbert (1994) recently rejected this suggestion and proposed the Crotonoideae origin of Euphorbieae from a *Jatropha*-like ancestor. The results of our analysis of morphological data are mostly consistent with the hypotheses of Croizat (1938) and Pax (1924).

However, our weighted analysis supports the alternative hypothesis that the cyathium is evolved from a common ancestor of the cyathium-bearing Euphorbieae and from the remaining taxa of Euphorbioideae plus *Acalypha australis* of the subfamily Acalyphoideae.

In conclusion, Webster's (1994) tribes Euphorbieae and Stomatocalyceae are well supported, but the tribe Hippomaneae does not form a clade consistently. The cyathium-bearing Euphorbieae is a well supported tribe, but whether the tribe originated within Hippomaneae or had an isolated origin from Euphorbioideae cannot be answered clearly. Therefore, a broad phylogenetic analysis including Acalyphoideae and Crotonoideae is needed to resolve the sister group of Euphorbieae.

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### Literature Cited

- Bremer, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42**: 795-803.
- Bremer, K. 1994. Branch support and tree stability. *Cladistics* **10**: 295-304.
- Croizat, L. 1937. Notes on Euphorbiaceae, with a new genus and a new subtribe of the Euphorbieae. *Philipp. J. Sci.* **64**: 397-412.
- Croizat, L. 1938. Glands of Euphorbiaceae and of *Euphorbia*. *Chron. Bot.* **IV**: 6: 512-514.
- Croizat, L. 1942. Peculiarities of the inflorescence in the Euphorbiaceae. *Bot. Gaz.* **103**: 771-779.
- Eriksson, T. 1998. AutoDecay ver. 4.0 (Program Distributed by the Author). Bergius Foundation, Royal Swedish Academy of Sciences, Stockholm.
- Esser, H.-J., P. van Welzen, and T. Djarwaningsih. 1997. A phylogenetic classification of the Malesian Hippomaneae (Euphorbiaceae). *Syst. Bot.* **22**: 617-628.
- Farris, J.S. 1969. A successive approximations approach to character weighting. *Syst. Zool.* **18**: 374-385.
- Farris, J.S. 1989. The retention index and the rescaled consistency index. *Cladistics* **5**: 417-419.
- Farris, J.S., V.A. Albert, M. Källersjö, D. Lipscomb, and A.G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* **12**: 99-124.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**: 783-791.
- Fitch, W.M. 1971. Toward defining the course of evolution: Minimum change for a specific tree topology. *Syst. Zool.* **20**: 406-416.
- Gilbert, M.G. 1994. The relationships of the Euphorbieae (Euphorbiaceae). *Ann. Missouri Bot. Gard.* **81**: 283-288.
- Gillespie, L.J. 1994. Pollen morphology and phylogeny of the tribe Plukenetieae (Euphorbiaceae). *Ann. Missouri Bot. Gard.* **81**: 317-348.
- Haber, J.M. 1925. The anatomy and the morphology of the flower of *Euphorbia*. *Ann. Bot.* **39**: 657-707.
- Hurusawa, I. 1954. Eine nochmalige Durchsicht des herkommlichen systems der Euphorbiaceen im weiteren Sinne. *J. Fac. Sci. Univ. Tokyo, III, Bot.* **6**: 209-342.
- Jensen, U., I. Vogel-Bauer, and M. Nitschke. 1994. Leguminlike proteins and the systematics of the Euphorbiaceae. *Ann. Missouri Bot. Gard.* **81**: 160-179.
- Jussieu, A. 1824. *De Euphorbiacearum Generibus Medicisque Earumdem Tentamen*. Didot, Paris.
- Kluge, A.G. and J. S. Farris. 1969. Quantitative phyletics and the evolution of the anurans. *Syst. Zool.* **18**: 1-32.
- Källersjö, M., J.S. Farris, A.G. Kluge, and C. Bult. 1992. Skewness and permutation. *Cladistics* **8**: 275-287.
- Levin, G.A. and M.G. Simpson. 1994. Phylogenetic implications of pollen ultrastructure in the Oldfieldioideae (Euphorbiaceae). *Ann. Missouri Bot. Gard.* **81**: 203-238.
- Mueller, J. 1866. Euphorbiaceae. In A.P. de Candolle (ed.), *Prodromus* 15 (2). Masson and Son, Paris, pp. 189-1269.
- Nowicke, J.W. 1994. A palynological study of Crotonoideae (Euphorbiaceae). *Ann. Missouri Bot. Gard.* **81**: 245-269.

- Park, K. 1996. Phylogeny of New World subtribe Euphorbiinae (Euphorbiaceae). *Kor. J. Plant Tax.* **26**: 235-256.
- Park, K. 1997. Pollen morphology of *Euphorbia* subgenus *Agaloma* section *Tithymalopsis* and related species (Euphorbiaceae). *Grana* **36**: 11-16.
- Park, K. and S. Lee. 1988. A palynotaxonomic study of the Korean Euphorbiaceae. *Kor. J. Plant Tax.* **18**: 69-94.
- Pax, F. 1924. Die Phylogenie der Euphorbiaceae. *Bot. Jahrb.* **59**: 129-182.
- Pax, F. and K. Hoffmann. 1931. Euphorbiaceae. In A. Engler and K. Prantl (eds.), *Die Natürlichen Pflanzenfamilien* ed. 2, 19C, Leipzig, pp. 11-233.
- Punt, W. 1987. A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. *Bot. J. Linn. Soc.* **94**: 127-142.
- Rudall, P. 1987. Laticifers in Euphorbiaceae - a conspectus. *Bot. J. Linn. Soc.* **94**: 143-163.
- Rudall, P. 1994. Laticifers in Crotonoideae (Euphorbiaceae): homology and evolution. *Ann. Missouri Bot. Gard.* **81**: 270-282.
- Sherff, E.E. 1940. The concept of the genus. *Bull. Torrey Bot. Club* **67**: 375-380.
- Swofford, D.L. 1999. PAUP\*: Phylogenetic Analysis Using Parsimony, version 4.0d65. Computer program. Sinauer, Sunderland, Massachusetts.
- Tokuoka, T. and H. Tobe. 1995. Embryology and systematics of Euphorbiaceae *sens. Lat.*: a review and perspective. *J. Plant Res.* **108**: 97-106.
- Venkata Rao, C. 1971. Anatomy of the inflorescence of some Euphorbiaceae. *Bot. Not.* **124**: 39-64.
- Webster, G.L. 1975. Conspectus of a new classification of the Euphorbiaceae. *Taxon* **24**: 593-601.
- Webster, G.L. 1994a. Classification of the Euphorbiaceae. *Ann. Missouri Bot. Gard.* **81**: 3-32.
- Webster, G.L. 1994b. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Ann. Missouri Bot. Gard.* **81**: 33-144.
- Webster, G.L. and F.A. Rupert. 1973. Phylogenetic significance of pollen nuclear number in the Euphorbiaceae. *Evolution* **27**: 524-531.
- Webster, G.L. and B.D. Webster. 1972. The morphology and relationships of *Dalechampia scandens* (Euphorbiaceae). *Amer. J. Bot.* **59**: 573-586.
- Wurdack, K.J. and M.W. Chase. 1999. Spurges split: molecular systematics and changing concepts of Euphorbiaceae. In anonymous (eds.), *Proceedings of the XVI International Botanical Congress, St. Louis, August 1-7, 1999, Abstracts, USA*, pp. 142.

## 具杯狀花序 (cyathium) 之大戟族 (大戟科) 植物的起源： 根據形態性狀之系統發育探討

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本文以大戟亞科 (Euphorbioideae) 之支序分類分析 (cladistic analysis) 闡明具杯狀花序 (cyathium) 之大戟族植物起源，並提供亞科內演化關係之假說。使用了 21 種植物以代表擬進行研究對象之大多數屬，並選取 3 種代表 Acalyphoideae 亞科及 Crotonoideae 亞科供對照之外群作最簡約分析法 (parsimony analysis)。對 24 個形態性狀進行未加權之最簡約分析法，可得到 5 個一致性指數 (consistency indices) 為 0.67 之同等簡約演化樹，演化樹有 39 次的改變。嚴格的共同樹支持具杯狀花序之大戟族植物為單一起源。具杯狀花序之大戟族與 *Maprounea* (Hippomaninae 亞族) 間之姊妹關係其支持度較弱。杯狀花序可能起源於 Hippomaneae 族，或者大戟族及大戟亞科其餘種類，加上 Acalyphoideae 亞科的共同祖先。在大戟族內，大戟亞族及 Neoguilauminiinae 亞族都是單源的，但特產非洲的 Anthosteminae 亞族則尚未確定。本研究所得之演化樹支持 Stomatocalyceae 族之單源性，但 Hippomaneae 族則非為單起源群。

**關鍵詞：**杯狀花序；大戟族；系統發育。