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CLASSIFICATION OF THE EUPHORBIACEAE¹

Grady L. Webster²

ABSTRACT

The family Euphorbiaceae appears to be monophyletic, despite proposals for segregate families. The Euphorbiaceae display a great variety of growth forms, including at least 17 "models" of Hallé. Anatomical characters particularly useful for classification include wood structure, laticifer type, trichomes, and stomata. Inflorescences are basically dichasial, and pseudanthia have evolved several times. Pollen nuclear number and exine structure provide useful criteria for characterizing genera, tribes, and subfamilies. Structure of the seed coat is characteristic for the family and does not provide evidence for a polyphyletic origin of the family. Pollination is prevalently entomophilous, and seed dispersal by ants is important in many taxa. Geographic distribution patterns of genera show a concentration of primitive taxa in Africa and Madagascar, although in subfamily Crotonoideae there is evidence of a neotropical center. Disjunctions between Africa and South America are common. Bentham's hypothesis of an Old World origin of the family appears well supported. The basic distribution patterns appear to reflect early (Cretaceous and Paleogene) dispersal across land or narrow water barriers and spectacular but rather trivial instances of long-distance dispersal in the late Tertiary and Pleistocene; Tertiary high-latitude dispersals via the Bering land bridge appear to have been relatively insignificant.

The Euphorbiaceae, although one of the largest dicot families and conspicuous throughout the tropics, have been relatively neglected by systematists in the 20th century. While other families such as Compositae, Leguminosae, and Solanaceae have been the subjects of various symposia, the very first international conference with a major focus on Euphorbiaceae was held at Kew in 1986 (Jury et al., 1987). The Kew symposium, on the Euphorbiales, was heavily biochemical in orientation and focused to a considerable extent on relationships between the Euphorbiaceae and other families. The present symposium in St. Louis is the first in which the classification of the family and its constituent infrafamilial taxa is the major focus of attention.

The history of classification systems for the Euphorbiaceae at the subfamilial and tribal level has been reviewed in the Kew symposium on Euphorbiales (Webster, 1987). In my opinion, the two major milestones in this history were the classifications of Adrien Jussieu (1824), who identified the major series of genera that (after much later revision) correspond roughly to current subfamilies, and Jean Mueller (1866), who provided the first detailed classification of the family into subfamilies, tribes, and subtribes. The originality of Mueller is particularly striking in comparison with the earlier system of Baillon (1858), which was disappointingly

uninformative about relationships, and the later ones of Bentham (1880) and Pax (1890), who accepted the general framework of Mueller with relatively minor exceptions. Later revisions by Pax & Hoffmann (1931) and the treatment by Hurusawa (1954) continued to reflect the original ideas of Mueller, despite considerable changes. Although my recent classification (Webster, 1975) appears very different from that of Mueller at first glance, I was struck by how many of the great Swiss systematist's ideas still survive. Even though he went astray in his major subdivisions (based on cotyledon shape) of the "Stenolobeae" and "Platylobeae," Mueller arranged the genera of Euphorbiaceae into subtribes that, in an impressively large number of instances, reflect phylogenetic affinity as presently understood. In reviewing our efforts at this symposium to improve the classification of Euphorbiaceae, it seems evident to me that it is Mueller's foundation we are standing on.

In my classification of 1975, the 300 genera of Euphorbiaceae were grouped into 52 tribes in five subfamilies, with several of the tribes divided into subtribes. The classification presented at this conference shows only a limited number of changes, even though it is quite probable that future research will show that substantial modifications will have to be made. As has often been remarked, the linear arrangement of taxa in a classification is an im-

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perfect way of indicating phylogenetic relationships. Cladistic analysis of the family is badly needed in order to provide a clear idea of the evolution of characters and to test the implicit phylogenetic hypotheses that are lodged in the classification scheme. Unfortunately, the information available for the Euphorbiaceae is imperfect and this, along with the size of the group, makes it difficult to proceed. In my discussion of the family at the Berlin congress in 1987 (unpublished), I provided some informally constructed "family trees" that reflected evolution of characters and used these as the basis for a schematic model of the evolutionary and biogeographic history of the subfamilies and tribes. The present essay is intended to set forth this model in greater detail, in the hope that it will suggest topics for discussion and criticism. In doing so, I emphasize that, while our classification system is a descendant of the system of Jean Mueller in 1866, my scenario for the evolution and biogeography of the Euphorbiaceae is indebted to the perspicacious essay of Bentham (1878), who from extremely imperfect data deduced a model that has proved to be almost clairvoyant in its anticipation of later work on the biogeography of major angiosperm taxa.

RELATIONSHIPS BETWEEN THE SUBFAMILIES

Since the perceptive discussion of Bentham (1878), it has been accepted by later workers (e.g., Pax, 1924), that the subfamily Phyllanthoideae is the primitive group from which other subfamilies are derived. Within the Phyllanthoideae, genera within the tribe Wielandieae, such as *Heywoodia* and *Savia*, appear to represent relicts of the original euphorbiaceous complex that arose probably in the late Cretaceous. These primitive Euphorbiaceae are dioecious shrubs or small trees of seasonal forest habitats in tropical latitudes. They have, as expected, relatively unspecialized flowers with well-developed petals, floral disk, and a pistillode in the staminate flower. The pistillate flower usually has a 3-locular ovary, with two anatropous ovules beneath an obturator. The fruit is a 3-celled capsule, and the seeds have a dry testa, copious endosperm, and a large embryo with a radicle much shorter than the cotyledons. As far as the evidence goes, the chromosome base number is $n = 13$ in these "archaic" taxa of subfamily Phyllanthoideae. Anatomically, the relict Phyllanthoideae have such unspecialized features as vessel elements with scalariform perforation plates, paracytic stomata, and unicellular nonglandular trichomes. Laticifers appear to be absent. If Geranialean families such as

Ixonanthaceae are accepted as possible "out-groups," as speculated earlier (Webster, 1967), then it is feasible to compile a list of characters in the Euphorbiaceae for which plesiomorphic (primitive) and apomorphic (advanced) states are defined (Table 1).

An important contribution to identifying significant synapomorphies in subfamily Phyllanthoideae has been made by Levin (1986c) in his cladistic analysis of the subfamily based on foliar characters. Pollen studies on the subfamily, mostly still unpublished (Punt, 1987) or in this symposium (Levin & Simpson, 1994a, b; Nowicke, 1994), show great promise of adding important information for constructing phyletic models. The really major lacuna in our knowledge, for this and other subfamilies, is in biochemical data. Although Hegnauer (1962–1973) and Gibbs (1974) have compiled informative resumes of reports from the biochemical literature, this information is frustrating to the systematist, because it demonstrates a great biochemical diversity in the Euphorbiaceae but at the same time reveals a meager and erratic level of sampling. As a consequence, biochemical data are still of limited usefulness for meaningful comparisons at the tribal and subfamilial levels.

In my 1987 review of the classification of the family, the Euphorbiaceae were implicitly treated as a monophyletic group by the inclusion of such proposed segregate families as Bischofiaceae and Hymenocardiaceae. However, for those interested in relationships within and outside the Euphorbiaceae, it should be noted that this delimitation of the family is not accepted by all of my colleagues. Hymenocardiaceae are accepted as a family by Léonard & Mosango (1985) and by Radcliffe-Smith (1987). Furthermore, Radcliffe-Smith accepts Pandaceae and retains three genera (*Antidesma*, *Bischofia*, and *Uapaca*) only provisionally within the Euphorbiaceae. Jensen (1994) suggests that on the basis of serological data there appear to be two main groups of Euphorbiaceae: Phyllanthoideae + Oldfieldioideae; and Acalyphoideae + Crotonoideae + Euphorbioideae. This binary arrangement of "bioovulate" and "unioovulate" taxa parallels the arrangement proposed by Mahlberg (1987) on the basis of laticifer morphology. On a phenetic basis, this basic dichotomy appears intuitively reasonable, but it remains to be seen whether it will be substantiated by critical phylogenetic studies.

Meeuse (1990) went much further and proposed recognizing nine families, with Euphorbiaceae being restricted mainly to the "unioovulate" subfamilies Acalyphoideae, Crotonoideae, and Euphorbioideae. There is not sufficient space here to analyze

TABLE 1. List of primitive (plesiomorphic) and derived (apomorphic) characters in the Euphorbiaceae.

Character	Primitive state	Derived state
1. Habit	Trees/shrubs	Herbs/vines
2. Branching	Monopodial	Sympodial
3. Phyllotaxy	Alternate	Opposite
4. Leaf shape	Simple	Lobed; compound
5. Leaf venation	Pinnate	Palmate
6. Stipules	Present	Absent
7. Vessel perforation	Scalariform	Simple
8. Vascular rays	Multiseriate	Uniseriate
9. Internal phloem	Absent	Present
10. Laticifers	Absent	Present
11. Trichomes	Simple	Stellate; lepidote
12. Foliar glands	Absent	Present
13. Inflorescence	Axillary	Terminal
14. Calyx aestivation	Imbricate	Valvate; reduplicate
15. Petals	Present; free	Absent; connate
16. Disk	Present	Absent
17. Stamen number	5-10	1-4; over 10
18. Filaments	Free	Connate
19. Anther dehiscence	Longitudinal (vertical)	Horizontal
20. Pollen nuclei	2-nucleate	3-nucleate
21. Pollen exine	Semitectate	Tectate; intectate
22. Pollen apertures	Colpi	Pores; inaperturate
23. Aperture number	3	4 or more
24. Pistillode	Present	Absent
25. Carpel number	3-5	1-2; 6 or more
26. Style branches	Bifid	Unlobed; multifid
27. Style union	Free	Connate
28. Ovule number	2/locule	1/locule
29. Ovule configuration	Anatropous	Hemitropous
30. Embryo sac	Monosporic	Disporic; tetrasporic
31. Fruit	Dehiscent	Indehiscent
32. Seeds	Ecarunculate	Carunculate
33. Seed testa	Dry	Fleshy
34. Endosperm	Present	Scanty or absent
35. Cotyledon/radicle length	2+	Less than 2
36. Cotyledon/radicle width	2+	Less than 2

his provocative arguments, but I believe that he has overemphasized the seed-coat data of Corner (1976) and that the case for fragmentation of the family remains unpersuasive. Clearly, though, the monophyly of the Euphorbiaceae as a whole, and of the individual subfamilies, needs to be more convincingly demonstrated in the course of any detailed analysis of the infrafamilial taxa.

REVIEW OF SYSTEMATIC CRITERIA

At present, the overwhelming preponderance of the data available for interpreting the patterns of phylogeny within the Euphorbiaceae comes from gross vegetative and floral morphological characters that have been used as diagnostic taxonomic features. In evaluating relationships within individ-

ual tribes or subfamilies, particular morphological characters have proven to be especially useful. So far only pollen morphology has provided micro-morphological characters that are useful in determining systematic affinities in all five subfamilies, as shown by the works of Erdtman (1952) and Punt (1962, 1987). However, the studies of Levin (1986a, b, c) demonstrate that foliar venation provides systematically valuable characters in subfamily Phyllanthoideae, and this may prove to be true for other characters as well. The survey of chromosome numbers by Hans (1973) indicates that these may well yield clues to defining lines of systematic affinity, but at present the available data are frustratingly incomplete. Biochemical data from comparative studies of secondary compounds such as alkaloids and terpenes can hardly fail to produce

results of great interest, especially at the tribal and generic levels, but at present we have only tantalizing scraps of data from scarcely more than a handful of genera.

In all of the classifications of the Euphorbiaceae proposed before 1975, the major criteria were drawn from details of gross morphology observable with the naked eye or a dissecting lens. Even after demonstrating the systematic importance of pollen characters by Erdtman (1952), the systems of Hurusawa (1954), Hutchinson (1969), and Airy Shaw (1972, 1975) still depended almost entirely on the same data sets available to Baillon, Mueller, Benthams, and Pax. In order to expedite future work on classification of the family, it seems appropriate in this essay to review the characters that show promise in interpreting evolutionary trends and lines of affinity. Ecological characters are not discussed, except for those relating to pollination and dispersal with a possibly significant effect on the evolution of reproductive structures.

A. GROWTH FORM

The Euphorbiaceae display an extraordinary range of growth forms, perhaps equaling or surpassing any other angiosperm family (Hallé, 1971). Trees and shrubs predominate, as one would expect of a primarily tropical family, but herbs have evolved independently in all five subfamilies. The greatest diversity of growth form is seen in the genera *Phyllanthus* (Webster, 1956) and *Euphorbia* (Croizat, 1972; Cremers, 1977), which show a wide range of adaptations to relatively mesic and xeric habitats, respectively.

In recent years the architecture of tropical trees has been studied on a comparative basis, so that for the first time the bewildering diversity of form in tropical taxa can be comprehended through the scheme of about two dozen basic models proposed by Hallé and coworkers (Hallé & Oldeman, 1970; Hallé et al., 1978). Determination of the membership of a particular taxon in the Hallé/Oldeman model system is difficult and sometimes impossible from examination of herbarium specimens; observations of the germination and ramification of seedlings or saplings may be required. Despite the considerable number of Euphorbiaceae that have been studied, the sampling of taxa in the subfamilies and tribes is still incomplete. However, further studies may provide important insights into the phylogeny of suprageneric taxa.

At the present time, no less than 17 models have been reported for the woody Euphorbiaceae; and a significant number of herbaceous, scandent, and

succulent Euphorbiaceae show additional variations that cannot be easily assigned to any of the Hallé models. All of the subfamilies except for the Oldfieldioideae show more or less comparable diversity, and there appear to be differences between some of the subfamilies that may be phylogenetically significant.

In subfamily Phyllanthoideae branching patterns tend to be monopodial and inflorescences axillary; the prevalent unspecialized patterns are those shown by the models of Attims, Aubreville, and Rauh. A striking tendency is that toward monopodial plagiotropic branching (Roux's model) as in *Flueggea*, *Phyllanthus* (input), and *Drypetes*. A further specialization of this pattern yields the deciduous, floriferous phyllomorphic branchlets (Cook's model) found in several genera of tribe Phyllantheae subtribe Flueggeinae, including *Breynia*, *Glochidion*, *Phyllanthus*, and *Sauropus*. This highly specialized growth form, first documented by Dingler (1885) and designated as "phyllanthoid branching" by Webster (1956), has been thoroughly analyzed by Roux (1968), Bancilhon (1971), and Rossignol & Rossignol (1985).

The subfamily Oldfieldioideae resembles the Phyllanthoideae in having relatively unspecialized monopodial branching patterns that agree with the models of Attims and Rauh. However, *Stachystemon polyandrus* (F. Muell.) Benth., and perhaps a few other taxa, appear to fit the model of Koriba, in which extension of the main axis is interrupted by a terminal inflorescence, leading to sympodial growth. In the three uniovulate subfamilies, determinate/sympodial growth patterns predominate. Among the Acalyphoideae studied, about half (20 genera) show the unspecialized patterns of Attims and Rauh, but a number of genera follow the models of Koriba and Leeuwenberg, in which the main axis is terminated by an inflorescence and branching is more or less dichasial in nature. In the Crotonoideae, the model of Koriba seems to be the most common, and that of Rauh is about as prevalent as that of Attims. Finally, in the Euphorbioideae, which are possibly the latest subfamily to evolve, the branching patterns are more specialized. Only six out of 32 genera show the patterns of Attims and Rauh, as compared to 15 for the models of Koriba and Leeuwenberg. Furthermore, the models of Prévost and Nozeran, almost or entirely absent in the other subfamilies, are well represented with nine genera. Even though these figures are influenced by the large number of models found in *Euphorbia*, the divergence of the subfamily Euphorbioideae in growth pattern is clear.

The vegetative and reproductive morphology of

Euphorbia has received a great deal of attention, and a striking sequence of modifications of growth form can be traced within the tribe Euphorbieae. It is particularly notable that the branching pattern of *Anthostema* is referred to the model of Nozeran by Hallé & Oldeman (1970); the ramification in that genus recapitulates the origin of the cyathium from a concrescent verticel of floriferous branches, with the abortive axis surmounted by a pistillate flower. Nozeran (1953) had appropriately applied the term "pre-cyathium" to the bisexual spikes of Hippomaneae such as *Sapium* or *Stillingia*. A whorl of four or five of these "spikes" (which are really thyrses) produced on a plant growing according to the model of Nozeran could indeed have given rise to the primitive cyathium, although there are still problems—in the absence of any living "missing link"—in specifying how the lateral and basal flower in the Hippomanean thyrse becomes the terminal flower in the cyathium (see Gilbert, 1994).

One can argue that the ultimate point in vegetative evolution in the Euphorbiaceae is attained in *Chamaesyce*, where the seedling axis is usually abortive above the cotyledons and the axial portion of the plant is virtually all sympodial. In the abortion of the main axis, the pattern suggests the model of Nozeran, but the subsequent dichasial pattern is a two-dimensional plagiotropic variant of the model of Leeuwenberg. Hurusawa (1954) has claimed that the conformation of axes in *Chamaesyce* represents the terminus of a reduction series beginning in *Euphorbia* subgenus *Esula* and progressing through subgenus *Agaloma* by retardation of the main axis relative to the lateral anthocladia. However, in a recent study, Hayden (1988) showed that the lateral branches in *Chamaesyce* arise at the cotyledonary nodes, and that the apparent homology with the terminal pleiochasial whorl in *Euphorbia* is doubtful.

The adaptive significance of the growth forms in the Euphorbiaceae is not as clear as their utility as systematic characters (a common situation in many angiosperm taxa). Part of the difficulty is that the changes in some ramification patterns are due to simple shifts in relative rates of meristematic activity, so that reversals of trends and convergences appear common indeed. A striking instance of this, for example, is shown by the distribution of Troll's model in the Euphorbiaceae: in the Phyllanthoideae, it is found in woody taxa of *Briedelia* and herbaceous *Phyllanthus*, where it appears derived from Attims's model; but in the Euphorbioideae, it seems to have evolved in *Pedilanthus* via Attims's model and in *Actinostemon* via Prévost's

model. Cremers (1977) demonstrated 10 different models in Madagascan *Euphorbia*, and there appear to be some species that do not fit any model. Even worse, species such as *Euphorbia stenoclada* Baillon and *E. abyssinica* Gmel., which conform to the models of Attims and Rauh, have surely been derived from ancestral taxa with the more "specialized" models of Prévost and Nozeran.

It is understandable that correlations between architectural models and ecological conditions are imperfect and often obscure, in view of the fact that the vegetative growth patterns interact with reproductive adaptations in a complicated fashion. Certain models, such as Cook's and Nozeran's, clearly predominate in rainforest habitats; but others, such as Attims's, are found in both rainforests and deserts. Evidently the Euphorbiaceae have entered such a wide variety of habitats during their radiation that no simple correlations can be expected. Nevertheless, the coevolution of branching patterns and reproductive structures in some taxa of Euphorbiaceae is sufficiently striking that more attention needs to be given to field observation of the architectural models.

B. ANATOMY

Anatomical characters have been regarded as important in the classification of the Euphorbiaceae since the essay of Pax (1884), which first established the importance of laticifers as a character for defining natural groups. Pax used laticifer type (articulated vs. nonarticulated), phloem characters, and trichome type as the major anatomical characters to support his redivision of the major suprageneric taxa. These studies were considerably extended in the following decade by Radlkofer and his students. Radlkofer (1870) emphasized anatomical characters in a paper establishing the new euphorbiaceous genus *Pausandra*; and a series of his students surveyed most of the family anatomically (Rittershausen, 1892; Froembling, 1896; Rothauscher, 1896; Herbert, 1897). The first really critical anatomical survey of the family was provided by Solereder (1899), who reviewed the contributions of Radlkofer's group and added many observations of his own. Gaucher (1902) published an independent anatomical survey of the family that curiously omits all mention of the works of the German school. He was criticized for this by Solereder (1908), who also pointed out mistakes in his observations. However, Gaucher's study did have the merit of providing a comparative review of anatomical characters arranged by tribe.

Anatomical studies of wood by Pax and others,

up to the turn of the century, seem mainly to have been made on twig material. The first important contribution based on studies of mature wood from tree trunks appears to be that of Janssonius (1929, 1930), based largely on Indonesian taxa. Janssonius pointed out the divergent wood structure of *Daphniphyllum* as an indication of its lack of relationship to the Euphorbiaceae. The most interesting of his findings was his designation of a group of genera of subfamily Phyllanthoideae (*Aporosa*, *Baccaurea*, *Drypetes*, and *Putranjiva*) as characterized by thick-walled nonseptate fibers, abundant metatracheal parenchyma, and scalariform vessel perforations. Bamber (1974) amplified the work on fiber morphology by showing that thick-walled fibers ("type II") also occur in genera of subfamily Oldfieldioideae (*Dissiliaria* and *Petalostigma*). Mennega (1987) expanded the survey and showed the presence of type II fibers in a number of additional genera of Phyllanthoideae and Oldfieldioideae. Hayden (1980) reviewed the wood anatomy of subfamily Oldfieldioideae as part of a comprehensive anatomical survey.

Metcalf & Chalk (1950), in the most recent comprehensive anatomical review of the entire family, created some anatomical groups that partly correspond to accepted subfamilial and tribal concepts but in a number of respects are contradictory. Their "Group A" of the Phyllanthoideae includes the genera with the syndrome of characters first identified by Janssonius: thick-walled (Bamber "type II") fibers, abundant parenchyma, and scalariform vessel perforations. It appears that "Group A" taxa such as tribes Wielandieae and Antidesmeae may indeed have the most anatomically primitive characters in the Euphorbiaceae. However, there are also some outstanding discrepancies between the arrangement of Metcalf & Chalk and the classification accepted currently. The most notable is the position of *Acalypha*, which is grouped by them (and Janssonius) with the Phyllanthoideae; but this disposition is contradicted by so much other evidence that the resemblances of *Acalypha* to the Phyllanthoideae must be due entirely to convergence. The studies of Mennega (1987) on wood anatomy in the Phyllanthoideae in general supported the relationships in the classification of Webster (1975), although some discrepancies remain.

Although Pax (1884) placed great emphasis on laticifer type in defining the major infrafamilial subdivisions, the use of laticifers to address problems at higher ranks was subsequently neglected despite the plea by Solereder (1908) for new developmental and comparative studies of laticifers. Dehgan & Craig (1978) reported a variety of la-

ticifers in the single genus *Jatropha*: single-celled idioblasts, coenocytic laticifers without cross-walls, and classic "articulated" laticifers. Their results in some respects contradict the findings of Rao & Malaviya (1964). Mahlberg (1975, Mahlberg et al., 1987), in a series of studies showed the systematic importance of laticifers in *Euphorbia*, particularly with respect to the type of starch grains produced. Only recently, however, has Rudall (1987) provided the first modern survey of laticifer types within the family and amply demonstrated the importance of laticifers in evaluating relationships. Rudall's survey indicates that articulated laticifers are confined to subfamily Crotonoideae and nonarticulated ones to the Crotonoideae and Euphorbioideae, except for a few reports (needing confirmation) of nonarticulated laticifers in the Acalyphoideae. Mahlberg et al. (1987) interpreted this laticifer data radically by proposing a subdivision of the Euphorbiaceae into three families based on the groups Phyllanthoideae, Acalyphineae, and Hippomanoineae of Pax (1884). Clearly there is still an urgent need for more intensive sampling of tribes in the uniovulate Euphorbiaceae for morphological and anatomical data.

Another important source of systematic data is furnished by trichomes. Mueller (1866) was the first to emphasize trichomes as a major character in his revision of the family. Froembling (1896) reviewed the trichome types in the Crotonoideae, which show the greatest diversity among the subfamilies. The subsequent neglect of trichome characters in the Euphorbiaceae is indicated by the fact that the last detailed systematic review is that of Solereder (1899). Inamdar & Gangadhara (1977) presented a survey of euphorbiaceous trichomes, but their sample of only 53 species was too limited to be systematically meaningful. A more comprehensive sample of 250 species by Rao & Raju (1985) provided a succinct review of the systematic distribution of trichome types. Most of the trichome variation of systematic interest is found in subfamilies Acalyphoideae and Crotonoideae, where various kinds of malpighiaceous, stellate, and lepidote types occur; in the other three subfamilies simple unicellular or multicellular hairs overwhelmingly predominate.

The most unusual trichomes found in the Euphorbiaceae are stinging hairs, which have evolved independently in the Acalyphoideae and Crotonoideae. The hairs in *Cnidioscolus* (Crotonoideae-Manihoteae) are of the common *Urtica* type, with a deciduous bulbous tip (Thurston & Lersten, 1969). Breckon (1975) has described considerable variation in morphology of the stinging hairs in Mex-

ican species of *Cnidocolus*. Within the Acalyphoideae, stinging hairs of a fundamentally different type are known from the tribe Plukenetieae. These were carefully described by Knoll (1905) as composed of a central crystaliferous cell of subepidermal origin surrounded by a jacket of three epidermal cells; Knoll's interpretation of these trichomes has been confirmed by the ultrastructural studies of Thurston (1976). The common possession of this unique type of trichome (along with other characters such as columnar compound styles) provides a powerful argument for assigning *Dalechampia*, which has been previously kept in a separate tribe, to the Plukenetieae.

The Euphorbiaceae are also impressively rich in foliar glands, which appear to have arisen de novo within the family, as they are absent in the Wielandiaeae and other apparently archaic taxa in the Phyllanthoideae. In both the Phyllanthoideae and Oldfieldioideae, foliar glands are restricted in occurrence, but they are very common in the uniovulate subfamilies. Diffuse pellucid-punctate glands have been reported in the unrelated genera *Clutia* (Acalyphoideae) and *Suregada* (Crotonoideae). Discrete embedded laminar glands are widespread, occurring in many Acalyphoideae (e.g., in Acalypheae, Alchorneae, Bernardieae, Chrozophoreae, Omphaleae, and Plukenetieae). In the Crotonoideae, glands most often occur at the junction of lamina and petiole (e.g., in Crotonaeae, Manihoteae, Micrandreae). In *Jatropha* (Dehgan & Webster, 1979), and many other Crotonoideae and Acalyphoideae, glands are very diverse; glands on leaf margins often appear to intergrade with petiolar glands.

Bernhard (1966), in a survey of the morphology and anatomy of euphorbiaceous foliar glands, has suggested that the marginal glandular teeth in many Euphorbiaceae may be of a separate origin from the laminar or petiolar glands. Belin-Depoux & Clair-Maczulajtys (1974, 1975) elucidated the anatomical structure of petiolar glands of *Aleurites* with light microscopy and TEM, and Belin-Depoux (1977) showed that the foliar glands of *Alchornea cordata* Benth. (Acalyphoideae) are fundamentally similar to those of *Aleurites* (Crotonoideae).

Stomatal development within the Euphorbiaceae shows considerable variation, as indicated by Raju & Rao (1977). They found an overwhelming predominance of paracytic stomata in the woody taxa of most of the 17 tribes sampled, with anisocytic stomata becoming prominent mainly in herbaceous Phyllanthoideae (as indicated earlier for *Phyllanthus* by Webster, 1956). The most aberrant situation reported by Raju & Rao is the high per-

centage of anomocytic stomata in *Chamaesyce* (Raju & Rao, 1987). Not unexpectedly, Kakkar & Paliwal (1974) found a considerable diversity of stomatal types in *Euphorbia*. Dehgan (1980) found that the two subgenera of *Jatropha* can be distinguished by stomatal type and also surface of hairs (smooth versus verruculose).

Foliar venation, a neglected character, has only recently been used by Levin (1986a, b, c) to provide new insights into relationships within subfamily Phyllanthoideae. Similar studies on the other subfamilies would no doubt be illuminating. So far, almost all of the work in other subfamilies has been done on tribe Euphorbieae (Sehgal & Paliwal, 1974). The characteristic jacketed venation in *Chamaesyce* has attracted interest because of its correlation with C₄ photosynthesis (Webster et al., 1975).

Although the vast majority of Phyllanthoideae and Euphorbioideae have simple entire leaves, the Acalyphoideae and Crotonoideae have predominately toothed or lobed leaves. Hickey & Wolfe (1975) have designated the Euphorbiaceae as having a "Dilleniid" leaf type on the basis of actinodromous venation and "Violoid" marginal teeth, in which the medial vein expands into a glandular termination without a deciduous apical seta. However, in the most primitive Phyllanthoideae the leaves are entire and campitodromous, so the "Violoid" teeth would appear to have arisen de novo within the family. Furthermore, the foliar teeth in Euphorbiaceae are variable; for example, deciduous setae occur in the Hippomaneae, which would make them "Theoid" instead of "Violoid." A survey of foliar venation and tooth types in the Acalyphoideae and Crotonoideae will be necessary to verify the claim by Hickey & Wolfe that the leaves of Euphorbiaceae betray a "Dilleniid" instead of "Rosid" affinity.

Vascular anatomy of petioles has been studied from cross sections by Dehay (1935), who showed considerable variation in stelar configurations. However, Dehay did not attempt to untangle variation correlated with leaf size from that due to systematic affinity, and it seems unlikely that this character will prove to be of general utility. However, on a more restricted level, Miller & Webster (1962) used differences in petiolar steles to separate *Cnidocolus* from *Jatropha*, and Dehgan (1982) found that different degrees of petiolar stelar dissection were significant at the sectional and subsectional level in *Jatropha*.

A significant foliar structure in many Euphorbiaceae are the stipules inserted at the base of the petiole (Uhlarz, 1978). In many of the Phyllan-

thoideae and occasional genera (e.g., *Manihot*) elsewhere, the stipules are early deciduous (caducous), even if they are rather large. Phyllanthoid stipules are entire, but in the Acalyphoideae and Crotonoideae they can become lobed, dissected, or glandular. In a considerable number of taxa, stipules have become reduced or even entirely suppressed. Sometimes one or a few species in a genus (e.g., *Hyeronima alchorneoides* F. Allemão) have stipules, whereas they are absent in related species. Many species of *Croton* lack stipules, whereas they are large and conspicuous in others. Most notably, in *Euphorbia* presence or absence of stipules is a diagnostic character for some sections and subgenera. Although stipules presumably play some adaptive role in protecting stem apices and leaf primordia, no convincing explanation has been given for their presence or absence in closely related taxa.

C. INFLORESCENCES AND FLOWERS

Since Euphorbiaceae have unisexual flowers that are often reduced, grouping of flowers into inflorescences is often important for pollination, and inflorescence structure is an important systematic character in many instances. Monoecious and dioecious flower production are widespread, with monoecious perhaps somewhat more common. It seems likely that dioecy is primitive in the family, judging from sexual dispositions in "basal" taxa (e.g., Wielandiaeae) in the subfamily Phyllanthoideae. However, this seems to have been readily reversible, since monoecious taxa appear to have given rise to dioecious ones in *Croton*, *Euphorbia*, *Phyllanthus*, and other genera. Inflorescences as a whole are proterogynous, although within some genera (e.g., *Euphorbia*) transitions can be found from proterogyny to proterandry. Pollination of Euphorbiaceae is mainly entomophilous, but wind pollination has evolved independently in all of the subfamilies (except in the Euphorbioideae, where anemophily may be absent): *Hymenocardia* (Phyllanthoideae); *Picrodendron* (Oldfieldioideae); *Acalypha* and a considerable number of other genera (Acalyphoideae); and *Borneodendron* and *Eremocarpus* (Crotonoideae). Wind-pollinated taxa usually have spicate inflorescences, but so do many entomophilous taxa.

It seems apparent that inflorescence structure in the Euphorbiaceae is fundamentally dichasial. This is most strikingly evident in genera of Crotonoideae such as *Cnidioscolus* and *Jatropha*, which have elaborate compound dichasia. However, in the Phyllanthoideae, it can usually be seen that

the flowers in axillary clusters are produced cymosely. The thyrses, often mistakenly described as a spike, is very common in all five subfamilies. In subfamily Euphorbioideae there is a striking reduction series from the diffuse "paniculate" inflorescences of *Senefeldera* through the thyrses of Hippomaneae such as *Sapium* or *Stillingia* to the pseudanthia (cyathia) of the Euphorbieae. Examples of pseudanthia or "subpseudanthia" can be found in isolated genera in most of the subfamilies: Phyllanthoideae (*Uapaca*), Oldfieldioideae (*Pseudanthus*), Acalyphoideae (*Dalechampia*, *Pera*), and Euphorbioideae (tribe Euphorbieae). In the tribe Euphorbieae there has been the greatest "radiation" of pseudanthial structure, with several cyathial genera apparently evolved from a common ancestor.

Floral form in the Euphorbiaceae shows tremendous diversity, partly as a consequence of independent evolution of staminate and pistillate flowers and partly as the result of adaptation to a variety of vectors (wind, bees, flies, butterflies, birds, and mammals). A masterly illustrated survey of floral gross morphology, with emphasis on ontogeny, was made by Baillon (1858), the most perceptive morphologist of the 19th-century specialists on the family. Since Baillon's work there has been only one other comprehensive survey, that of Michaelis (1924). However, Venkata Rao more recently (1971, 1972) studied vascular anatomy of a considerable number of genera and attempted to relate his findings to the phylogeny of the family. Unfortunately, he sometimes generalized excessively from single instances, as when he suggested that the flowers of *Jatropha* are the most primitive in the family because they are often hermaphroditic; this is contradicted by the specialized pollen grains and secretory apparatus in that genus.

Venkata Rao pointed out a number of trends in floral morphology within the Euphorbiaceae, the most obvious being that of reduction in size and number of parts. Reduction is sometimes correlated with shift to wind pollination, as in tribe Acalyphaeae; but in other instances (Phyllanthaeae, Euphorbieae) it clearly is not. As noted by Venkata Rao, there are also trends to increase the number of floral parts; here again, there is no correlation with anemophily, since the highest numbers of stamens, for example, occur in *Croton* (entomophilous) and *Ricinus* (anemophilous). A particularly evident reduction tendency is loss of the corolla, which is so prevalent that Euphorbiaceae are often placed in "apetalous" groups. This affects both sexes but is most striking for the pistillate flowers; petaliferous staminate flowers and apetalous pistil-

late flowers occur in most species of *Croton* and in other Crotonoideae, as well as many Acalyphoideae (e.g., Agrostistachydeae, Chrozophoreae). Two subfamilies, Oldfieldioideae (except *Croizatia*) and Euphorbioideae, are apetalous in both sexes. In the presumably wind-pollinated oldfieldioid genera *Androstachys* and *Stachyandra*, the staminate flowers have a chaotic organization of tepals and stamens that led Leroy (1976) to propose a curious theory suggesting that the staminate flowers in these genera are modified inflorescences.

The calyx in Euphorbiaceae varies greatly in configuration and number of parts. Where the corolla is absent, petaloid calyces may occur, as in *Cnidocolus* and *Manihot*. Croizat (1943) suggested that the perianth of *Cnidocolus* is corolline and that the calyx had been lost; however, the evidence from vascular traces in *Manihot* contradicts this idea (Venkata Rao & Ramalakshmi, 1968; Venkata Rao, 1971). In past systems of classification of the Euphorbiaceae, great stress has been placed on aestivation of the calyx (whether imbricate or valvate), a practice initiated by Mueller (1866). Although Baillon (1873) rightly objected to the excessive weight accorded the character by Mueller, it was still extensively used by Pax (1890) and Pax & Hoffmann (1931). Comparison of the aestivation character with evidence from other characters (wood anatomy, trichomes, and pollen) strongly suggests that it must be used with caution.

The euphorbiaceous corolla, where present, is variable in size and color; large showy red or white flowers occur mainly in the Crotonoideae (e.g., in *Aleurites*, *Jatropha*). The petals are usually distinct, but may be coherent or connate in some Crotonoideae such as *Jatropha* (Dehgan & Webster, 1979) and some Aleuritideae (Léonard, 1962). Venkata Rao & Ramalakshmi (1968) reported that vascularization of petals (with three bundles) is usually similar to that of the sepals, although it may be obsolete in the reduced petals of *Codiaeum* and *Croton*.

The floral disk (nectary) is a conspicuous feature of many euphorbiaceous flowers. Baillon (1858) regarded it as receptacular in nature and was followed in this interpretation by most later workers (e.g., Bentham, 1880; Pax & Hoffmann, 1931). On the other hand, Michaelis (1924) proposed that the disk is of staminodial origin, partly because of the apparent obdiplostemony in flowers of taxa such as *Jatropha*, and partly because of the staminodelike appearance of disk-segments in various genera such as *Chiropetalum*, *Clutia*, and *Poranthera*. However, Venkata Rao & Ramalakshmi

(1968) have shown that the vascularization of the disk is highly variable; and Webster (1956) found that in *Phyllanthus* the degree of vascularization seems to be correlated with mass; small disk-segments are usually nonvascularized. The preponderance of evidence seems to be against the view of Michaelis and in favor of the classical concept of Eichler (1875) that the floral disk is of receptacular nature and not an independent whorl of the flower.

The euphorbiaceous androecium displays a protean diversity that has provided many characters used by Mueller (1866) and later workers to diagnose subtribes, genera, and infrageneric taxa. Michaelis (1924) hypothesized that the primitive condition in the family was an androecium of an indefinite number of stamens in many whorls. Venkata Rao & Ramalakshmi (1968), in contrast, suggested that the primitive condition is 10 stamens in two whorls, as in *Jatropha*. However, on the basis of the prevalent condition in the Wielandiaeae and associated tribes of the Phyllanthoideae, I think that an androecium of a single whorl of five or six stamens is most likely to be ancestral within the family. Mueller (1866), in defining subtribes, placed great emphasis on the insertion of the stamens; in practice, this usually depended on whether they were inserted around a pistillode or disk. However, in some groups such as the Drypeteae it is difficult to distinguish a pistillode from a confluent central disk; and in Crotonoideae such as *Cnidocolus* or *Jatropha*, it is not easy to tell whether the slender projections at the top of the staminal column represent staminodes or a pistillode.

Mueller was sharply criticized by Baillon (1873) for placing undue emphasis on anther form and dehiscence as generic characters. Because of transitional situations, distinctions between extrorse and introrse dehiscence are sometimes difficult to verify. There are all degrees of shift of the plane of anther dehiscence, not only between extrorse and introrse but between basifixed/versatile and longitudinal/horizontal. The most bizarre specializations are found in the Acalyphaeae (subtribe Lasio-coccinae), where the filaments of the stamens are united into branching fascicles and the number of anthers proliferated, reaching the extreme degree of elaboration in *Ricinus*. Although there has been much profitless spilling of ink in speculations about the androecium of *Ricinus*, it tells us nothing about the role of telomes in the angiosperm flower, as pointed out by van der Pijl (1952). Venkata Rao & Ramalakshmi (1968) made the fantastic suggestion that the branched stamen complex of *Ricinus* is primitive and that conventional ditheous

anthers are derived by reduction; abnormal super-numerarily lobed anthers in *Jatropha curcas* L. are supposed to represent an intermediate condition. In fact, the derivation of the androecium of *Ricinus* is clearly suggested by comparison with the related genus *Adriana*, which has a large number of completely separate stamens. Although more careful morphological study is needed, it appears that Airy Shaw (1980) may have been correct in suggesting that the fascicled stamens in *Homonioia* and *Lasiococcus* were derived independently from those in *Ricinus*.

Pollen grains of the Euphorbiaceae are produced in tetrads by simultaneous cytokinesis, as in most dicots (Davis, 1966), and are always monads at maturity. At anthesis the pollen grains may be either binucleate or trinucleate. Webster & Rupert (1973) showed that the nuclear condition of pollen is a significant taxonomic character in defining major phyletic lines in the family: the Phyllanthoideae, Oldfieldioideae, and Acalyphoideae appear to be entirely binucleate, while in the Crotonoideae and Euphorbioideae both binucleate and trinucleate pollen occur. In a study of the tribe Euphorbieae, Webster, Rupert & Koutnik (1982) showed that trinucleate pollen originated several times and that the distribution of pollen nuclear number is an important criterion in defining subgenera and sections. These observations support the "Schürhoff-Brewbaker Law," which postulates that the shift from binucleate to trinucleate pollen is irreversible.

The morphology of pollen grains in Euphorbiaceae is so diverse that only the Acanthaceae can rival it. Although Mueller (1874) illustrated a considerable number of pollen grains of Brazilian Euphorbiaceae, he made no use of pollen morphology in defining taxa at any level. Pax (1884) dismissed the systematic utility of pollen despite the paper by Radlkofer (1870) emphasizing the pollen characters of *Pausandra*. We owe to Erdtman (1952) the first convincing demonstration that pollen morphology offers decisive clues to systematic relationships within the Euphorbiaceae. Erdtman's suggestion that genera with crotonoid sexine patterns should be associated irrespective of their positions in the system of Pax & Hoffmann (1931) has been supported by Punt (1962) and later workers. Köhler (1965), on the basis of a survey of pollen of the biovulate taxa, was able to make a persuasive argument for recognizing a new subfamily, the Oldfieldioideae. The reclassification of subfamilies and tribes by Webster (1975) was strongly influenced by these light microscopic studies and by unpublished SEM observations (Webster et al., un-

published). The importance of palynological characters is further highlighted by the studies in this issue on Oldfieldioideae, Crotonoideae, and tribe Plukenetieae.

The great pollen diversity in Euphorbiaceae makes it difficult to identify consistent trends. As one might expect, taxa that are presumed to be wind-pollinated share a tendency toward reduction of colpi and sexinous ornamentation, e.g., in *Hymenocardia* (Phyllanthoideae), *Longetia* (Oldfieldioideae), *Acalypha* (Acalyphoideae), and *Borneodendron* (Crotonoideae). However, *Ricinus* is a partial exception; although the sexinous ornamentation is reduced, the grains have very prominent colpi. Within all of the subfamilies except the Euphorbioideae, there is a tendency for multiplication and shortening of apertures that leads to polyporate grains; in the Crotonoideae, the apertures become obsolete. Crotonoid sexinous ornamentation is a unique synapomorphy within subfamily Crotonoideae. Transmission electron microscopy will no doubt provide even more valuable insight into tribal relationships within the subfamilies.

The gynoecium in Euphorbiaceae is almost as diversely modified as the androecium. Although the carpel number is three in the majority of taxa, it is reduced to two in a number of genera and to one in several, including *Antidesma* (in part), *Crotonopsis*, *Drypetes* (in part), and *Jatropha*. On the other hand, it is increased to six or more in species of a number of genera, including *Glochidion*, *Hippomane*, *Hura*, and *Phyllanthus*. It is not even certain that 3-carpellate gynoecia represent the plesiomorphic condition in Euphorbiaceae, since within the Wielandioideae there are genera characterized by four carpels (*Heywoodia*) and five (*Wielandia*). In *Margaritaria* carpel number fluctuates between two and six, and varies from three to six in the single species *M. nobilis* L.f. (Webster, 1979).

Stylar variation is marked and has been used often for specific, generic, and even tribal diagnoses. In the majority of genera the styles are elongated and bifid (often so deeply as to be bipartite); in scattered genera and in the subfamily Euphorbioideae, they are undivided in most genera (but usually bifid in *Euphorbia*). On the other hand, the two style branches may be further subdivided so that each style may have four or eight stigmas, or even more; this is particularly common in *Croton*. Usually the styles are connate, if at all, only at the base, but in the tribe Plukenetieae they are often connate to the tip into a long stylar column which may be modified in bizarre shapes. Finally, in a number of genera (e.g., *Endospermum*, *Glo-*

chidion, *Tetrorchidium*) the styles are reduced to sessile, often petaloid, stigmas. Rather unexpectedly, styler morphology is not clearly correlated with pollination vectors: anemophilous taxa may have either highly dissected styles (*Acalypha*) or undivided entire styles (*Alchornea*).

Ovular characters have been regarded as significant within the Euphorbiaceae since A. Jussieu (1824) originally established the distinction between biovulate and uniovulate taxa as a diagnostic criterion. There is no evidence of reversion from the presumed derived condition, uniovulate, to the biovulate condition. However, it remains unclear whether the transition from gynoecea with biovulate locules to gynoecea with uniovulate locules occurred only once. In other words, we cannot yet be certain that the uniovulate taxa, treated by Pax (1890) as subfamily Crotonoideae, represent a monophyletic group.

As pointed out by Baillon (1858), ovules of Euphorbiaceae are characteristic in their epitropous orientation and the presence of an obturator that fits over the micropyle of one or both ovules and fills the gap between the styler conducting tissue and the nucellus. Within the Phyllanthoideae, some taxa (e.g., *Aporusa*, *Drypetes*) have a single massive obturator, while others (e.g., *An-drachne*, *Phyllanthus*) have tenuous separate obturators. Schweiger (1905) surveyed the variation in ovular form in the Euphorbiaceae and found it to be of considerable importance systematically. In some Phyllanthoideae, especially tribe Phyllantheae, the ovules are distinctly hemitropous, instead of anatropous as in the great majority of genera in the family. Singh (1962) has contrasted the anatropous and hemitropous types and illustrated an unusual variation in *Trevisa*, where the ovule is ventrally adnate to the placenta and lacks a distinct funicle. The ovules of *Croton* and *Trevisa* illustrated by Singh are characteristic of the subfamilies Crotonoideae and Acalyphoideae respectively; in the Crotonoideae the ovule tends to be elongated and has a nucellar beak projecting beyond the micropyle, whereas in the Acalyphoideae the ovule is less elongated with a thickened inner integument and without a projecting nucellus. Ovules in the Euphorbioideae conform to those of the Acalyphoideae.

Considerable embryological work has been done on the Euphorbiaceae (Davis, 1966; Rao, 1970), showing that embryo sac development is of the normal *Polygonum* type in most of the family. Aberrant development has been reported only in the Acalyphoideae and Euphorbioideae: disporic (*Allium*) types occur in *Chrozophora* and *Eu-*

phorbia, and tetrasporic types in *Acalypha*, *Euphorbia*, and *Mallotus*. A characteristic of most euphorbiaceous female gametogenesis is the early disappearance of the antipodals, which in the older literature led to a number of misinterpretations of embryo sac development in genera such as *Phyllanthus* and *Codiaeum* (Maheshwari, 1942). Apomixis is rare in Euphorbiaceae, even though the earliest report of apogamy is from the genus *Coelebogyne* (Smith, 1841); it has been verified mainly in temperate species of *Euphorbia* such as *E. dulcis* L. (Carano, 1926; Cesca, 1961; Kapil, 1961).

D. FRUIT AND SEEDS

The fruit in most Euphorbiaceae is an explosively dehiscent schizocarp, but indehiscent fruits have evolved repeatedly in all of the subfamilies. The schizocarpous fruit appears to be the primitive state, both in the family as a whole and within individual genera. In *Phyllanthus* (Webster, 1956–1958) there is a particularly complete morphological series: typical capsules (most sections) to baccate fruits (sect. *Anisonema*), drupaceous but dehiscent (sect. *Embllica*), and finally drupaceous and indehiscent (sect. *Cicca*). It must be admitted, however, that this linear sequence does not clearly represent morphological transition within a single phyletic line.

Berg (1975a, b) has provided the most thorough description of the development, anatomy, and ecology of the typical euphorbiaceous fruit as represented in the Australian genus *Micrantheum*. Berg related many of the distinctive features of the euphorbiaceous pistillate flower, such as the vascular pattern in the columella, to adaptive aspects of fruit dehiscence and seed dispersal. He regarded the placentation in *Micrantheum* as not typically axile because the three columellar bundles lie on different radii from the dorsal bundles; he thus described the columellar portion of the axis of the ovary as “an internal carpophore congenitally fused with down-hanging lobes from carpels attached to its tip.” However, as shown in the descriptions and illustrations of Venkata Rao & Ramalakshmi (1968), the three basal central strands in the axis each give rise to paired strands that represent the ventrals of the carpel margins; this strongly implies that the placentation in the euphorbiaceous flower is typically axile, and Berg’s ingenious hypothesis is unnecessary.

Another provocative suggestion of Berg is that the primary function of the obturator is not to facilitate passage of the pollen tube but rather to displace the seed lower into the coccus for more

effective seed dispersal. Against this view may be cited the great variation in obturator dimensions within the capsular-fruited taxa (although it is possible that size variation could be correlated with differential growth of the ovary overall).

Euphorbiaceous seeds show variation in size, shape, seed-coat ornamentation and anatomy, endosperm development, and configuration of the embryo; seed characters are taxonomically important, especially at specific and generic levels. In the biovulate taxa, there are typically two seeds per locule, but the number is often reduced to one (e.g., in *Amanoa*, *Meineckia*, and *Savia*). In biovulate taxa with drupaceous fruits, only one or two seeds per fruit may develop (e.g., in *Antidesma*, *Aporusa*, *Baccaurea*, and *Drypetes*). Seed size varies greatly, from less than 1 mm in herbaceous species of *Chamaesyce* or *Phyllanthus* to over 4 cm in *Hevea* and *Omphalea*.

Netolitzky (1926), Wunderlich (1968), and Corner (1976) have shown that the anatomical structure of the seed coat is of considerable importance in relating the Euphorbiaceae to other families, as well as providing clues about infrafamilial relationships. The testa (from the outer integument) persists in the mature seed and sometimes is thickened and fleshy (e.g., in *Baccaurea*, *Mallotus*, *Margaritaria*, *Melanolepis*, *Sapium*, and *Tetrorchidium*). The mechanical layer of the seed is formed from the outer epidermis of the tegmen (inner integument), and Corner reported that it is different in the uniovulate and biovulate taxa. In the Phyllanthoideae, the mechanical cells consist of cuboid (or only slightly radially elongate) sclerotic cells or of tangentially elongated fibers. In contrast, in the uniovulate taxa the mechanical layer is usually formed of radially elongated palisade sclerenchyma ("Malpighian") cells. On the basis of this difference in seed structure, Corner referred the uniovulate taxa (Crotonoideae sensu Pax) to a Malvacean affinity and the Phyllanthoideae to a Celastracean affinity, but frankly admitted that the picture is not crystal-clear.

In my opinion, the primitive condition in the family would seem to be the fibrous exotegmen as found in Phyllanthoideae such as *Andrachne*, *Antidesma*, *Aporusa*, *Baccaurea*, and *Briedelia*. The palisade cells in *Glochidion* seem to be derived from the shortened fibers found in *Breynia*, *Flueggea*, and *Phyllanthus*; but contrary to Corner's interpretation, the condition in *Glochidion* does not seem to be transitional to that found in the uniovulate taxa. Instead, the tegmen with cuboidal mechanical cells of *Drypetes* may be closer to the main line of specialization. Although the uniovulate

subfamilies differ from the Phyllanthoideae in sometimes having tegmic vascular bundles, this character is inconsistent: Corner's groups 1 and 3 contain representatives of all three uniovulate subfamilies, and group 2 contains both Acalyphoideae and Crotonoideae. Nevertheless, it is quite possible that this character is phylogenetically significant. Most of the genera with tegmic vasculature belong to the Crotonoideae, and *Gelonium*, with a "tegmic pachychalaza," may be closest to the ancestral condition.

Although the caruncle is by no means a ubiquitous feature of the euphorbiaceous seed—Baillon (1873) censured Mueller for using it as a generic character—it still is of considerable taxonomic and evolutionary interest. Bresinsky (1963) and Berg (1975a, b) described the structural and functional features of the caruncles in *Euphorbia* and *Micrantheum*. As Schweiger (1905) demonstrated, the caruncle always arises from the micropylar region (exostome) of the outer integument. In *Euphorbia*, *Micrantheum*, and doubtless the other genera with carunculate seeds, the caruncle functions as an elaiosome to attract ants for dispersal. Berg noted that in *Micrantheum* it may also play a role in the build-up of tension within the developing capsule, leading up to the explosive dehiscence.

Carunculate seeds have been recorded from all of the subfamilies except the Phyllanthoideae (and even in that subfamily there are sometimes micropylar outgrowths that could be regarded as incipient caruncles). However, their distribution within each subfamily is inconsistent; closely related genera may differ in presence or absence of a caruncle, while in various genera (e.g., *Euphorbia*, *Stillingia*) some species have a caruncle and others lack it. Caruncles are invariably lacking on seeds from indehiscent fruits, which accounts for part (but by no means all) of the spottiness in reports of distribution.

A seed character that appears particularly important in the Phyllanthoideae is the presence or absence of endosperm, which develops as the Nuclear type (Rao, 1970). It is copious in most genera, but scanty or absent in relatively primitive genera such as *Actephila*, *Amanoa*, *Spondianthus*, and *Wielandia*. In exalbuminous seeds, the cotyledons are often distinctly folded. Outside the Phyllanthoideae, seeds normally have well-developed endosperm, but there are a few exceptions (e.g., *Elateriospermum* in the Crotonoideae).

Cotyledon characters have been given exceptional weight in the classification of Euphorbiaceae since they were strongly emphasized by Mueller

(1866), who erected his two primary infrafamilial divisions, *Platylobeae* and *Stenolobeae*, on the basis of cotyledon shape. Baillon (1873) rightly objected to this overemphasis on the cotyledon character, and his rejection of Mueller's scheme has been substantiated by the palynological studies of Erdtman (1952), Punt (1962), and Köhler (1965), which clearly demonstrated that the *Stenolobeae* are an artificial group. One can sympathize with Bentham (1880) in his decision to maintain the *Stenolobeae* as a tribe because of the striking correlation between cotyledon shape, ericoid habit, and Australasian distribution. As a matter of fact, it is still not clear why the character of narrow cotyledon shape should be almost confined to Australia, except for the anomalous North American genus *Reverchonia* (Webster & Miller, 1963).

E. CYTOLOGICAL CHARACTERS

Perry (1943) was the first to provide a survey of chromosome numbers for the Euphorbiaceae, but his sample was very small, and a considerable number of his counts have proved to be erroneous. Three decades later, Hans (1973) presented a much more extensive (and reliable) survey of chromosome numbers; and there have been a few additional surveys since then, such as that of Urbatsch et al. (1975). Although the percentage of species sampled is still very low (below 5%), there are now data on a sufficient number of genera to discuss the possible implications for phylogeny and classification. Hans concluded that there are two fundamental basic numbers in the family: $x = 7$ and $x = 13$, of which the latter is presumed to be derived from the first by doubling and aneuploid reduction. Although this scenario cannot be disproved, it is notable that $x = 13$ is the prevailing number in the "lower" *Phyllanthoideae*, and it seems unwarranted to invoke a hypothetical ancestral complement of $x = 7$. Hans's reason for doing so is probably a consequence of his following Bentham's (1880) tribal arrangement, and unfortunately the worst mistake in Bentham's treatment is his inclusion of the *Buxaceae* (with $x = 7$) as one of the tribes.

Hans (1973) is probably correct in concluding that $x = 11$ is the original base number in the *Acalyphoideae* and *Crotonoideae*. The same conclusion can also be made for the *Euphorbioideae*, as $x = 11$ is prevalent in the *Hippomaneae*. Hans regarded $x = 7$ and 10 as the primary base numbers for *Euphorbia*, but this implies that the genus is polyphyletic, which is scarcely warranted. In my opinion, the evidence clearly suggests an original

number of $x = 10$, with other numbers originating in a descending aneuploid series. Jones & Smith (1969) reported a surprising diversity of basic numbers in *Monadenium*: $x = 12, 16, 17, 18$, and 19. Since the prevalent number in *Monadenium* is $x = 18$, and the lowest number of $x = 12$ occurs in a species (*M. echinulatum* Stapf) ranked as highly specialized in the monograph of Bally (1961), the most probable hypothesis is that these numbers are of polyploid origin from an ancestor with $x = 9$, followed by a mostly decreasing aneuploid series. Unfortunately, all of the cytologically known potential succulent ancestral species in *Euphorbia* subg. *Euphorbia* are reported to have $x = 10$, so the case remains not proven.

SUMMARY OF TAXONOMIC CHARACTERS IN THE EUPHORBIACEAE

At this writing, only one comprehensive phylogenetic analysis of Euphorbiaceae using both phenetic and cladistic methods has been made. Levin (1986b, c) classified the genera of subfamily *Phyllanthoideae* primarily on the basis of leaf anatomical data. A cladistic study of *Oldfieldioideae* based on pollen characters has recently been completed (Levin & Simpson, 1994a, b). However, critical phylogenetic analysis of the family is really just beginning. Considerably more morphological, anatomical, and biochemical (not to mention molecular) work needs to be done before the data set is adequate.

In Table 1 are listed a basic set of primitive and derived character states for the Euphorbiaceae, based on both the literature and personal observations. It is focused on the *Phyllanthoideae* as the sister group of the other subfamilies, and also the sister group of the unknown collateral (or ancestral) closest related family. I have used a pastiche of several potential "ancestral" families as a composite sister group; this includes families of *Linales* and *Sapindales* (sensu Cronquist, 1981) such as *Ixonanthaceae*, *Irvingiaceae*, and *Linaceae*. The ovular structure in these *Linales* is suggestively similar to that in the Euphorbiaceae (Webster, 1967). Other possible families, such as the *Thymelaeaceae*, should be tested as sister groups, and this might well alter the list of characters.

Further refinement of this crude and preliminary list of character states in Euphorbiaceae can be expected from more intensive study of fossils as well as living plants. Since I reviewed the earlier reports of euphorbiaceous fossils (Webster, 1967), data provided by fossil wood and fruits has been supplemented by discoveries of euphorbiaceous

flowers in the Eocene. Crepet & Daglian (1982) have described a genus *Hippomaneoides* from the Eocene Claiborne formation that appears similar to the modern genus *Senefeldera*. This raises the encouraging possibility that further discoveries may provide a picture of the past evolution of euphorbiaceous reproductive structures and a firmer basis for polarizing character states. Although the systematic affinities of fossil fruits have proved more difficult to establish, the study of Mazer & Tiffney (1982) on fruits of Hippomaneae from the North American Eocene indicates that it may be possible to correlate flower and fruit characters in fossil taxa of Euphorbiaceae.

THE ECOLOGICAL AND BIOGEOGRAPHIC BACKGROUND

1. POLLINATION

Despite the reproductive diversity in the Euphorbiaceae, the limited studies on pollination indicate that the flowers of the majority of genera are not highly specialized for a single kind of pollination vector. Although wind pollination is presumably the norm in a limited number of genera (e.g., *Acalypha*, *Macaranga*, *Mallotus*) with anemophilous characteristics such as reduced perianth and nectar, it has been demonstrated experimentally only in a few genera such as *Mercurialis* (Daumann, 1972) and *Ricinus* (Alex, 1957). Perhaps the typical situation might be that demonstrated for three species of *Chamaesyce* in Arizona by Ehrenfeld (1976), who collected 175 species of insects, including small bees, flies, and wasps. A similar spectrum of visitors was reported for a North American and a South American species of *Jatropha* by Simpson (1977), and for *Jatropha gossypifolia* L. in India by Reddi & Reddi (1983). Steiner (1983) reported visits by a variety of bees, flies, and butterflies to the flowers of *Croton draco* Cham. & Schtdl. in Panama. Recently it has been claimed (Dominguez & Bullock, 1989; Dominguez et al., 1989) that the Mexican species *Croton pseudoniveus* Lundell and *C. suberosus* HBK are wind-pollinated, even though nectaries are present in both staminate and pistillate flowers. The argument is made that the role of nectar in *Croton suberosus* is to attract wasps that deter lepidopteran predators from attacking the foliage. However, other reports such as that of Jose & Inamdar (1989) on the role of floral nectaries in *Croton bonplandianus* Baill. support adaptation for insect pollination. In my opinion, the arguments for wind pollination in *Croton*, in view of the floral and pollen morphology, are not entirely persuasive; Domin-

guez and his collaborators have not yet demonstrated convincingly that the benefit from visits of *Polistes* wasps is not merely incidental (or superfluous) with respect to a pollination system that depends on visitations by a variety of generalist visitors. It should be noted, though, that *Eremocarpus*, a specialized derivative group surely derived from within *Croton* (and better treated as a section of that genus), does appear to be wind-pollinated. The situation in *Croton suberosus* could represent a preliminary step toward anemophily and merits further experimental study.

The lack of specificity in most euphorbiaceous flower/pollinator relationships clearly has not impeded diversification in floral and inflorescence structure; however, the number of genera that have received even superficial study is very small. A number of instances of more unusual adaptations for pollination have been demonstrated, and no doubt many remain to be detected. Pollination by Diptera is no doubt usually unspecialized, as recorded by Hauman-Merck (1912) for a species of *Sapium* in Argentina, where species of genera such as *Eristalis* and *Sarcophaga* were recorded removing nectar from extra-floral nectaries on the floral bracts; as Hauman suggested, a similar syndrome may occur in other taxa of tribe Hippomaneae, but there are few recent observations. In contrast to this, however, Warmke (1952) demonstrated that *Hevea* in Brazil is naturally pollinated by midges (Heleidae). Although further verification of this is desirable, it appears that *Hevea* may depend on midges of a single family for pollination, and this might well prove to be the case for other euphorbiaceous genera.

In a few genera of Euphorbiaceae, floral structure has become modified for pollination by Lepidoptera. Perkins et al. (1975) reported nocturnal pollination of *Cnidocolus texanus* (Muell. Arg.) Small in Oklahoma by two species of hawkmoths. However, Breckon, in observations on four species of *Cnidocolus* in Mexico (pers. comm.), found pollination primarily by sphingids in *C. herbaceus* (L.) I. M. Johnston, but mostly by butterflies in *C. aconitifolius* (Miller) I. M. Johnston and *C. multilobus* (Pax) I. M. Johnston; the most important butterfly families were Papilionidae and Nymphalidae, but significant numbers of visits were made by taxa of Heliconidae, Pieridae, and Hesperidae. In Brazil the situation in *Cnidocolus* is similar, except that near Jequié, Bahia, visits to *Cnidocolus urnigerus* Pax were seen to be almost entirely by hummingbirds (Webster, unpublished). The peculiar urn-shaped corolla and the androecium of

distinct (not monadelphous) stamens appear to have evolved in this one species concomitantly with a shift from lepidopteran to ornithophilous pollination.

Pollination by small Hymenoptera is doubtless very widespread in the Euphorbiaceae. In California, wasps were found to be the most important pollinators for *Croton* and *Euphorbia* by Moldenke (1976). In Suriname, pollination of *Tragia lesser-tiana* (Baill.) Muell. Arg. appeared to be primarily by *Melipona* (Webster & Dobson, unpublished), although species of *Trigona* were common visitors to this and other Euphorbiaceae. Further observations of pollination by small wasps and bees may help to elucidate some of the variations in euphorbiaceous floral structure that at present appear mysterious.

Larger bees presumably are major pollinators for Euphorbiaceae with relatively large and showy flowers, such as *Aleurites*, *Manihot*, and species of *Croton*; however, critical field observations are still almost entirely lacking. The major exception involves *Dalechampia*, which has small flowers aggregated into a conspicuous pseudanthium that in most species produces resin for a floral reward (Webster & Webster, 1972). Armbruster & Webster (1979) demonstrated that in Mexico pollination of one species, *Dalechampia magnistipulata* Webster & Armbruster, was affected by female euglossine bees visiting the inflorescence to gather the resin; in the other species, *D. spathulata* (Scheidw.) Baill., which has modified resin glands, visits were by male euglossine bees gathering volatile terpenoids. Subsequently, in a series of papers Armbruster (1984; 1988; Armbruster & Herzog, 1984) described pollination of a large number of *Dalechampia* species, which depend on visits by anthidiine and euglossine bees. The considerable speciation in *Dalechampia* (over 100 species) may plausibly be related to exploitation of this unique "niche" in the pollination spectrum of tropical plants. Armbruster (1992) showed a fascinating correlation between phylogeny of taxa in *Dalechampia* and evolution of pollination mechanisms; he convincingly demonstrated that pollination by fragrance-collecting euglossine bees has evolved independently in three different species lineages.

The other major occurrence of pseudanthial inflorescences in the Euphorbiaceae is in the tribe Euphorbieae, where modification of floral structure has occurred along an entirely different pathway. As indicated by Venkata Rao (1971), the inflorescence structure of *Dalechampia* may be derived from the thyrse of Acalyphaeae, in which the floral

bracts are usually glandless. In contrast, the cyathium of the Euphorbieae appears derived from the spicate thyrse of the Hippomaneae, in which the nectaries of the floral bracts have become incorporated as the nectaries of the pseudanthium; theories about the nature of the cyathium have been reviewed by Dressler (1957) and Webster (1967). Other pseudanthia, of quite a different nature, are known in *Uapaca* (Phyllanthoideae) and *Pera* (Acalyphoideae); but nothing is known about their reproductive biology.

The pseudanthium of *Euphorbia* and *Chamaesyce* is generally pollinated by small generalist insects (flies, wasps, bees) as reported by Ehrenfeld (1976) and earlier workers. However, the type species of *Euphorbia* subgenus *Poinsettia*, *Euphorbia pulcherrima*, has very conspicuous red bracts subtending the cyathia (forming a second-order pseudanthium); this, and the copious nectar, suggest hummingbird pollination. Indeed, Dressler (1957) clearly illustrated how the more or less radially symmetrical cyathium of *Euphorbia* has been highly modified into the bilaterally symmetrical cyathium of *Pedilanthus* that is pollinated mainly by hummingbirds.

At least fragmentary accounts of most major pollination syndromes of Euphorbiaceae were published by the end of the 19th century. However, Steiner (1981, 1983) demonstrated mammal pollination of *Mabea occidentalis* Benth. by bats (*Glossophaga*, *Carollia*) and the red woolly possum (*Caluromys*), which visit the inflorescences to obtain nectar from the extrafloral nectaries on the bracts. An even more remarkable instance of bat pollination has been reported by Steiner (1982) in another genus of Hippomaneae, the sandbox tree (*Hura*). In contrast to *Mabea*, in which the staminate and pistillate flowers are associated in the same inflorescence, in *Hura* the fleshy staminate inflorescences and the solitary pistillate flowers with bizarrely enlarged stigmas behave as separate pollination units. Steiner suggested that the staminate "cones" are taken by bats mistaking them for fleshy fruits—certainly the most striking case of "mistake pollination" in the Euphorbiaceae.

These examples indicate that the great diversity of euphorbiaceous floral structure is at least partly related to a long history of shifting adaptation to different pollinators. However, because the flowers of most Euphorbiaceae are less than 1 cm in diameter, the effective unit of pollination has often been the inflorescence or subinflorescence. Functional studies of evolution of reproductive structures must therefore take into account the inflo-

TABLE 2. Taxonomic distribution of disseminule types in the Euphorbiaceae. A number of genera have not been scored due to lack of definite information.

Subfamily	Num- ber of genera	Seeds carun- culate	Seeds ecarun- culate	Testa fleshy	Fruit inde- his- cent
Phyllanthoideae	58	0	38	5	12
Oldfieldioideae	28	11	14	0	2
Acalyphoideae	118	18	77	13	5
Crotonoideae	61	19	29	5	8
Euphorbioideae	42	16	18	1	4
Totals	307	64	176	24	31

rescence as a whole, as well as its constituent parts. Furthermore, as discussed below, adaptations for dispersal may also have a "retrospective" effect in projecting developmental restraints back onto the flowers.

2. DISPERSAL

The prevalent fruit type in the primitive Euphorbiaceae (Phyllanthoideae), and indeed in most of the taxa of the family, is the 3-carpellate schizocarp that dehisces explosively into three segments (cocci) each with one or two seeds. Typically, the central axis of the flower (carpel margins and placentae) remains in the fruit as a columella after the cocci have dispersed. In the subfamily Phyllanthoideae, the individual seeds may have a dry or fleshy testa, but there is never the large conspicuous elaiosome (caruncle) found in other subfamilies; the caruncle appears to be a novelty (independently evolved?) in the subfamilies Oldfieldioideae and Acalyphoideae.

Under the description of fruit and seed morphology, Berg's (1975b) detailed study on the Aus-

tralian oldfieldioid genus, *Micranthemum*, is mentioned, in which dispersal of the carunculate seeds depended on attraction of ants to the elaiosome. Berg's study remains unique in its synthesis of field observations on ant dispersal of *Micranthemum* seeds with a careful anatomical study of fruit and seed development; he also provided comparative data on myrmecochory in several other Australian genera of Euphorbiaceae (1975a, 1981). Since a very rudimentary elaiosome occurs in some Phyllanthoideae (e.g., *Phyllanthus*), it is not unreasonable to suggest that selection for ant dispersal was an important factor in the evolution of fruit and seed morphology in the Euphorbiaceae. Berg plausibly suggested that the diagnostic character syndrome of the euphorbiaceous gynoecium and fruit—including the reduced ovule number, obturator, the axis becoming a persistent columella, and the closed ventral wall of the coccus—represent a specialized derivation from an ancestral state of nonexplosive capsular fruits, and that morphological changes involved in dispersal have as a consequence relayed from the fruit back into the flower. Berg also suggested, somewhat less persuasively, that this characteristic euphorbiaceous gynoecium/fruit/seed character syndrome arose in a tropical monsoon climate; this could be so, but there are many taxa with typical explosive fruits in the tropical rainforest. Intensive investigations on other genera are badly needed in order to test Berg's hypotheses.

Some of the relationships involved in the adaptive aspects of dispersal are given in Tables 2–4. It is notable from Table 2 that "unspecialized" seeds (i.e., ecarunculate, with dry seed coat) predominate in all five subfamilies. However, in the Oldfieldioideae and Euphorbioideae there are nearly as many carunculate as ecarunculate genera. The Acalyphoideae have the lowest percentage of the four subfamilies with carunculate seeds, but in compensation have the largest number of seeds with fleshy testa.

Geographically (Table 3), there are some interesting differences in average dispersal type, since the neotropical and Australasian genera have many more myrmecochorous genera than ornithochorous, whereas in the rest of the paleotropical area the situation is reversed.

In view of the interest tropical ecologists have taken in the role of dioecy as a reproductive adaptation, it is of some interest to compare the types of fruits and seeds with the monoecious versus dioecious conditions within Euphorbiaceae (Table 4). The data support the predictions of Bawa (1980), Givnish (1982), and Steiner (1988) that dioecious taxa should have a higher percentage of ornitho-

TABLE 3. Relation of dispersal type to geographic distribution of genera: carunculate seeds are treated as myrmecochorous; fleshy seeds and indehiscent fruits as ornithochorous. Many genera, not enumerated in the table, are probably autochorous.

	Myrmeco- chorous	Ornitho- chorous
Neotropics	18	10
Africa/Madagascar	8	21
Tropical Asia	6	28
Australasia	21	6
Holarctic	4	0
Totals	57	65

chorous disseminules than do monoecious taxa. In contrast, there appears to be no significant difference in the expectation of monoecy or dioecy in myrmecochorous taxa, or in the "unspecialized" taxa, which are presumably mostly autochorous.

Although Berg is surely correct in suggesting that the autochorous tricocous fruits represent a primitive state, and myrmecochory developed subsequently, further evolution to fleshy, more or less indehiscent fruits has occurred in all of the subfamilies. Within the Phyllanthoideae there are also a number of fruits that appear adapted for dispersal by birds: examples include berries in *Breynia*, and drupes in *Drypetes* and *Uapaca*. In *Phyllanthus* (Webster, 1956), there is a particularly marked progression from schizocarps (subgenus *Isocladus*) to berries (subgenus *Kirganelia*) and finally to drupes (subgenus *Cicca*). Within dry fruits, there has also been an elaboration of seeds with sarcotesta; this is very often reddish, as in *Macaranga* or *Mallotus*, but in *Margaritaria* it is blue or green. The baccate fruits in Euphorbiaceae are watery and dispersed by nonspecialist frugivores (Snow, 1981). Presumably, drupaceous fruits are dispersed by specialist frugivores, but we have very little data on Euphorbiaceae. A striking development in Acalyphoideae and Crotonoideae is the evolution of large oily seeds in genera such as *Caryodendron*, *Hevea*, *Joannesia*, *Aleurites*, and *Omphalea*. The seeds of *Hevea* are explosively dispersed to great distances (up to 45 m according to van der Pijl, 1982) and then dispersed by rivers in the Amazon basin. *Hevea* and these other large-seeded taxa are mostly rainforest dominants (*Omphalea* is a liana), but another group of genera such as *Homonoia*, rheophytes that are adapted to extensive periods of submergence, also presumably depend mainly on water dispersal. According to Gottsberger (1978), none of the Euphorbiaceae observed in the Amazon basin (including *Hevea*) are dispersed by fish, but rather the seeds are preyed upon. Wind dispersal is rare in Euphorbiaceae and occurs mainly in taxa with samaroid fruits adapted for open tropical woodland (e.g., *Hymenocardia*); there are no good examples of winged seeds in the Euphorbiaceae.

Bresinsky (1963), on the basis of studies of elaiosomes, hypothesized that seed morphology in temperate taxa with myrmecochory has been derived from ornithochory in tropical taxa. This assumes that seeds with sarcotesta (tropical forms) have evolved into carunculate seeds (temperate forms), with *Mercurialis* showing an intermediate condition. However, the real situation appears much more complex. Primitively, seeds in the Euphor-

TABLE 4. Relation of sexual expression to dispersal type in genera of Euphorbiaceae. M indicates genus is monoecious; M/D, monoecious or dioecious (in same or different species of a genus); D, consistently dioecious.

Subfamily	Seeds dry (autochorous)	Seeds carunculate (myrmecochoorous)	Seeds fleshy (ornithochorous)	Totals for each subfamily
Phyllanthoideae				
M	11	0	3	14
M/D	5	0	1	6
D	22	0	9	31
Oldfieldioideae				
M	1	3	0	4
M/D	1	1	0	2
D	12	7	3	22
Acalyphoideae				
M	44	4	6	54
M/D	3	0	1	4
D	30	14	11	55
Crotonoideae				
M	15	13	4	32
M/D	0	2	0	2
D	14	4	9	27
Euphorbioideae				
M	14	13	0	27
M/D	2	2	1	5
D	2	1	4	7
Totals				
M	85	33	13	131
M/D	11	5	3	19
D	80	26	36	142
	176	64	52	292

biaceae appear to have been ecarunculate, and well-developed caruncles are unknown in the Phyllanthoideae. It is interesting that carunculate seeds occur in "basal" taxa of the Oldfieldioideae (*Tetracoccus*), Acalyphoideae (*Clutia*), and Crotonoideae (*Micrandra*, *Manihot*). Seeds with sarcotesta are found in relatively "advanced" genera (e.g., *Margaritaria*, *Breynia*) in Phyllanthoideae, but in relatively "basal" genera in Acalyphoideae (*Cheilosa*) and Crotonoideae (*Tetrorchidium*, *Klaineanthus*). It appears that diaspore evolution has followed a tortuous path, with many reversals between dry/fleshy and carunculate/ecarunculate testa. There is a general tendency for seeds with sarcotesta to occur in closed forested habitats and for those with caruncles to occur in open dry habitats. What is evident, however, is there is no unilinear direction

TABLE 5. Summary of diversity in subfamilies and tribes of Euphorbiaceae as measured by numbers of native and endemic genera (endemic genera indicated in parentheses). Tropical Arabia is counted as part of Africa, Pacific islands with Australasia.

Subfamily	America	Africa	Madagascar	Asia	Australasia
Phyllanthoideae					
Wielandieae	4 (3)	4 (3)	3 (2)	1 (0)	1 (0)
Amanoeae	1 (0)	2 (1)			
Bridelieae		2 (0)	2 (0)	2 (0)	2 (0)
Phyllantheae	8 (3)	14 (4)	6 (1)	10 (1)	7 (0)
Drypeteae	1 (0)	3 (2)	1 (0)	2 (1)	1 (0)
Antidesmeae	6 (5)	7 (4)	4 (1)	4 (1)	5 (2)
Hymenocardieae	1 (1)	1 (0)		1 (0)	
Bischofieae				1 (0)	1 (0)
Totals	21 (12)	33 (14)	16 (4)	21 (3)	17 (2)
Oldfieldioideae					
Croizateae	1 (1)				
Podocalyceae	3 (3)				
Caletieae		1 (1)		2 (1)	13 (12)
Picrodendreae	4 (4)	4 (3)	3 (2)	1 (1)	
Totals	8 (8)	5 (4)	3 (2)	3 (2)	13 (12)
Acalyphoideae					
Clutieae		1 (1)			
Pogonophoreae	1 (0)	1 (0)			
Chaetocarpeae	1 (0)	1 (0)	1 (0)	2 (1)	
Pereae	1 (1)				
Cheiloseae				2 (1)	1 (0)
Erismanthaeae				3 (2)	1 (0)
Dicoelieae				1 (1)	
Galearieae		2 (1)		2 (0)	1 (0)
Ampereae					2 (2)
Agrostistachydeae		2 (2)		2 (1)	1 (0)
Chrozophoreae	5 (4)	2 (0)		6 (4)	1 (0)
Caryodendreae	2 (2)	1 (1)			
Bernardieae	2 (2)	2 (2)		1 (1)	
Pycnocomaeae		2 (1)	2 (1)	4 (2)	2 (0)
Epiprineae		2 (1)	2 (0)	8 (6)	
Adelieae	4 (4)	1 (1)			
Alchorneae	5 (4)	1 (0)	3 (2)	1 (0)	2 (2)
Acalypheae	3 (1)	11 (6)	10 (5)	14 (4)	11 (3)
Plukenetieae	11 (8)	3 (1)	3 (1)	5 (3)	
Omphaleae	1 (0)	1 (0)	1 (0)	1 (0)	1 (0)
Totals	36 (26)	33 (17)	22 (9)	52 (26)	23 (7)
Crotonoideae					
Micrandreae	4 (4)				
Manihoteae	2 (2)				
Adenoclineae	3 (2)	3 (2)		1 (0)	
Gelonieae		1 (0)	1 (0)	1 (0)	1 (0)
Elateriospermeae				1 (1)	
Jatropheae	3 (2)	2 (1)		3 (2)	
Codiaeae	4 (4)	1 (0)		8 (5)	5 (3)
Trigonostemoneae				1 (0)	1 (0)
Ricinocarpeae				1 (1)	6 (6)
Crotonaeae	4 (3)	2 (1)	1 (0)	2 (1)	1 (0)
Ricinodendreae		2 (1)	1 (0)	1 (0)	
Aleuritideae	2 (2)	7 (6)	3 (2)	4 (3)	1 (0)
Totals	22 (19)	18 (11)	6 (2)	23 (13)	15 (9)

TABLE 5. Continued.

Subfamily	America	Africa	Madagascar	Asia	Australasia
Euphorbioideae					
Stomatocalyceae	1 (1)	2 (2)		1 (0)	1 (0)
Hippomaneae	14 (10)	4 (2)	1 (0)	5 (1)	4 (0)
Pachystromateae	1 (1)				
Hureae	4 (4)				
Euphorbieae	4 (2)	7 (4)	3 (0)	2 (0)	4 (2)
Totals	24 (18)	13 (8)	4 (0)	8 (1)	9 (2)
Grand totals	111 (83)	102 (54)	51 (17)	107 (45)	77 (32)

of seed-coat specialization in any of the subfamilies except for the Phyllanthoideae, which lack myrmecochory, and the Oldfieldioideae, which are overwhelmingly myrmecochorous (Table 2). The geographical distribution of myrmecochorous and ornithochorous diaspores (Table 3) is interesting, with the neotropical and Australian regions mainly myrmecochorous, and the paleotropical region ornithochorous. Particularly notable is the prevalence of seeds with fleshy testa in the paleotropical region, and the overwhelming predominance of myrmecochorous dispersal in Australia, confirming the statements of Berg (1975a, b, 1981).

Little has been studied so far on the effects of seed predation on dispersal systems in Euphorbiaceae. The seed-coat toxins of such genera as *Ricinus* could be explained as a deterrent to predators, but this apparently has not been studied in the field in Africa, where natural predators might be expected. However, there is a suggestive study by Cook et al. (1971) on the effects of seed predation by doves on the seed morphology of *Croton setigerus* Hook. in California. Here there is a kind of "balanced polymorphism" between gray unpatterned seeds with toxins produced by plants in the deserts and mottled palatable seeds that are produced by coastal populations. Cook et al. (1971) argued plausibly that the mottled seed patterns of coastal plants are maintained by the adaptive advantage of camouflage, whereas the unpatterned seeds of desert areas indicate lower levels of predation. The situation is reminiscent of that in *Ricinus*, which also has notoriously variable seed-coat patterns.

3. GEOGRAPHIC DISTRIBUTION

A detailed analysis of the geographic distribution patterns of the 50 tribes of Euphorbiaceae is clearly beyond the scope of this essay. However, it seems appropriate here to outline some of the major geographic patterns of the five subfamilies and indicate

some of the most striking disjunct or relict distributions. There do not appear to be any critically documented maps of suprageneric taxa in the literature, and since the discussion of Bentham there have been few analyses besides the study of the distribution of Jatrophae by Pax (1910), and (partially) of the Euphorbieae by Croizat (1972) and Leach (1976).

A review of the geographic distribution of the tribes and genera of subfamily Phyllanthoideae brings out the striking prominence of Africa and Madagascar (Table 5). The highly disjunct distribution of the primitive genus *Savia* is striking (Fig. 1); including the related genus *Heywoodia*, the diversity in Africa/Madagascar is clearly greater than the New World. The occurrence of the relict genus *Wielandia* in Madagascar and the Seychelles is noteworthy; together with the endemic genera *Blotia* and *Petalodiscus*, it indicates a major center in Malagasia (Fig. 2). *Discocarpus* and *Lachnostylis* apparently form a vicariant pair in South America and Africa, and the neotropical and paleotropical species of *Savia* seem equally vicariant. This South American/African disjunction is repeated at the level of groups of species within a number of other genera of Phyllanthoideae, such as *Amanoa*, *Drypetes*, *Margaritaria*, *Meineckia*, and *Phyllanthus*. It also occurs in other subfamilies, as noted in Table 5. It seems particularly informative to look at the distribution of the more primitive genera within each subfamily. It is notable that in the Oldfieldioideae the "basal" tribes Croizateae and Podocalyceae are entirely neotropical (Fig. 3), whereas the Caletieae are entirely Old World, and only the Picrodendreae (Fig. 4) are represented in both hemispheres. Within the Picrodendreae, the genera *Celaenodendron*, *Piranhea*, and *Oldfieldia* appear to be vicariants that link America and Africa in the manner of *Savia*. The Laurasian genus *Tetracoccus* is taxonomically isolated, but clearly seems to belong in the Podocalyceae; it may represent the taxon in which the important

PHYLLANTHOIDEAE

Wielandieae

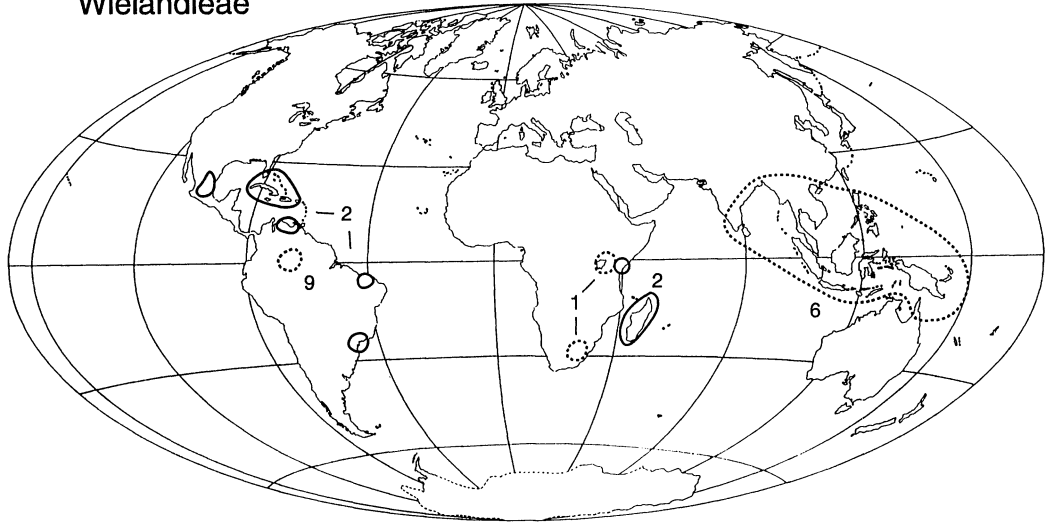


FIGURE 1.³ Distribution of Phyllanthoideae, tribe Wielandieae: 1, *Heywoodia* (dotted line, Africa); 2, *Savia* (continuous line); 6, *Actephila* (dashed line); 9, *Chonocentrum* (dotted line, America).

apomorphy of carunculate seeds first appeared in the family.

In the Acalyphoideae, there is one relict neotropical/African genus, *Pogonophora*, one of east and southern Africa, *Clutia*, one neotropical and Asiatic, *Chaetocarpus*, and three Asiatic, *Cheilosa*, *Neoscortechinia*, and *Trigonopleura* (Figs. 5, 6). Africa does not appear to be the epicenter for oldfieldioids and especially acalyphoids that it is for the Phyllanthoideae. It is notable that in the Acalyphoideae, in contrast to the biovulate subfamilies, basal taxa such as Cheiloseae and Chaetocarpeae are well developed in the Oriental region.

The Crotonoideae (Figs. 7, 8) differ from all the other subfamilies in a clear predominance of neotropical relict genera: *Ditta*, *Glycydendron*, *Hevea*, *Micrandra*, *Micrandropsis*, and *Tetrorchidium*. However, *Tetrorchidium* also occurs in Africa, and *Adenocline* and *Klaineanthus* are confined there. The Crotonoideae therefore show considerable parallelism to the Phyllanthoideae, except that the center of gravity is definitely to the west of the Atlantic rather than to the east. Finally, the primitive Euphorbioideae of tribe Stomatocalyceae (Fig. 9) give an ambiguous picture, with one neo-

tropical genus, *Nealchornea*, two African, *Hamilcoa* and *Plagiostyles*, and one oriental, *Pimelodendron*. It is interesting that the "advanced" tribe Euphorbieae (Fig. 10) has a distributional pattern somewhat paralleling the Stomatocalyceae, with tribe Anthosteminae in Africa/Madagascar, the Neoguillauminiinae in Australia/New Caledonia, and the Euphorbiinae (via shrubby species of subg. *Esula*) with an apparent focus in Africa/Madagascar. To me, this suggests that as stated by Raven & Axelrod (1974), deployment of a significant number of tribes of Euphorbiaceae may have taken place before Cretaceous plate tectonic movements separated the taxa of the family into their present disjunct situations. Fossil evidence (summarized for North America by Taylor, 1990) is still limited, but the fact that fossils of the relatively "advanced" tribe Hippomaneae have been recorded from the Eocene (Crepet & Daglian, 1982; Dilcher & Manchester, 1988) suggests that the origin and initial spread of all five subfamilies may go back into the Cretaceous, or the earliest Tertiary. For example, the pollen records from Australasia discussed by Martin (1974, 1978) indicate that relatively "advanced" genera of Oldfieldioideae were in place in Australia in the Paleocene, which surely implies differentiation of the subfamily well back into the Cretaceous.

It is not easy to summarize the overall distributional history of the Euphorbiaceae, but I am struck by the remarkable insightfulness of the essay

³ Distributions are based on references cited in Webster (1994) and examination of herbarium specimens, primarily at DAV. Genus numbers are the same as in Webster (1994). Distributions are necessarily somewhat generalized and do not show minor gaps.

PHYLLANTHOIDEAE
Wielandieae

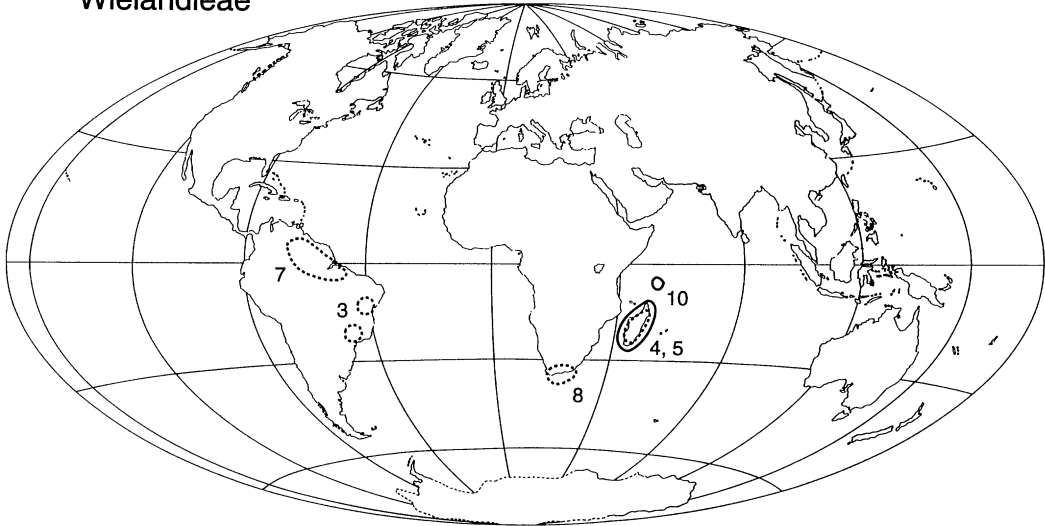


FIGURE 2.³ Distribution of Phyllanthoideae, tribe Wielandieae (continued): 3, *Gonatogyne*, (dotted line, Brazil); 4, 5, *Blotia*, *Petalodiscus* (dotted line, Madagascar); 7, *Discocarpus* (dashed line, America); 8, *Lachnostylis* (dashed line, Africa); 10, *Wielandia* (solid line).

by Bentham (1878), who presented the first model for the geographic patterns involved in the origin and radiation of the Euphorbiaceae. Bentham's words deserve to be quoted: "... we may be led to conjecture that the most ancient home of the

Order was in the Old World, but that several of the principal forms were differentiated and widely spread before that remote period when the present impassible barriers opposed by the Atlantic and Pacific did not exist, or were crossed over in some

OLDFIELDIOIDEAE
Croizateae
Podocalyceae

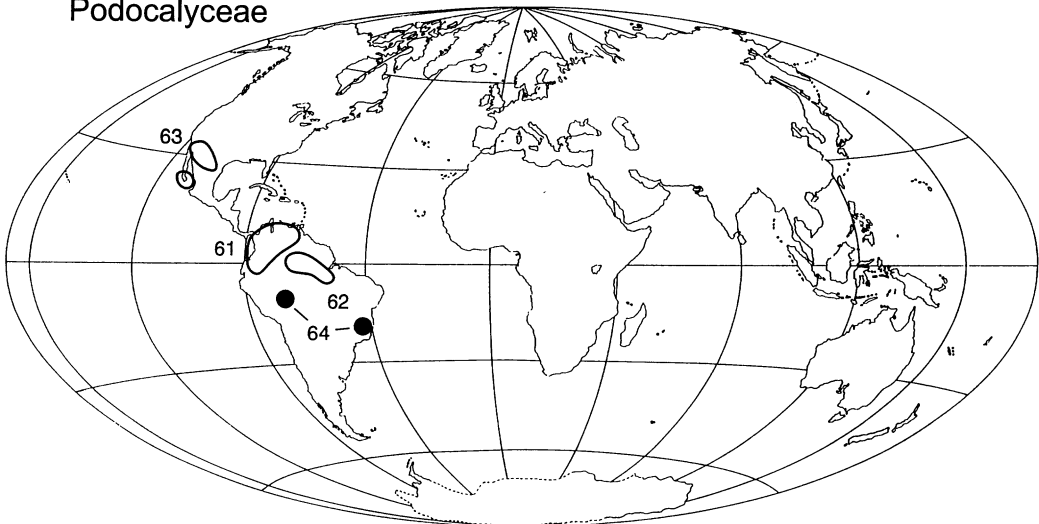


FIGURE 3.³ Distribution of Oldfieldioideae. Tribe Croizateae: 61, *Croizatia*. Tribe Podocalyceae: 62, *Podocalyx*; 63, *Tetracoccus*; 64, *Paradrypetes*.

OLDFIELDIOIDEAE

Picrodendreae

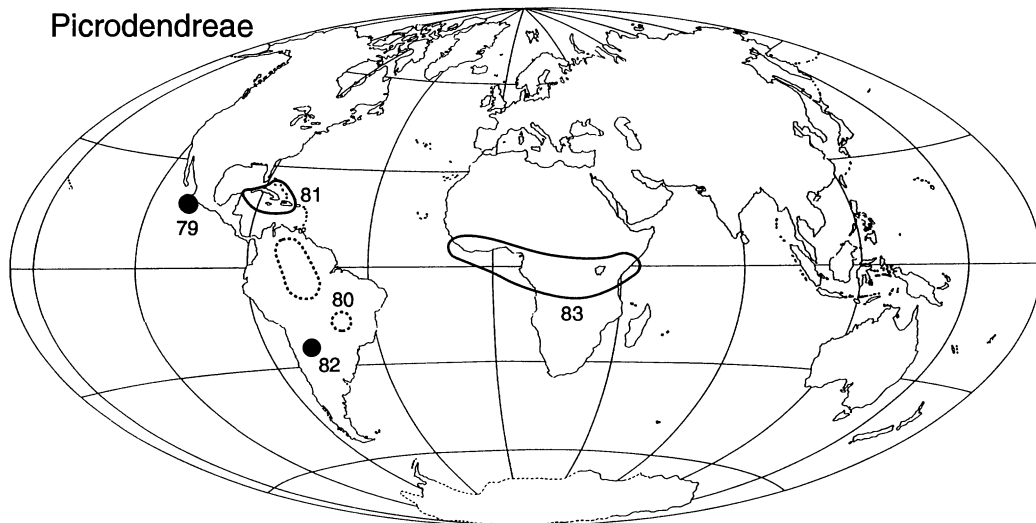


FIGURE 4.³ Distributions of Oldfieldioideae, tribe Picrodendreae: 79, *Celaenodendron* (dot, North America); 80, *Piranhea* (dashed line); 81, *Picrodendron* (solid line, North America); 82, *Parodiodendron* (dot, South America); 83, *Oldfieldia* (solid line, Africa).

manner of which no plausible explanation has been suggested. It would also appear that interchange of forms between the principal Old-World centres of differentiation . . . continued long after the interposition of the obstacles preventing the spread

of the new American forms.” Later in this essay Bentham clearly stated “that the most ancient home of the order was in the Old World, whence it spread in very remote times to America.”

This scenario proposed by Bentham over a cen-

ACALYPHOIDEAE

Clutieae

Pogonophoreae

Cheiloseae

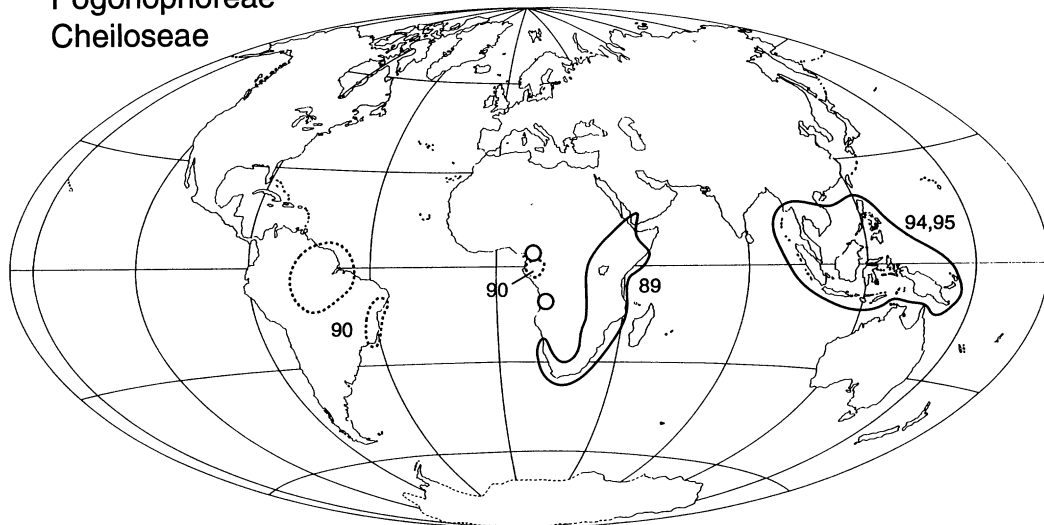


FIGURE 5.³ Distribution of Acalyphoideae. Tribe Clutieae: 89, *Clutia* (solid line, Africa). Tribe Pogonophoreae: 90, *Pogonophora* (dashed line). Tribe Cheiloseae (solid line, Asia; ranges of the two genera combined); 94, *Cheilosa*; 95, *Neoscortechinia*.

ACALYPHOIDEAE
Chaetocarpeae

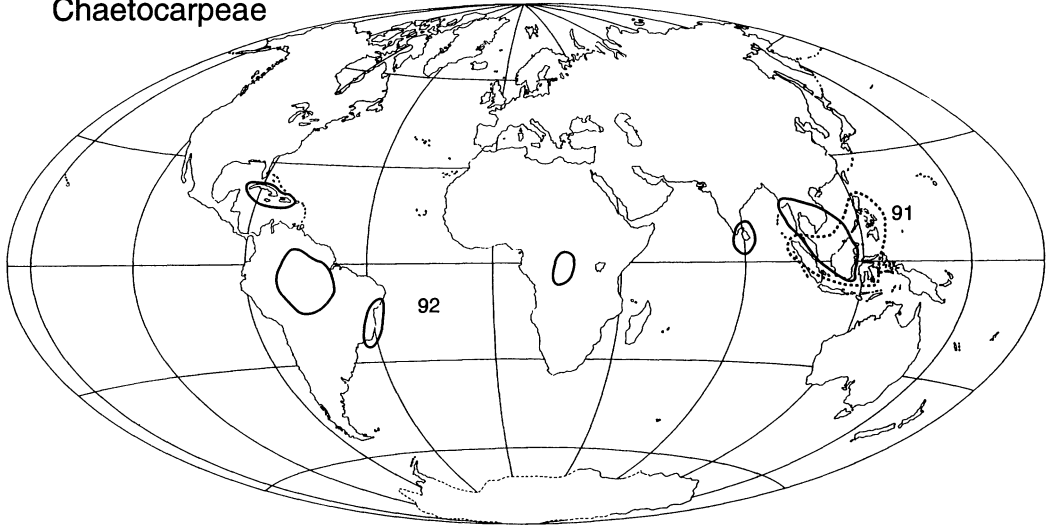


FIGURE 6.³ Distribution of Acalyphoideae, tribe Chaetocarpeae: 91, *Trigonopleura* (dashed line); 92 *Chaetocarpus* (solid line).

ture ago now appears as a prescient anticipation of models of intercontinental relationships based on plate tectonic models. Pax (1924), although not mentioning Bentham's essay, accepted much the same overall explanation of intercontinental "land bridge" distributions in Euphorbiaceae, and—un-

like most plant geographers of his time—did not reject "continental drift" as an explanation. The very limited paleontological record still does not provide critical evidence for Euphorbiaceae, but the distributions and relationships of the taxa are now better understood, so that Bentham's model

CROTONOIDEAE
Micrandreae
Manihoteae

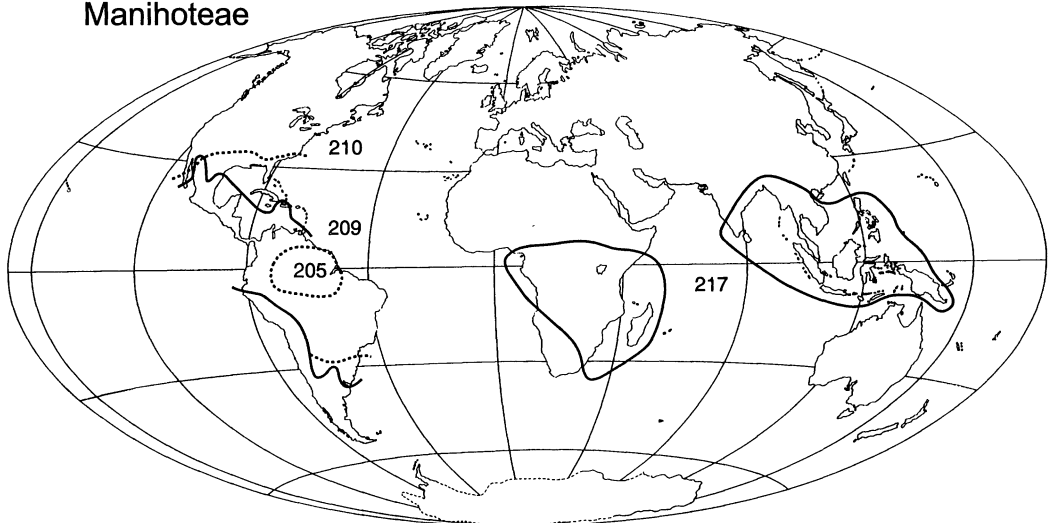


FIGURE 7.³ Distribution of Crotonoideae. Tribe Micrandreae (dotted line, generic ranges combined); 205, *Micrandra* [and 206, *Micrandropsis*; 207, *Cunuria*; 208, *Hevea*]. Tribe Manihoteae (northern and southern limits): 209, *Manihot*; 210, *Cnidioscolus*. Tribe Gelonieae: 217, *Suregada*.

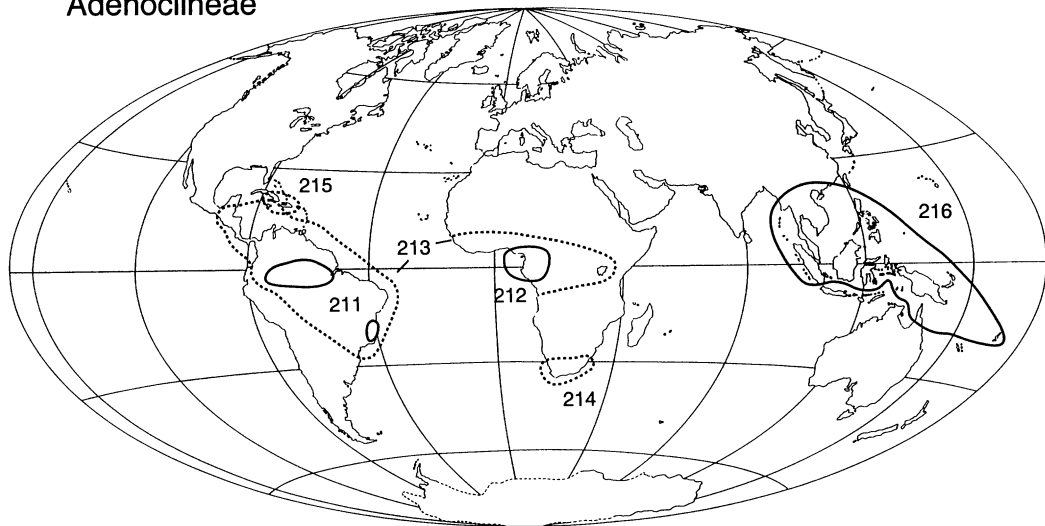
CROTONOIDEAE
Adenoclineae

FIGURE 8.³ Distribution of Crotonoideae, tribe Adenoclineae: 211, *Glycydendron* (solid line, America); 212, *Klaineanthus* (solid line, Africa); 213, *Tetrorchidium* (dashed line); 214, *Adenocline* (dotted line, Africa); 215, *Ditta* (dotted line, North America); 216, *Endospermum* (solid line, Asia & Australasia).

can be refined. It now appears that Africa/Madagascar retains the largest number of primitive taxa of Phyllanthoideae, and is the most likely center of origin for the family, but South America would seem to be the cockpit of initial differentiation for both the Oldfieldioideae and Crotonoideae. For both

the Acalyphoideae and Euphorbioideae, the trail of clues leads back to a joint South American/African center, but a narrower designation of original locality must await further studies.

With regard to the role of long-distance dispersal in possibly accounting for these geographic pat-

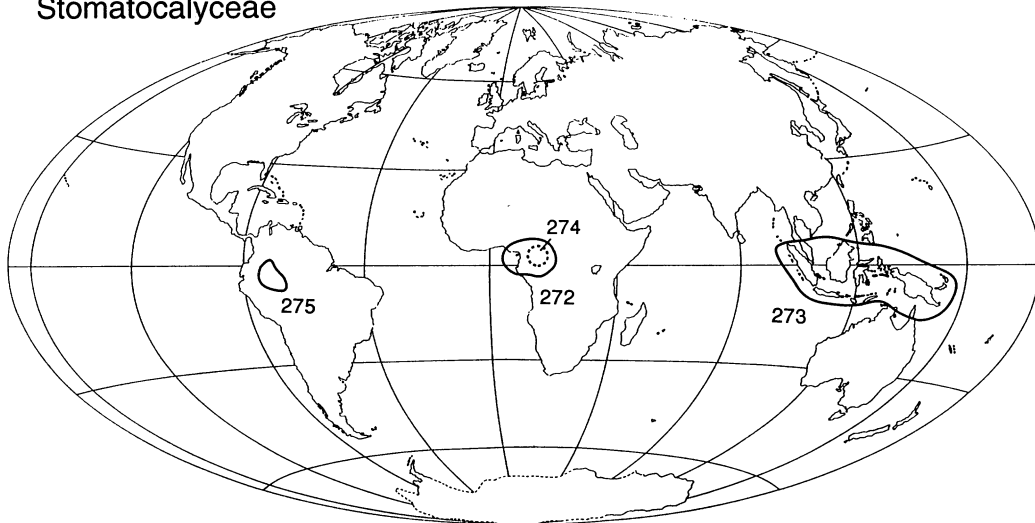
EUPHORBIOIDEAE
Stomatocalyceae

FIGURE 9.³ Distribution of Euphorbioideae, tribe Stomatocalyceae: 272, *Plagiostyles* (solid line, Africa); 273, *Pimelodendron* (solid line, Asia); 274, *Hamilcoa* (dotted line); 275, *Nealchornea* (solid line, America).

EUPHORBIOIDEAE Euphorbieae

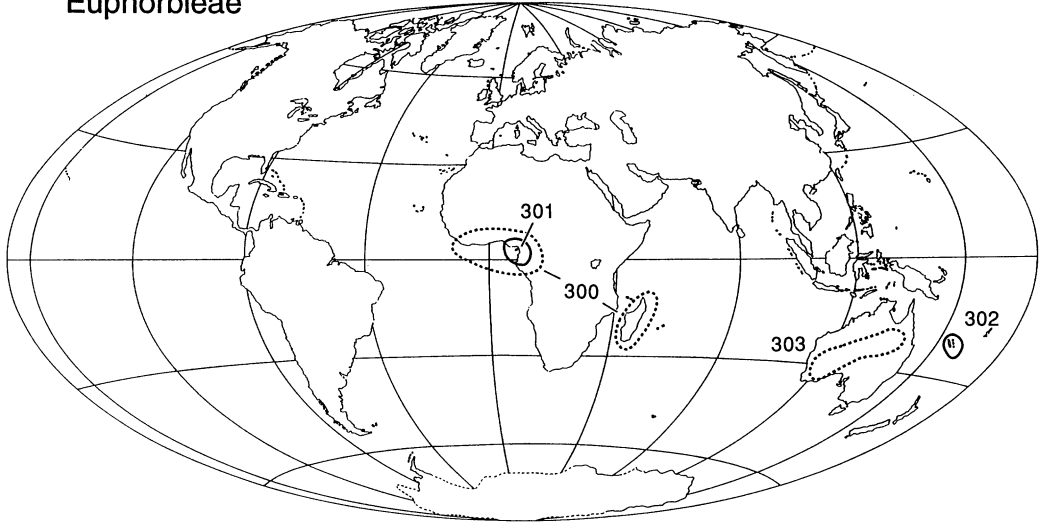


FIGURE 10.³ Distribution of Euphorbioideae, tribe Euphorbieae. Subtribe Anthosteminae: 300, *Anthostema* (dashed line, Africa & Madagascar); 301, *Dichostemma* (solid line, Africa). Subtribe Neoguillaumininae: 302, *Neoguillauminia* (solid line, New Caledonia); 303, *Calycopeplus* (dashed line, Australia).

terns, which Thorne (1972) and more recently Carlquist (1983) implied may be operative for many tropical intercontinental disjunctions, it is notable that the “basal” taxa in the Phyllanthoideae, Oldfieldioideae, and Acalyphoideae have capsular fruits with dry seed-coats, which certainly do not suggest a high degree of “preadaptation” for transoceanic dispersal. Only in the Adenoclineae of the Crotonoideae (Fig. 8) and the Stomatocalyceae of the Euphorbioideae (Fig. 9) do fleshy fruits or seeds occur that seem more likely to have been transported by birds. The weedy nature of many Euphorbiaceae would indeed appear to predispose them for success in establishment after transoceanic dispersal. However, the patterns reviewed above suggest that in the Euphorbiaceae, as in many other angiosperm families, the spectacular ocean crossings have been achieved by taxa (e.g., *Euphorbia*) that appear to have evolved later in family evolution, at a time when the continents were known to be widely separated. As suggested by Schuster (1976), the progressive refinement of dispersal capabilities during the course of the Tertiary leads to the paradox that the most widely dispersed genera are the latest evolved, and so the dramatic cases of long-distance transoceanic dispersal often noted in the literature tell us a great deal about the geologically recent stocking of oceanic islands but very little about the migrational history of less highly evolved taxa that were dispersing in the late Cretaceous or earliest Tertiary. Because of this paradox, Thorne (1973)

appears correct in claiming that American/African disjuncts such as *Mayaca*, *Pitcairnia*, and *Saccoglottis* represent recent long-distance dispersal, but he goes too far in concluding that this explanation may be extended to all of the taxa that link America with Africa. The transoceanic vicariant patterns of genera and tribes in the Euphorbiaceae agree with those of many other tropical families mapped and discussed by Axelrod (1970, 1972, 1975); these strongly suggest that the differentiation of genera and tribes was decisively influenced by ocean-floor spreading.

There is a third alternative explanation for trans-Atlantic or trans-Pacific distributions in Euphorbiaceae, and that is overland migration at high latitudes during the early Tertiary; Wolfe (1972) proposed that some tropical groups crossed into America from Asia during the Eocene by the Bering land bridge. It is notable, however, that the genera he cited—*Meliosma*, *Sagaretia*, and *Saurauia*—are cloudforest rather than lowland tropical taxa; the suggested presence of Lecythidaceae and Myristicaceae is more significant, but requires confirmation. The distribution of Euphorbiaceae does not offer much support for this Beringian alternative migrational pathway. In the Phyllanthoideae, a possible example is *Flueggea* (Webster, 1984); however, this genus has also colonized Hawaii (Hayden, 1987). There are also possible trans-Pacific or trans-Atlantic links in the subtribe Antidesminae. The Oldfieldioideae show no indication of possible use

of the Alaskan corridor. In the Acalyphoideae and Crotonoideae, an intrusion from Asia into America is suggested by the Tertiary records of *Aleurites* and *Macaranga* (Wolfe & Leopold, 1967). There is little sign of this in living taxa, however; perhaps the best example is in Crotonoideae tribe Codiaeeae, where the North American genus *Acidocroton* appears to be a vicariant of the Asian *Blachia*. In the Euphorbiaceae, therefore, an Eocene migration into America from Eurasia seems to have been an unimportant pathway. For explaining transoceanic links at the tribal level, a convincing model will have to involve plate tectonics as a major determinant.

Although the overall ecology of the Euphorbiaceae has not been reviewed in detail, it is worthwhile noting that genera of subfamily Phyllanthoideae with many plesiomorphic characters (e.g., *Heywoodia*, *Savia*) occur as shrubs or small trees in seasonal woodlands or scrub formations in the Southern Hemisphere. Except for the Acalyphoideae, the "basal" genera in the other subfamilies occur in rainforest or at least more mesic habitats; thus the spectacular efflorescence of xerophytes such as the African succulent Euphorbieae, *Jatropha*, and *Manihot*, appears to be a later development. In all five subfamilies, insect pollination is the plesiomorphic condition, and wind pollination has evolved independently within each subfamily. Relatively few Euphorbiaceae have become canopy trees in rainforest; rather, the family has specialized in an opportunistic life-style involving colonization of fragmented, shifting, or extreme (e.g., desert) habitats.

In closing this essay, I feel obliged to emphasize the large amount of conjecture that has been necessary in discussing the major patterns of tribal differentiation and continental deployment in the Euphorbiaceae. Perhaps we can keep our feet on the ground if we imagine our reconstructed phylogenies as a fireworks display: colorful, intricate, cleverly contrived, and evanescent. There may be a correspondence here between the mental activity of the systematist and the master-plan of evolution: if we allow the rockets to represent family ancestors (or plesiomorphic states), and their trajectory the onward rush in evolutionary time, then the first burst of the rocket's red glare will represent the formations of tribes, subsequent pops genera, and the final transient fizzles, the species. The sedate appearance of cladograms in our scholarly papers represents an austere, abstract schematization of the turbulent, convoluted, and ultimately partly unknowable history of the Euphorbiaceae and other plant taxa.

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