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Journal Title: Botanical Journal of the Linnean Society.

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Maxcost: \$25.00

Volume: 94 **Issue:**
Month/Year: 1987 **Pages:** 3-46

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Article Author: Linnean Society of London.

Article Title: ; The saga of the spurses; A review of classification and relationships in the Euphorbiales.

Fax: 717/337-7001
Ariel: 138.234.152.5

ILLiad TN: 7580



Imprint: [London, New York] Academic Press.

ILL Number: 12821083



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The saga of the spurges: a review of classification and relationships in the Euphorbiales

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Received June 1986, accepted for publication September 1986

WEBSTER, G. L., 1987. **The saga of the spurges: a review of classification and relationships in the Euphorbiales.** The order Euphorbiales, defined by Lindley in 1836, has undergone many vicissitudes to the present day. Over 30 families have been referred to the Euphorbiales by various authors, but most of them no longer appear closely related to the Euphorbiaceae. Several families commonly referred to Euphorbiales (or Tricoccae) in the 19th century now appear better located in other orders: Buxaceae in Hamamelidales (*sensu lato*), Empetraceae in Ericales, and Callitrichaceae in Lamiales. Several putatively related families, including the Aextoxicaceae, Stackhousiaceae, and Dichapetalaceae, appear to be of Celastralean affinity. The Simmondsiaceae, a problematical family once referred to the Buxaceae, have been included in the Euphorbiales in recent classifications, but the evidence for this is still inconclusive. Thymelaeaceae show a number of similarities to Euphorbiaceae, but share a greater number of distinctive characters with Malvales. The Euphorbiales show affinities to both the Malvales and Geraniales (*sensu lato*), and separation of these three orders between two major dicotyledon subclasses (Dilleniidae and Rosidae) appears questionable. The evidence does not support recognizing segregate families from the Euphorbiaceae such as the Bischofiaceae, Picrodendraceae and Stilaginaceae; the Euphorbiales are therefore best construed as containing a single major family, the Euphorbiaceae, as suggested by Hutchinson; the small family Pandaceae is also included in the Euphorbiales but may not be separable from the Euphorbiaceae. The recent classifications of Airy Shaw and Webster agree in many respects, and areas of disagreement indicate the need for additional data gathering and analysis.

ADDITIONAL KEY WORDS:—Aextoxicaceae – Buxaceae – Dichapetalaceae – Euphorbiaceae – Malvales – Simmondsiaceae – Thymelaeaceae.

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INTRODUCTION

The first detailed treatment of the Euphorbiales was by Lindley (1836), and it is somewhat sobering to consider that after a century and a half we are still debating many of the same taxonomic questions.

Before reviewing the taxonomic history of the Euphorbiales, we have to face the fact that the order has been given very different circumscriptions by different systematists. To go back no further than the most recent treatments, we find that Croizat (1973) and Hutchinson (1973) include only one family, the Euphorbiaceae, in the Euphorbiales, whereas the order includes four to six families in the classifications of Stebbins (1974), Takhtajan (1980), Cronquist (1981), Dahlgren (1983) and Thorne (1983); and the family composition is different in all five of the multi-family classifications! This disagreement among both contemporary and past authors is indeed a major justification for holding this symposium.

To approach the problem of the history of the Euphorbiales, perhaps the most pragmatic solution is to begin with the uni-familial concept of Hutchinson, as the Euphorbiaceae is clearly the 'core' family in the circumscriptions of all workers. Let us then briefly review the salient characteristics of the Euphorbiaceae as defined by Webster (1967, 1975), Hutchinson (1969b, 1973), and Cronquist (1981). This will establish a central mode, or standard, for the Euphorbiales, and the problem then becomes how to decide which other families show sufficient similarity to the Euphorbiaceae that they should be included in the same order.

The Euphorbiaceae, with about 8000 species in 300 genera, are one of the largest and most diversified families of angiosperms. Although all taxa have unisexual flowers, pollination is achieved by a wide variety of agents, including wind, insects, birds, bats and non-flying mammals. There is great diversity in growth form, from tall rain forest trees to lianas, shrubs, perennial and annual herbs, geophytes, succulents, and floating aquatics; only the epiphytic habit is lacking among the major 'niches' of vegetative adaptation. However, because of the primarily tropical distribution of the family, and the often minute flowers, the Euphorbiaceae have been much less thoroughly studied than other large angiosperm families, and there have previously not been any symposia on Euphorbiaceae such as those treating the Compositae, Cruciferae, Gramineae, Leguminosae, Solanaceae and Umbelliferae.

Nevertheless, despite this relative neglect, the classification of the Euphorbiaceae has been studied during the past 150 years by a number of outstanding systematists, including Adrien de Jussieu (1823, 1824), Baillon (1858), Boissier (1862), Jean Mueller (1866a), Bentham (1878, 1880), Pax (1890-1931), Hurusawa (1954), Hutchinson (1969b), and Airy Shaw (1971, 1975, 1980a). However, the last complete monographic treatment of the family is that of Boissier (1862) and Mueller (1866a) in A. P. de Candolle's *Prodromus Systematis Naturalis Regni Vegetabilis*, and only one large genus, *Manihot*, has been recently monographed (Rogers & Appan, 1973). Since the time of Pax & Hoffman (1931), considerable outstanding systematic work has been accomplished on individual groups of Euphorbiaceae, especially the tribe Euphorbieae (Allem & Irgang, 1975; Anton, 1974; Bally, 1961; Carter, 1982; Croizat, 1938, 1939, 1940, 1972; Dressler, 1957, 1962; Leach, 1976; Mahlberg & Pleszczynska, 1984; Wheeler, 1941, 1943; White, Dyer & Sloane, 1941). Important regional contributions to our knowledge of Euphorbiaceae have been provided for Asia and Australia (Airy Shaw, 1971, 1975, 1980a, b, 1981, 1982), Africa (Leonard, 1962; Vindt, 1953), Madagascar (Leandri, 1957); North America (Webster, 1967; Webster & Burch, 1968; Webster & Huft, 1987) and

South America (Jablonski, 1967; Lanjouw, 1931; Lourteig & O'Donell, 1943). Many other important contributions (partly cited in Webster, 1967) to the systematics of the family are not mentioned here because they fall outside the scope of this review.

In technical terms, the outstanding diagnostic characteristics of the Euphorbiaceae include the stipulate simple or palmately compound leaves; basically cymose inflorescences (often highly modified and raceme-like or capitulate); hypogynous radially symmetrical unisexual flowers; a receptacular nectary disk (sometimes secondarily lost); petals showy to absent; stamens 1 to many and often connate; pollen grains 2- or 3-nucleate and very diverse in exine sculpturing; gynoecium of mostly 3-5 connate carpels with styles undivided to multifid; the ovules solitary or paired in each carpel, anatropous (or less commonly hemitropous) and epitropous, crassinucellate, with two integuments; fruits mostly capsular (but sometimes drupaceous or baccate), primarily septicial, the carpels (cocci) separating from a central columella on dehiscence; seeds 1 or 2 in each coccus, with exotegmic seed coat development, with or without endosperm, often carunculate; embryo large, often with broad cotyledons (Webster, 1967).

This characterization of the Euphorbiaceae understates the considerable morphological variation within the family. Relationships among the 300 genera are still poorly understood, but I have proposed to group them in five subfamilies (Webster, 1975); salient characters of the subfamilies are given in Table 1. Biochemically, the family is very diverse as indicated in the summaries of Hegnauer (1966) and Gibbs (1974); alkaloids, cyanogenic glycosides, fatty acids, glucosinolates and terpenoid compounds have provided a large body of biochemical information of great systematic interest.

Considering its size, the family is rather poorly known with respect to morphological and biochemical characters, although there are summaries of the work on anatomy by Metcalfe & Chalk (1950), laticifers by Mahlberg (1975), cytology by Hans (1973), floral morphology by Michaelis (1924), pollen by Punt (1962) and Köhler (1965), seed coat anatomy by Netolitzski (1926) and Corner (1976), and embryology by Davies (1966) and Rao (1970). Our knowledge in all these areas is very uneven and is much more satisfactory for a small minority of genera of economic importance (*Hevea*, *Manihot*, and *Ricinus*) or horticultural interest (succulent *Euphorbia*).

I now consider those families that have been added to make up the membership of the Euphorbiales. As indicated in Table 2, at least 30 families have been proposed for membership. It is especially interesting to see how fashions have changed; of those families placed in the Euphorbiales by 19th century systematists, only one, the Buxaceae, is still considered as possibly Euphorbialean in the late 20th century (and that is a minority opinion). In the following survey of the taxonomic history of the Euphorbiales, the reasons for this striking shift in opinion are given.

TAXONOMIC HISTORY OF THE EUPHORBIALES

Although the order Euphorbiales technically dates from the publication of the name in the *Nixus Plantarum* of Lindley (1833), groupings of plants that included the spurges (Euphorbiaceae) and supposedly related taxa were recognized much

Table 1. Summary of characteristics of the taxa of Euphorbiales; the five subfamilies of Euphorbiaceae are given as circumscribed by Webster (1975); characters of the Pandaceae are mostly from Forman (1966, 1968, 1971) and Villiers (1973, 1975)

Euphorbiaceae A. L. de Jussieu, *Genera Plantarum*: 384 (1789)

Petals imbricate or valvate but rarely hooded or concave; disk present or absent; fruits capsular, baccate, or drupaceous; ovules anatropous to hemitropous, obturator present

Subfamily 1. Phyllanthoideae Ascherson, *Flora der Provinz Brandenburg, 1*: 59 (1864). Laticifers absent; leaves stipulate, simple (except *Bischofia*), usually alternate, and entire; petals and disk present or absent; pollen grains 2-nucleate, exine not spinulose; ovules 2 per locule; seeds rarely carunculate. 13 tribes with 50 genera, c. 2000 species; common in wet to seasonal habitats, but rare in deserts

Subfamily 2. Oldfieldioideae Köhler & Webster, *Journal of the Arnold Arboretum, 48*: 308 (1967). Laticifers absent; leaves exstipulate, simple or compound, alternate to opposite or whorled, entire or dentate; petals and disk absent; pollen grains 2-nucleate, exine usually distinctly spinulose; ovules 2 per locule; seed often carunculate. 4 tribes with 25 genera and c. 100 species; in wet to desert habitats

Subfamily 3. Acalyphoideae Ascherson, *Flora der Provinz Brandenburg, 1*: 58 (1864). Laticifers generally absent; leaves stipulate, simple to lobed (rarely compound), alternate (rarely opposite), entire to dentate; petals and disk present or absent; pollen grains 2-nucleate, exine neither spinulose nor with 'croton' pattern; ovules 1 per locule; seeds carunculate or not. 19 tribes (some of which perhaps should be combined) with 110 genera, c. 1500 species; in many habitats

Subfamily 4. Crotonoideae Pax, *Natürlichen Pflanzenfamilien, 3(5)*: 14 (1890) Articulated and/or non-articulated laticifers usually present; leaves stipulate, simple to compound, alternate (rarely opposite), entire to dentate; sepals mostly imbricate; petals and disk usually present; pollen grains 2-nucleate or 3-nucleate, exine mostly with 'croton' pattern; ovules 1 per locule; seeds often carunculate. 11 tribes with c. 70 genera, c. 2000 species; well represented from rain forest to desert

Subfamily 5. Euphorbioideae. Non-articulated laticifers usually present; leaves mostly stipulate (except in *Euphorbia*), simple to lobed, alternate (rarely opposite), entire to dentate; calyx mostly valvate to obsolete (rarely imbricate); petals and usually disk absent; pollen grains 2-nucleate or 3-nucleate, exine reticulate or tectate; ovules 1 per locule; seeds carunculate or not. 5 tribes with c. 40 genera, c. 2500 species; commonest in seasonal to arid regions.

Pandaceae Pierre, *Bulletin de la Société Linnéenne de Paris*, 1255 (1896); Engler & Gilg, *Syllabus der Pflanzenfamilien, Ed. 7*: 223 (1913)

Petals slightly imbricate to valvate, often hooded; disk absent; fruits drupaceous, endocarp often with processes or canals; ovules anatropous to orthotropous, obturator absent

Tribe 1. Dicoelieae Hurusawa, *Journal of the Faculty of Science, University of Tokyo, III. Botany, 6*: 322 (1954). 1 genus, *Dicoelia* Bentham, with 1 or possibly 2 species. Monoecious; flowers in axillary thyrses; pistillode with slender branches; styles entire, elongated; ovules 2 in each locule; fruit capsular

Tribe 2. Galearieae Bentham, *Genera Plantarum, 3*: 247, 287 (1880) Bennettieae R. Brown ex Schnizlein, *Iconographia Familiarum Naturalium Regni Vegetabilis, 3*: pl. 172 (1860?). 3 genera, *Galearia*, *Microdesmis*, and *Panda*, with c. 30 species. Dioecious; flowers in terminal thyrses or axillary clusters; pistillode unlobed; styles bifid; ovules 1 in each locule; fruit drupaceous

earlier. Morison (1680) appears to have been the earliest botanist to publish a distinct group, under the name *Plantae tricoccae purgatrices*. Linnaeus, in collaboration with van Royen (1740), established a class Tricoccae that included several Euphorbiaceous genera as well as a number of extraneous ones (*Cneorum*, *Montia*, *Phyllica*, *Osyris*). He proposed a similar treatment in the *Philosophia Botanica* (1751) under the name Tricocca, and (as Tricoccae) in an appendix to the sixth edition of the *Genera Plantarum* (1764). Of the 26 genera listed by Linnaeus under Tricoccae, only 16 are now considered Euphorbiaceous, and only five of the ten extraneous genera (*Buxus*, *Carica*, *Cneorum*, *Sterculia* and *Thryallis*) belong to families considered by later writers as of Euphorbialean affinity.

The name Tricoccae, for the group including the Euphorbiaceae and related families, continued to be used for more than two centuries; it was adopted by

Table 2
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Family

Aextoxica
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Buxaceae
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Empetrae
Forestier
Fouquier
Geissolon
Gyrostem
Haloragch
Lacistem
Lophopy
Malpigh
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Table 2. Families that have been included in the Euphorbiales (or Tricoccae) by major botanical authors. Segregate families (see Table 3) are not listed, except for Pandaceae. Only selected citations are included for some families. Incidental and provisional placements have mostly been omitted.

Family	Reference
Aextoxicaceae	Barkley, 1948; Dahlgren, 1980; Takhtajan, 1980; Thorne, 1980
Aquifoliaceae	Bartling, 1830
Batidaceae	Lindley, 1853
Buxaceae	Eichler, 1878; Gundersen, 1950; Cronquist, 1981
Callitrichaceae	Horaninov, 1847; Lindley, 1853; Wettstein, 1935
Celastraceae	Bartling, 1830; Lindley, 1833, 1836
Daphniphyllaceae	Wettstein, 1935; Emberger, 1960; Novák, 1961; Soó, 1967; Stebbins, 1974
Dichapetalaceae (Chailletiaceae)	Baillon, 1873; Pulle, 1938; Emberger, 1960; Novák, 1961; Thorne, 1983
Didymelaceae	Novák, 1961
Empetraceae	Lindley, 1836; Endlicher, 1841; Eichler, 1878; Warming, 1904
Forestieraceae	Brongniart, 1850
Fouquieriaceae	Lindley, 1836
Geissolomataceae	Hooker, 1876
Gyrostemonaceae	Lindley, 1853
Haloragchaceae	Horaninov, 1847
Lacistemaceae	Hooker, 1876
Lophopyxidaceae	Emberger, 1960
Malpighiaceae	Lindley, 1833
Nepenthaceae	Lindley, 1847
Pandaceae	Webster, 1967; Cronquist, 1968, 1981; Thorne, 1983
Penaecaceae	Hooker, 1876
Pittosporaceae	Bartling, 1830
Polygalaceae	Grisebach, 1854
Rhamnaceae	Bartling, 1830
Simmondsiaceae	Takhtajan, 1980; Cronquist, 1981; Dahlgren, 1983; Thorne, 1983
Stackhousiaceae	Bartling, 1830; Martius, 1835; Lindley, 1836
Thymelaeaceae	Thorne, 1968, 1983
Tremandraceae	Grisebach, 1854
Trigoniaceae	Grisebach, 1854

Endlicher (1841), Klotzsch (1859, 1860), Eichler (1878), Rendle (1925), Wettstein (1935), Copeland (1957) and Lanjouw *et al.* (1968). However, although its use still appears to be legal in the International Code Of Botanical Nomenclature (Voss *et al.*, 1983), the overwhelming number of 20th century systematists have used the name Euphorbiales. However, this nomenclatural consensus is rather misleading since, as mentioned earlier, the circumscription of the order Euphorbiales has been extremely variable.

The only other ordinal name that gained any currency during the 19th century is Cocciferae, which appears to have been introduced by Batsch (1802), who included the family Tricoccae. Martius (1835) treated Cocciferae as a "Cohors" apparently equivalent to the order Euphorbiales of Lindley. Grisebach (1854), the last major systematist to use the name Cocciferae, treated it as a Nexus with four families: Polygalaceae, Tremandraceae, Trigoniaceae, and Euphorbiaceae in an inclusive sense (including Putranjiveae, Pseudantheae, Scepaceae, Batideae, and Antidesmeae).

In reviewing the literature, I find that over 30 families have been included in the Euphorbiales by leading botanists in the 19th and 20th centuries (Table 2);

and the number would be considerably higher if all of the families segregated from the Euphorbiaceae were included. Redefinitions of the boundaries of the Euphorbiales have steadily gone on since the initial listing of the constituent genera of Tricoccae by Linnaeus (1751, 1764). During the critical period 1825-1840 when the natural system was replacing the Linnean system, the publications of Lindley (1833, 1836) were most influential in establishing the order as the standard hierarchical group that includes one or more families (despite the fact that Lindley used the term "alliance" in place of order, and "order" for family, his use of the endings -ales and -aceae established the precedent for later usage). Lindley (1836) included five families within Euphorbiales: Euphorbiaceae, Empetraceae, Stackhousiaceae, Fouquieriaceae, and Celastraceae. Although the latter three families were not regarded as Euphorbialean by subsequent workers, the Empetraceae continued to be assigned to the Euphorbiales by Endlicher (1841), Eichler (1878), and Warming (1904). In the third edition of his *Vegetable Kingdom*, Lindley (1853) offered his matured judgement about the membership of the Euphorbiales, and, as sometimes happens, it was retrogressive; Stackhousiaceae, Fouquieriaceae, and Celastraceae were excluded, but their replacements were families that on the whole would be regarded as even less closely related to the Euphorbiaceae: Batidaceae, Callitrichaceae, Gyrostemonaceae, and Nepenthaceae.

A particular role in the taxonomic history of the Euphorbiales has been played by the family Buxaceae. The boxwoods were included in Linnaeus's Tricoccae, and in the Euphorbiaceae by Adanson (1763; as Tithymali), A. L. Jussieu (1789), and Adrien Jussieu (1824). Since Lindley (1836) also included Buxaceae within Euphorbiaceae, the Euphorbiaceous core of the order was tainted with Buxacean characters. Baillon (1856, 1858, 1859) deserves the credit for clearly demonstrating that *Buxus* does not belong to the Euphorbiaceae, although he appears to have been anticipated by Plée (1854). Baillon (1859), in his monograph of the Buxaceae, reaffirmed his earlier statements by providing a detailed description and excellent illustrations of floral morphology in *Buxus* and related genera. He showed clearly that the Buxaceae differ significantly from the Euphorbiaceae in characters of the gynoeceum, especially in the peripheral position of the styles on the carpels and the apotropous ovules. Agardh (1857) had recently described and illustrated the differences in ovule position that involve the relative placement of the funiculus (raphe) with respect to the placentation. Although Baillon did not use Agardh's terminology, it is clear from his description that the ovules of *Buxus*, with the raphe turned away from the placenta (outside the micropyle), are strikingly different in orientation from the ovules of typical Euphorbiaceae, where the raphe is next to the placenta (and the micropyle outside) and the ovules would be described as apotropous. The systematic value of this character has been disputed, for example by Asa Gray (1879); and Bentham (1878, 1880), after finding exceptions to most of Baillon's diagnostic characters for Buxaceae, did not consider epitropous ovules of sufficient weight to merit placing *Buxus* in a family separate from Euphorbiaceae. However, Mueller (1866a) and Pax (1884, 1890) were convinced by Baillon's arguments and accepted Buxaceae as a distinct family. Although Eichler (1878) retained Buxaceae in the Euphorbiales (Tricoccae), Engler (1892, 1897) transferred the Buxaceae to the Celastrales. During the 20th century, the influence of Bentham and Eichler is apparent in the retention

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of the Buxaceae in the Euphorbiales by Rendle (1925), Wettstein (1935) and Cronquist (1981).

Although Dang-Van-Liem (1962) affirmed an embryological similarity between Buxaceae and Celastrales, the preponderance of evidence pointed toward a position in or near the Hamamelidales; this is well summarized by Takhtajan (1980). Some floral features of Buxaceae, such as the tardily closing carpels with peculiar development of placentation, interpreted as parietal by Baillon, and elongated outer integuments suggest features of the Hamamelidales as discussed by Endress (1977). Also, the presence of laterocytic stomata in Buxaceae (Baranova, 1983) supports a connection with Hamamelidales. Embryologically, the Buxaceae diverge sharply from the Euphorbiaceae in the presence of cellular endosperm and a different pattern of differentiation of the integuments (Davis, 1966; Wiger, 1935; Wunderlich, 1968). At the same time, it must be noted that the Buxaceae differ from other Hamamelidalean taxa in embryological characters and other features. Behnke (1982) has recently shown that the sieve-tube plastids of Buxaceae (*sensu stricto*) are of a unique type different from *Daphniphyllum* and other Hamamelidales, as well as *Simmondsia* and the Euphorbiaceae.

A recurrent problem with the Buxaceae is the controversial circumscription of the family, due mainly to questions regarding the aberrant genus *Simmondsia*, which was described by Nuttall (1844) as resembling Garryaceae and Euphorbiaceae, and placed in the Euphorbiaceae by Lindley (1853). Baillon (1858) followed Nuttall in assigning it to the Garryaceae, a disposition rejected by Mueller Argoviensis (1866a, 1869), who referred *Simmondsia* to the Buxaceae. van Tieghem (1897a, 1898) removed *Simmondsia* to a separate family, which he suggested belonged to the Centrospermae in the neighborhood of the Tetragnoniaceae. Until recently, most botanists followed Mueller in treating *Simmondsia* as a genus of Buxaceae, although Melikian (1968) supported van Tieghem on the basis of seed coat structure. Wagenitz (1975) notes that the ovular structure in *Simmondsia* is incompatible with membership in the Centrospermae, but doubts that Simmondsiaceae, Buxaceae, and Daphniphyllaceae are closely related to the Hamamelidales. Scogin (1980) has claimed support for Lindley's Euphorbiaceous assignment on the grounds of similarities in serological experiments. Thorne (1981, 1983), on the basis of Scogin's evidence, now classifies Simmondsiaceae as a family of Euphorbiales closely related to Euphorbiaceae and far removed from Buxaceae (*sensu stricto*), which Thorne refers to the Pittosporales.

The decision of Scogin and Thorne to place Simmondsiaceae in the Euphorbiales is contested by Köhler & Bruckner (1983), who find that the pollen of *Simmondsia*, as originally indicated by Erdtman (1952), is quite different from other taxa assigned to Buxaceae. In its large rather poorly defined operculate apertures it is also different from any known Euphorbiaceae (Köhler & Bruckner, 1983; Webster, unpubl.). Corner (1976) regards the seed coat structure in *Simmondsia* as typical for Buxaceae, which belongs to his mesotestal class, in contrast to the exotegmic Euphorbiaceae. In view of the ambiguity that surrounds interpretation of many serological studies, and the contrary evidence from pollen and seed structure, I think that the case for assigning Simmondsiaceae to Euphorbiales is weak. Furthermore, the recent study of sieve-element plastids in Buxaceae by Behnke (1982) shows that *Simmondsia*,

with S-type plastids, strongly differs from the Buxaceae (*sensu stricto*), which have a unique type of plastid with a central globular protein crystal. This would seem to leave the Simmondsiaceae as a very isolated group without close relationship to either Buxaceae or Euphorbiaceae. Nevertheless, as Köhler & Bruckner (1983) point out, the resemblances between *Simmondsia* and the Buxaceae in wood anatomy, stomatal type, chromosome number, pollen exine stratification and seed coat development do not preclude a taxonomic association, even if not very close, between the two families. On the basis of present evidence, I believe that there is support for the decision of Novák (1961) to place Buxaceae in a separate order Buxales; and perhaps the Simmondsiaceae should be referred to the same order.

A genus that has at times accompanied the Buxaceae in these labyrinthine taxonomic paths is *Daphniphyllum*. Lindley (1853) originally followed the suggestion of Blume (1826) that *Daphniphyllum* might belong to the Rhamnaceae, but Planchon (1854) referred it to the Scapeaceae (i.e. Euphorbiaceae tribe Aporuseae), and Baillon (1858) accepted it as a genus of Euphorbiaceae. Mueller (1866a) disagreed and suggested that it might belong to the "Ilicineae"; later (1869) he proposed the family Daphniphyllaceae and noted resemblances to Buxaceae, Euphorbiaceae and Ilicineae. Bentham (1880) returned to Baillon's opinion that *Daphniphyllum* belongs in the Euphorbiaceae, and due perhaps to his influence the Daphniphyllaceae, although usually treated as a family distinct from the Euphorbiaceae, was often juxtaposed in taxonomic treatments (e.g. by Rosenthal, 1919, 1931). Hallier (1904) broke radically with this tradition by transferring *Daphniphyllum* into a tribe of the Hamamelidaceae, an opinion that displayed great taxonomic insight. Support has been given to Hallier's position on the basis of wood anatomy by Janssonius (1950), and on grounds of general morphology by Hutchinson (1959) and Airy Shaw (1966). Although some recent workers (Novák, 1961; Scholz, 1964; Soó, 1967; Stebbins, 1974) have continued to place Daphniphyllaceae in the Euphorbiales, it is excluded by others. Bhatnagar & Garg (1977) note that Daphniphyllaceae differ from Euphorbiaceae in their cellular endosperm development, as well as in pollen characters. Takhtajan (1980) has the Daphniphyllaceae, associated with the Simmondsiaceae, in suborder Buxineae in the Hamamelidales; Cronquist (1981, 1983) recognizes a separate order Daphniphyllales (Hurusawa, 1954) in the Hamamelidae; Dahlgren (1983) places it in the Buxales along with Buxaceae and Didymelaceae; and Thorne (1983) puts it in suborder Buxineae of Pittosporales. Based on the characters discussed above, it appears to me that the classifications of Takhtajan and Cronquist best agree with available evidence.

A recent phenetic study of families in the Hamamelidae by Barabé *et al.* (1982) found the Daphniphyllaceae, Buxaceae, Simmondsiaceae and Didymelaceae to be most closely related not to the 'classic' Hamamelidalean families but rather to fringe families such as the Leitneriaceae, Barbeyaceae, Balanopaceae and Eucommiaceae. The authors note a closer phenetic resemblance of Daphniphyllaceae to Balanopaceae rather than with Buxaceae, and suggest that the Buxaceae and Simmondsiaceae should probably be excluded from the Hamamelidales. These results are not necessarily incompatible with the classifications of Takhtajan, Dahlgren, and Thorne, but seem inconclusive; a thorough cladistic analysis of the complex of families might well produce a more significant insight into relationships.

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The small Madagascar genus *Didymeles* has been regarded as allied to the Leitneriaceae by some workers (Baillon, 1873b; Leandri, 1937) and with Euphorbiaceae by others (Novák, 1961; Thorne, 1968, 1976). However, the suggestion of a Hamamelidalean affinity made by Hallier (1912) has been supported on anatomical grounds by Melikian (1973) and Cronquist (1981), who both accept a separate order Didymelales, adjacent to Hamamelidales. In contrast, the palynological study of *Didymeles* by Köhler (1980) indicates a resemblance to Buxaceae; and Carlquist (1982) detects anatomical similarities to Buxaceae. Thorne (1983), therefore, places the Didymelaceae along with Buxaceae, Daphniphyllaceae and Balanopaceae in a suborder of his Pittosporales.

Whether the Hamamelidalean or the Pittosporalean affinity of Buxaceae and Daphniphyllaceae is preferable remains an open question, but at least there is something of a consensus (not entirely shared by Cronquist, 1981) that the Buxaceae and Daphniphyllaceae are not closely related to Euphorbiales. Another family whose Euphorbialean connections are now generally discredited is the Callitrichaceae. Lindley (1853), approving an earlier suggestion by Reichenbach (1837), placed the Callitrichaceae in the Euphorbiales and questioned whether it should even be considered distinct from the Euphorbiaceae. Baillon (1957, 1858) concurred and actually demoted the Callitrichaceae to a tribe of Euphorbiaceae. This was rejected by Mueller (1866a), who accepted the older view of Robert Brown that *Callitriche* is related to the Hippuridaceae. Notwithstanding, the prevailing opinion in the century after Baillon was that Callitrichaceae were close to Euphorbiaceae; Pax (1890, 1931) associated *Callitriche* with Euphorbiaceae in a common suborder; and Rendle (1925) and Wettstein (1935) had both families in the Euphorbiales (Tricoccae). However, Clarke (1865) noted a gynoeceal resemblance between Callitrichaceae and Boraginaceae, and much later Jorgensen (1923, 1925) pointed out that the 4-lobed gynoeceum and seeds with cellular, haustorial endosperm development are characteristic of taxa in the Tubiflorae (Asteridae). There is still some disagreement about the position of the Callitrichaceae, since Cronquist (1981) associates it with the Hippuridaceae in an order Callitrichales, whereas Takhtajan (1980) and Thorne (1983) put it into the Lamiales; but since Cronquist's Callitrichales immediately follows Lamiales, the difference is not very significant.

A more difficult case than that of the Callitrichaceae is presented by the Dichapetalaceae, which Lindley (1853) placed in the Rhamnales (under the old family name Chailletiaceae). Baillon (1874) included the Dichapetalaceae as a tribe within the Euphorbiaceae. Engler (1897), perhaps influenced by Baillon, placed the Dichapetalaceae in a separate suborder of the Geraniales adjacent to the suborder Tricoccae. Van Tieghem (1903), on the other hand, related the Dichapetalaceae to the Convolvulaceae because of the sympetalous corolla of some taxa. The Dichapetalaceae have more recently been classified in the Euphorbiales by Wettstein (1935), Novák (1961), Takhtajan (1980), Dahlgren (1983) and Thorne (1983).

However, the resemblances of Dichapetalaceae to Euphorbiaceae are not very convincing, and alternative suggestions of relationship have been made, especially with the Celastrales. Lobreau (1969) indeed suggested a relationship between Dichapetalaceae and Euphorbiaceae on the basis of pollen morphology, but later (Lobreau-Callen, 1976) she decided that Euphorbiaceous

pollen itself shows similarities to Celastralean families such as the Aquifoliaceae and Icacinaceae. Punt (1975), on the basis of a detailed survey of the pollen of Dichapetalaceae, disagrees that there is any significant similarity with the pollen of Euphorbiaceae, studied by him earlier (Punt, 1962). Punt suggests that there are more impressive resemblances between the pollen of Dichapetalaceae and Malpighiaceae. Prance (1972), in a revision of the neotropical Dichapetalaceae, also supports a Celastralean affinity, with particular ties to the Celastraceae and Icacinaceae. In this instance, it appears that the concensus of our phylogeneticists is not very well-founded, and the best classification appears to be that of Cronquist (1981), who places the Dichapetalaceae in the Celastrales (but admittedly hedges his bets by having it immediately precede the Euphorbiales).

A small family that has long been associated in the literature with the Euphorbiales is the Aextoxicaceae, a monogeneric family endemic to Chile. W. J. Hooker (1836), when describing the genus *Aextoxicon*, ascribed it with some doubt to the Euphorbiaceae; similar opinions were indicated by Endlicher (1841) and Lindley (1853). Baillon (1858) regarded it as forming a group intermediate between the Celastraceae and "Ilicinées"; Miers (1862) related *Aextoxicon* to Icacinaceae (as part of Aquifoliaceae). Decaisne (1858), possibly influenced by the prominence of Monimiaceae in Chile, suggested a comparison with Monimiaceae, which was viewed with approval by Mueller (1866a). Bentham (1878, 1880), who was impressed by the resemblance of the lepidote indumentum of *Aextoxicon* to that of *Hyeronima*, as well as other resemblances between the Chilean plant and various Euphorbiaceae, firmly placed *Aextoxicon* in the tribe Phyllanthae of the Euphorbiaceae. Pax (1890) at first followed Bentham, but later (Pax & Hoffmann, 1917) reconsidered and created a separate family, the Aextoxicaceae, located adjacent to the Icacinaceae. In the latest edition of Engler's *Syllabus*, Scholz (1964) assigns the Aextoxicaceae to the Sapindales. Both 19th century alternative traditions have persisted into recent times, with Takhtajan (1980) and Thorne (1983) referring the Aextoxicaceae to the Euphorbiales, while Hutchinson (1973) and Cronquist (1981) follow the tradition of Baillon, Miers and Pax in treating them as a family of Celastrales. In my opinion, the preponderance of evidence favours the Celastralean view, but *Aextoxicon* is still a very poorly known plant and needs much more detailed study before its relationships can be clarified.

Another small family that has been referred to the Euphorbiales is the Lophopyxidaceae. Although only relatively recently given family status by Pfeiffer (1951), *Lophopyxis* was originally described by J. D Hooker (1887) as a genus of Euphorbiaceae, but of doubtful affinity. Pax (1890) expressed even greater doubt about relationship with the Euphorbiaceae, and Engler (1893) created a subfamily Lophopyxidoideae within the Icacinaceae. Van Tieghem (1897b) recognized it as a distinct family, but with the invalid name Lophopyxidacées. Although Hallier (1910) and Emberger (1960) have reaffirmed the affinity with Euphorbiaceae, most recent workers would disagree. Airy Shaw (1966) indicated a relationship with the Rhamnaceae (tribe Gouanieae), but this also has received little support. Hutchinson (1959) referred *Lophopyxis* to the Celastraceae, and Scholz (1964) placed it in the subfamily Tripterygioideae of Celastraceae. Sleumer (1968), on the other hand, argues that although related to Celastraceae, Lophopyxidaceae should be recognized as

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a distinct family. Sleumer's argument is reinforced by the pollen study of Lobreau (1969), who found the pollen structure of *Lophopyxis* to be more similar to Tiliales than to Celastrales. Takhtajan (1980) accepts the Lophopyxidaceae as a distinct family of Celastrales, but Cronquist (1981) regards it as only an aberrant genus of Celastraceae. Here we seem to have a recent consensus, at least at the ordinal level; Lophopyxidaceae is Celastralean in affinity and not related to the Euphorbiales.

The family Caricaceae has not often been mentioned as a candidate for admission into the Euphorbiales, although Adanson (1763) included *Carica* in the Euphorbiaceae. However, Hallier (1896, 1903) argued for a close relationship between Papayaceae (= Caricaceae) and Euphorbiaceae on the basis of resemblance in seed coat structure. As indicated by Corner (1976), the seed coat in Caricaceae is indeed exotegmic in development, but differs in a number of ways that are more like Violaes than Euphorbiales. The rather striking vegetative and floral resemblances between *Carica* and the Euphorbiaceous genus *Cnidocolus* appear to be only a striking example of convergence (it is notable that the flowers in both are primarily lepidopteran-pollinated). There is a rather tenuous biochemical similarity in the presence of glucosinolates in both Caricaceae and Euphorbiaceae (Kjaer, 1973), but so far glucosinolates are reported only from the isolated tribe Drypetae in the Euphorbiaceae, and the resemblance seems more likely to be a convergence. Spencer & Seigler (1984) show that *Carica papaya* is the only known species to produce both glucosinolates and cyanogenic glycosides. These glycosides are of two types: prunasin, a phenylalanine-derived glucoside; and tetraphyllin B, with a cyclopentene ring. The latter compound is characteristic of the Violalean families Flacourtiaceae, Turneraceae and Passifloraceae; so the biochemical evidence at least in part agrees with morphological similarities in suggesting a Violalean position for Caricaceae; and there is indeed a consensus on this point in the classifications of Takhtajan (1980), Cronquist (1981), Dahlgren (1983) and Thorne (1983).

The last, but definitely not the most insignificant, family to be discussed with regard to possible Euphorbialean affinities is the Thymelaeaceae. Although traditionally placed in the Myrtales (e.g. by Cronquist, 1981; Eichler, 1878; Grisebach, 1854; and Wettstein, 1935) or in a separate order Thymelaeales (Gundersen, 1950; Hutchinson, 1973; Pfitzer, 1894; Wagenitz, 1964), the alternative of a relationship with the Euphorbiaceae has surfaced in recent years. Domke (1934), on the basis of floral morphological characters, suggested an overall Malvalean affinity, with particular floral resemblances between Thymelaeaceae and Euphorbiaceae/Dichapetalaceae. Erdtman (1952) emphasized the palynological similarities ("crotonoid" exine) between genera of Euphorbiaceae and Thymelaeaceae, which apparently influenced Thorne (1968) in his placement of the Thymelaeaceae in the Euphorbiales. There are also some biochemical similarities. Paris (1963) notes that the coumarin glycoside daphnetin has been reported only from Thymelaeaceae and Euphorbiaceae. Ourisson (1973) indicates that Thymelaeaceae and Euphorbiaceae also share common diterpenes (phorbol esters). In opposition to these tantalizing suggestions of phylogenetic affinity must be set some considerable morphological differences: Thymelaeaceae have exstipulate leaves, polytelic inflorescences, strongly perigynous flowers with anthers inserted on the

hypanthial tube, and often a pseudomonorous gynoecium. The study of floral anatomy by Heinig (1951) does not indicate any special resemblance to the Euphorbiales. The most impressive recent evidence for a relationship comes from studies of seed coat anatomy by Wunderlich (1968) and Corner (1976), who find that most genera in both families have an exotegmic seed coat with a palisade layer derived from the outer epidermis of the inner integument. As pointed out by a number of writers, this also furnishes evidence in favour of a placement of both Thymelaeaceae and Euphorbiaceae near the Malvales. In my opinion, the many floral differences make it undesirable to locate the Thymelaeaceae within the Euphorbiales, as is done by Thorne (1983). The classifications of Takhtajan (1980) and Dahlgren *et al.* (1981), in which the Euphorbiales and Thymelaeales are juxtaposed within a superorder Malviflorae, would better accord with the facts. My own inclination is to tentatively associate the Euphorbiales and Thymelaeales together, but in a superorder separate from the Malviflorae. However, it is not yet certain that this is the best solution, and there is still the alternative of a Myrtalean affinity for the Thymelaeales, which we must now consider.

Dahlgren & Thorne (1985) argue that the Thymelaeaceae cannot be regarded as related to typical Myrtales because of a number of biochemical and embryological characters (e.g. lack of ellagic acid, presence of coumarins, different pollen grains, ovules with obturator, and exotegmic seed coat development in Thymelaeaceae). They therefore reaffirm the Malvalean/Euphorbialean position of Thymelaeaceae proposed by Thorne (1968, 1983) and adopted by Takhtajan (1980) and Dahlgren (1983). On the other hand, characters of Thymelaeales more or less concordant with Myrtales are reported in leaf histology (Keating, 1985), wood anatomy (van Vliet & Baas, 1985), sieve-element plastids (Behnke, 1985), and a number of reproductive features (Schmid, 1985). Cronquist (1985) provides a vigorous rebuttal to the Dahlgren/Thorne classification, and notes that most of the resemblances between Thymelaeales and Euphorbiales cited by those authors are either primitive (plesiomorphic) or else, e.g. the common occurrence of daphnetin in *Daphne* and in *Euphorbia*, may represent convergence. It is clear that the jury is still out, and more evidence and analysis is needed to break this deadlock between the experts. However, whatever the position of the Thymelaeaceae may prove to be, I am in sympathy with Cronquist's opinion that it should be assigned to a separate order, and not be included within the Euphorbiales. Perhaps it is worth reconsidering the earlier classification of Dahlgren (1975), in which the Thymelaeales are placed in a superorder Thymelaeanae immediately following the Euphorbiales.

Looking back over the families we have reviewed as candidates for admission to the Euphorbiales, it is apparent that the credentials of most of them are seriously defective. The Buxaceae, although long included within the Euphorbiaceae, now appear to lie outside the Euphorbiales because of both reproductive characters (carpel morphology, apotropous ovules, cellular endosperm and mesotestal seed coat development). The Simmondsiaceae, although approaching the Euphorbiaceae in some respects, differ fundamentally in pollen structure, and may be aberrant relatives of the Buxaceae. Daphniphyllaceae, although not closely related to Buxaceae as has sometimes been suggested, may also be of general Hamamelidalean affinity, and this is

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probably also true of the Didymelaceae. Certain small families, notably the Aextoxicaceae, Lophopyxidaceae, Stackhousiaceae, and perhaps the Dichapetalaceae, appear to lie closer to the Celastrales. The Callitrichaceae are now generally accepted as belonging in the Asteridae in or near the Lamiales.

After excluding all of these families, there is only one remaining to consider for inclusion in the Euphorbiales: the Pandaceae. This small Old World group was first recognized as possibly meriting family status by Robert Brown (Bennett & Brown, 1852) when he published the genus *Bennettia* from Java, based on the plant now treated as *Galearia filiformis* (Bl.) Boerl. (Forman, 1971). Brown's family name Bennettiaceae is invalid because he proposed it only in a provisional sense, but the name was validated (with the spelling Bennettiaceae) by Schnizlein (c. 1860). Schnizlein agreed with Brown that *Bennettia* showed resemblances to Euphorbiaceae, and especially with Antidesmaceae, then generally considered a distinct family. Schnizlein also suggested a possible affinity between *Bennettia* (i.e., *Galearia*) and *Phytocrene* (Icacinaeae).

Mueller (1866a) demoted the Bennettiaceae to a subtribe of his tribe Hippomaneae, noting that it was atypical in having the sepals scarcely imbricate. Bentham (1878, 1880) clearly considered *Galearia* and allied genera as occupying a distinctive position in the Euphorbiaceae, since he created Galearieae as one of the six major groups (tribes) in the family. Bentham specifically noted an affinity between *Pentabrachion*, a genus of subfamily Phyllanthoideae, and *Microdesmis*, a genus described by Hooker (1848). Bentham's Galearieae was heterogeneous, as he also included in it *Pogonophora* and *Tetrorchidium*, two genera of subfamily Acalyphoideae and Crotonoideae, respectively. Pax (1890) at first improved the definition of the group, treated by him as subtribe Galeariinae of tribe Clutiae, by removing *Tetrorchidium*; however, he later (Pax, 1911) added the genus *Syndyophyllum* Schum. & Lauterbach, which differs from the other Galearieae in opposite leaves, monoecious flower production and capsular fruit. Airy Shaw (1960) has shown that the branching pattern in *Syndyophyllum* is quite different from that in *Galearia* or *Microdesmis*, and that it has much more in common with *Erismanthus* and *Moultonianthus*. In the system of Webster (1975), *Syndyophyllum*, *Erismanthus* and *Moultonianthus* are associated in tribe Erismantheae of subfamily Acalyphoideae.

After it had been relegated to obscurity for the better part of a century due to the influence of Pax, the Bennettiaceae of Robert Brown and Schizlein was revived by Forman (1966) as the family Pandaceae. Forman provides a detailed history of the family, beginning with the recognition of the Pandaceae by Pierre (1896) concomitantly with his description of the new genus *Panda*. Pierre, in the same publication, recognized the affinity of *Microdesmis* with *Panda*; and the following year (Pierre, 1897) he added *Galearia* to the family. Engler (1912a, b) disagreed with Pierre's conclusions, mainly because the orthotropous ovules of *Panda* contrasted with the more-or-less anatropous ovules of *Galearia* and *Microdesmis*; he restricted the Pandaceae to include only *Panda*, and erected a new order, the Pandales. Forman (1966) confirmed the disposition of Pierre with a detailed study of fruit structure and branching pattern, with contributions on anatomical characters by Metcalfe and Parameswaran.

In a review of the problems of circumscription of the family Euphorbiaceae (Webster, 1967), I agreed that it appeared expedient to recognize the Pandaceae as a distinct family because of a constellation of distinctive features

(unusual configuration of petals and stamens in male flowers, divergent fruit type, orthotropous ovules in *Panda*, and the unusual chromosome number of $n=15$ in *Microdesmis*). In my synopsis of the subfamilies and tribes of Euphorbiaceae (Webster, 1975), I omitted mention of the genera of Pandaceae, thus implicitly continuing recognition of Forman's family concept.

Now, two decades after Forman's proposal to reinstate the Pandaceae, my opinion is still equivocal. The three genera of Pandaceae *sensu* Forman appear to form a natural group, but they show many similarities to the Euphorbiaceae. It seems probable that the ancestry of the Pandaceae is to be sought within the subfamily Phyllanthoideae, and a significant clue to phylogenetic relationships was given by Bentham (1878), who noted the resemblance in floral structure between *Dicoelia* and *Galearia*, and in his arrangement of genera (1880) placed *Dicoelia* as the final genus of Phyllanthaeae, immediately preceding *Galearia*. Admittedly, *Dicoelia* differs from *Galearia* in its capsular fruit, monoecious flower production (in axillary thyrses), and undivided styles, but it nevertheless is similar in its habit, in the conformation of the staminate flowers (due to position of anthers in concavities in the petals), and in the lack of a floral disk. Although *Dicoelia* is still very poorly known, my own impression is that Bentham's intuition is probably well founded, and that *Dicoelia* stands in an ancestral or collateral relationship to *Galearia* and the other Pandaceae. The separation of *Dicoelia* from these other genera because of its biovulate locules has been overemphasized; there is no reason, after all, why reduction to uniovulate locules could not have occurred, along with other specialized characters, during the evolution of the Pandaceae. In the tabulation of the taxa of Euphorbiales in this paper, I have therefore transferred tribe Dicoelieae from the Euphorbiaceae to the Pandaceae.

However, this does not really solve the problem of family delimitation. Adding a monoecious genus with biovulate carpels to the Pandaceae blurs the distinctions, already difficult to articulate, from the Euphorbiaceae. As Backhuizen van den Brink (1968) remarked, it is a weak argument to recognize the Pandaceae as distinct in order to make the Euphorbiaceae more homogeneous. I believe that the addition of *Dicoelia* to the Pandaceae is an improved reflection of phylogenetic relationships, but it admittedly raises at least as many questions as it answers. Although *Dicoelia* is certainly an isolated genus when placed in the Euphorbiaceae subfamily Phyllanthoideae, it does not appear totally alien either. One could argue that the recognition of the relationship between *Dicoelia* and *Galearia* just as logically suggests incorporating the Pandaceae into the Euphorbiaceae, perhaps as a separate subfamily. The phylogeny of subfamily Acalyphoideae is still very poorly understood, but it is possible that the genera of the Pandaceae represent the sister group to other tribes of Acalyphoideae, such as Erismantheae and Cheiloseae, and perhaps lie near the stem of the Acalyphoideae as a whole. If that proved to be so, the Pandaceae might shrink to the status of a tribe within the Acalyphoideae. The recognition of the Pandaceae as a family distinct from Euphorbiaceae in this paper is therefore done provisionally and for reasons of expedience, not because I am convinced that these two families represent the optimal suprageneric grouping for the taxa of Euphorbiales. In effect, I agree with Croizat (1973) and Hutchinson (1973) in accepting the Euphorbiaceae as the only major family within the Euphorbiales.

RELATIONSHIPS OF THE EUPHORBIALES

To a considerable extent, the history just reviewed of the varying concepts of membership in the Euphorbiales gives an impression of the way systematists have interpreted the relationships of the order to other suprafamilial groups of dicotyledons. The early treatments by Linnaeus (1751, 1764), Adanson (1763) and A. L. de Jussieu (1789) included genera that would now be referred to Malvales, Rhamnales, Geraniales, Sapindales and Violales (in the broad Englerian sense of these orders). However, from the beginning systematists also offered speculations about possible relationships of the Euphorbiaceae; Adanson (1763), for example, noted that his Tithymali approached the Pistaciae (a mixture of mostly Geraniales and Sapindales) in characters of stamens, ovules, and stem exudates.

Ventenat (1799) remarked that "les Tithymaloïdes se rapprochent, par plusieurs caractères, des Rhamnoides". Adrien de Jussieu (1824), the first monographer of the Euphorbiaceae, did not offer any speculations about its affinities with other families (perhaps reflecting his greater knowledge of the magnitude of the problem!). Lindley (1836) listed the Euphorbiales immediately after the Rhamnales, and commented on similarities of the Euphorbiales with both Malvales and Rhamnales; all three orders were included in a common group Syncarposae. However, later he placed Euphorbiales following Urticales (Lindley, 1853), but with lateral affinities to the Malvales and Rhamnales. Lindley in 1853 appears to have had a working model of a progression from a simpler to more complex floral form, as he says: "Euphorbiaceae may be regarded then as a higher form of Urticads, and accordingly we find their lateral affinities also pointing to groups with a more complicated structure; as for example to the Rhamnads in the perigynous, and Malvads in the hypogynous Sub-class".

The first really detailed consideration of the affinities of the Euphorbiaceae was provided by Baillon (1858). Baillon, who always expressed his systematic conclusions in an idiosyncratic form, did not explicitly define an order Euphorbiales, but his discussion implies that the Euphorbiaceae represented an independent order. He found the greatest affinity of the Euphorbiaceae to be with the Malvales, and detected a parallel set of taxa, with different tribes of Euphorbiaceae corresponding to various families of Malvales. In a striking geometrical model (reconstructed in Fig. 1A), he imagined the Euphorbiaceae and Malvales arranged in parallel on the triangular face of a pyramid, with *Euphorbia* and *Malva* (an odd couple!) at the base, ascending through the families Byttneriaceae, Bombacaceae, and Sterculiaceae, with the "Helicterées" opposite the Scopaeeae, and at the apex of the triangle (and pyramid) the Urticaceae, reflecting the double relation of that family (in Baillon's mind) to both Malvales and Euphorbiaceae. On the second face of this pyramid he placed the Rhamnales, with emphasis on the Chailletiaceae (Dichapetalaceae), at the margin opposite the Euphorbiaceae, and the Rutales on the more distant margin; the third face to be occupied by the Geraniales, especially the Linaceae. This model can reasonably be converted into a dendrogram of putative relationships between the orders (Fig. 1B). It should be noted that Baillon's pyramidal design was probably copied from that of Weddell (1857), who used a very similar model (with many of the same families) to illustrate the affinities of the Urticaceae.

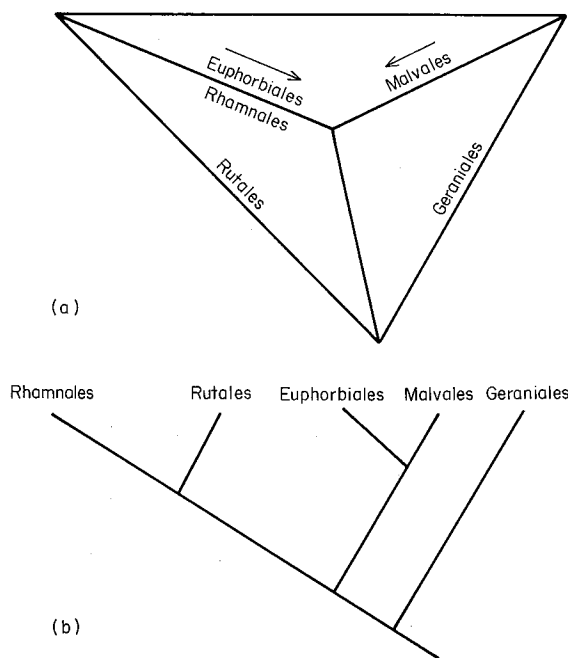


Figure 1. Baillon's model of relationships of Euphorbiaceae with other taxa. A. Pyramidal model described by Baillon (1858). B. Cladogram inferred from Baillon's description of relationships.

This model of Baillon epitomizes relationships observed by Lindley earlier, and other botanists who published later. Mueller (1866a) noted for the Euphorbiaceae that "affinitas ordinis vasti est multiplex", and gave priority of position to ties with Malvaceae and Urticaceae, but also mentioned possible affinities with Rhamnaceae, Dichapetalaceae, Sapindaceae, Burseraceae and Menispermaceae. Bentham (1878, 1880) was very non-committal about ordinal relationships, but he was impressed by the resemblances between tribe Phyllantheae of Euphorbiaceae with Rhamnaceae and Celastraceae, and between the Hippomaneae and Urticaceae. Eichler (1878) emphasized the taxonomic isolation of the Euphorbiales more than any previous systematist by creating for them a Reihe Tricoccae, one of his nine major groups of the dicotyledons (equivalent to the subclasses or superorders of contemporary botanists). In recent times, a similar degree of isolation has been proposed only by Emberger (1960), whose Phylum (=superorder) Tricoques has a single order Tricoques including Euphorbiaceae, Daphniphyllaceae, Dichapetalaceae and Lophopyxidaceae. Pax (1890) assigned the Euphorbiaceae to a suborder of Geraniales, a position probably dictated for him by Engler. It is rather surprising, incidentally, that Engler's system, which seems to have evolved from Eichler's (Staffeu, 1965), demoted the Euphorbiales from a superorder to a suborder of Geraniales. In an explication of his system, Engler (1897) does not offer any indication why this change was made.

An original but uninfluential hypothesis about the phylogenetic placement of the Euphorbiales was offered by Wettstein (1901, 1935). He regarded the apetaly of Euphorbiaceae as primitive, apparently due to his inability to

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imagine the biological reasons for reversion of bisexual flowers to unisexual ones, or the poor development of a corolla in insect-pollinated plants. In Wettstein's phyletic diagram (Fig. 2A) the Tricoccae are indicated as a connecting link between the Amentiferae and the Malvalean line, with the "Columniferae" derived from an Euphorbialean ancestry. In the "Stammbaum" of Wettstein's system published posthumously by Janchen (1932), the Euphorbiaceae are shown as a nodal family leading to the origin of both the Malvalean and Geranialean families; this resembles the model of Pax, discussed below, but with the direction of evolution reversed. Wettstein's theory that the Euphorbiaceae link the Amentiferae and Malvales has found little support among subsequent authors, although it appears to have influenced Däniker (1946), who found similarities between the Euphorbiaceae and Balanopaceae, and sought to derive the Juglandaceae from the Euphorbiaceae via the Balanopaceae.

When given the opportunity to express his own opinions, Pax (1924) did so in a discussion that summed up his conclusions after 40 years of work on the Euphorbiaceae. His solution to the problem of multiple affinities suggested by previous workers was to propose a frankly polyphyletic origin from both the Malvales and Geraniales (Fig. 2C), although he did not consider this to be true polyphyletic, since the Euphorbiaceae were considered to have branched off early in the evolution of both Malvales and Geraniales ("... die Euphorbiaceen sich sehr früh von den Urtypen der Geraniales und Malvales lösten und zu einer gewissen Selbständigkeit entwickelten"). Pax suggested that the euphorbiaceous taxa with basically imbricate sepals evolved from near the Geraniales, and those with valvate sepals from the Malvales. As an evolutionary model, this is defective because the 'valvate' taxa of Euphorbiaceae belong mainly to the derived subfamilies Acalyphoideae and Crotonoideae, and appear to be derived from 'imbricate' ancestors within the Euphorbiaceae (Webster, 1967, 1975).

The Paxian concept of a polyphyletic origin of the Euphorbiaceae apparently influenced Hutchinson (1926), who in his phyletic diagram indicated an origin of the Euphorbiales from the Malvales and Sapindales, an opinion concurred with by Croizat (1940). Later (1969a), Hutchinson explicitly stated (but without producing any new evidence) that the Euphorbiaceae are a composite group derived from a number of other families, including Tiliaceae, Sterculiaceae, Malvaceae, Celastraceae, Rhamnaceae, and Sapindaceae. In his last phyletic diagram (Hutchinson, 1973), the Euphorbiales are indicated as derived from the Malpighiales, Celastrales and Malvales; and they are the only order of dicotyledons shown to have a composite origin!

At about the same time as Pax's essay on the phylogeny of the Euphorbiaceae, serological workers also placed the Euphorbiaceae into juxtaposition with both Geraniales and Malvales, as is shown in the phylograms of Hoeffgen (1922) and Mez & Ziegenspeck (1926; Fig. 3). Similar placement of Euphorbiales in the vicinity of both Malvales and Geraniales has been made by a number of subsequent workers, such as Novák (1961, Fig. 2E) and Soó (1967, Fig. 2D).

We have already discussed some of the suggestions of affinity between the Euphorbiales and Thymelaeaceae, most of which seem to have been inspired by the similarity in pollen grains pointed out by Erdtman (1952). Croizat (1960), although most strongly favouring a Sterculiacean affinity for Euphorbiaceae, was also impressed by the similarity to the Thymelaeaceae. As I have noted,

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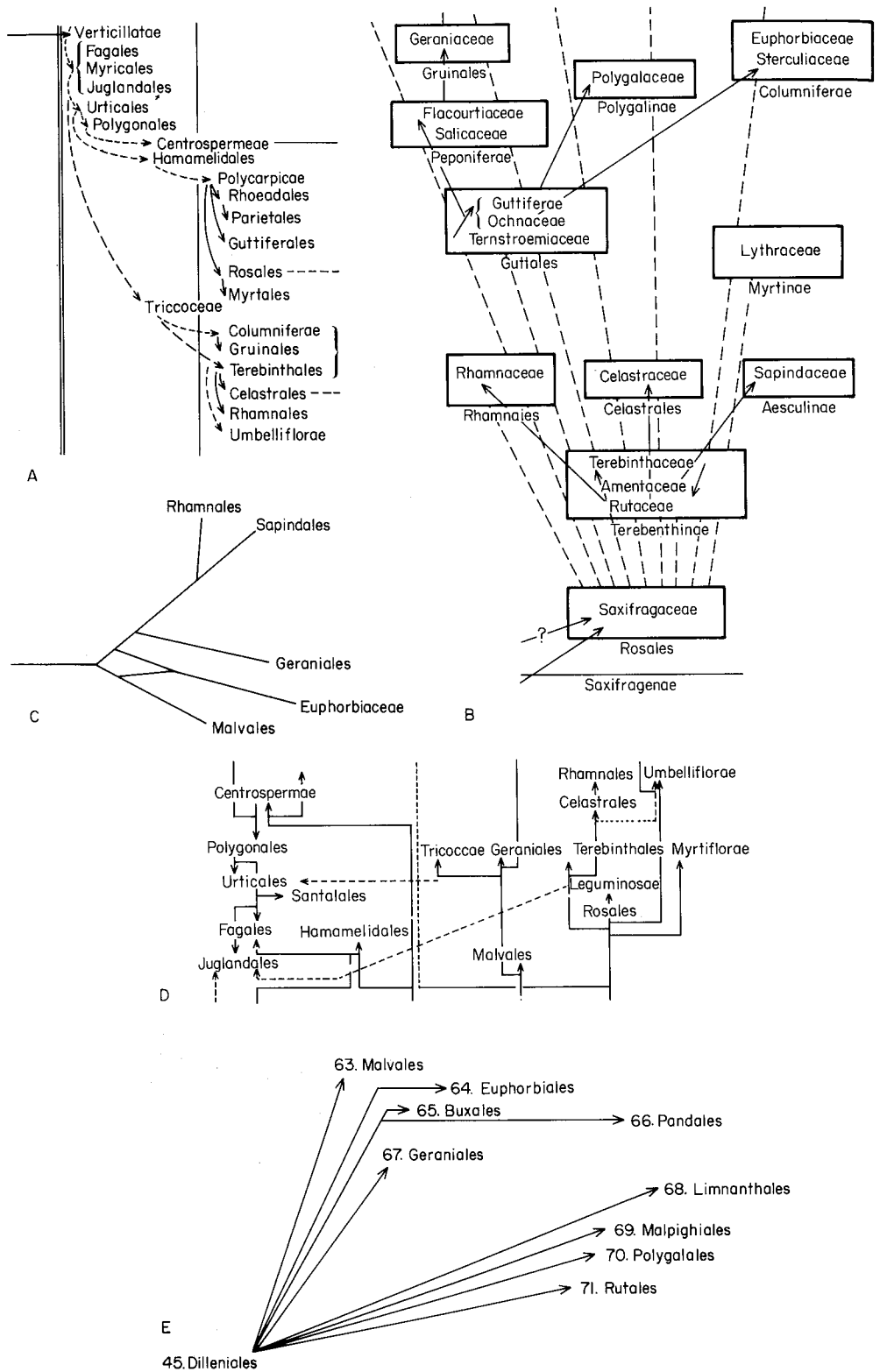


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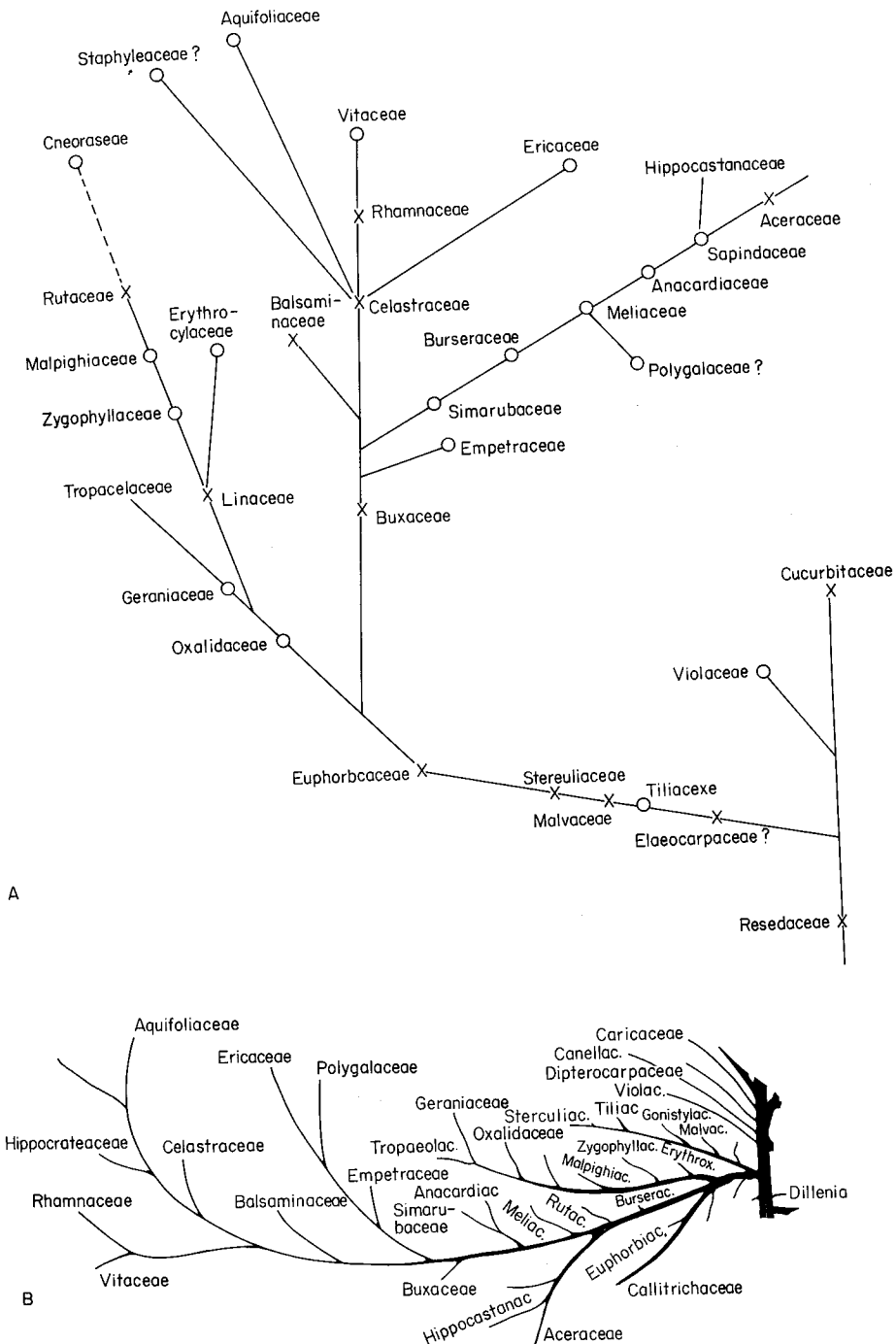


Figure 3. Phylograms based on serological studies. A. Hoeffgen (1922). B. Mez & Ziegenspeck (1926).

Figure 2. Phylograms proposed by various authors to illustrate the putative geneological relationships of the Euphorbiaceae (partly adapted from Grossheim & Sakhokia, 1966). A. Wettstein (1905). B. Hallier (1912). C. Pax (1924). D. Soó (1967). E. Novák (1961).

there is still uncertainty about the relative merits of a Myrtalean or Euphorbialean affinity for the Thymelaeaceae.

Another order that has been mentioned as having Euphorbialean connections is the Violales. The possible affinity of Caricaceae to Euphorbiaceae has already been mentioned, but in addition to that suggestion, Hallier (1903, 1912) also emphasized a possible relationship between Flacourtiaceae and Euphorbiaceae (Fig. 2B). This seems not to have been suggested by any prominent 19th century systematist, perhaps because the difference in placentation seemed too great. However, Janssonius (1950) commented on the resemblance in wood anatomy between certain genera in the two families, and Miller (1975) also sees some similarities. Croizat (1960) regarded a link between Flacourtiaceae and Euphorbiaceae as patently obvious, and Hutchinson (1967) pointed out similarities in gross floral morphology. Takhtajan (1966, 1969) stated that the Euphorbiaceae showed affinities to both Malvales and Flacourtiaceae. Keating (1973) has demonstrated palynological similarities between the Flacourtiaceae and Euphorbiaceae subfamily Phyllanthoideae. However, it is notable that in their recent treatments, Takhtajan (1980), Cronquist (1981) and Thorne (1983) do not mention any Violalean affinities of the Euphorbiales. I believe that this reflects a consensus (however subconscious) among our phyleticians that the similarities between Flacourtiaceae and Euphorbiaceae mentioned above are mainly unspecialized (plesiomorphous) characters that do not provide any compelling evidence for a common origin.

The most emphatic recent claim of Violalean ancestry for the Euphorbiales is made by Hickey & Wolfe (1975), on the basis of the occurrence of "Violoid" teeth in both groups. In the Euphorbiaceae subfamily Phyllanthoideae, Levin (1986) reports "Theoid" teeth in the genera *Drypetes*, *Putranjiva* and *Bischofia*; presumably the "Violoid" teeth of Hickey & Wolfe were reported from subfamilies Acalyphoideae and Crotonoideae. The presence of "Violoid" or "Theoid" teeth in both Euphorbiaceae and Flacourtiaceae could be regarded as significant if indeed this represents a shared advanced character due to common ancestry (synapomorphy). However, within the Euphorbiaceae subfamily Phyllanthoideae, the genera *Drypetes*, *Putranjiva* and *Bischofia* have advanced floral characters and cannot be regarded as primitive in the family; the genera that appear basal, such as *Heywoodia*, *Savia* and *Wielandia*, have entire leaves. It appears that the "Theoid" teeth in subfamily Phyllanthoideae, and the "Violoid" teeth in subfamilies Acalyphoideae and Crotonoideae, were "reinvented" from ancestral forms with entire leaves, so it can be argued that the similarity in the leaf tooth character does not represent a significant homology useful in determining the phyletic relationships between Euphorbiaceae and Flacourtiaceae. In order to justify use of this character, one would have to invoke the principle of "apomorphic tendencies" advanced by Cantino (1982, 1985). This idea that shared tendencies to change in morphological characters can be used to define phylogenetic relationship has been criticized as unrigorous by Rasmussen (1983), although it looks as if such a principle indeed reflects the thinking of phylogeneticists such as Cronquist, Takhtajan and Thorne. There is some evidence for relating Flacourtiaceae to Euphorbiaceae because of similarities in seed coat development (Corner, 1976), but these are also shared by taxa of Celastrales. In my opinion, the failure so far to demonstrate additional synapomorphies between Euphorbiales and

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Flacourtiaceae or Celastrales puts the burden of proof on those who follow either the claim of Hickey & Wolfe (1975) that the Euphorbiales came from the Violalean branch of the "palmate Dilleniidae", or the assertion of Cronquist (1981) that they should be associated with the Celastrales.

We have seen that with the exception of the Violalean connection initiated by Hallier and by Hickey and Wolfe, most suggestions of the affinity of Euphorbiales by 20th century systematists fall into two classes with regard to a putative sister group: Celastralean, supported by Stebbins (1974) and Cronquist (1981); and Malvalean, supported by Croizat (1973), Takhtajan (1980), Dahlgren (1983) and Thorne (1983). Nevertheless, I still believe that my own suggestion of Geranialean affinity (Webster, 1967) also merits consideration. The flowers in families such as Ixonanthaceae (Forman, 1965; Noteboom, 1967) appear closer to those of primitive Euphorbiaceae (subfamily Phyllanthoideae) than do those of corresponding genera in Celastrales or Malvales. I suggest that the Linales (*sensu* Cronquist, 1981) must be taken into account in searching for the closest phyletic lines to Euphorbiaceae.

CLASSIFICATION OF THE TAXA OF EUPHORBIACEAE

Although there have been many changes in the circumscription of the Euphorbiales during the past 150 years, these have generally not involved questions of delimitation of the family Euphorbiaceae, with the notable exception of the position of Buxaceae. The outstanding problems of interest, both in the 19th century and now, involve intergeneric relationships and delimitation of the infrafamilial taxa of Euphorbiaceae.

In the first family treatment, that of Adanson (1763), 32 genera were enumerated, of which nine are extraneous (*Buxus*, *Carica*, *Cissampelos*, *Clusia*, *Cupania*, *Hernandia*, and three genera of Polygalaceae). Adanson also attempted the first infrafamilial division of the family, but his two sections (founded on whether the stamens are free or united) are wholly unnatural. The treatment by A. L. de Jussieu (1789) is more impressive in terms of generic placement, since only five of 86 genera admitted into the Euphorbiaceae are not Euphorbiaceous: three Buxaceae, *Lacistema* and *Xylosma*. However, Jussieu's attempt to subdivide the family on the basis of stylar, rather than stamen union, was no more successful than that of Adanson.

The first great advance in taxonomic insight was provided by Adrien de Jussieu (1824), who subdivided the Euphorbiaceae into six well-defined sections based on several characters: ovule number, stamen insertion, presence of petals and type of inflorescence. Although Jussieu unfortunately did not provide names for his sections, they were recognized and given formal status as tribes by Dumortier (1829), Bartling (1830) and Spach (1834). The classification based on these six tribes (Buxaceae, Phyllanthaceae, Ricineae, Acalypheae, Hippomaneae and Euphorbieae) has provided the paradigm for all later work on classification of the groups of genera within the family.

The most important insight of Adrien de Jussieu was to recognize the taxonomic importance of ovule number; the distinction between taxa with uniovulate and biovulate ovary loculi has been accepted as fundamental by subsequent workers. Zollinger (1845) was the first to use this character to divide

the family into two subfamilies: Monosporae and Disporae. Pax (1884, 1890) assigned most of the genera in the Euphorbiaceae into two subfamilies, Phyllanthoideae and Crotonoideae, that correspond to Zollinger's Monosporae and Disporae. Mueller (1866a) and Bentham (1880) did not recognize subfamilies, but the ovule number character was still important in their definition of tribes.

In addition to providing the first monograph of the Euphorbiaceae, Adrien de Jussieu (1823) also wrote an interesting essay in which he analysed character variation and described his systematic methodology. Here he noted the primary importance of ovule number in establishing taxa, and he showed a pragmatic approach to choice of characters: for example, he observed that the pistillode character used to establish two sections in the biovulate taxa was of no use for the uniovulate taxa, where it had to be replaced with inflorescence characters.

Although he stated that his selection of characters to define major taxa was based on a modification of the Aristotelian method of logical division, A. Jussieu went on to explain that his actual working method was to select a few large and clearly delimited genera (*Buxus*, *Phyllanthus*, *Croton*, *Acalypha*, *Sapium* and *Euphorbia*) and then to build up his tribes by accretion, adding genera to the core of each group according to progressively decreasing strength of resemblance. The result of this typological procedure, which in fact is still one of the basic approaches used by taxonomists today, is that the groups are modally well-defined but not always sharply circumscribed. In Jussieu's words: "... le limites de ces sections ne sont pas bien tranchées, et certains genres établissent le passage de l'une à l'autre. Ce qui me semble important, c'est que les genres s'y trouvent placés toujours près de ceux avec lesquels ils ont les affinités les plus fortes et les plus nombreuses; c'est que la série soit la plus naturelle possible". It is clear that although Jussieu was playing by the rules of De Candolle's *Theorie Elementaire* (1813), his actual practice in constructing a classification was largely empirical and inductive (as indeed that of De Candolle and most other leading contemporaries was in large part).

Immediately following the monograph of A. Jussieu (1824), these followed what we might call the 'romantic period' in Euphorbiaceous taxonomy, in which attempts were made to recognize a number of small families segregated from the Euphorbiaceae (Table 3). These included Stilaginaceae for *Antidesma* (Agardh, 1825), Scepaceae for *Aporusa* and *Hymenocardia* (Lindley, 1836), Putranjiveae for *Putranjiva* (Endlicher, 1837) and Prosopidoclineae (later Peraceae) for *Pera* (Klotzsch, 1841, 1859, 1860). Most of these segregations involved genera with reduced flowers, and the proposed new families were associated with wind-pollinated groups; thus, Lindley (1836) juxtaposed the Stilaginaceae with Urticaceae, and Scepaceae with Betulaceae.

Reichenbach (1828, 1837, 1841) was the first major systematist after A. Jussieu to propose an original classification of the Euphorbiaceae. He treated it as a subordinate group of the Rutaceae, a proposal that has not been followed by anyone else, and created the most complex classification before that of Mueller (1866a). There are three tribes, each with three subtribes: Euphorbieae genuinae (Callitrichineae, Tithymaleae, Ricineae); Crotoneae (Micrantheae, Argythamneae, Crozophoreae); and Buxae (Phyllantheae, Cluytieae, Buxae genuinae). Reichenbach's Crotoneae is on the whole a natural taxon, roughly corresponding to Pax's Crotonoideae. Reichenbach did not provide detailed

Table 3. Enumeration of family names referable to the Euphorbiales (the family Euphorbiaceae as defined by Webster, 1975); family references are given by Bullock (1958a, 1958b). Names are given in their original form of publication, except where noted. The names of some taxa that have been included in the Euphorbiales are here omitted because of typification they must be excluded from the order (e.g. Forestieraceae Endl., based on a genus of Oleaceae)

- Acalyphaceae J. G. Agardh, *Theoria Systematis Plantarum*: 258 (1858) = Euphorbiaceae subfamily Acalyphoideae Ascherson (*pro. parte*).
- Antidesmeae Endlicher, *Genera Plantarum secundum Ordines Naturales Disposita*: 287 (1837); Antidesmeaceae Walpers, *Annales Botanices Systematicae*, 3: 391 (1852) = Euphorbiaceae tribe Antidesmeae (Endl.) Hurusawa.
- Aporoseae Lindl. ex Planchon, *Annales des Sciences Naturelles, Botanique, IV, 1*: 265 (1854); ex Miquel, *Flora van Nederlandsch Indie, 1(2)*: 430 (1859) = Euphorbiaceae tribe Aporuseae Airy Shaw.
- Bennettiaceae R. Brown, in J. J. Bennett & R. Brown, *Plantae Javanicae Rariorum*: 250 (1852; *nom. prov.*); Bennettieae Schnizlein, *Iconographia Familiarum Naturalium Regni Vegetabilis*, 3: 172 (c. 1860; *nom. illegit.*, based on *Bennettia* R. Brown, a later homonym of *Bennettia* S. F. Gray) = Pandaceae.
- Bertyaceae J. G. Agardh, *Theoria Systematis Plantarum*: 190 (1858) = Euphorbiaceae tribe Ricinocarpeae Muell. Arg.
- Bischofiaceae (Muell. Arg.) Airy Shaw, *Kew Bulletin*, 18: 261 (1965) = Euphorbiaceae tribe Bischofiaceae (Muell. Arg.) Hurusawa.
- Crotonaceae J. G. Agardh, *Theoria Systematis Plantarum*: 258 (1858) = Euphorbiaceae subfamily Crotonoideae Pax.
- Euphorbiaceae A. L. Jussieu, *Genera Plantarum*: 384 (1789; as Euphorbiaceae).
- Galeariaceae Pierre, *Bulletin de la Société Linnéenne de Paris*, 1327 (1897; *nom. illegit.*) = Pandaceae.
- Hippomaneae J. G. Agardh, *Theoria Systematis Plantarum*: 244 (1858) = Euphorbiaceae tribe Hippomaneae A. Juss. ex Spach.
- Hymenocardiaceae Airy Shaw, *Kew Bulletin*, 18: 261 (1965) = Euphorbiaceae tribe Hymenocardiaceae (Muell. Arg.) Hutchinson.
- Linostoeae Sprengel, *Anleitung zur Kenntnis der Gewächse, Zweite . . . Ausgabe, 2(1)*: 371 (1817; rank of "Ordnung" probably equivalent to subfamily).
- Micrantheae J. G. Agardh, *Theoria Systematis Plantarum*: 182 (1858) = Euphorbiaceae tribe Caletieae Muell. Arg.
- Pandaceae Pierre, *Bulletin de la Société Linnéenne de Paris*, 2: 1255 (1896).
- Peracées A. Jussieu in C. V. D. D'Orbigny, *Dictionnaire Universel d'Histoire Naturelle*, 5: 773 (1844; *nom. illegit.*); Peraceae Klotzsch, *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1859: 246 (1859) = Euphorbiaceae tribe Peraceae (Kl.) Pax & Hoffm.
- Phyllanthaceae J. G. Agardh, *Theoria Systematis Plantarum*: 249 (1858); Phyllanthaceae Klotzsch, *Monatsberichte der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1859: 246 (1859) = Euphorbiaceae subfamily Phyllanthoideae Ascherson (*pro parte*).
- Picrodendraceae Small, *Journal of the New York Botanical Garden*, 18: 184 (1917) = Euphorbiaceae tribe Picrodendreae (Small) Webster.
- Porantheraceae (Muell. Arg.) Hurusawa, *Journal of the Faculty of Science, University of Tokyo, Section III Botany*, 6(6): 224 (1954) = Euphorbiaceae tribe Poranthereae (Muell. Arg.) Grüning.
- Pseudanthaeae Endlicher, *Genera Plantarum Secundum Ordines Naturales Disposita*: 328 (1838; probably of subfamilial rank) = Euphorbiaceae tribe Caletieae Muell. Arg.
- Putranjiveae Endlicher, *Genera Plantarum Secundum Ordines Naturales Disposita*: 287 (1837) = Euphorbiaceae tribe Drypetaceae (Griseb.) Hurusawa.
- Ricinocarpaceae (Muell. Arg.) Hurusawa, *Journal of the Faculty of Science, University of Tokyo, Section III Botany*, 6(6): 224 (1954) = Euphorbiaceae tribe Ricinocarpeae Muell. Arg.
- Scepaceae Lindley, *A Natural System of Botany, Second Edition*: 171 (1836) = Euphorbiaceae tribe Aporuseae Airy Shaw.
- Stilagineae C. A. Agardh, *Aphorismi Botanici*, 14: 199 (1824); Stilaginaceae Lindley, *The Vegetable Kingdom, Third Edition*: 259 (1853) = Euphorbiaceae tribe Antidesmeae (Endl.) Hurusawa.
- Tithymali Adanson, *Familles des Plantes*: 346 (1763; *nom. illegit.*) = Euphorbiaceae A. L. Jussieu (*nom. cons.*)
- Trewiaceae Lindley, *A Natural System of Botany, Second Edition*: 174 (1836) = Euphorbiaceae tribe Acalyphaceae Dumort. (subtribe Rottlerinaceae Meisn.).
- Uapacaceae (Muell. Arg.) Airy Shaw, *Kew Bulletin*, 18: 270 (1965) = Euphorbiaceae tribe Uapacaceae (Muell. Arg.) Hutchinson.

descriptions or documentation, and his treatment appears to have had little influence on later taxonomic work.

More in the mainstream was the classification of Meisner (1841), which was clearly influenced by that of A. Jussieu. Meisner's tribe *Crotoneae* included a subtribe, *Jatrophaeae*, in which *Aleurites*, *Jatropha*, *Manihot*, *Ricinocarpus*, and *Trigonostemon* are correctly associated; this appears to be the first published system in which there is a clearly defined taxon for genera with 'crotonoid' pollen.

With the publication of *Étude Générale du Groupe des Euphorbiacées* by Baillon (1858), a significant milestone in Euphorbiaceous classification was attained. This great work is Baillon's major effort at a monograph of a plant family, even though he went on in the *Histoire des Plantes* to accomplish the only extensive multi-volume monograph of the angiosperms attained by a single individual. In the *Étude*, Baillon demonstrated a dazzling virtuosity in morphological observation (especially as seen with the microscope), and his superb analytical drawings (which make the plates of A. Jussieu seem extremely crude by comparison) remain unsurpassed. Baillon created many new genera and sections, redefined the circumscription of the family by excluding the Buxaceae, and provided many interesting discussions of relationships between genera, often with great insight. However, as remarked by both Mueller and Bentham, Baillon's work is regrettably marred by its failure to provide a classification appropriate to reflect degrees of affinity. Instead of using a proper hierarchical system, Baillon created 14 "series", within which each genus was usually characterized by its differences from a previously cited genus. This method of creating a classification by a chain of archetypes was contrary to better systematic practice, even in Baillon's day, and it fortunately did not have any appreciable influence on the next generation of workers on Euphorbiaceae.

Baillon's monograph appeared almost simultaneously with two other systems and shortly was followed by that of Jean Mueller, so that the decade following 1858 can well be considered the 'golden age' of Euphorbiaceous classifications. The treatment by Klotzsch (1859, 1860) initiated a new tradition of splitting and inflation of rank in the Euphorbiaceae. Klotzsch treated the Euphorbiaceae as an order ("Klasse") divided into six families ("Ordnungen"): Euphorbiaceae (*sensu stricto*), Peraceae, Acalyphaceae, Buxaceae, Phyllanthaceae and Antidesmaceae. Although this classification has six major taxa, as did that of A. Jussieu, the two are not very similar. Only the Euphorbiaceae (*sensu stricto*), Buxaceae and Phyllanthaceae correspond fairly closely to the comparable sections of Jussieu; the Peraceae and Antidesmaceae are segregate groups, while the Acalyphaceae combine the Jussieu/Spach tribes Ricineae, Acalypheae and Hippomaneae in a rather infelicitous juxtaposition. Subsequent work has not dealt very kindly with this classification, since not a single one of Klotzsch's major taxa is currently accepted with the same circumscription, and only a few recent workers (e.g. Barkley, 1948; Hurusawa, 1954) have accepted such narrowly circumscribed families.

Grisebach (1859, 1860), in a contribution that has been neglected, discussed the criteria for infrafamilial subdivision, and proposed a new classification of the Euphorbiaceae that in some respects was the best published up until that time. Although he unfortunately retained the tribe Buxaceae in the family (despite Baillon's well-founded assertion that they should be excluded), Grisebach placed

all of the uniovulate taxa into a single tribe Crotonae with seven subtribes: Jatrophaeae, Ricineae, Eucrotoneae, Ditaxideae, Acalypheae, Hippomaneae and Euphorbieae. This may be criticized as placing too much emphasis on the peculiarities of *Ricinus*; but the subtribes Jatrophaeae and Crotonae, characterized largely on inflorescence characters, contain mostly genera now referred to subfamily Crotonoideae; the Ditaxideae and Acalypheae mostly belong to subfamily Acalyphoideae; and the Hippomaneae and Euphorbieae to subfamily Euphorbioideae. Grisebach based his classification mostly on Caribbean taxa, and it was soon eclipsed by that of Mueller.

The first, and only, monograph of the Euphorbiaceae to the species level appeared in de Candolle's *Prodromus* in two sections, the tribe Euphorbieae by Boissier (1862), and the other tribes by Jean Mueller (Mueller Argoviensis) in 1866. Boissier's revision of *Euphorbia*, the last complete review of the genus, is justly famous for its judicious use of characters in defining species groups; Boissier's sections have survived remarkably intact (although recently challenged; Gilbert, in press), considering the fact that the number of species of *Euphorbia* has at least tripled since his work.

Mueller's infrafamilial classification of the Euphorbiaceae (1864, 1866a) was, if anything, more revolutionary than that of A. Jussieu four decades earlier; it is much more complex and sophisticated than its predecessor. The hierarchy of taxa in Euphorbiaceae as developed by Mueller was probably the most elaborate devised for any plant family up to that time. The major infrafamilial division is the novel recognition of two "tribal series" Stenolobeae and Platylobeae, defined on cotyledon shape; although accepted by Bentham (1880) and Pax (1890, 1931), this division appears now to have been an unfortunate choice, since it results in unnatural associations of genera.

Within each "series", Mueller's system has tribes characterized on the basis of a sequential hierarchy of three characters: ovule number, aestivation of calyx, and orientation of anthers in the bud. Within most of the tribes, subtribes are defined on the basis of the presence or absence of an involucre or of petals; an additional character of subordinate value is the position of insertion of the stamens. An outstanding peculiarity of Mueller's system arises from his use of disk-segments and petals as characters. Some apetalous taxa are placed among those with "flores petalis praediti", because the disk-segments are opposite the sepals; taxa with disk-segments alternate to the sepals are assigned to groups with "flores absolute apetalii." However, since the disk-segments are often united, partially fused, or absent, this character is in practice difficult, or impossible, to use. Furthermore, it is most doubtful that the theoretical distinction intended by Mueller is valid; the disk is more plastic and variable within the basic floral plan than Mueller's scheme would allow.

Mueller's classification, with 10 tribes instead of the six recognized earlier by A. Jussieu, was actually not as different at the tribal level as might appear at first sight. With exclusion of the Buxaceae, it continued use of the five other Jussieuian tribes and added three Stenolobeae (Caletieae, Ricinocarpeae and Ampereae) plus two new Platylobeae (Bridelieae and Dalechampieae). The recognition of these five new tribes depended on Mueller's systematic philosophy and use of characters. Fortunately, we have his own testimony as to his working methods published shortly after the treatment in the *Prodromus* (Mueller, 1866b). Reflecting the philosophy of De Candolle in his *Théorie Élémentaire de*

Botanique (de Candolle, 1813), Mueller states as self-evident that the reproductive parts of the flower should receive highest value because of their functional importance; this is the familiar Aristotelian precept inherited from Caesalpino and Linnaeus. However, in the selection of characters, Mueller claimed that he had tested them as to their generality of occurrence and hence had used an inductive method. This is true to a certain extent, but Mueller seems not to have realized that he had pre-selected the characters to be tested on the basis of *a priori* philosophical biases.

As noted by Briquet (1896, 1940), Mueller showed a very strong mathematical bent as a student, and it would appear that he had an inherently formalistic cast of mind. It is perhaps not surprising that he erected a rigid scaffolding for his systematic work, or that he followed strict Aristotelian practice in selecting an embryonic character (cotyledons) as his *fundamentum divisionis*. Here he was unlucky, for it happens that the narrow cotyledons of the Australian Stenolobeae represent a striking instance of morphological convergence between unrelated taxa now referred to four different subfamilies. The likelihood of such convergence happening only in Australia (and not in other climatic areas with ericoid-leaved Euphorbiaceae) would indeed seem rather small, and it still has not been satisfactorily explained; however, there are some non-Australian taxa with narrow cotyledons, such as *Reverchonia* in the Phyllanthaceae (Webster & Miller, 1963). Bentham (1878, 1880), evidently impressed by the geographical correlation of the cotyledon character, recognized the Stenolobeae as a natural tribe, and Pax (1931) retained the group for 40 years after he had already decided that it was polyphyletic.

However, while he was simply unfortunate in selecting an embryo character for his primary division, Mueller was even less justified in his use of floral aestivation for the major tribal divisions. Adrien de Jussieu (1823) had already pointed out the differences in "préfloraison" of the perianth, but had not placed great weight on the character. The peculiarity of Mueller's usage resides in his apparent assumption that this character, once tested and found to show strong correlations with generic differences, could be applied across the board to separate nearly all of the groups at tribal rank. This assumption that a character found to yield correlations could be assigned an absolute weight or value in assigning rank to taxa occurs in the work of other 19th century systematists, but is nowhere as consistently and uncompromisingly pursued as in the work of Mueller.

Mueller's insistence on the hierarchical value of perianth aestivation had the most pernicious consequences in his tribe Hippomaneae, which, in his circumscription, included most of the uniovulate taxa with imbricate sepals. Baillon (1858) had already shown a number of instances in which this character was variable or inconstant, and in the Hippomaneae (*sensu stricto*), which have a more-or-less reduced calyx it is particularly difficult to interpret. Furthermore, recent studies, especially of pollen (Erdtman, 1952; Punt, 1962; Webster, unpublished) clearly show that the valvate/imbricate dichotomy separates many natural lines of affinity and makes both the Acalypheae and Hippomaneae of Mueller highly unnatural groups. The case of the Hippomaneae is particularly striking, since all of the 13 genera assigned to the tribe (as section V) by A. de Jussieu (1824) are retained in it by Pax & Hoffmann (1931), except for the Buxaceous genus *Styloceras*. In contrast, Mueller's Hippomaneae also included a

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large number of genera now assigned to subfamilies Acalyphoideae or Crotonoideae, such as *Chaetocarpus*, *Clusia*, *Jatropha* and *Manihot*.

The unanalysed assumption by Mueller that biased his approach was specified by himself (Mueller, 1866b) as a dogma: "In jeder systematischen Einheit muss der innere Werth des Characters dem hierarchischen Höhengrad der Einheit entsprechen". This can only mean that the classification is intended to reflect a descending series of Platonic archetypes. For Mueller, this principle of the near-absolute equivalence between character and rank extended down to the level of genera, sections, and species. However, in his actual work at the level of genera and species, Mueller followed a more empirical procedure. He reported that he carefully analysed three or four well-separated species of a genus in order to arrive at the most useful characters, and that he then applied these character differentials in placing all of the other taxa. Nevertheless, it is notable that in descriptions of genera, sections, and species only, reproductive characters are given as diagnostic; vegetative characters are always relegated to a second section of less important supplementary characters.

Mueller's realignments in classification were accompanied by many nomenclatural changes. He adopted a strict rule of priority, including the priority of species epithets over species names that was common practice in the mid-19th century, but in addition cited himself as the authority for the names of genera to which he had given a different circumscription. These innovations in nomenclature occasioned more discussion from other botanists (as noted below) than the changes in classification itself.

Mueller's monograph of the Euphorbiaceae was generally well received, although there were various complaints and reservations by his peers. Jaubert (1866) was dissatisfied with the use of the embryo character to separate the primary groups Stenolobeae and Platylobeae, mainly because he felt that it was too difficult to use in practice. Seemann (1866) applauded the competence of Mueller while deploring his nomenclatural innovations. Gray (1867) was unfavourably disposed towards Mueller's citations of authority as well as his practice of adopting herbarium or manuscript names without crediting them to the original 'author'; this went against the prevailing standards of gentlemanly practice. Alphonse de Candolle (1867), in reply to Seemann, disavowed responsibility for Mueller's innovations with the candid statement that he did not edit any of the manuscripts submitted for the *Prodromus*; but he did defend Mueller's work for its great precision and characterized it as "un véritable travail monographique".

Mueller's work could hardly have escaped some critical review from the acidulous pen of Henri Baillon, since many of his dispositions contradicted those in Baillon's classification of 1850. Even before the *Prodromus* volume appeared, Baillon (1865) had already criticized Mueller's generic circumscriptions in the Hippomaneae. Later (1867) he adversely commented on Mueller's placement of *Petalostigma* near *Phyllanthus*, arguing that it belonged closer to *Drypetes* and *Longetia*. Finally, in a long article titled *Nouvelles Observations sur les Euphorbiacées* (Baillon, 1873a), he launched a full-scale attack on Mueller's classification. After briefly complimenting Mueller on his reductions of a number of genera, Baillon stated: "Mais je cesse de partager la manière de voir de l'auteur du *Prodromus* quant à la valeur générique qu'il accorde à la forme des anthères, au degré de développement de la caroncule, et quant aux caractères de tribus qu'il fonde sur

le préfloraison. Je pense qu'en l'imitant, on briserait à chaque pas les liens les plus naturels". Baillon decisively rejected the cotyledon character used by Mueller for the primary division of the family, partly for the practical reasons already stated by Jaubert. With considerable asperity, he also contested the circumscription and placement of many taxa. A number of his strictures, such as his disapproval of the calyx aestivation character to separate Acalypheae from Hippomaneae, today seem well targeted. However, in several instances Baillon went to almost grotesque lengths of amalgamating genera in opposition to Mueller's concepts; for example, he proposed to unite *Pentabrachium*, *Bridelia* and *Cleistanthus* with *Amanoa*.

Mueller replied with an angry counter-attack (Mueller, 1875) which is full of sarcasm and in places shows a surprising lapse in decorum. In replying to Baillon's major criticisms, Mueller made few concessions, and in turn pointed out some supposed errors committed by Baillon (e.g. in calling the corolla of *Jatropha* subgenus *Curcas* gamopetalous). After reviewing the characters that had been contested by Baillon, he concluded sarcastically that following Baillon would logically lead to amalgamating all of the Euphorbiaceae into a single genus. Finally, Mueller framed a rhetorical question: how could two outstanding botanists, after working for years, come to such diametrically opposed conclusions? His explanation is: "Dr. Baillon ist Adansonianer, er zählt die Differenzen, er perhorrescirt mehr oder weniger die Subordination der Charactere; ich dagegen gehöre dem systematischen Bekenntniss der Jussieu, R. Brown, de Candolle, etc., an, ich lege der Charactere auf die Wagschale, ich taxire die Differenzen, und die Subordination der Charactere ist für mich elementares und absolutes Bedürfniss".

This exchange between Mueller and Baillon, which seems to have been the first full-scale confrontation between two outstanding taxonomists of Adansonian and non-Adansonian persuasions, was not to be equalled for three-quarters of a century. In terms of our present-day knowledge, the verdict is curiously mixed. Some of Baillon's criticisms, especially the use of cotyledon shape and calyx aestivation as major characters, have been fully substantiated. On the other hand, Mueller's system of tribes and subtribes, despite his problems with the Hippomaneae, has held up much better than that of Baillon. Mueller's polemic against Baillon would have been much more effective if he had had in hand volume five of the *Histoire des Plantes*, which appeared in 1874 but which Mueller obviously had not seen when he sent his reply to the *Botanische Zeitung* on 29 December 1874. In volume five, Baillon presented his own mature (and final) system of the Euphorbiaceae, in which the genera (reduced to 146) are grouped in six series (not counting the Dichapetalaceae and Callitrichaceae, which were erroneously included). These six series are of extremely unequal size, with Euphorbieae, Ricineae, and Crotoneae each containing only two, three and four genera, respectively, while the Jatropheae have 88. In terms of circumscription (exclusion of extraneous elements) and information content (explication of relationships between taxa), it is probably the worst major classification of the Euphorbiaceae ever published. Mueller's accusation that Baillon merely enumerated the differences underscores the major weakness of Baillon as a systematist: he excelled in analysis but seems to have lacked the capacity (or interest) for synthesis. Baillon could also be just as dogmatic as Mueller, as is indicated, for example, by his stubborn anachronistic

insistence that the cyathium of *Euphorbia* is a hermaphroditic flower. He believed as strongly as did Mueller that genera should be sharply defined, and an excessively rigorous logic led him to reject even slightly unreliable characters and to combine genera separated by such characters. In this practice he was curiously non-Adansonian.

Stevens (1984) has cited Baillon (in a later work, Baillon, 1891) as a promoter of the "chaining technique" of producing higher taxa by stringing related taxa together. It is not surprising that Baillon and Mueller, writing during the decade immediately following the publication of Darwin's *Origin of Species*, do not express themselves in phylogenetic terms. However, it is clear that Mueller's elaborate hierarchical system produced nested arrays of taxa and hence came far closer to being a representation of evolutionary affinities than did the classification of Baillon.

As pointed out by Leandri (1962), Baillon had little interest in the historical (phylogenetic) aspects of systematics; and judging from his published works, the same could be said of Mueller. At about the time of their exchange of polemics, a third botanist of very different temperament, George Bentham, was taking up a study of the family for the *Genera Plantarum*. Bentham's essay on Euphorbiaceae (1878) remains today as readable and interesting as his better-known review of the Compositae. It provides a judicious history of earlier taxonomic work, with major emphasis on Baillon and Mueller, both of whom he chided for their arbitrariness in use of characters.

Since Bentham appeared to be less constrained by preconceptions and dogmatic attitudes than other 19th century students of the Euphorbiaceae, it is of some interest to see how this was reflected in his classification. Bentham frankly acknowledged that his own classification was based on that of Mueller, but he was closer to Jussieu in recognizing only six tribes: Euphorbieae, Stenolobeae, Buxeeae, Phyllanthaeae, Galearieae and Crotonaeae. By present standards, his treatment was retrograde in including Buxaceae within the family after both Baillon and Mueller had excluded it. His unfortunate adoption of the Stenolobeae was perhaps influenced by the striking resemblances in habit that he must have noticed while preparing the Euphorbiaceae for the *Flora Australiensis* (1873). On the other hand, his recognition of the Galearieae as a distinct tribe was an improvement on the treatments of Baillon and Mueller, since *Galearia* and *Microdesmis* are indeed divergent from typical Euphorbiaceae and have recently been removed to the family Pandaceae by Forman (1966, 1968, 1971).

Within his large tribe Crotonaeae, which includes most of the uniovulate Euphorbiaceae, Bentham created subtribes comparable to some of Mueller's tribes, and made a number of perceptive indications of affinity. Particularly felicitous were his demotion of Mueller's tribe Crotonaeae to subtribal rank, and his creation of a subtribe Plukenetiinae. Bentham's demotion of the Dalechampiae to an element of the Plukenetiinae gave a much better expression of affinity for *Dalechampia* than indicated in most other classifications. Despite various defects of Bentham's system, it was the most nearly natural that had been produced up until that time. However, today perhaps the major interest in his essay is in the final section on geographical distribution, which appears very modern because of its patently phylogenetic reasoning, even though Bentham did not use evolutionary phraseology.

Shortly after Bentham's treatment in the *Genera Plantarum* (1880), a young German botanist, Ferdinand Pax, began working on the systematic anatomy of the Euphorbiaceae. His first paper (Pax, 1884) initiated a series of publications that extended over more than 50 years. In his essay of 1884 Pax reviewed the previous systems of Klotzsch, Baillon, Mueller and Bentham, and then offered his own findings based on anatomical observations (mainly on cross-sections of twigs on herbarium specimens, many of which were furnished by Mueller from the Geneva herbarium). In one of the most striking cases of a missed opportunity in 19th century plant systematics, he considered using pollen characters but rejected them as taxonomically useless!

Pax in 1884 offered his own original classification, based on anatomical characters, and in some respects it was superior to those he produced later. He presented for the first time since Zollinger in 1845 a bipartite classification with all of the biovulate taxa in the subfamily Phyllanthoideae and the uniovulate in Crotonoideae. Perhaps his most important innovation was the use of laticifers as a primary character; this was the first time that non-floral characters had been given such emphasis, and reflects a further decline in the use of Linnaean essentialistic criteria. His other major innovation in classification was to divide the Crotonoideae into two taxa of supertribal rank, the Acalyphoideae and Hippomanoideae, defined on the presence of articulated and non-articulated laticifers, respectively. This was not a very natural division, since the Ricinocarpeae and Joannesiaeae, with 'crotonoid' pollen, were placed in the Acalyphoideae, while the Crotonaeae, with similar pollen, went into the Hippomanoideae. As various authors pointed out later, Pax's observations on laticifers were inexact, and he did not always distinguish articulated laticifers from rows of tannin cells. Nevertheless, description and definition of laticifers still plagues workers in the 20th century, and I agree with Dr Mahlberg (pers. comm.) that Pax's classification of 1884 deserves re-examination.

With a display of that curious inconsistency that he was to show to the end of his career, Pax concluded that his findings supported the system of Mueller, despite the fact that they clearly contradicted it in some important aspects. For example, his anatomical work showed the heterogeneity of the Stenolobeae of Mueller and demonstrated that Baillon (1873a) was correct in dismembering it and referring the genera to appropriate positions among the biovulate and uniovulate taxa. In his dendrogram illustrating phylogenetic relationships among the tribes (Fig. 4A), the first published for the family, Pax showed the Stenolobeae as biphyletic, and in his systematic table of tribes, he referred the Stenolobeae Caletiaeae to the Phyllanthoideae and the Ricinocarpeae to the Crotonoideae; yet in his concluding discussion he appears to have accepted the Stenolobeae as a legitimate taxon ("systematisch jedenfalls gut begründete").

As a result of his studies, Pax arrived at several conclusions about the phylogeny of the Euphorbiaceae that had been partly anticipated by Bentham and that have been accepted by most later workers: greater antiquity of the Phyllanthoideae, early separation of the two subfamilies, origin of the 'acalyphoid' line mainly in the Old World and the 'hippomanoideae' mainly in the New World, as well as the biphyletic origin of the Stenolobeae. In his treatment in the first edition of *Die Natürlichen Pflanzenfamilien* (1890), he contradicted some of his conclusions of 1884 and reverted to Mueller's treatment in retaining Platyllobeae and Stenolobeae as the major divisions of the family. Otherwise, in

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was to show to the end of the system of Mueller, the important aspects. For the tribe of the Stenolobeae of Mueller correct in dismembering it among the biovulate and phylogenetic relationships of the family, Pax showed the importance of tribes, he referred to the Ricinocarpeae to the tribe. Pax has to have accepted the conclusion (falls gut begründete"). His conclusions about the tribe anticipated by Bentham greater antiquity of the tribe, origin of the 'acalphyoid' tribe mainly in the New World. In his treatment in 1924, he contradicted some of his treatment in retaining the tribe of the family. Otherwise, in

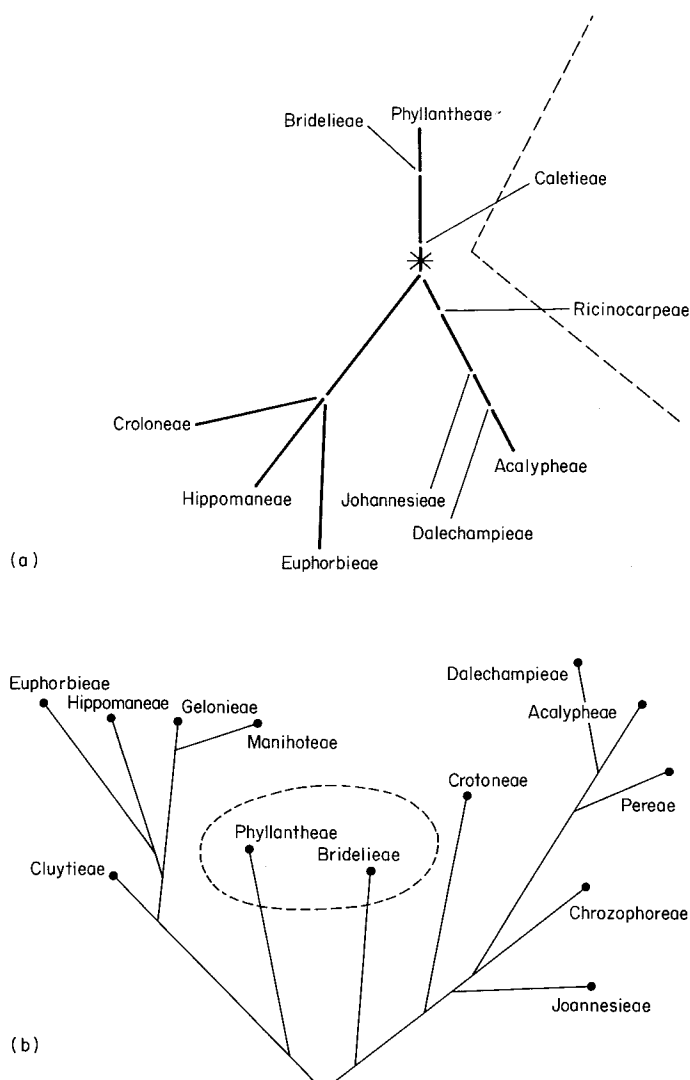


Figure 4. Phylograms proposed by Pax to illustrate putative relationships among the tribes of Euphorbiaceae. A. Version of 1884. B. Version of 1924.

his divisions into tribes and subtribes Pax usually followed the dispositions of Mueller, but did accept many of Bentham's suggestions. However, one suggestion of Bentham that he should have ignored was the re-inclusion of *Daphniphyllum* in the Euphorbiaceae after its earlier exclusion by Mueller (1869). Some of Pax's changes were distinct improvements; for example, he brought together most of the Oldfieldioideae into two adjacent subtribes, Toxicodendrinae and Bischofinae.

Pax's treatment of the Crotonoideae as comprising eight tribes was heavily dependent on Bentham, with Bentham's subtribes raised to tribal rank. His tribes Acalyphaceae and Jatropheae were largely natural, but in following Bentham in the circumscription of the tribe Manihoteae (based on Bentham's

Adrianeae), he seconded one of Bentham's worst mistakes. Pax degraded Bentham's tribe Galearieae by renaming it Cluytieae and including many extraneous elements. On the other hand, by associating the Plukenetiinae with the Acalypheae and making the Hippomaneae (*sensu* A. de Jussieu) coordinate in rank with the Euphorbieae, Pax provided a classification that reflected relationships better than previous systems.

Beginning with the treatment of the Jatrophaeae in *Das Pflanzenreich*, Pax (1910) initiated a series of monographic treatments of the Euphorbiaceae (assisted after 1910 by Käthe Hoffmann) that ran for 17 instalments with over 2200 pages (summarized in Webster, 1967), thus establishing a quantitative superiority over Mueller. With the completion of the treatment of the Acalyphinae in 1924, most of the family had been covered, except for the subtribes with the three largest genera: *Phyllanthus*, *Croton*, and *Euphorbia*.

Pax did not introduce any important modifications of his system of 1890 until the publication of Additamentum VI in *Das Pflanzenreich* (Pax & Hoffmann, 1919). Here he remarked that in 1890 he had based his tribes Jatrophaeae and Manihoteae on Bentham's corresponding subtribes of Crotonaeae, but that he had gradually come to see the Benthamian taxa as unnatural. In effect, Pax in 1919 largely returned to the system of Mueller and readopted calyx aestivation as a primary diagnostic character. With regard to the Manihoteae, Pax was on firm ground when he restricted the tribe to *Manihot* and expelled the other genera included by Bentham. However, in realigning the genera of Jatrophaeae Pax was disastrously mistaken, for this was one of the most natural of all Bentham's taxa. Now *Aleurites*, *Jatropha*, *Hevea*, and *Micrandra* were widely separated in four different tribes; and 11 genera of the Jatrophaeae of 1890 were referred to eight different subtribes. In his final general review of the phylogeny of the family, Pax (1924) presented a phylogram (Fig. 4B) in which the Phyllanthoideae is straightforwardly shown as an unnatural group. In this essay he did associate *Hevea* and *Joannesia* together in the tribe Joannesieae, but otherwise this fragmentation of the original Jatrophaeae was allowed to stand in the final version of Pax's classification (Pax & Hoffmann, 1931). On the whole, the classification of 1931 now appears only marginally better than that of 1890, and was definitely inferior in its treatment of genera with 'crotonoid' pollen.

In the 55 years since the last detailed classification of Pax & Hoffmann (1931), three complete classifications of the family down to the tribal level have been produced: Hurusawa (1954), Hutchinson (1969) and Webster (1975). Because of the shorter historical perspective, it is difficult to evaluate these more recent classifications, but a brief discussion seems warranted. Hurusawa's classification is the only 20th century system to return to the tradition of Klotzsch, in which the Euphorbiaceae are dismembered into several families. However, Hurusawa's four families, Antidesmataceae, Euphorbiaceae, Porantheraceae and Ricinocarpaceae, really represent the four subfamilies of Pax raised to family rank, and hence do not indicate any novelty of classification. On the other hand, Hurusawa provides a more original treatment at the subfamily level, with three biovulate subfamilies (Bridelioideae, Antidesmatioideae and Phyllanthoideae) and four uniovulate (Euphorbioideae, Acalyphoideae, Crotonoideae, and Sapioidae). The value of Hurusawa's paper would appear to rest mainly on his detailed discussions of Oriental taxa and delimitation of the new tribes Epiprineae, Aleuritideae, Hureae, Drypeteae and Bischofieae. To

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the best of my knowledge, none of Hurusawa's proposed segregate families have been accepted.

Hutchinson (1969b), in contrast, produced a very original classification in which subfamilies are abandoned and the genera assigned to 40 tribes, many of them new. Hutchinson had begun work on the family over 50 years earlier with his treatment of part of the Euphorbiaceae for the *Flora of Tropical Africa* (Hutchinson, 1911-1912). In his first classification of the families of dicotyledons (1926), he enumerated no subfamilial taxa, but did characterize the family as polyphyletic. His classification of 1969 is featured by a synoptic key to tribes, illustrations, tribal descriptions and enumerations of genera.

How well does Hutchinson's system reflect affinities? If it is measured against the treatment of Webster (1975), it is notable that 11 of the 40 Hutchinsonian tribes have genera belonging to at least three different tribes (*sensu* Webster). Among the taxa that were placed in Acalyphaeae subtribe Mercurialinae by Pax & Hoffmann (1931), Hutchinson's treatment appears especially unfortunate. His tribe Malloteae includes genera belonging to five different tribes, while he refers to seven different tribes genera that in my opinion should be brought together in the single tribe Acalyphaeae. On the other hand, his classification does have the virtue of awarding tribal status to phylogenetically isolated genera such as *Uapaca*, and largely natural groups of genera, such as the Codiaceae and Alchornieae.

Overall, Hutchinson's system does not appear greatly superior to that of Pax in terms of elucidating phylogenetic affinities, and in some respects it is retrograde. Partly, this disappointing result seems due to Hutchinson's reliance on Gestalt of habit and gross floral morphology without seeking correlations among anatomical, cytological, or palynological characters. It is apparent that in the Euphorbiaceae Hutchinson's intuition was not very successful in identifying lines of natural affinity. His insistence on using only a single rank between family and genus would in itself result in considerable distortion of relationships compared to a more hierarchical system.

Some of the most significant contributions to improving our understanding of the classification of the Euphorbiaceae have been made by the late Mr H. K. Airy Shaw. Although he dealt primarily with taxa of tropical Asia and Australia, he also had occasion to consider the problem of delimitation of the family (Airy Shaw, 1965; Willis, 1966). He concluded that in addition to the Euphorbiaceae *sensu stricto*, a number of small segregate families should be recognized: Androstachyaceae, Bischofiaceae, Hymenocardiaceae, Pandaceae, Peraceae, Picrodendraceae, Stilaginaceae and Uapacaceae. Earlier (Webster, 1967) I expressed scepticism about some of these segregations, and, on the basis of studies done since then, I am not persuaded that any of the splinter-families should be recognized, except possibly the Pandaceae.

Within the scope of the present review, it is not practicable to discuss in detail the arguments for and against recognizing these small families. However, it seems worthwhile to note recent studies that provide evidence for evaluating Airy Shaw's proposals. Evidence from pollen (Punt, 1962; Köhler, 1965) and wood structure (Metcalf & Chalk, 1950; Mennega, this volume) does not support recognition of the Stilaginaceae and Uapacaceae (Airy Shaw in his revision of Willis, 1966) as distinct families. My suggestion (Webster, 1967, 1975) that *Picrodendron* should be located in the Euphorbiaceae subfamily

Oldfieldioideae is supported on anatomical and palynological grounds by Hayden (1977) and Hayden *et al.* (1984). Inclusion of *Androstachys* in subfamily Oldfieldioideae is also supported by anatomical studies of Hayden (1980).

There is no doubt that *Bischofia* is an isolated genus in the Euphorbiaceae, without any morphologically similar neighbours in the subfamily Phyllanthoideae. However, Airy Shaw's claim (Airy Shaw, 1965; Willis, 1966) that it is not only a distinct family but is more closely related to the Staphyleaceae is contradicted by the study of Bhatnager & Kapil (1974, 1979), who demonstrate that *Bischofia* is fully compatible with Euphorbiaceae in embryological characters and quite different from Staphyleaceae.

The proposal by Airy Shaw (1965) to create a segregate family Hymenocardiaceae remains controversial. Leonard & Mosango (1985) accept family status for *Hymenocardia*, citing floral and pollen differences. It is true that both Punt (1962) and Köhler (1965) have remarked on the palynological distinctiveness of *Hymenocardia*; however, this could possibly reflect the shift to wind pollination in the genus, rather than a wide phylogenetic divergence. Against the pollen evidence, one may cite the ovule structure, typical for Euphorbiaceae (Baillon, 1858); chromosome number of $n=13$ as in other Phyllanthoideae (Hans, 1973); and wood anatomy similar to Antidesmeae (Metcalfe & Chalk, 1950; Mennega, this volume). A very interesting contribution towards resolving the problem is the discovery by Pais *et al.* (1967) of a new alkaloid, hymenocardine, in *Hymenocardia acida* Tul.; this belongs to an unusual class ("alcaloides peptidiques") that has also been isolated from Rhamnaceae and Pandaceae. Whether or not this furnishes evidence for placing *Hymenocardia* in a separate family, it provides a very suggestive indication of its relationships. The conflict between evidence from pollen and possibly alkaloids versus that from other organs clearly requires explanation, but at present I see no compelling need to remove *Hymenocardia* from the Euphorbiaceae, unless indeed it is shown to be more closely related to the Pandaceae.

It is unfortunate that Airy Shaw never found time to complete his system of suprageneric taxa in the Euphorbiaceae. However, in his revision of Willis's dictionary and in various floristic treatments (Airy Shaw, 1972, 1975, 1980; Willis, 1966), he has offered a fragmentary draft of his revised system, which is based mainly on taxa of the Oriental and Australasian regions; a brief modified version of his system is given by Radcliffe-Smith (1978). For comparison with the system of Webster (1975), his taxa are listed in Table 4. If one ignores differences in rank, it can be seen that the two systems show many correspondences overall. Airy Shaw's tribes Crotonae, Jatropheae, and Euphorbieae are more-or-less comparable to the subfamilies Acalyphoideae, Crotonoideae and Euphorbioideae *sensu* Webster. The main differences are due to the recognition (by creation of suprageneric taxa) that Airy Shaw has given to certain individual genera, such as *Acalypha*, *Baloghia*, *Borneodendron* and *Ricinus*. His suggestions for placement of genera in his enlarged tribe Jatropheae are based on considerable personal experience and merit serious consideration where they differ from those of other workers.

For obvious reasons of self-reference, an objective appraisal of the system of Webster (1975) cannot be offered in this review. Eventually, it will no doubt be at least partly superseded by a different classification, as the Euphorbiaceae is still a very poorly understood family and much work at the alpha taxonomic

Table 4. Comparison of the classifications of Euphorbiaceae by Airy Shaw 1972, 1975, 1980; Willis 1966) and Webster (1975); segregate families recognized by Airy Shaw are given in capitals; taxa not treated by Airy Shaw are indicated by —. The infrafamilial taxa of Airy Shaw, as explicitly noted by him, are mostly 'informal' taxa that have not been validly published

	Webster	Airy Shaw
Subfamily	PHYLLANTHOIDEAE	
Tribe	Wielandieae	—
	Amanoeae	(Phyllanthae)
	Brideliaceae	Brideliaceae
	Porantheraceae	—
	Spondiantheae	—
	Antidesmeae	STILAGINACEAE
	Aporuseae	Aporuseae, Baccaureae
	Drypeteae	Drypeteae
	Phyllanthaceae	Phyllanthaceae
	Hymenocardiaceae	HYMENOCARDIACEAE
	Uapaceae	UAPACACEAE
	Bischofiaceae	BISCHOFIACEAE
Subfamily	OLDFIELDIOIDEAE	
	Hyaenancheae	Dissiliariaceae, Austrobuxaceae
	Petalostigmateae	Petalostigmateae
	Caletieae	Drypeteae (ex parte)
	Picrodendreae	—
Subfamily	ACALYPHOIDEAE	
	Clutieae	—
	Pogonophoreae	—
	Chaetocarpeae	Chaetocarpeae
	Cheiloseae	Cheiloseae
	Erismanthaceae	Crotoneae-Erismanthinae
	Ampereae	—
	Chrozophoreae	Crotoneae-Chrozophorinae
	Agrostistachyidae	Crotoneae-Agrostistachyidinae
	Caryodendreae	—
	Pycnocomaceae	Crotoneae-Blumeodendrinae, Mallotinae
	Bernardieae	—
	Epiprineae	Crotoneae-Epiprininae
	Adelieae	—
	Alchorneae	Crotoneae-Alchorneinae
	Acalypheae	Acalypheae; Crotoneae-Mallotinae, Homonoiiinae, Mercurialinae; Ricineae
	Plukenetieae	Crotoneae-Plukenetiinae
	Dalechampiaceae	Crotoneae-Dalechampiinae
	Omphaleae	Jatropheae-Jatrophinae
	Pereae	PERACEAE
Subfamily	CROTONOIDEAE	
	Micrandreae	—
	Manihoteae	Jatropheae-Manihotinae
	Adenoclineae	Crotoneae-Endosperminae
	Gelonieae	Suregadeae
	Elaterospermeae	Jatropheae-Jatrophinae
	Joannesieae	Jatropheae-Jatrophinae
	Codiaeaceae	Baloghieae; Crotoneae-Codiaeinae, Ostodinae
	Ricinocarpeae	Borneodendreae; Crotoneae- Alphandiinae
	Trigonostemoneae	Jatropheae-Ostodinae
	Aleuritideae	Jatropheae-Jatrophinae
	Crotoneae	Crotoneae-Crotoninae
Subfamily	EUPHORBIOIDEAE	
	Stomatocalyceae	Euphorbieae-Pimelodendrinae
	Hippomaneae	Euphorbieae-Hippomaninae
	Pachystromateae	—
	Hureae	Euphorbieae-Hippomaninae
	Euphorbieae	Euphorbieae-Euphorbiinae

level still remains to be done, to say nothing of what will be possible with more sophisticated techniques. I would predict that if currently espoused practices in cladistic taxonomy (Wiley, 1981) are followed, the boundaries of the subfamilies and many tribes would have to be drastically modified; it is evident, for example, that the subfamilies Phyllanthoideae, Crotonoideae, and Acalyphoideae, as presently constituted, are paraphyletic taxa.

CONCLUSIONS

The complexity of relationships within the Euphorbiales has challenged the best efforts of systematists for two centuries, and the resolution of problems will probably continue for many more years. The greatest uncertainty remaining at present is the position of the entire order on the phylogenetic map of the angiosperms. The competing claims of Malvales and Geraniales for the status of sister group makes it impossible at present to confidently assign the Euphorbiales to the appropriate superorder.

A striking result of researches during the 20th century has been to remove, one after another, extraneous families that do not belong in the Euphorbiales. The most recent classifications by well-known students of phylogeny all list families that I believe should be excluded from the Euphorbiales: Aextoxicaceae (Dahlgren, 1983; Takhtajan, 1980; Thorne, 1983); Buxaceae (Stebbins, 1974; Cronquist, 1981); Simmondsiaceae (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1980; Thorne, 1983); and Thymelaeaceae (Thorne, 1983). Only the Pandaceae survives a close scrutiny of characters to emerge as the only other family of the order besides Euphorbiaceae. However, despite the arguments of Forman (1966, 1968, 1971), the evidence to support status of the Pandaceae as a separate family is very weak, and rests more on our ignorance than on our knowledge. The Pandaceae is very tentatively accepted in this paper as the only other family of Euphorbiales, with the understanding that future studies may demonstrate that it is better treated as a group within the Euphorbiaceae.

The question of the position of the Euphorbiales in the phylogenetic system of the dicotyledons remains unresolved. During the years since my earlier statement favouring a placement of the Euphorbiaceae in the Rosidae (Webster, 1967), I have come to be less certain about rejecting a Malvalean affinity. The morphological and biochemical similarities between Euphorbiales and various taxa of the superorders Malvanae, Rutanae and Celastranae (*sensu* Takhtajan, 1980) appear to me to contradict the assignment of these groups to two different dicotyledon subclasses, the Dilleniidae and Rosidae (*sensu* Cronquist, 1968, 1981). It is notable in this regard that Kubitzki (1969, 1977) and Merxmüller (1972), on the basis of biochemical and floral characters, have pointed out the arbitrariness of the boundary between Dilleniidae and Rosidae. There are other indications, besides problems in tracing affinities of the Euphorbiales, that there is a serious problem with the delimitation of the two dicotyledon subclasses by Cronquist. Lobreau-Callen (1977), for example, considers that the pollen of Celastrales *sensu stricto* agrees with that in the Rosidae, whereas other families that have been placed in the Celastrales (e.g. Aquifoliaceae, Icacinaceae) are palynologically closer to Dilleniidae. Therefore, I am in sympathy with the criticisms of Kubitzki, Merxmüller, and the recent statement by Ehrendorfer (1983) expressing an agnostic point of view towards recognizing the currently

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defined limits of Dilleniidae and Rosidae. At present, it appears that the best reading of the evidence is to associate the Euphorbiales with the Malvales and Geraniales, and possibly with the Celastrales, in a superorder that straddles the arbitrary boundary between Dilleniidae and Rosidae suggested by Cronquist (1981). Among recently published classifications, phylogenetic affinities seem to be best expressed in the system of Soó (1967), who links the Malvales, Geraniales and Euphorbiales into a single phyletic line (Fig. 2D), even though he does not create a formal supraordinal taxon.

Despite over 150 years of study of infrafamilial relationships in the Euphorbiaceae, following the pioneering work of A. de Jussieu (1824), the subfamilies and tribes of Euphorbiaceae are still not satisfactorily defined. The system of Webster (1975), with five subfamilies and over 50 tribes, is broadly compatible with data from the fields of wood anatomy, cytology, and biochemistry, but detailed morphological and anatomical studies are still needed for many genera before the scaffolding of the classification of Euphorbiaceae can be considered secure.

ACKNOWLEDGEMENTS

The conclusions in this paper have been strongly influenced by research done over the past 30 years with support from the National Science Foundation. I am indebted to Mr Radcliffe-Smith and the staff of the library at Kew for assistance in completing the bibliographic work.

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