Taxonomic and Phylogenetic Assessment of the Euphorbiaceae: A Review

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ABSTRACT: The family Euphorbiaceae is assessed taxonomically and phylogenetically in the light of different disciplines of botany. It lacks anatomical homogeneity, probable because of diverse habit and habitat. It is heterogenous palynologically, chemically and embryologically. It is, however, fairly homogenous from embryological point of view. The floral anatomical investigations indicate reduction in the number of floral whorls as well as the number of members of whorls from a supposedly 5 - merous, dichlamydeous, heterochlamydeous ancestral flower. A review of taxonomic features especially those from exomorphology, have always remained changing. The present review based on all pervasive examination of exomorphology and endomorphology suggests close affinities of certain families of this alliance. However, few of them apparently closer because of unisexuality and reduced floral structure.

Key words: Taxonomy, Phylogeny, Euphorbiaceae

Introduction

The family Euphorbiaceae is generally distinguished by the milky sap (when present), the unisexual flower, ovary superior and generally trilocular, placationt axile, ovules collateral, pendulous with ventral raphe and usually carunculate. Although so, the family received varied treatments in the Englerian and Ranalian systems of plant classification. The ordinal, familial, subfamilial and tribal boundaries of the euphorbiaceous plexus has always remained uncertain. All pervasive scrutiny of features divulged from different disciplines appear worthwhile. In past, alliance has received fair attention in various domains of plant morphology. The present investigators assessed the said alliance synthetically, inclusive of their vegetative anatomical evidence. Discussion of the same is avoided for the sake of precision here.

Taxonomic history and significance

In Bentham and Hooker's treatment (1862 - 1883), the family Euphorbiaceae is kept under the series Unisexualae based on unisexual or polygamous flowers. It is placed alongwith other families such as Balanopceae, Urticaceae, Platanaceae, Leitnerieae, Juglandaceae, Myricaceae, Casuarinaceae and Cupuliferae. They divided Euphorbiaceae into six tribes viz., Viz., Euphorbeae, Stenolobieae, Buxeae, Phyllanthaceae, Galeareae, and Crotonaceae. They included some genera in their 'Formae Abnormes'. They employed the features especially of embryo, ovule, distinctiveness of flowers, etc. at tribal level.

Bessey (1915) included the family Euphorbiaceae in his order Geraniales under subclass Strobiloideae. However, he referred the family Buxaceae, which is sometimes included in the family Euphorbiaceae, to his order Celastrales under his subclass Cotyloideae. His Strobiloideae represents Ranalian line characterised by vertical conations of like parts, whereas his Cotyloideae represented by transverse adnation of unlike parts.

Hutchinson (1959) included a single family Euphorbiaceae in his order Euphorbiales. He regards the family heterogenous and derived probably from several stocks viz., Bixales Tiliales, Malvales, Celastrales and Sapindales. He included Pandaceae and Aextoxicaceae in his order Celastrales. He regarded Apetalae as primitive. His Tricoccae are indicated as a connecting link between Amertiferae and Malvalean ancestry. However, this theory received a little support among subsequent
workers. Rendle's order Tricoccae (1969) comprises families viz., Euphorbiaceae, Buxaceae and Callitrachraceae. He includes Daphniphylaceae as a tribe under the Euphorbiaceae. However, Simmondsiaceae is merged under the Buxaceae. He is silent in regard to the taxonomic treatment of the family Dichapetalaceae, Aectoxiaceae, Pandaceae, Picrodendraceae, etc. He divided family Euphorbiaceae, after following Pax in the 'Pflanzen Familien', into two groups viz., Platylaboeae and Stenolaboeae. The former is characterised by broad cotedyles. He divided the former into two families e.g. Phyllanthoideae and Crotonoideae. He also divided later into two subfamilies Porantheroideae and Ricinocarpoideae. He emphasized aestivation of calyx, size of embryo, number of ovules per locule, etc. for the tribal and subfamilial delineations. In his opinion, the Buxaceae differs from Euphorbiaceae in the dorsal raphe of the anatropus ovule and loculcial dehisence of fruit. Benson (1957) referred the families Euphorbiaceae and Buxaceae in his order Euphorbiales. He characterised the former by fruit septicidal, ventral raphe, whereas the latter by fruit loculical and dorsal raphe. Melchior (1964) placed the family Euphorbiaceae in his suborder Euphorbineae under Geraniales, whereas Buxaceae is kept under Buxineae under the order Celastrales.

The preceding resume of the systematic accounts of the family Euphorbiaceae and its alliance indicates that there has been no unanimity of opinions in the task of systems of plant classification. They revealed considerable diversity of opinions in regard to their tribal, subfamilial, familial and ordinal circumscriptions. There are certain parameters that lump them together into some larger groups, while there are others which split / distinguish and delimit them.

**Synthetic assessments**

While anatomical evidence are of utility in the assessments and appraisals, they have their own limitations as an effective tool in interpreting phylogenetic evaluations and systematic delineations. The present investigators, in addition to their own observations of the family Euphorbiaceae, data from past studies have employed for a more comprehensive description of the problem. An attempt had been made to evaluate the Euphorbiaceae in the following to focus on the intricacies of these situations. Evidence from other disciplines of plant morphology are freely borrowed in this assessment.

**(i) Vegetative anatomy**

Metcalfe and Chalk (1950) recorded paracytic stomata in the tribe Acalyphae, Dalechampiaceae, Euphorbiaceae, Hippomaneae (except *Manihot*), Phyllantheae (except some Euphyllantheae) and in the genera *Glochidion*, *Excoecaria*, *Stillingia*. They also noted anomocytic stomata in some genera viz., *Andrachne*, *Aporosa*, *Baccaurea* and *Richeria*. Inamdar and Gangadhar (1978) noted paracytic, anomocytic, anisocytic and diacytic stomata in 53 species belonging to three tribe's viz., Euphorbiaceae, Phyllantheae and Crotonoideae. More than one type on stomata occurs on the same surface of lamina in majority of species studied. Rao and Raju (1977) reported stomata paracytic most common. They also noted anomocytic, anisocytic, and diacytic stomata in 50 species belonging to different 17 tribes of the Euphorbiaceae. In their opinions the paracytic type forms the basic stomatal type for the family Euphorbiaceae because of common occurrence in majority of tribes studied. Dehgan (1980) reported paracytic stomata as basic in different species of the genus *Jatropha*. Sehgal and Pillaiwal (1974) investigated 130 species of the genus *Euphorbia* and stated that most of them belong to dicotyledon met with in the genus *Euphorbia*. Anomocytic type being most preponderant. Khatijah Hussein et al. (1996) in their studies of some species of *Malolius* observed paracytic stomata. Levin (1986) noted anomocytic type in *Podocalectyranas* and paracytic in *Paradrypetes* within the subfamily Phyllanthoideae. Paracytic stomata are characteristic of the tribe Bridelieae, Dendrophyllaeae, Phyllantheae, Fleuggegeneae and some genera of Wielandieae.

The present authors noted mostly anomocytic type in Euphorbiaceae and Phyllantheae. The anomocytic and paracytic types are reported on the same foliar surface in the tribe Hippomaneae, anomocytic being most common. In the tribe Crotoneae anomocytic type is more or less common, except *Parviceps indica*, *Jatropha panuraefolia*, *Tragia involucrata* wherein paracytic type is observed. *Simmondsia chinensis* presently studied by present investigators shows anomocytic type of stomata. Metcalfe and Chalk (1950), however, documented anomocytic stomata in this genus. Metcalfe and Chalk (loc. cit.) described the stomata for the genus *Buxus* surrounded by rosettes of more or less clearly defined subsidiary cells.

The observations made by present investigators and those documented above by the different authors indicate that the stomata is characteristic of the any tribe *sensu* Bentham and Hooker (1862 – 1883) of the family Euphorbiaceae. Also their distribution, whether hypostomatic or epistomatic, is not tribe - characteristic. It is to be noted that paracytic type is more or less common in the genera of the Phyllantheae as well as family Euphorbiaceae. The other types such as anomocytic, anisocytic and diacytic appear to have been derived from it in the euphorbiaceae allium. Epidermal outgrowths such as unicellular, stellate and peltate scales have been observed by present authors in 18 species belonging to the tribes *sensu* Bentham and Hooker 1862 – 1883 Euphorbiaceae, Phyllantheae and Crotonoideae (Thakur and Patil, 2005). The genera *Neoscodechinia*, which are not, mentioned in Genera Plantarum (Bentham and Hooker, 1862 – 1883) also show unicellular trichomes, the stellate trichomes are found in two genera (*Chrozophora rotteri* and *Trewia polyacarpa*) of the tribe Conoideae. The peltate scales are found in one genus *Chrozophora* (*Chrozophora kingii* and *Dimophocalyx lawianus*) of the tribe Conoideae. In the rest others, genera belonging to tribes Euphorbiaceae, Phyllantheae and Crotonoideae the trichomes are generally unicellular, but unlike the genera of the other tribes mentioned, the basic trichomes are basically three types of trichomes, viz., glandular, unicellular, and stinging types. They grouped glandular trichomes in six different types, which are mostly included multicellular ones. They categorized non-glandular trichomes into six types covering unicellular and multicellular types. The latter included stellate trichomes and peltate scales. These authors have not pointed out taxonomic significance of the trichomes. However, it appears that the category of stinging hairs is generally found in the tribes Dalechampiaceae and Plukenetiaeae. Likewise, the simple unicellular and uniseriate trichomes are generally found in Phyllantheae, Bridelieae, Acalypheae and also in some members of Crotoneae, Hippomaneae and Dalechampiaceae.

Sastry and Kannabiran (1994) observed stellate and candelabral (dendroid) trichomes in the tribe Crotoneae. On account of unicellular conical hairs in the genus *Micrococoa*, Sastry and Kannabiran (loc. cit.) recommended segregation of the genus from the subtribe Acalyphinae. They also noted unicellular trichomes in this tribe. Baruah and Nath (1997) formulated a key on the basis of presence or absence of trichomes in the two genera viz., *Crotone* and *Croton*. Stellate trichomes usually occur in the species of the genus *Croton* and trichomes do not occur in the case of *Codiaeum variegatum*. Webster et al. (1996) investigated 120 species for their trichomes in the genus *Croton*. They noticed stellate, fasciculate, multiradiate and rosulate, denticrict, lepidote, papillate and glandular types. They characterised 40 sections of the genus on the basis of trichome morphology. Although *Crotoneae* is similarly characterised by the occurrence of stellate trichomes, one of the genus *viz.*, *Pedilanthus*. His reported to have uniseriate branched or unbranched trichomes by Dave et al. (1979). Rao and Raju (1985) investigated trichome types and their distribution in 250 species of the family. They particularly noted malpighiaceous, stellate and lepidote types in the subfamilies Acalyphoideae and Crotonoideae, whereas in rest other subfamilies they are predominantly unicellular or multicellular ones. In their opinion, the stinging hairs evolved independently in the members of the subfamilies Acalyphoideae and Crotonoideae. The stinging hairs in the Acalyphoideae are fundamentally different from those of the tribe Plukenetieae. The trichomes in Plukenetieae composed of a central crystalliferous cells of subepidermal origin surrounded by a jacket of the epidermal cells (Krook, 1955). The presence of unicellular type of trichome provided a basis for assigning the genus *Dalechampia* to the tribe Plukenetieae, which is sometimes referred outside it.

The present authors observed *Brenyina nivoso*, *Macaranga peltata* and *Malolius stenanthes* for foliar glands especially present on the lower surface. These taxa belong to the tribes Phyllantheae and Crotoneae. They are reported in some genera of Acalyphoideae, Crotonoideae and confined to some genera of the Phyllantheae, Oldfieldiaceae and few other genera (Webster, 1994). The foliar
glands are also generally noted in some taxonomic accounts (Hooker, 1885; Cooke 1958; Gamble, 1972). It appears that the occurrence of foliar glands in the family Euphorbiaceae is sporadic and not restricted to any group within it. Probably, these have arisen de novo within this alliance (cf. also Webster loc. cit.). Metcalfe and Chalk (1950) recorded their occurrence in the genera like *Asclepias*, *Chamaesyce*, *Macaranga*, *Malolitus*, *Acalypha*, *Hymenocardia*, *Trewia*, etc.

Stern (1967) while studying xylem anatomy of the genus *Kleinotheca* and tribe Clutiaee (Euphorbiaceae) reminded the remarks made by Metcalfe and Chalk (1950) that 'the anatomical structure exhibit a wide range of variation in correlation with a diversity of habit and no important characters occurs throughout the numerous tribes into the families divided'. Stern (loc. cit.) further opines that this statement applies equally to the xylem anatomy of the species Clutiaeae because no single anatomical characteristic is common to all the species. Although so, in his opinion, there are no anatomically related objections to the inclusion of the genus *Kleinotheca* under the tribe Clutiaeae as treated by Pax (1890) and Pax and Hoffmann (1931).

Foliar venation patterns, although very important for the taxonomic and phyllogenetic considerations, have largely remained neglected for the family Euphorbiaceae. The genus *Euphorbia* of the tribe Euphorbieae have been investigated by Sehgal and Palival (1974). They found the features such as number of strands entering a leaf, presence or absence of sheath around the vein, organization of midrib and behaviour of strands in the areoles, size, number of veins - endings and their tips per areole, as also the organization of terminal vein endings are plastic and bear little taxonomic significance. In their opinion, the venation patterns of the leaves are widely divergent, and in part confirmatory and in part conflicting with the proposed arrangement of sections and subsections of the genus sensu Pax and Hoffmann (1931).

The family Buxaceae is revealed anatomically by Metcalfe and Chalk (1950). The type of stomata, petiolar vasculature, clustered crystals, wood parenchyma apotracheal, and vessel specialization are more or less similar to the majority of the Euphorbiaceae. However, fibers with border pits and cortical vascular bundles in the stem of *Buxus* and *Notobuxus* do not ally with the members of Euphorbiaceae. *Simmondsia* sometimes included under the family Buxaceae (Bentham and Hooker, 1862 - 1883; Engler and Diels, 1936; Benson, 1975; Cronquist, 1968, 1981; Takhtajan 1969, 1973). It is also treated separately in its own family Simmondsiaceae. The present authors observed foliar stomata are anisocytic in the genus *Simmondsia*. These results revealed that the members of Euphorbiaceae is to be segregated from *Buxus*. The leaves are isobilateral. Remarkable anomalous growth in thickness of stem by the development of successive concentric rings of xylem and phloem is noted. Roots are also marked having phloem in each consecutive ring of isolated strands, vessels with spiral thickenings with simple perforation are encountered in the Buxaceae as well as in the Euphorbiaceae (Metcalfe and Chalk, 1950). The eglandular trichomes, arc - shaped vascular strand in the petiole, presence of clustered crystals are, however, found in the genus *Simmondsia*. These are also noted in the Buxaceae and Euphorbiaceae (Metcalfe and Chalk, 1950). *Simmondsia* shows S - type sieve - element plastids which strongly differs from the Buxaceae. These render *Simmondsia* a very isolated genus without close relationship to either Buxaceae or Euphorbiaceae. Kokubun (loc. cit.) pointed out the resemblances between *Simmondsia* and Buxaceae in wood anatomy, stomatal type, pollen exine stratification, seed coat development and chromosome number, etc. These, in their opinion, do not preclude a taxonomic association, although not very close between these two families viz., Buxaceae and Euphorbiaceae. Paracytic stomata, petiole supplied with solitary vascular strand, paired root of clustered crystals are recognized in the Daphniphyllaceae and Euphorbiaceae as well. However, wood anatomically it is different from the Euphorbiaceae. The wood in the Daphniphyllaceae is characterised by vessels small, solitary numerous perforation plates, scalariform, intervacular pitting scalariform to opposite, parenchyma diffuse, rays upto two cells wide. Daphniphyllaceae are very distinctively and anatomically similar to the Euphorbiaceae. Bhatnagar and Garg (1977) noted difference in the cellular endosperm development, and also in pollen character of the Daphniphyllaceae and Euphorbiaceae.

Metcalfe and Chalk (1950) described family Dichapetalaceae anatomically. He noted unicellular trichomes, paracytic stomata, vessels with simple perforation or scalariform intervacular pitting usually alternate, wood parenchyma predominantly paratracheal, vasicentric to alliform, fibers with bordered pits, markedly heterogeneous, etc. All these anatomical features are generally encountered in the members of Euphorbiaceae. The family Dichapetalaceae is referred under the order Euphorbiales by some systematists (Takhtajan 1969, 1980; Wettstein 1935). Its placement within the order Euphorbiales or even near the family Euphorbiaceae is amply justified on anatomical grounds.

Vascular anatomy of petiole studied by the present authors (Thakur and Patil, 2009) revealed few variations. The petioles receive 3 - 8 vascular bundles or a ring of 8 - 13 or continuous ring of vascular tissue is generally found in members of tribe Crotoneae (sensu Bentham and Hooker, 1862 - 1883). In the members of tribe Phyllanthaeae, the petioles receive either a continuous ring of vascular tissue or solitary prominent bundle or arc. The petiolar vasculature in the tribe Euphorbeae is either in the form of a ring of vascular bundle of three separate vascular bundles centrally. The tribe Hipppomaneeae shows separate 5 - 8 vascular bundles or a ring of vascular bundles. The different stellar configuration of the petioles do not appear tribe - specific. This configuration, however, can be employed to distinguish between the genera at least. Miller and Webster (1962) used differences in petiolar steles to segregate the genus *Jatropha* from the tribe *Chondrocalyx*. Dehgan (1982) postulated these features significantly at the sectional and subsectional level in *Jatropha*. Dehgan (1935) found resemblance between the Euphorbiaceae on the one hand and Malvaceae, Tilliaceae and related families on the other based on petiolar structure. He also pointed out close relationship between Buxaceae and Euphorbiaceae on the basis of petiolar structure.

The laticifers in the Euphorbiaceae have been fairly investigated by different workers such as Metcalfe and Chalk (1950), Mahlberg (1975, 1993), Spillato and Mahlberg (1986), Mahlberg and Sabharwal (1968), Rao and Malviya (1981), Rao, Menon and Malviya (1964), Fineran (1982, 1983), Balaji, Subramanian and Inamdar (1996). However, it is only Dehgan and Craig (1978) and Rudall (1994) commented on their taxonomic importance in the family. Dehgan and Craig (loc. cit.) could distinguish the subgenus *Curcas* based on the presence of chambered crystalliferous cells and their absence in the subgenus *Jatropha*. In their opinion, use of laticifer as a taxonomic criterion is only relevant if supported by other lines of evidence. They further pointed that much new work and reevaluation of older studies are needed if the taxonomic dilemma of the laticifers is to be alleviated. Webster (1987) postulated that Crotonoideae and Euphorbioideae (latex and laticifers usually present) evolved independently from *Acalyphoideae* (latex and laticifers rarely present). The subfamilies viz., Oldfieldioideae and Phyllanthoideae (latex and laticifiers absent) are closely linked to each other. He opined that latex - producing dicotyledonous families such as Apocynaceae, Asclepiadaceae, Moraceae and Sapotoaceae are widely distributed throughout the dicotyledonous orders, but the capacity for latex production does not in itself necessarily imply relationships inter se.

Behnke (1982) showed that *Simmondsia* with S - type plastids in the element which strongly differs from the Buxaceae (sensu stricto). The Buxaceae have a unique type of plastids with a globular photosynthetic crystal. Behnke (loc. cit.) considered the Simmondsiaceae as a very isolated group without close relationship to either Buxaceae or Euphorbiaceae. There are few variations in the photosynthetic process among green plants called C4 type, C3 type and CAM. The species of the genus *Euphorbia* have been detected for CAM; C4 photosynthesis. Depending on these the genus *Euphorbia* is divided into two subtribes viz., *Euphorbioideae* which is restricted to the subgenus *Chamaesyce* such plants are termed as C4 plants. These plants have specialized chlorenchymatous leaf bundle sheath in which chloroplasts have a slightly granular and wall structure. These anatomical specializations are called Kranz syndrome and the species are therefore called as Kranz species. Webster et al. (1975) suggested a distinct morphological feature as the origin of C4 plants showing Kranz anatomy. They also suggested a distinct generic status for the subgenus *Chamaesyce*. 

(ii) Palynology
Palynology of the Euphorbiaceae and related families has been fairly investigated. Erdtman (1952) described the pollen grains in the family are corporeal, forate, rugorate, foraminoidate or non-aperturate, oblate to prolate. He thought the family clearly multi-specific and also commented on the palynological hierarchy e.g. pollen morphology in his opinion, supported the subdivisions of the Euphorbiaceae into 'Platylobae, Stenolobae' as unnatural. Porantheroideae should probably be referred to subdivisions of the Euphorbiaceae into 'Platylobeae, Stenolobeae' as investigated. Erdtman (1952) described the pollengrains polyf-orate. He described the genera Buxus, Notobuxus, Pachysandra, Sarcococca, Simmondsia and Sterculiosia. According to him, the pollengrains of Buxaceae are similar to certain types Euphorbiaceae and Thymelaeaceae. He further stated that the pollen grains in Pachysandra and Sarcococca are more or less reminiscent of certain Crotonoid pollen grains in Euphorbiaceae and Thymelaeaceae, The pollen grains of Aextoxicaceae, Dichapetalaceae and Pandaceae are similar to those of some Euphorbiaceae. The pollen grains of Picrodendraceae are slightly similar to those of Pseudanthus and Acidocrotonoideae to Crotonoideae. Nowicke (1994) investigated pollen morphology of 69 species representing 34 genera of 12 tribes of Crotonoideae using L M, S E etc. Erdtman (loc. cit.) described the pollengrains polyf-orate. He described the genera Buxus, Notobuxus, Pachysandra, Sarcococca, Simmondsia and Sterculiosia. According to him, the pollengrains of Buxaceae are similar to certain types Euphorbiaceae and Thymelaeaceae. He further stated that the pollen grains in Pachysandra and Sarcococca are more or less reminiscent of certain Crotonoid pollen grains in Euphorbiaceae and Thymelaeaceae. The pollen grains of Aextoxicaceae, Dichapetalaceae and Pandaceae are similar to those of some Euphorbiaceae. The pollen grains of Picrodendraceae are slightly similar to those of Pseudanthus and Acidocrotonoideae to Crotonoideae. Nowicke (1994) investigated pollen morphology of 69 species representing 34 genera of 12 tribes of Crotonoideae using L M, S E etc. Erdtman (loc. cit.) recognized five subfamilies viz., Phyllanthoideae, Oldfieldioidae, Acalyphoideae, Crotonoideae and Euphorbioidae. Nowicke (loc. cit.) supported Webster’s idea of dividing the Euphorbiaceae into five subfamilies on palynological basis. He opined that each subfamily is more or less characterised by a basic pollen type with the exception of subfamilies Acalyphoideae. Nowicke (1994) investigated pollen morphology of 69 species representing 34 genera of 12 tribes of Crotonoideae using L M, S E M and T E M. He observed the pollen mostly inaperturate and having similar architecture. He opined that pollen morphologically the three subfamilies viz., Oldfieldioidae, Crotonoideae and Euphorbioidae are natural assemblages. He further observed that the pollens of Crotonoideae resemble to those of Thymelaeaceae. Takhtajan (et al., 1980) studied palynologically 30 genera. They described and illustrated with light microscopy, scanning and T E M covering the tribes Epirrheae, Adelaeae, Alchorneae and Acalyphae pro parte. Pollen data support the concept of subtribe Epirrheae but indicate that subtribe Cephalomppinaceae is not related and should be considered for separate tribal status. There is close relationship among Adelae, Lasciocroton and Leucocroton but not with the two remaining members of Adelaeae, which do not appear closely related with each other. These authors pointed out that the genus Wettinia is not closely related to Cleidion. They tentatively supported concept of Macarangiae comprising only Macaranga. Nowicke (1994) based the concept of Crotonoideae on his palynological studies. He showed every species having pollen with Croton structure within the family. Pollen data suggested Micrandraceae and Adencoclineae primitive retaining only apertured but exines with well developing foot layers. They have the Crotan structure and are clearly allied to inaperturate Crotonoideae. The exine structure of Crotonoideae is similar to Thymelaeaceae than any two remaining subfamilies of Euphorbiaceae and Thymelaeaceae is sometimes acknowledged (cf. Cronquist 1981, 1988). Cronquist (loc. cit.) assigned Thymelaeoideae to Euphorbiaceae. Thymelaeaceae may fit in the Myrtales on other bases but pantoporate pollen is virtually unknown in the order. Nowicke (loc. cit.) thought the Euphorbiaceae perplexing on the basis of pollen data. The Oldfieldioidae, Crotonoideae and Euphorbioidae have basic pollen type. The Phyllanthoideae and Acalypheoidae have basic pollen type. The Oldfieldioidae, Crotonoideae and Euphorbioidae, in his opinion, are natural assemblage. The genus Platygyna shows pollen grains inaperturate with rugulate tectum. The generic status of this genus is much debated (cf. Liogier, 1971; Borhidi et al., 1973). It is separated from the genus Tragia on the basis of a globose or convex staminate receptacle and thickened papillose style. The genus Platygyna is quiet distinct from Tragia palynologically. The genus Euphorbiaceae is controversial. Hutchinson (1969) included Buxaceae under the family Euphorbiaceae. Airy Shaw (1965) disband the genus and placed in its own family - the Hymenocardiaceae. Radcliffe - Smith (1973, 1987a,b) and Leonard and Masango (1985) also placed it under the Hymenocardiaceae. Airy - Shaw (1965) observed male flowers lacking both petals and disc and considered it decisively ualumeaceae or urticaeous. The winged fruit of Hymenocardia also resembles to those of Holoptelea of the Ulmaceae. It is to be noted that the fruit of the Hymenocardia are bilocular, while samara producing Ulmaceae is always unilocular. Also, carpels of Hymenocardia are biővulate, they are always uniovulate in the Ulmaceae. Geoffrey et. al. (1994) noted palynological features of Hymenocardia similar to those Phyllanthoideae and remarked for its retention in the Euphorbiaceae. Wood anatomically it is also similar to the members of the Phyllanthoideae (Euphorbiaceae) (Metcalfe and Chalk, 1950). Muller (1981) assessed record of fossil angiosperms pollen types and gave the appearance of angiospermic families based on it. He recorded Phyllanthoideae and Crotonoideae of the Euphorbiaceae as appearing in Paleocene of Tertiary. Likewise, the family Buxaceae, which is sometimes included under the Euphorbiaceae, made appearance in Oligocene. However, further studies in the Euphorbiaceae may clarify this situation in future.

(iii) Embryology
Rao (1970) stated comparative embryology of the Euphorbiaceae and assessed its taxonomy and phylogeny based on the evidence then available to him. The family Callitrichaceae is included under the Euphorbiaceae. Airy Shaw (1874), Engler and Diels (1936) placed Callitrichaceae under the suborder Callitrichinae near the suborder Tricoceae of the Euphorbiaceae, both being placed under the main order Geraniales. Wettstein (1935) placed the family Callitrichaceae under the order Tricoccae alongwith the Euphorbiaceae. Rao (loc. cit.) reiterated the similarities between Callitrichaceae and Euphorbiaceae. The embryological features such as anisogamous unitegmic ovules, differentiation of endosperm, cellular endosperm with terminal haustoria, long filamentous proembryonal suspensor and minute seedcoat with membranous seedcoat, etc. do not allow one to ally the Callitrichaceae with the Euphorbiaceae. On the other hand, these embryological features are not found in any two remaining subfamilies of Euphorbiaceae. It is similarly discredited by Webster (1987). Embryologically, the Callitrichaceae are nearer the Lamiales. Takhtajan (1980, 1970) reiterated the similarities between Callitrichaceae and Euphorbiaceae. Rao (loc. cit.) opined that the family Euphorbiaceae is polyphyletic in origin with several lines of evolution and specialisation. Bentham and Hooker (1862 – 18883) placed the genus Daphniphyllum under the family Daphniphyllaceae. Cronquist (1968) treated as a separate family Daphniphyllaceae. Under the order Euphorbiales, Takhatajan (1969) included Buxaceae and Euphorbiaceae as separate families under the order Euphorbiales. However, later (1980) he made no clear reference to the Buxaceae. Cronquist (1968) recognized Buxaceae and Euphorbiaceae as distinct families under the Euphorbiaceae. In his later systems (1981, 1988) he maintained similar treatment for them. Benson (1957) also maintained them as such. Kapil and Bhatnagar (1994) pointed out the differences between Buxaceae and Euphorbiaceae. The former differs from the latter in multilayered anther tapetum, ovules with a dorsal raphe, dermal inner and subdermal outer integument, persistent antipodal cells which even multiply, and fusion of polar nuclei at the chalazal part of the central cell, cellular development of endosperm and the seeds exo - mesotestal. These embryological features, in their opinion, do not support to the inclusion of Buxaceae under Euphorbiaceae. Similar treatment is given by Webster (1987) remarked that it is neglected to retain the Buxaceae under the Euphorbiaceae on embryological ground. Rao (loc. cit.) opined that the family Euphorbiaceae is polyphyletic in origin with several lines of evolution and specialisation.

(iv) Floral Anatomy

The affinities of Euphorbiaceae have been discussed in past into two different groups of angiospermic families. Some suggested affinities to monocotyledonous families like Urticaceae and Centrospermales (Bentham and Hooker 1862 – 1883: Wettstein, 1935). Others thought the family derived from reduction of petaloid ancestors similar to those of Malvales and Geraniales (Engler and Diels, 1936). However, their viewpoints are based on embryonic features of flowers. Comparative floral anatomical studies are helping in solving such problems. Rao and Ramalakshmi (1968) investigated floral anatomy of 23 genera belonging to eight tribes of the Euphorbiaceae. In their opinion, the ancestral flower of Euphorbiaceae conforms to the primitive dicot plant, most commonly found in Malvales and the Geraniales viz. K3, C5, A5+5, G5. In their opinion, reduction have occurred in pistil to three carpels which later became separate family Bischofia (Hutchinson, 1969, 1973; Webster, 1980, 1987; Pax and Hoffmann, 1931, Backer and Bakhuizen 1963). However, it is placed under separate family Bischofia (Hutchinson, 1969, 1973) and Emberger (1960) referred it to a distinct position from the Euphorbiaceae. Kapil and Bhatnagar (1973, 1979), Bhatnagar (1978), Kapil and Bhatnagar (1980) revealed embryological features of the genus Bischofia such as tetrasporangiate anther, anther wall 5 - layered, endothecium fibrous, tapetum secretory, multinucleate pollen grains, binucleate crassinucellate anatropous placental obturator, nucellar cap and hypostase present, embryosac Polygonum type, endosperm nuclei observed 8 – 10 layered, radial and inner tangential wall of the endothecium, 2 or 3 layered tapetum, bicellar ovary with parietal ovules, subdermal outer and dermal inner integuments. Obturate is absent in Daphniphyllum. These features rendered the genus Daphniphyllum to a distinct position from the Euphorbiaceae. Kapil and Kaul (1972) and Kaul and Kapil (1974) noted embryological features of Daphniphyllum resembling the Hammamelidales. In their opinion, inclusion of the genus Daphniphyllum under an independent family Daphniphyllaceae under the Daphniphyllales of Hammamelidales is more satisfactory.

Cronquist (1981, 1983) Thorne (1983) and Dahlgren (1983) placed the Simmondsiaceae in the Euphorbiaceae. Engler (1960) referred it to the Buxaceae, whereas Takhtajan (1980) placed it to the Buxaceae. Bentham and Hooker (1862 – 1882) placed it under the Euphorbiaceae. The genus Simmondsia shares a few embryological features with the Euphorbiaceae in having anatropus, bitegmic, crassinucellate ovules and nuclear endosperm. However, it differs from Euphorbiaceae in having the ovules with a dorsal raphe, absence of obturator and hypostase and in possessing exotesta, mesostesta, exalbuminous seed. It is little related to the Euphorbiaceae, Buxaceae or even Hamamelidales. It shows better embryological similarities with the Fagales (cf. Wiger, 1935; Davis, 1966; Corner 1976).

Dichapetalaceae is referred under the order Euphorbiaceae by some systematists (Takhtajan 1969, 1980; Wettstein, 1935; Thorne 1983; Dahlgren, 1983). Hutchinson (1969, 1973) treated Dichapetalum or Dichapetalaceae under the order Rosales. Takhtajan (1969, 1980) placed this family under Euphorbiales. Engler and Diels (1930) included Dichapetalaceae in the suborder Dichapetalinae near the suborder Tricoccaceae of the Euphorbiaceae both being placed under the order Geraniales. Cronquist (1981) Goldberg (1986) referred it to Celastrales. Mezger (1964) included under the order Thymeleales. The family Dichapetalaceae contains genera with bi to tri - carpellary ovary, two ovules per loculus, axile placentaion with carunculate seeds similar to the members of Euphorbiaceae. However, it is different in unitegmic ovule and exalbuminous seeds. It resembles more with the Celastrales (Goldberg, 1986).

Aextoxicaceae is a monotypic family. It is referred to it under the Euphorbiaceae by Takhtajan (1980), Hutchinson (1973, Cronquist 1968, 1981), Thorne (1980, 1983). Webster (1975) included it under the order Celastrales. The family Aextoxicaceae shows anatropus, bitegmic crassinucellate ovule with massive nucellar beak (Mauritzon, 1936). But its bicellular unilocular ovary with divided two subapical ovules, endosperm extending beyond the exostome, embryo extending only up to half the length of endosperm and ruminate endosperm, etc. do not ally with the Euphorbiaceae. Davis (1996), Corner (1976) and Wunderlich (1967) revealed embryological and seed characters of the family Thymeleaceae. They recorded exotegmic seeds, tetrasporangiate anther, fibrous endothecium, ephemeral middle layer, secretory tapetum, bitegmic crassinucellate, anatropus or hemianatropus ovule, nucellar beak and 99, 1969 and 1973) and whatever is known about these does not satisfy their inclusion in the Euphorbiaceae. Bischofia and Picrodendron can be retained on this basis.

According to Corner (1976), the paucisepalous - like exotege of the Crotonoideae are the Bombacaceae, Malvaceae, Sterculiaceae and Tiliaceae. On the other hand, fibrous exotege of Phyllanthoideae appear closer to the Celastraceae, Flacourtiaceae and Violaceae. Corner (loc. cit.) proposed a cleavage in the Euphorbiaceae based on this fact. Kapil and Bhatnagar (1994) opined that the differences in seed structure should not be construed indicative of a diphyletic origin of the Euphorbiaceae. This is particularly so when various intermediates are seen in the family itself.
viz., Codiaeum, Manihot, Fleuggea, Croton, Homononia, Glochidion, Breynia, etc. Evolution in case of androecium is noted along three lines: 1) reduction in number of whorls or number of members in whorls. 2) increase in number of stamens in one or both whorls, 3) connession. reduction of stamens noticed in Jatropha and Acalypha wherein 5+3 and 4+4 conditions are observed respectively. Some genera e.g. 1) Kigelia and Simmondsia, the androecium consists of only five stamens. Further reduction has occurred e.g. Cicca, in which only four stamens are present. The genera like Sebastinia, Excoecaria, Phyllanthus, Breynia, Tragia have only three stamens. They further reduced to two e.g. in Sapium and Maprounea. This trend culminated into the one - stamened, male flower of the genera like Anthostema and Euphorbia. A trend towards increase in number of stamens also noticed in Phyllanthus, inclusive of Cicca. He considered it to closer to Margaritaria and Cicca together with the genus Phyllanthus section Maprounea. This study revealed definite proof that the flower is an inflorescence. The flower is not hermaphrodite one, it is considered as a cyathium consisting of very highly specialized glands and reduction of individual flowers to naked monandrous flower.

Jussie (1789) and Jussieu (1824) both regarded Margaritaria, a genus of uncertain position within the Euphorbiaceae. The latter author thought possible relationship of Margaritaria with Cicca. Baillon (1858) referred it differently to the sections of Cicca as well as in a separate genus Zygospermum. Hooker (1887) lumped Margaritaria and Cicca together with the genus Phyllanthus section Cicca. Webster (1957, 1968) thought Margaritaria quiet distinct from Phyllanthus, inclusive of Cicca. He considered it to closer to Fleuggea in Phyllanthaceae. However, the unique seed with fleshy exotesta, thick and bony endotesta render Margaritaria distinct from all other Phyllanthaceae. The seeds of this genus with a little irregularly shattering papery endocarp are equally distinctive. Margaritaria also lacks pistilode and staminate flower. Cicca differs from it in drupaceous fruits with thin walled dry seeds. The fruit of Margaritaria is different from those of other Phyllanthaceae. The triloculate, semitectate pollen grains of Margaritaria are typical of many unspecialized Phyllanthaceae and are similar to those species of Fleuggea (cf. Punt 1962, Kohler 1965). The genus revealed 2n = 26, with a base number 13, like many taxa of subfamily Phyllanthoideae (Webster and Ellis 1962, Bancilone 1971).

(v) Phytochemistry

Gibbs (1974) summarized and reviewed phytochemical constituents of Euphorbiaceae and its allied families. In his opinion, the relationship of the family are obscure since a great array of families are involved. He pointed out peculiar interest in the stinging hairs. He listed stinging plants group Platylobaeae and indicated probable abscence of these hairs in Sterculiobaeae. Stinging members, in his opinion, seem to be confined to few genera placed relatively close together. Webster and Webster (1966) recognized relationship which is not acknowledged. They also stated that the seed fats of Euphorbiaceae may not be valid based on X = 8, 10, 19, 23. Likewise the Genus lack 7 and 13 chromosomal series. The Flacourtiaceae shows a different base number X = 11. Hutchinson (1969) visualized ancestry of the Euphorbiaceae from the Malvaceae on the basis of constant characters of axile placenta, this may be particularly true because majority of the Malvaceae are based on X = 7 and 13.

(vi) Karyology

Hans (1973) studied chromosomal conspectus of the Euphorbiaceae and shed more light on the genetic interrelationship, ancestry and evolution of the family. In main, the Buxaceae are Asiatic in origin and primitive Phyllanthaceae have evolved in New World. He also opined that both polyploidy and aneuploidy are effective in speciation and as much as 48 % of the known as exhibiting polyploidy.

The largest genus Euphorbia exhibits great diversity not only in habit but also chromosome number and size, basically the species from neotropical are 2n = 6, 7, 8, 9, 10. In this series, polyplody is effective in speciation. Hans (loc. cit.), however, remarked for further thorough revision of the genus from taxonomic, nomenclatural and cytological point of view.

Webster (1967), however, recorded n = 11 for the genus Chamaesyce but thought the possible connecting link between Euphorbia and Chamaesyce. He made another genus Euphorbia and Chamaesyce on cytological ground. The tribe Buxae whether or not treated as a family Buxaceae shows the relationship with the Euphorbiaceae. The genus Buxus and Sarcococca have base number X = 7, which is also encountered in the Euphorbiaceae. Simmondia has no equal base number X = 13 which is out of place within the Buxaceae. Willis (1966) treated Simmondia in the monogenic family of its own - the Simmondsiaceae apart from Buxaceae. It is justified on chromosomal ground. Some genera e.g. Excoecaria, Kigelia and Simmondsia, the androecium consists of only five stamens. Further reduction has occurred e.g. Cicca, in which only four stamens are present. The genera like Sebastinia, Excoecaria, Phyllanthus, Breynia, Tragia have only three stamens. They further reduced to two e.g. in Sapium and Maprounea. This trend culminated into the one - stamened, male flower of the genera like Anthostema and Euphorbia. A trend towards increase in number of stamens also noticed in Phyllanthus, inclusive of Cicca. He considered it to be closer to Margaritaria and Cicca together with the genus Phyllanthus section Maprounea. This study revealed definite proof that the flower is an inflorescence. The flower is not hermaphrodite one, it is considered as a cyathium consisting of very highly specialized glands and reduction of individual flowers to naked monandrous flower.

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such as coumarins, flavonoids, lignan, monoterpenes, sesquiterpenes, amino acids, etc. are widely distributed within the Euphorbiaceae. The alkaloids like harmane, piperidine, pyrrolidine, tropane, quinolizidine, imidazole, glochidine, glochidisine, pyrimidine, guanidine, etc. are of widespread occurrence and have sporadic distribution among Euphorbiaceae. Seigler (loc. cit.) further opined that their presence is not suggestive of confirmative familial or subfamilial relationship. Seigler (loc. cit.) also noted securinine alkaloids produced only by the members of the subfamily Phyllanthoideae. Their presence in several members of the Phyllanthoideae, in his opinion, reinforces the close relationship of the genera like Phyllanthus, Fieuggea and Securinega. Peptide alkaloids are known for Hymenocardia. Similar alkaloids such as hemconcardine have been isolated from Pandá (Pandaceae). Webster (1994), Hegnauer (1989), Seigler (1994) merges with the Euphorbiaceae. His contention is thus supported. Many species of the genera Buxus, Pachysandra and Sarcococca yield steroidal and triterpenoid alkaloids. These are distinct from those of euphorbiaceous taxa. Simmondsia is sometimes included under Buxaceae or Euphorbiaceae. It is devoid of alkaloids. Thus it is distinct from both of them. It also produced unusual nitriles which are also not recorded in the Buxaceae as well as Euphorbiaceae (Hegnauer, 1989). The triterpenal alkaloids are found in the Daphniphyllaceae. They are unique and do not resemble to those of the Euphorbiaceae. Thus there is no chemical similarities between Daphniphyllaceae and Euphorbiaceae (cf. Hegnauer, 1989; Rizk, 1987). The family Malvaceae, Sterculiaceae and Bombacaceae contain unusual lipids in their seeds. Cycloprenenoid fatty acids are particularly common amongst these (Hegnauer, 1989; Smith, 1970). Although there is some chemical similarity. It does not strongly resemble that of Euphorbiaceae. Likewise, the chemistry of the Geraniaceae does not greatly resemble that of the Euphorbiaceae. The floral lipids of the Malpighiaceae and Krameriacae produced unusual fatty acid and glyceride mixtures. However, these are not found in the Euphorbiaceae (cf. Seigler, 1994). Cyanogenic glycosides are present of subfamilies in the Phyllanthoideae, Crotonoideae and Acalypoideae of the Euphorbiaceae. They are also reported from Euphorbiodeae but the cyanogentic compounds of Euphorbiaceae have not been characterised. A large variety of diterpenes occur in the Euphorbiaceae (Hegnauer, 1966, 1989). Precursors of the tiglianes, ingenanes and daphane type cocarcogenic diterpenes have been isolated from the Euphorbiaceae as well as Thymeleaceae (cf. Seigler, 1994) Jensen et al. (1994) studied the Euphorbiaceae and related families' serotaxonomically. They attempted to find out similarities between major seed storage proteins present in them. Their study does not support the separation of five subfamilies but clearly suggest separation of the Acalypoideae, Crotonoideae, Euphorbiodeae and the Phyllanthoideae as two phylogenetic groups. Dahlgreen (1980) and Ehrendorfer (1991) divide the Euphorbiaceae only in two subfamilies viz., Phyllanthoideae and Hippomanaeae. The above conclusion is in agreement with such systematic treatments. These authors also reached to such a conclusion that neither the Malvales nor the Rhamnales are serologically related to the Euphorbiaceae. On the contrary, they proved to be serologically closely allied with the Euphorbiaceae. Likewise, the members of the Violales share relatively high portion of serological characters with the Euphorbiaceae. The families viz., Tropaeoideae, Cneoraceae and Linaceae of Rutidilloae revealed important positive cross-reactions. These authors thought the Euphorbiaceae as closely related to Dilleniidae (i.e. Malviflorae, Violiflorae) as well as to the Rosidae (i.e. Rutiflorae), which are two distinct subclasses in the systems of Cronquist (1981) and Takhtajan (1980). In a nutshell, the family Euphorbiaceae lacks anatomical homogeneity throughout and anatomical structures show wide range of variations. This is probably in correlation with the diversity of habit. The family, therefore, shows diverse affinities of its various members. Palynologically the family is also fairly heterogenous. This is indicated by the palynological study to date. Embryological evidence is by far decisive and appears fairly homogeneous, with the possible exclusion of its suspected allies. The karyological study of euphorbiaceous taxa also revealed diversity with the chromosome number ranging from the lowest is 2n = 12 to the highest 2n = 224. The basic chromosome numbers usually vary from 7 to 13 and rarely 18. Thus a wide cytological spectrum is divulged by the members of the Euphorbiaceae. Chemical diversity covering majority of chemical classes is widely acknowledged from the recent studies. The floral anatomical study indicated reduction in the number of whorls and also number of members of the whorl from a supposedly pentamous, dichlamydeous, heterochlamydeous ancestral flower. This trend of reduction, coupled with the trends of connesion, adhesion and amplification has culminated in the diversity of the family Euphorbiaceae and the members, which have been included or excluded from the euphorbiaceous plexus. The taxonomic features which have been employed for delineations at various levels have remained ever-changing. A review of the taxonomic features in a bird's eyeview appears pertinent. It was Adanson (1763) who for first time used the staminal features whether free or united. Jussieu (1789) employed styril features in his treatment. The features such as number of ovules, insertions of stamens, presence of petals and type of inflorescence were exploited for taxonomic purpose by Jussieu (1824). Meisner (1941) emphasized Crotroid pollen as a taxonomic marker. Mueller (1864, 1866) found shape of cotyledon useful for dividing the Euphorbiaceae into two separate primary groups viz., Stenolobae and Platylobaeae. Mueller (loc. cit.) also employed the features like ovule number, aestivation of calyx, orientation of anthers in bud and presence or absence of petals for other taxonomic category within the above primary groups. The employment of these taxonomic characters in different periods have obviously changed the circumscriptions or delimitations of the family Euphorbiaceae and its allied taxa. Accordingly, the ordinal, familial and infrafamilial relationship have been largely debated and has challenged the efforts of systematists in solving complexity of relationships of the euphorbiaceous plexus. Kubitzki (1977) and Merxmuller (1972) have pointed out the arbitrariness of the boundary between Dilleniidae and Rosidae within which the cradle of euphorbiaceous plexus swings. Uncertain number of families have been included in the Euphorbiaceae by leading botanists in the last two centuries. This number would increase if all of the families are segregated from the Euphorbiaceae. A sum total of evidence based on all - pervasive examination of features of anatomy, palynology, embryology, karyology and chemistry of the euphorbiaceous alliance suggest close affinities of some families, however, few of them appear apparently closer just because of unisexuality and reduced floral structures prevalent in them. These are better treated isolated within this alliance. This would render the family Euphorbiaceae homogenous. The present investigators however, inclined to align and accommodate the euphorbiaceous taxa as the following:
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