

Regular Article

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 trilobular, placentation axile, ovules collateral, pendulous with ventral raphe and usually carunculate. Although so, the family received varied treatments in the Englerian and Ralian 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 Unisexuales based on unisexual or polygamous flowers. It is placed alongwith other families such as Balanopceae, Urticaceae, Platanaceae, Leitneriaceae, Juglandaceae, Myricaceae, Casuarinaceae and Cupuliferae. They divided Euphorbiaceae into six tribes viz., Euphorbieae, Stenolobieae, Buxeeae, Phyllantheae, Galearieae, and Crotonaeae. 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 Ralian line characterised by vertical connations 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 Tiliiales, Malvales, Celastrales and Sapindales. He included Pandaceae and Aextoxicaceae in his order Celastrales. He included Buxaceae and Daphniphyllaceae in his order Hammamelidales. Likewise, he refers Dichapetalaceae and Chaillietaceae under order Rosales, whereas Picrodendraceae is kept under order Juglandales.

Hutchinson (1969) includes only the family Euphorbiaceae in the order Euphorbiales. His Euphorbiaceae contains Tithymalaceae, Stilaginaceae, Antidesmadaceae, Putranjivaceae, Peraceae,

Porantheraceae, Ricinocarpaceae, Androstachydeaceae, Bischofiaceae, Hymenocardiaceae, Uapacaceae and few others. In his opinion, the family Euphorbiaceae is composed of genera derived from different stocks like those of Tiliaceae, Sterculiaceae, Malvaceae and also from Celastraceae. He placed Pandaceae and Aextoxicaceae under his order Celastrales, whereas families Buxaceae, Simmondsiaceae and Daphniphyllaceae find place in the order Hammamelidales. The families Dichapetalaceae and Picrodendraceae are referred to the order Rosales and Juglandales respectively. Hutchison (*loc. cit.*) discarded the cotyledonary character whether broad or narrow than radicle. He emphasized primitiveness of euphorbiaceous taxa based on imbrication of sepals, presence of petals, lack of disc, retention of vestigial ovary in the male flower and numerous stamens. Hutchinson (1973) maintained his system similar to the one appeared in 1959 and 1969.

Cronquist (1968) includes other four families viz., Buxaceae, Daphniphyllaceae, Pandaceae and Aextoxicaceae, apart from proper Euphorbiaceae under the order Euphorbiales in the Rosiidae. He retained the family Dichapetalaceae in the order Celastrales. He emphasized type of fruit and its dehiscence, ovule anatropus, epitropus, raphe dorsal or ventral, number of ovules, etc. while recognising familial status of the families included in this order. Cronquist (1981) included four families viz., Buxaceae, Simmondsiaceae, Pandaceae, and Euphorbiaceae. He transferred Aextoxicaceae to the order Celastrales. He also included the family Dichapetalaceae in the Celastrales. Daphniphyllaceae is also kept as a distinct family under the order Daphniphyllales under Hammamelidales. Later, Cronquist (1988) maintained his earlier treatment appeared in 1981 for this alliance. He characterised these families on similar characteristics used in the system which appeared earlier in the 1968.

Takhtajan's Euphorbiales (1969) contained the families viz., Buxaceae, Simmondsiaceae, Daphniphyllaceae, Dichapetalaceae, Pandaceae, Picrodendraceae, apart from the Euphorbiaceae. He presumed that the Euphorbiales arose from ancient group intermediate between the Flacourtiaceae and Malvales. His order Euphorbiales is kept under super order Malvaceae. In his later system, Takhtajan (1980) included the families viz., Euphorbiaceae, Pandaceae, Dichapetalaceae and Aextoxicaceae. His Euphorbiaceae includes Androstachydeaceae, Bischofiaceae, Hymenocardiaceae, Peraceae, Picrodendraceae, Stilaginaceae and Uapacaceae. He doughtfully includes Aextoxicaceae in his order Celastrinae.

Soo (1975) considered the Euphorbiaceae and Buxaceae as distinct families in the order Euphorbiales under his subclass Malvidae. He is silent in regard to related families of Euphorbiales. Airy Shaw (1965, 1975, 1980) segregated family Hymenocardiaceae, Bischofiaceae, Picrodendraceae, Androstachydeaceae distinct from the Euphorbiaceae.

Engler and Diels (1936) included the Euphorbiaceae in the order Geraniales alongwith other 20 families. The family Buxaceae, is however, treated under their order Sapindales. The placement of Euphorbiaceae is based on the ovule pendulous with a ventral raphe and the micropyle pointing upwards, or erect with dorsal raphe and micropyle pointing downwards. While the family Buxaceae is referred under Sapindales on account of pendulous ovules with a dorsal raphe and micropyle pointing upwards or erect with ventral raphe and micropyle pointing downwards. Wettstein (1935) placed the family Euphorbiaceae in Reihe Tricoccae, while the Buxaceae is treated distinctly under the order Celastrales. He regarded Apetalae of Euphorbiaceae as primitive. His Tricoccae are indicated as a connecting link between Amentiferae and Malvacean ancestry. However, this theory received a little support among subsequent

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workers. Rendle's order Tricoccae (1969) comprises families *viz.*, Euphorbiaceae, Buxaceae and Callitrichaceae. He includes Daphniphyllaceae 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, Aextoxicaceae, Pandaceae, Picrodendraceae, etc. He divided family Euphorbiaceae, after following Pax in the 'Pflanzen Familien', into two groups *viz.*, Platylobeae and Stenolobeae. The former is characterised by broad cotyledons. He divided the former into two families e.g. Phyllanthoideae and Crotonoideae. He also divided later into two subfamilies Porantheroideae and Reginocarpoideae. 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 anatrochus ovule and loculicidal dehiscence of fruit. Benson (1957) referred the families Euphorbiaceae and Buxaceae in his order Euphorbiales. He characterised the former by fruit septical, ventral raphe, whereas the latter by fruit loculicidal and dorsal raphe. Melchior (1964) placed the family Euphorbiaceae in his suborder Euphorbiineae 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 phyletic 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

Metcalf and Chalk (1950) recorded paracytic stomata in the tribe Acalyphaeae, Dalechamptaeae, Euphorbieae, Hippomaneae (except *Manihot*), Phyllanthaeae (except some Euphyllanthaeae) and in the genera like *Glochidion*, *Excoecaria*, *Stillingia*. However he also noted anomocytic stomata in the genera *Andrachne*, *Aporosa*, *Baccaurea* and *Richeria*. Inamdar and Gangadhara (1978) noted paracytic, anomocytic, anisocytic and diacytic stomata in 53 species belonging to three tribe's *viz.*, Euphorbieae, Phyllanthaeae and Crotonaeae. 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 Paliwal (1974) investigated 150 species of the genus *Euphorbia* and stated that most of the stomatal type recognized for dicotyledons met with in the genus *Euphorbia*. Anomocytic type being most preponderant. Khatijah Hussin *et al.* (1996) in their studies of some species of *Mallotus* observed paracytic stomata. Levin (1986) noted anomocytic type in *Podocalyx* and paracytic in *Paradrypetes* within the subfamily Phyllanthoideae. Paracytic stomata are characteristic of the tribe Brideliaceae, Drypeteae, Phyllanthaeae, Fleugggenae and some genera of Wielandiaeae.

The present authors noted mostly anomocytic type in Euphorbieae and Phyllanthaeae. The anomocytic and paracytic types are reported on the same foliar surface in the tribe Hippomaneae, anomocytic being most common. In the tribe Crotonaeae anomocytic type is more or less common, except *Acalypha indica*, *Jatropha panuraefolia*, *Tragia involucreta* wherein paracytic type is observed. *Simmondsia chinensis* presently studied by present investigators

shows anisocytic 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 no 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 Phyllanthaeae as well as family Euphorbiaceae. The other types such as anomocytic, anisocytic and diacytic appear to have been derived from it in the euphorbiaceous alliance.

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) Euphorbieae, Phyllanthoideae and Crotonoideae (Thakur and Patil, 2005). The genera *Neoscortechinia*, 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 rottleri* and *Trewia polycarpa*) of the tribe Crotonoideae. The peltate scales are found in one genus each (*Neoscortechinia kingii* and *Dimorphocalyx lawianus*) of the tribe Crotonoideae. In the rest others, genera belonging to tribes Euphorbieae, Phyllanthoideae and Crotonoideae the trichomes are generally unicellular. Metcalfe and Chalk (1950) documented basically three types of trichomes, *viz.*, glandular, non-glandular 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 Dalechamptaeae and Plukenetiaeae. Likewise, the simple unicellular and uniseriate trichomes are generally found in Phyllanthaeae, Brideliaceae, Acalyphaeae and also in some members of Crotonaeae, Hippomaneae and Dalechamptaeae.

Sastry and Kannabiran (1994) observed stellate and candelabra (dendroid) trichomes in the tribe Crotonaeae. On account of unicellular conical hairs in the genus *Micrococca*, 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.*, *Croton* and *Codiaeum*. 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, dendritic, lepidote, papillate and glandular types. They characterised 40 sections of the genus on the basis of trichome morphology. Although Crotonaeae 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 malpighiaceae, stellate and lepidote types in the subfamilies Acalyphoideae and Crotonoideae, while in rest other subfamilies they are predominantly simple 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 Plukenetiaeae. The trichomes in Plukenetiaeae composed of a central crystalliferous cells of subepidermal origin surrounded by a jacket of three epidermal cells (Knoll, 1905). The possession of unique type of trichome provided a basis for assigning the genus *Dalechampia* to the tribe Plukenetiaeae, which is sometimes referred outside it.

The present authors observed *Breynia nivosa*, *Macaranga peltata* and *Mallotus stenanthus* for foliar glands especially present on the lower surface. These taxa belong to the tribes Phyllanthaeae and Crotonaeae. They are reported in some genera of Acalyphoideae, Crotonoideae and confined to some genera of the Phyllanthoideae, Oldfieldioideae 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 *Acidocroton*, *Coccolobos*, *Coelodiscus*, *Macaranga*, *Mallotus*, *Acalypha*, *Hymenocardia*, *Trewia*, etc.

Stern (1967) while studying xylem anatomy of the genus *Kleindendron* and tribe Clutieae (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 Clutieae 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 *Kleindendron* under the tribe Clutieae as treated by Pax (1890) and Pax and Hoffmann (1931).

Foliar venation patterns, although very important for the taxonomic and phylogenetic considerations, have largely remained neglected for the family Euphorbiaceae. The genus *Euphorbia* of the tribe Euphorbieae have been investigated by Sehgal and Paliwal (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 vein – 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; Soo, 1975; Wettstein, 1935) or placed under the family Euphorbiaceae (Melchior, 1964; Hutchinson, 1959, 1969, 1973). It is also treated separately in its own family Simmondsiaceae. The present authors observed foliar stomata are anisocytic in the genus *Simmondsia*. They are reported ranunculaceous (Metcalfe and Chalk, 1950). 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. Kohler and Bruckner (1983) also 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, presence of clustered crystals are recorded 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, markedly heterogenous and fibers with distinctly bordered pits. 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 heterogenous, 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 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 Crotonae (*sensu* Bentham and Hooker, 1862 – 1883). In the members of tribe Phyllanthae, the petioles receive either a continuous ring of vascular tissue or solitary prominent bundle or arc. The petiolar vasculature in the tribe Euphorbieae is either in the form of a ring of vascular bundle of three separate vascular bundles centrally. The tribe Hippomaneae shows separate 5 – 8 vascular bundles or a ring of vascular bundles. The different stelar 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 *Cnidioscolus*. Dehgan (1982) employed these features significantly at the sectional and subsectional level in *Jatropha*. Dehay (1935) found resemblance between the Euphorbiaceae on the one hand and Malvaceae, Tiliaceae 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), Spilatro 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 penned that much new work and reevaluation of older studies are needed if the taxonomic dilemma of the Euphorbiaceae 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 laticifers absent) are closely linked to each other. He opined that latex-producing dicotyledonous families such as Apocynaceae, Asclepiadaceae, Moraceae and Sapotaceae 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 protein 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 C³ type, C⁴ 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 subgenera *viz.*, *Euphorbia* and *Chamaesyce*. C⁴ photosynthesis 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) sought completely independent 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 colpate, forate, rugulate, foraminoidate or non-aperturate, oblate to prolate. He thought the family clearly multipalynous. He also commented on taxonomic utility at different hierarchy e.g. pollen morphology in his opinion, supported the subdivisions of the Euphorbiaceae into 'Platylobeae, Stenolobeae' as unnatural. Porantheroideae should probably be referred to Phyllanthoideae and Stenolobeae; Ricinocarpoideae to Crotonoideae. Bentham and Hooker (1862 – 1883) placed *Jonnesia* near *Jatropha* and *Acidocroton*. It is not supported on palynological ground. He found some slight similarities of the pollen grains of Euphorbiaceae in some Geraniales like Linaceae, Zygophyllaceae, Malpighiaceae etc. Erdtman (*loc. cit.*) described the pollen grains polyforate. He described the genera *Buxus*, *Notobuxus*, *Pachysandra*, *Sarcococca*, *Simmondsia* and *Styloceros*. According to him, the pollen grains of Buxaceae are similar to certain types Euphorbiaceae and Thymeliaceae. He further stated that the pollen grains in *Pachysandra* and *Sarcococca* are more or less reminiscent of certain Crotonoid pollen grains in Euphorbiaceae and Thymeliaceae, 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 related genera of the Euphorbiaceae. The pollen grains of five species are very similar to each other. Therefore Robbrecht (1985) remarked the genus homogeneous. He found no palynological features to point a relationship with the Euphorbiaceae. On the contrary, the pollen grains of *Hymenocardia* resemble much more that found in Moraceae, Urticaceae and Ulmaceae. Punt (1987) discussed the role of pollen morphology and taxonomy and compared with the classification of Webster (1975). Webster (*loc. cit.*) recognized five subfamilies viz., Phyllanthoideae, Oldfieldioideae, Acalyphoideae, Crotonoideae and Euphorbioideae. Punt (*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., Oldfieldioideae, Crotonoideae and Euphorbioideae are natural assemblages. He further observed that the pollens of Crotonoideae resemble to those of Thymeleaceae. Takashi *et. al.* (2000) studied palynology of 96 species belonging to 30 genera. They described and illustrated with light microscopy, scanning and T E M covering the tribes Epiprineae, Adeliaeae, Alchorneae and Acalyphaeae *pro- parte*. Pollen data support the concept of subtribe Epiprininae but indicate that subtribe Cephalomappinae is not related and should be considered for separate tribal status. There is close relationship among *Adelia*, *Lasciocroton* and *Leucacroton* but not with the two remaining members of Adeliaeae, which do not appear closely related with each other. These authors pointed out that the genus *Wetria* is not closely related to *Cleidion*. They tentatively supported concept of Macaranginae 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 Micrandreae and Adenoclineae primitive retaining only aperture but exines with well developing foot layers. They have the *Croton* structure and are clearly allied to inaperturate Crotonoideae. The exine structure of Crotonoideae is similar to Thymeleaceae than any two remaining subfamilies of Euphorbiaceae and Thymeleaceae is sometimes acknowledged (*cf.* Cronquist 1981, 1988). Cronquist (*loc. cit.*) assigned Thymeleaceae to Myrtales and Euphorbiaceae to Euphorbiales. Thymeleaceae 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 Oldfieldioideae, Crotonoideae and Euphorbioideae have basic pollen type. The Phyllanthoideae and Acalyphoideae have diverse pollen types. The Oldfieldioideae, Crotonoideae and Euphorbioideae, in his opinion, are natural assemblage. The genus *Platygyne* 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 *Platygyne* is quiet distinct from *Tragia* palynologically. The genus *Hymenocardia* is controversial. Hutchinson (1969) included under the family Euphorbiaceae, Airy Shaw (1965) disbanded 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 ulmaceous or urticaceous. 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 biovulate, 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) (Metcalf 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 companion of the Cretaceous. This record indicates more primitiveness of the Buxaceous taxa than the euphorbiaceous ones. However, further studies in the Euphorbiaceae may clarify this situation in future.

(iii) Embryology

Rao (1970) studied 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 (Baillon, 1874). Engler and Diels (1936) placed Callitrichaceae under the suborder Callitrichineae near the suborder Tricoccae 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 unitegmic tenuinucellate ovules, differentiation of endothelium, cellular endosperm with terminal haustoria, long filamentous pro - embryonal suspensor and minute seed with membranous seedcoat, etc. do not allow one to ally the Callitrichaceae with the Euphorbiaceae. It is similarly discredited by Webster (1987). Embryologically, the Callitrichaceae are nearer the Lamiales (Takhtajan, 1980; Stebbins, 1974; Thorne 1983; Dahlgren, 1983). Bentham and Hooker (1862 – 1883) thought Buxaceae constituting a tribe Buxaeae within the Euphorbiaeae. Soo (1975) included Buxaceae and Euphorbiaceae under the order Euphorbiales. Takhtajan (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 Euphorbiales. 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 or both of them under the same order. Rao (1970) 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. Bentham and Hooker (1862 – 1883) placed the genus *Daphniphyllum* under the tribe Phyllanthaeae of the Euphorbiaceae. Cronquist (1968) treated as a separate family Daphniphyllaceae under the order Euphorbiales (placed near the Euphorbiaceae).

However, in his later treatment (1981, 1988), he kept Daphniphyllaceae distinctly under its order Daphniphyllales. Cronquist (1981) also thought it closer to the Hammamelidales. Takhtajan (1969) included Daphniphyllaceae near the Euphorbiaceae under the order Euphorbiales. Later (1980, 1983, 1987) he considered it closer to the Hammamelidales. Hutchinson (1959, 1969, and 1973) considered the Daphniphyllaceae under the order Hammamelidales. Melchior (1964) included the Daphniphyllaceae near the Euphorbiaceae under the order Geraniales. Engler and Diels (1936) also kept in the order Geraniales.

Bhatnagar and Kapil (1982), Bhatnagar and Garg (1977), Kapil and Bhatnagar (1980) investigated embryology of the genus *Daphniphyllum*. They observed 8 – 10 anther wall layers, thickened radial and inner tangential wall of the endothecium, 2 or 3 layered tapetum, bicarpellary ovary with parietal ovules, subdermal outer and dermal inner integuments. Obturation 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 Euphorbiales. Emberger (1960) related it to the Buxaceae, whereas Takhtajan (1980) referred it to the Hammamelidales. Hutchinson (1969, 1973) considered *Simmondsia* under 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 exomesotestal, exalbuminous seed. It is little related to the Euphorbiales, Buxales or even Hammamelidales. It shows better embryological similarities with the Fagales (cf. Wiger, 1935; Davis, 1966; Corner 1976).

Dichapetalaceae is referred under the order Euphorbiales by some systematists (Takhtajan 1969, 1980; Wettstein, 1935; Thorne 1983; Dahlgren, 1983). Hutchinson (1969, 1973) treated *Dichapetalum* or Dichapetalaceae under the Rosales. Takhtajan (1969, 1980) placed this family under Euphorbiales. Engler and Diels (1930) included Dichapetalaceae in the suborder Dichapetalinae near the suborder Tricoccae of the Euphorbiaceae both being placed under the order Geraniales. Cronquist (1981) Goldberg (1986) referred it to Celastrales. Melchior (1964) included under the order Thymeleales. The family Dichapetalaceae contains genera with bi to tri - carpellary ovary, two ovules per loculus, axile placentation 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 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 bicarpellary unilocular ovary with divided two subapical ovules, endostome extending beyond the exostome, embryo extending only upto half the length of endosperm and ruminant 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 hypostase present, seeds mostly carunculate and straight, embryo extending all along the seed. However, Thymeleaceae exhibit stilar obturator, persistent and multiplicative antipodal cell and endosperm scanty or absent. Kapil and Bhatnagar (1994) based on these embryological features recommended to assign the Thymeleaceae in an order of its own; the Thymeleales near the Euphorbiales under the superorder Malviflorae. The Thymeleaceae is sometimes allied with the Myrtales (Cronquist, 1981; Benson, 1957, 1969). The Myrtaceae shows numerous ovules in the ovary and

devoid of obturator and hypostase, frequently polyembryonous and seed carunculate with a testal seed coat (Netolitzky, 1926; Corner, 1976).

The genus *Bischofia* is monocarpic and retained by some in the Euphorbiaceae (Hutchinson, 1969, 1973; Webster, 1987, Pax and Hoffmann, 1931; Backer and Bakhuizen 1963). However, it is placed under separate family Bischofiaceae Airy – Shaw (1965, 1966 1973). Bhatnagar and Kapil (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 anatropus placental obturation, nucellar cap and hypostase present, embryosac Polygonum type, endosperm nuclear, embryogeny Onagrad type and seed coat exotegmic. All these features are also shared by the euphorbiaceous taxa particularly the subfamily Phyllanthoideae (Mukherjee and Padhye, 1964; Chopra and Singh, 1969; Singh 1970) and do not support disbanding genus *Bischofia* from the Euphorbiaceae as thought by Airy – Shaw (*loc. cit.*). The genus *Picrodendron* is treated variously and placed in the families Anacardiaceae, Bombacaceae, Burseraceae, Euphorbiaceae, Juglandaceae, Sapindaceae and Simarubiaceae (cf. Hakki, 1985). Hutchinson (1969) placed it in a separate family Picrodendraceae under the order Juglandales. According to Hutchinson (1969), male flowers of *Picrodendron* greatly resemble to those of certain Euphorbiaceae. Hakki (*op. cit.*) investigated embryology of the genus *Picrodendron* and marked out its similarity with the Euphorbiaceae in bitegmic crassinucellate, anatropus ovule, placentae axile, ovules collateral, hypostase, nucellar cap and obturator present. It is still lacking information for female gametophyte, anther, and endosperm. These data would be of further taxonomic interest.

In a nutshell, embryological evidence lends supports to the monophyletic origin of the Euphorbiaceae. The embryological data of Dichapetalaceae, Aextoxicaceae and Pandaceae are poorly revealed and whatever is known about these does not satisfy their inclusion in the Euphorbiales. The family such as Buxaceae, Callitricaceae, Daphniphyllaceae and Simmondsiaceae although better known embryologically, but have hardly anything in common with Euphorbiaceae. *Bischofia* and *Picrodendron* can be retained on this basis.

According to Corner (1976), the palisade - like exotegmen of the Crotonoideae aliened with the Bombacaceae, Malvaceae, Sterculiaceae and Tiliaceae. On the other hand, fibrous exotegmen 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.

(iv) Floral Anatomy

The affinities of Euphorbiaceae have been discussed in past into two different groups of angiospermic families. Some suggested affinities to monochlamydeous families like Urticaceae and Centrospermales (Bentham and Hooker 1862 – 1883; Wettstein, 1935). Others thought the family derived by reduction from petaloidous ancestors similar to those of Malvales and Geraniales (Engler and Diels, 1936). However, their viewpoints are based on exomorphic features of flowers. Comparative floral anatomical studies are helpful 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.*, K5, C5, A5+5, G5. In their opinion, reduction have occurred in pistil to three carpels which later became established in the family. The ancestral pistil of Euphorbiaceae consisted of five carpels as in the Malvales and Geraniales. This is clearly evident by five carpellary pistil in female flower and 5 – lobed pistillode in the male flowers of euphorbiaceous genus *Wielandia*. Female flowers shows pentamerism in this genus. Their study also indicated the typical pentamerous dichlamydeous, heterochlamydeous perianth as ancestral type. Reduction occurred both in the number of whorls and also number of members of whorl. This is demonstrated by the floral anatomical studies in the genera

viz., *Codiaeum*, *Manihot*, *Fleuggea*, *Croton*, *Homonoia*, *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) connesion. reduction of stamens noticed in *Jatropha* and *Acalypha* wherein 5+3 and 4+4 conditions are observed respectively. Some genera e.g. *Hevea*, *Kirganelia* and *Flueggea*, the androecium consists of only five stamens. Further reduction has occurred e.g. *Cicca*, in which only four stamens are present. The genera like *Sebastiania*, *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 the number of stamens is also noticed in some euphorbiaceous taxa e.g. *Chrozophora*, *Mallotus*, *Trewia*, *Lasiococca*. Connesion of stamens is also visualized in *Jatropha*, *Chrozophora* and *Acalypha*. These authors attempted to bring the picture of ancestral flower of Euphorbiaceae close to that of Malvales and Geraniales. Their study suggested that Euphorbiaceae are derived mainly by reduction from ancestors with hermaphrodite, dichlamydeous, heterochlamydeous and pentacyclic flowers. They also endeavored to seek common ancestry for the Euphorbiaceae, Malvales and Geraniales.

Haber (1925) studied floral anatomy and morphology of the flower of *Euphorbia*. The genus *Euphorbia* exhibits much uniformity in its general morphology although it is largest genus of family Euphorbiaceae. 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 inflorescence involving primary, secondary and tertiary branches. Extreme complexity and congestion as well as evolutionary reduction have resulted in a suppression of nodes and internodes, aggregation of branches, cohesion of bracts, abortion of bracteoles, elaboration of glands and reduction of individual flowers to naked monandrous flower.

Jussieu (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 *Zygosperrum*. 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 *Flueggea* in Phyllanthaceae. However, the unique seed with fleshy exotesta, thick and bony endotesta render *Margaritaria* distinct from all other Phyllanthaceae. The fruits are 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 tricolporate, semitectate pollen grains of *Margaritaria* are typical of many unspecialized Phyllanthaceae and are similar to those species of *Flueggea* (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, Bancilon 1971).

(v) Karyology

Hans (1973) studied chromosomal conspectus of the Euphorbiaceae and shed more light on the generic interrelationship, ancestry and evolution of the family. In main, the Euphorbiaceae, in his opinion is 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 aneuploidy series of 6,7,8,9,10. In this series, polyploidy 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 *Anthostema*. He made no difference between the 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. *Simmondsia* has no equal base number $X = 13$ which is out of place within the Buxaceae. Willis (1966) treated *Simmondsia* in the monogeneric family of its own - the Simmondsiaceae apart from Buxaceae. It is justified on chromosomal ground. Willis (*loc. cit.*) also visualized a possible relationship of the Buxaceae ($X = 7$) with Celastraceae ($X = 8$). Hans (*loc. cit.*) conceived the former as a result of aneuploid decrease from $X = 8$. Hutchinson (1959) also related the Buxaceae to the Hammelidaceae, however Hans (*loc. cit.*) thought it not true as the latter has base number $x = 12$. The genus *Drypetes* sometimes considered synonymous with *Putranjiva* differs from *Putranjiva*. All species of *Drypetes* have $2n = 40$, whereas *Putranjiva* shows $2n = 14$. Thus, they differ in base number also. The genus *Bischofia* as treated variously as stated earlier. *Bischofia* shows $X = 7$, a base number which is encountered in the Euphorbiaceae. It also differs from Staphyleaceae to which relationship of which is indicated by Airy Shaw (1972). Staphyleaceae are characterised by base number $X = 13$. A spectrum of chromosome number is known to exist in the Euphorbiaceae between the lowest number $2n = 12$ to the highest $2n = 224$. The base number for various genera within the family are revealed as 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 17 and 18 series. The predominant base number in the primitive Phyllanthaceae is $X = 13$ followed distinctly by $X = 7$. Hans (*loc. cit.*) considered the family Euphorbiaceae having at least two base numbers *viz.*, $X = 7$ and 13. The original base number for the most advanced tribe Euphorbiae is believed by him to be $X = 11$.

One should look for relationship of Euphorbiaceae to other families which have genera predominantly based on $X = 7 / 13$ and their possible derivatives. Willis (*loc. cit.*) indicated relationship with the Malvaceae, Geraniaceae and Flacourtiaceae. In the order Malvales especially Sterculiaceae may not be valid based on $X = 8, 10, 19, 23$. Likewise the Geraniaceae 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 placentation, this may be particularly true because majority of the Malvaceae are based on $X = 7$ and 13.

(vi) 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 Platylobeae and indicated probable absence in Stenolobeae. 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 reveal the heterogeneity of the family. Evans and Kinghorn (1977) made a comparative phytochemistry of diterpenes of some species of *Euphorbia* and *Elaeophorbia*. Pax and Hoffmann (1931) recognized separate generic status for these two taxa. They bear drupe and not a capsule. Both of them produced white latex. Webster (1967) proposed on morphological grounds alone that these should be reclassified as a subgenus of *Euphorbia*. Latex samples of *Elaeophorbia* produced ingenol which further supported the suggestion concerning the reclassification in the genus *Euphorbia* (Anton, 1974). Acharya and Radhakrishnaiah (1997) studied 10 species of *Euphorbia*. The infrageneric segregate of *Euphorbia viz.*, *Chamaesyce* is sometimes elevated to an independent genus (Croziat, 1936). Webster (1967) found the genus critical in having flavones, syringin and iridoids in addition to the uncommon amino acids B, E and thus supported the segregation as an independent taxon.

Seigler (1994) evaluated systematic and evolutionary relationship in the Euphorbiaceae. He recorded large number of compounds from many different chemical classes from the members of the Euphorbiaceae. In his opinion, chemistry of the family is the most diverse and interesting and is comparable to be biological diversity of the family. He further stated that of all chemical classes, the alkaloids, cyanogenic glycosides, diterpenes, glucosinolates, seed and other lipids, tannins and triterpenes, are the most useful for chemotaxonomic purpose at the generic levels. Other compounds

such as coumarins, flavonoids, lignan, monoterpenes, sesquiterpenes, amino acids, etc. are widely distributed within the Euphorbiaceae. The alkaloids like harmaline, piperidine, pyrrolidine, tropane, quinolizidine, imidazole, gluchidine, gluchidisine, 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*, *Fleuggea* and *Securinega*. Peptide alkaloids are known for *Hymenocardia*. Similar alkaloids such as hymenocardine have been isolated from Panda (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. Cyclopropenoid 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 Geraniales does not greatly resemble that of the Euphorbiaceae. e.g. the floral lipids of the Malpighiaceae and Krameriaceae produced usual 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 Acalyphoideae of the Euphorbiaceae. They are also reported from Euphorbiaceae but the cyanogenic compounds of Euphorbiaceae have not been characterised. A large variety of diterpenes occur in the Euphorbiaceae (Hegnauer, 1966, 1989). Precursors of the tiglanes, ingenanes and daphnane type cocarcinogenic diterpenes have been isolated from the Euphorbiaceae as well as Thymeleaceae (*cf.* Seigler, 1994)

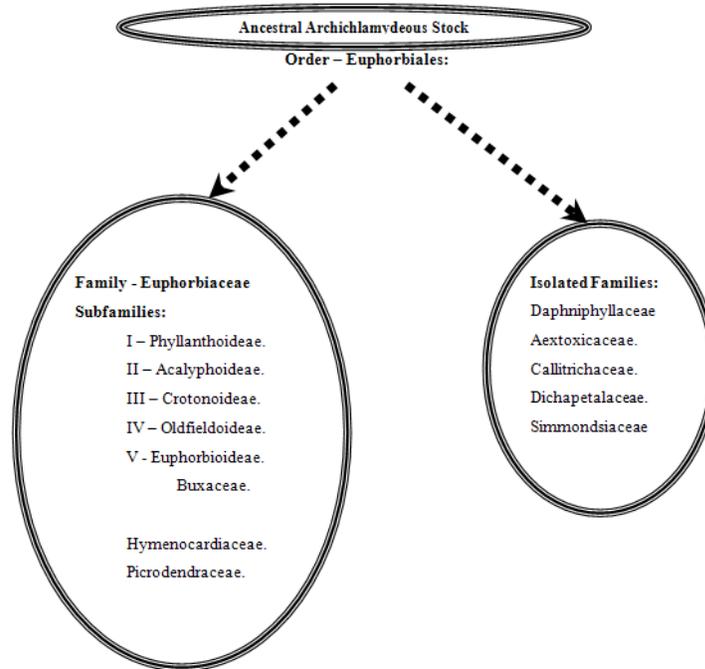
Jensen *et al.* (1994) studied the Euphorbiaceae and related families' serotaxonomically. They attempted to find out similarities between major seed storage proteins present in them. Their study does not support the separation of five subfamilies but clearly suggest separation of the Acalyphoideae, Crotonoideae, Euphorbioideae and the Phyllanthoideae as two phylogenetic groups. Dahlgreen (1980) and Ehrendorfer (1991) divide the Euphorbiaceae only in two subfamilies *viz.*, Phyllanthoideae and Hippomaneae. 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.*, Tropaeolaceae, Cneoraceae and Linaceae of Rutiflorae 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 heterogeneous. 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 pentamerous, 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 stylar 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 Crotonoid pollen as a taxonomic marker. Mueller (1864, 1866) found shape of cotyledon useful for dividing the Euphorbiaceae into two separate primary groups *viz.*, Stenolobeae and Platylobeae. 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 Rosiidae within which the cradle of euphorbiaceous plexus swings.

Uncertain number of families have been included in the Euphorbiales 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 homogeneous.

The present investigators however, inclined to align and accommodate the euphorbiaceous taxa as the following:



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*Original not consulted.