Taxonomic and phylogenetic census of the Celastrales: 
A synthetic review

Shisode S.B.¹ and D.A. Patil²

¹ Department of Botany L. V. H. College, Panchavati, Nashik–422003 (M.S.) India
² Post-Graduate Department of Botany S.S.V.P. Sanstha’s L.K.Dr.P.R.Ghogrey Science College, Dhule – 424 005, India

**Abstract**
A comprehensive assessment of the taxonomic and phylogenetic status of the celeastralean plexus is presented. An attempt has been made to review synthetically based on the data from different disciplines divulged by earlier authors and from present author's study on the alliance. The taxonomic literature indicated that the Celastrales (sensu latè) are a loose-knit assemblage. The tribal, subfamilial, familial and even ordinal boundaries are uncertain and even criss-cross each other. It appeared that the alliance can be grouped under two taxonomic entities viz., the Celastrales and the Rhamnales which appear evolved convergently.

**Introduction**
The order Celastrales (sensu lato) is a loose-knit assemblage. The taxonomic history clearly reflected that this alliance is not restricted to any taxonomic entity. The boundaries between the various taxonomic entities based on exomorphic characteristics are uncertain. The alliance has been investigated fairly in different domains of endomorphology. However, the data so accrued is not assessed critically to date. If at all assessed, they are assessed using information from a single discipline. The present authors studied vegetative anatomy of some Celastraceae, Hippocrateaceae and Rhamnaceae. They are also borrowed evidence from past literature and reviewed synthetically. The result of our in-depth study in this alliance are being presented in this communication.

**Taxonomic history**
In the treatment of Bentham and Hooker (1862-1883), the genera of the family Celastraceae and Hippocrateaceae constitute a composite family, the Celastraceae (sensu latè). They categorised these genera into two tribes - Celastraceae and Hippocrateaceae. The tribe Hippocrateae included only four genera viz., Hippocratea, Salacia, Siphonodon and Llavea, whereas the others are kept under the tribe Celastraceae. The family Celastraceae (sensu latè), in their scheme, is kept under the order Celastrales alongwith the families such as Rhamnaceae, Vetaceae and Stackhousiaceae. The family Rhamnaceae is divided into four tribes viz., Ventilagineae, Zizyphoeae, Rhamneseae and Gouanieae. Bessey (1915) included the families Rhamnaceae, Vetaceae, Celastraceae and an independent family Hippocrateaceae in the same order Celastrales alongwith some others.

In the Englerian treatment, Engler and Diels (1936), the three families - Celastraceae, Hippocrateaceae and Rhamnaceae are treated under two independent orders viz., the Sapindales and Rhamnales. The former two families are included in the Sapindales alongwith other 22 families. The Hippocrateaceae are accorded an independent familial status. The family Rhamnaceae is included under the Rhamnales alongwith the Vitaceae only. In the latest Engler's syllabus, Melchior (1964), included the Celastraceae and Hippocrateaceae as two independent families within his order Celastrales alongwith other 11 families. The family Celastraceae in his system is divided into five subfamilies viz., Celastridoideae, Tripterygioideae, Cassinoideae, Goupioideae and Siphonanthoideae. The families have been divided again into different tribes. However, he is silent about further categorization of his family Hippocrateaceae. His order Rhamnales contains the families Rhamnaceae, Vitaceae and Leeaceae. The family Rhamnaceae has been divided into five tribes viz., Rhamneseae, Zizyphoeae, Ventilagineae, Colletieae and Gouanieae. Treatment by Wettstein (1835) is essentially similar in regard to the placement of the three families - the Celastraceae, Hippocrateaceae and Rhamnaceae. Only Melchior (1964) included Leeaceae under the family Vitaceae and accorded to it a subfamilial status.

Rendle (1959) included the family Celastraceae in the order Celastrales, alongwith Staphyleaceae, Aquifoliaceae and Empetraceae, whereas the family Rhamnaceae is kept under the order Rhamnales alongwith the family Vitaceae. He included the Hippocrateaceae (sensu stricto) under the Celastrales (sensu latè) the Leeaceae under the Vitaceae. Benson's (1957) order Sapindales contains the Celastraceae and Hippocrateaceae as separate families alongwith many others, few of which he considered of uncertain position. He also included the families Rhamnaceae and Vitaceae (sensu latè) under his order Rhamnales. Hutchinson (1959, 1969, 1973) in his revised system placed the Celastraceae and Hippocrateaceae as distinct families alongwith few others under the order Celastrales, whereas his Rhamnales contained the families viz., Rhamnaceae and Vitaceae alongwith Heteropyxidaceae and Elaeagnaceae. Takhtajan (1969, 1980) recognised the
Celastraceae and Hippocrateaceae as independent families and included them under his Celastrales along with some others: few of which, in his opinion, are of doubtful position. He includes the Rhamnaceae and Vitaceae under a single order Rhamnales: however, the latter has been divided into two separate families: the Vitaceae and Leeaceae. Cronquist (1968, 1981, 1988) treated the order Celastrales into three separate families Celastraceae and Hippocrateaceae along with few others. His order Rhamnales includes the families Rhamnaceae and Vitaceae: the Leeaceae has been given a separate familial status.

Soo (1975) in his review of the new classification systems of flowering plants included only two families within the Celastrales viz., Celastraceae and Hippocrateaceae. Likewise, his order Rhamnales contains the Rhamnaceae and Vitaceae only. He appears to have included Hippocrateaceae under the Celastraceae (sensu latu) and Leeaceae under the Vitaceae (sensu latu).

Thorne (1992) in his recent treatment included Celastraceae under his order Celastrales but divided it into five subfamilies viz., Celastrinae, Tripteryginoideae, Cassinoideae, Hippocrateoideae and Siphonodontoideae. The genera Goupia and Lophopyxis are kept under their independent families - the Goupiaeceae and Lophopyxidaceae respectively. Hippocrateaceae (sensu stricto) is accorded a subfamilial rank under the family Celastraceae (sensu latu). He included the family Hippocrateae and Elaeagnaceae in his order Rhamnales interesting to note that the family Vitaceae has been kept under the order Cornales. The family Vitaceae has been divided into two subfamilies viz., Vitoideae and Leeoideae.

### Exomorphological significance and taxonomy

Some systematists (Bentham and Hooker, 1862-1883; Rendle, 1959; Soo, 1975; Thorne, 1992), submerged the genera of Hippocrateaceae into the Celastraceae (sensu latu), while others (Engler and Diels, 1936; Melchior, 1964; Westtein, 1935; Benson, 1957; Hutchinson, 1959, 1967, 1973; Takhtajan, 1969, 1980; Cronquist, 1968, 1981, 1988), and split the latter into the Celastraceae proper and the Hippocrateaceae. Engler and Diels (1936) distinguish the family Celastraceae on the basis of two ovules per locule and seeds arillate from the family Hippocrateaceae exhibiting predominant linnas habit, usually opposite leaves and winged angular seeds. However, Melchior (1964) delimits these two families on the basis of stamen number and type of seeds, stamens 4-5 (rarely 10) and seeds arillate in the Celastraceae whereas stamens are mostly three in the Hippocrateaceae. Benson (1957) emphasizes other characters-anthers introrse in the Celastraceae and extrorse in the Hippocrateaceae.

Hutchinson (1959) also laid emphasis on number of stamens (usually four to five) and nature of seeds, and the seeds with copious endosperm in Celastraceae, whereas stamens only three and seeds without endosperm in Hippocrateaceae. Cronquist (1981, 1988) employed the number and position of stamens, presence or absence of endosperm, aril and latex system to circumscribe these two families. Bentham and Hooker (1862-1883) although include the Hippocrateaceae into the Celastraceae, they divide the latter into two tribes viz., the tribe Celastraceae and the tribe Hippocrateaceae based on stamen number and albuminous or exalbuminous seeds. This clearly shows that these authors are not consistent in regard to the taxonomic criteria to be used to delimit the families Celastraceae and Hippocrateaceae.

Engler and Diels (1936) kept the families Celastraceae, Hippocrateaceae and few others under their order Sapindales but distinguished from the order Geraniales in the ovules pendulous with the dorsal raphe and micropyyle upward or erect with the central raphe and micropyle downward. They entreated the families Rhamnaceae and Vitaceae in the order Rhamnales and distinguished it from the order Geraniales and Sapindales by the stamens in a single whorl, as many as sepal and opposite the petals, the ovary usually with one or two ascending ovules. Benson (1957) employed the same features of staminal position in the flower of this alliance. The features which have been exploited at ordinal level also do not appear uniform for this alliance in the different systems of classification. Engler and Diels (1936) stressed simple leaves, perigynous flowers, antipetalous stamens and basal ovules in the Rhamnaceae to distinguish it from the family Vitaceae which show predominantly climbing habit, presence of tendril, antipetalous stamens, axile placentation and berried fruit. Benson (1957) emphasized the characters of sepals, fruits and tendril to delimit these families. Rendle (1959) characterizes the order Celastrales by flowers bissexual or unisexual by abortion, regular hypogynous cyclic, four to five numerous petals free or sometimes connect at base, stamens alternate to petals and few other ovarian and ovular features. He distinguishes the order Rhamnales from the Celastrales giving emphasis on antipetalous stamens, the other features are overlapping in the Celastrales. Melchior (1964) and Wettstein (1935) emphasized similarity. Hutchinson (1959, 1973) stressed more on position of nectariferous disc in the flowers, position of stamens, aestivation of petals, presence or absence of endosperm and nature of leaves while defining these orders. Hutchinson (1959) used pellicid, punctate leaves, infloesence leaf opposed, presence of tendril and fruit baccate in Vitaceae, whereas these are not so in the Rhamnaceae. Cronquist (1981) in his synthetic assessment of this alliance used large number of exomorphic as well as endomorphic features. Takhtajan (1969, 1980) also distinguishes the order Rhamnales by the antipetalous stamens from that of the Celastrales whereas the stamens are alternate to petals. Bentham and Hooker (1862-1883) placed the families Celastraceae and Rhamnaceae under the same order Celastrales and differentiated on the basis of stamens alternate to petals in the Celastraceae and opposite petals in the Rhamnaceae. These families also find place in different orders, the Celastraceae in the order Celastrales and the Rhamnaceae under the order Rhamnales. Cronquist (1968, 1981, 1988) employed the position of stamens in relation to the petals for the delimitation of the orders Celastrales and Rhamnales. They are similarly treated by Takhtajan (1969, 1980).

### Synthetic assessment of Celastraceae and Rhamnaceae

The above resume of systematic treatment of the families Celastraceae (sensu stricto), Hippocrateaceae (sensu stricto) and Rhamnaceae reveals that there has been no unanimity of opinions in earlier and even in the current systems of classification. They reveal considerable diversity of opinions in regard to their position, familial circumscriptions and association with other families in a group. There are certain criteria which distinguish and delimit certain subgroups, while there are others that hold them together into larger groups.

### Vegetative anatomical evidence

While epidermal and other vegetative anatomical evidence are of utility in the appraisal and evaluations, they have their own limitations as an effective tool in interpreting the putative phylogenetic assessments and taxonomic delineations. The present authors, in addition to their own observations, employed data from studies of earlier authors for a more comprehensive discussion of the problem. In the following paragraph is attempted an assessment of the Celastroids and Rhamnoids to focus the intricacies of the situation. Evidence from other domains of plant morphology is in brevity in this assessment. Based on this resume, conclusions, as reasonably as can be arrived at, are drawn.

Majority of plants of the three families exhibit three-lacunar, three-traced nodes (Shisode and Patil 2000a, 2005a) few taxa, however, show unilacunar one-traced nodes, the intermediate two-lacunar condition is found in Zizia pinnata, Buxus sempervirens and Z. multifida. Hence this family is characterized by three-lacunar, three-traced nodes.

Engler and Diels (1936) kept the families Celastraceae, Hippocrateaceae and few others under their order Sapindales, whereas stamens only three and seeds without endosperm in Celastraceae, whereas stamens only three and seeds without endosperm in Hippocrateaceae. Cronquist (1981, 1988) employed the number and position of stamens, presence or absence of endosperm, aril and latex system to circumscribe these two families. Bentham and Hooker (1862-1883) although include the Hippocrateaceae into the Celastraceae, they divide the latter into two tribes viz., the tribe Celastraceae and the tribe Hippocrateaceae based on stamen number and albuminous or exalbuminous seeds. This clearly shows that these authors are not consistent in regard to the taxonomic criteria to be used to delimit the families Celastraceae and Hippocrateaceae.
tricytic, cyclocytic and co-pericytic are found sporadically in the taxa studied. Hartog and Bass (1978) made more or less similar observations in the members of Celastraceae. It is interesting to note that hexactyl stomata occur exclusively in Colletia cruciata for which it is of diagnostic value. Likewise, paracytic type is noted for Kurrimia. The present study shows that majority of species in the three families have higher degree and are amphistomatic. Pant and Kidwai (1966) and Metcalfe and Chalk (1950) also noted hypostomatic condition of the leaves in the Celastraceae. Similar condition is also noted in Hippocrateaceae by Metcalfe and Chalk (loc.cit.). This may be a significant ecological parameter but it is of little phyletic value. Tannins are common in most of the plants in the three families investigated (Shisode and Patil 2006 b).

Clustered crystals are common in the petiole of Rhamnaceae. They are totally absent in the Hippocrateaceae and present only in Euonymus fortunei of the Celastraceae. (Shisode and Patil 2008 b). They are, however, occasionally present in the stem-axis. However, they are exclusively present in the leaves of Gouania microcrapa of the Rhamnaceae. Metcalfe and Chalk (1950) considered the occurrence and distribution of crystals of specific rather than generic diagnostic value. It is interesting to note that raphides occur only in the leaves of Euonymus fortunei of the Celastraceae. The occurrence of clustered crystals and raphides are of diagnostic value but appear to be of little phylogenetic significance. Anatomy of the petals, stem and leaves in the three families presently studied reveals an interesting fact that secretory cavities are present only in the species of Rhamnaceae (Shisode and Patil 2008 a, 2010 a). They are totally wanting in the Celastraceae and Hippocrateaceae (Shisode and Patil, 2005 b).

Metcalfe and Chalk (1950) summarized and reviewed different anatomical characters of the three families presently investigated and indicated the general similarity of the anatomical characters of Hippocrateaceae to those of majority of the Celastraceae. They further stated that these two families are closely related to one another. They also supported close relationship on the basis of exomorphic features of these two families.

Metcalfe and Chalk (loc.cit.) drew attention to the inclusion of some genera like Kurrimia, Perrottetia and Triptyergium in the Celastraceae. In their opinion, these genera differ considerably from one another and also from the remainder of the Celastraceae. In their opinions, these genera differ considerably from one another and also from the remainder of the Celastraceae. They considered it definitely aberrant within the Celastraceae and erected an independent family Gouipaceae (Shisode and Patil, 2010 b). Metcalfe and Chalk (1950) pointed out to the occurrence of grouping of the species of Ziziphus on wood anatomical features: one is characterized by diffuse apotracheal parenchyma as in Ziziphus angustula, Z. sonorensis, Z. miltost and Z. spinachristi. Likewise, they also recognised grouping of species within the genus Rhamnus based on wood anatomical features.

The outer surface of epidermis is smooth or may show cuticular ornamentation in the form of papillae or striations. (Shisode and Patil 2000 b). The development of epidermal papillae is notable in Maytenus ovata and M rhothiana of the Celastraceae. They are formed on the adaxial surface of leaf in case of Maytenus ovata, whereas on the abaxial in case of Maytenus rothiana (Shisode and Patil, 2000 b). They have been also noticed in case of Celastrus paniculatus and Castanosus on the midrib and venetals of the abaxial foliar epidermis by Pant and Kidwai (1965). The cuticular striations on the foliar surface of the cells of midvein and venetals. The occurrence of cuticular striations appears to be of systematic value. These are also thought in so other taxa of angiosperms (Cuttlle, 1978, 1992; Stace, 1965, 1980; Vaikos, 1982, 1987). Very rarely trichomes are also found striated in case of Celastrus paniculatus and Ventilago denticulata (Shisode and Patil 2005 b).

Hartog and Bass (1978) studied leaf epidermal diversity of the Celastraceae (sensu lato). They investigated characters of stipitifolium types, occurrence of crystaliferous epidermal cells and indumentum. These authors are inclined towards the inclusion of Hippocrateaceae (sensu stricto) in the Celastraceae proper. They employed anatomical characters to arrive at a natural classification below and above generic level. This is dilated later. The present author’s study (Shisode and Patil 2005 b, 2005 d, 2010 c) of foliar trichomes shows that unicellular conical or cylindrical trichomes are in ulmiiform type in all the three families investigated. Few other types especially unicellular two-armed, unicellular bulbous, bicellular trichomes occur sporadically in combination with other types. No trichome type is characteristic for a family. The stellate scales are recorded only in case of Pomaderris apetala of the Rhamnaceae. This obviously helps earmark the taxa within the Rhamnaceae. Behnke (1970) noted P-type and S-type of plastids in angiosperms. According to him the family Rhamnaceae have S-type, whereas Vitaceae as well as Leeaceae have P-type. This evidence does not help visualise affinity between Rhamnaceae and Vitaceae (sensu lato). At the same time, it does not favour splitting of the latter into two separate families.

Ultrastructural evidence

Mennega (1972) investigated wood anatomy of some Hippocrateaceae. In her opinion, the absence or presence of intraxylary phloem has no bearing with the systematic position of the species. However, she recognized two groups based on the wood structure. The first group, embracing Anthodon Cuevo, Elaeocarpus, Homingium, Hippocratea, Hylneaea, Pristinera and Prionostomma, can be characterised by broad and very high rays, mainly composed of procumbent cells, by the presence of septate fibres, tracheids and the absence of intraxylary phloem. The second group, consisting of Cheiloclinium, Perristasa, Tontelea and Salacia, is characterised by almost exclusively uniseriate rays, composed of square and upright cells, septate fibres in 2 to 5 cells wide concentric bands, intraxylary phloem of the foraminate or circumvallate type. She sheds more light on the genera thought ‘intermediate’ or ‘links’ between the Hippocrateaceae and Celastraceae. Cheiloclinium is one such genus. Loesener (1942) includes it in the Celastraceae. However, the genus evidently is in good agreement with species of Salacia. Another genus viz., Camptorhodon kept under the Celastraceae by Loesener (loc.cit.) was returned by Lawrelre (1947) to the Hippocrateaceae because its wood exactly matches that of Hippocratea of the Hippocrateaceae. Kokouna sometimes thought Celastraceous belonged to the Hippocrateaceae. This is, however, contradicted by very regular concentric parenchyma bands and by the absence of septate fibres. Stenzi (1882) finds certain resemblance in petiolar anatomy of Kokouna to the genus Maytenus.

Mennega (1997) studied some more genera of the Hippocrateaceae. Campyloestemon is thought by some taxonomists as belonging to the Celastraceae or as intermediate between the Hippocrateaceae and Celastraceae. In her opinion, the genus Campyloestemon resembles closely in its wood anatomy to the Hippocrateaceae. Mennega (op.cit.) still adheres to the concept of Hippocrateaceae as a family of its own since no intermediate linking Hippocrateaceae with Celastraceae. Moreover, she agrees with the independent familial status - Celastraceae and Hipporcrateae, assigned by Cronquist (1981) and Lawrelre (1947) to the Hippocrateaceae because its wood exactly matches that of Hippocratea of the Hippocrateaceae. Kokouna sometimes thought Celastraceous belonged to the Hippocrateaceae. This is, however, contradicted by very regular concentric parenchyma bands and by the absence of septate fibres. Stenzi (1882) finds certain resemblance in petiolar anatomy of Kokouna to the genus Maytenus.
dehiscent apocarpic fruits, an often winged seeds, have stems showing a thick bark deeply intruding to the woody cylinder, irregular or as regular deltoid intrusions, wide rays and intraxylary phloem lacking.

Zheng and Mennega (1990) extended their wood anatomical observations on the basis of Bhesa. A comparison with other Celastraceae genera revealed that the comparison also the salient wood anatomical features of Bhesa e.g. exclusively scalariform perforations, vessels mainly in radial multiples, large vessel-ray pits, non septic thick walled labriform fibres, fine apotracheal parenchyma bands, many-celled parenchyma strands and chambered prismatic crystals are unique within the family. Thus the genus Bhesa is an isolated one in the Celastraceae. An isolated position for Bhesa (previously named GUES) is also advocated (cf. Hou, 1962: Metcalfe and Chalk, 1950) and to a position in the Saxifragaceae (sensu lato) or as a separate family Kurrtimiaeae closer to the Celastraceae. A computer search of the GUES wood identification database with information of over 500 wood species (Wheelar et al., 1988) revealed that outside the Celastraceae the genus Bhesa matches rather closely with the tribe Couleae of the family Olacaceae.

Haller (1912 and Bentham Hooker-1862-1883) included the genus Hippocratea in the Celastraceae. However, Engler and Prantl (1889): Bessey (1915) and Hutchinson (1959) divided the Celastraceae into two independent families viz., the Celastraceae and the Hippocrateaceae. There are evidence for and against the inclusion of Hippocrateaceae with the Celastraceae. Smith (1940) showed many differences between these two but emphasized on their closer affinities. Smith and Bailey (1941) thought the division between the two families Celastraceae and Hippocrateaceae as artificial, Metcalfe and Chalk (1950) have pointed out a very close relation between the two families anatomically. Erdtman (1952) also noted great resemblance between the pollen grains of the two families.

Wood anatomical evidence
Ghosh and Shahi (1963) studied wood anatomical properties especially of the two Indian genera Rhamnus and Ziziphus. According to them, these can be distinguished easily by the flame-like arrangement of vessels which is striking feature for species of Rhamnus, however, this totally lacks in the species of Ziziphus.

Floral anatomy
Floral anatomy of some genera of the Celastraceae has been attempted by Berkeley (1953). The families Rhamnaceae and Vitaceae have been also studied similarly by Nair and Sharma (1961), Prichard (1955), Kashyap (1956, 1957). According to Prichard (1955) the Rhamnaceae and Celastraceae have arisen from a hypothetical ancestor of obdiplostemonous stamens. The loss of anisogamous stamens resulted in the former, while the disappearance of the antipetalous whorl is noted in the latter. He also stated that there is very little in common floral anatomically in these two families. The floral anatomical features of the Rhamnaceae and Vitaceae such as antipetalous stamens, conjoint petal—stamen trace, conspicuous interstaminal disc and basically parietal placmentation derived from axile condition hold them together (Nair and Sharma, 1961: Prichard, 1955: Kashyap, 1957).

Embryological evidence
Adatia and Gavade (1962) studied embryology of some Celastraceae. They showed main similarities as well as differences in the embryology of Hippocratea and Celastraceae. The genus Hippocratea is similar to Celastraceae in glandular tapetum, antipetalous and bitemgic ovules, Polygonum type of embryo sac, presence of endothecium and nucellar type of embryo sac, presence of endothecium and nuclear type of endosperm development. According to them, the genus Hippocratea differs from the Celastraceae in tenuinucellate ovules and exalbimingous, winged and exarillate seeds. They suggested differentiating Hippocratea from the Celastraceae and the inclined to place in a separate family - the Hippocrateaceae but closer to the former. It appears from their account that there are more similarities of Hippocratea with the Celastraceae than their differences. This led to controversy in the taxonomic position of the genus Hippocratea on the basis of their results. They considered Hippocratea belonging to the Celastraceae. Guadalupe (1994) and Espinosa et al. (1994) extended embryological observations of some more species of Hippocratea. Their study showed similarity between Hippocratea and the family Celastraceae.

The Stackhousiaceae and Rhamnaceae have certain embryological similarities e.g. extension of funicular vascular strand beyond the chalazal, Polygonum type of embryo sac nucellar endospem and Asterad type of embryo. The family Stackhousiaceae differs from Rhamnaceae in having a single anther middle wall layer, tenuinucellate ovules on basal placenta, absence of apotracheal parenchyma, single layered archesporium, embryosac absorbing inner integument and seed coat formed by outer integument alone (Maurizen, 1936; Narang, 1953). Embryologically, Rhamnaceae and Vitaceae share many common features e.g. antipetal wall consisting of five layers of cells, multinucleate Secretory tapetum, bitemgic crassinucellate antropous ovules with downwardly directed microphyte, thick integument, a nucellar caps, a well developed hypostase, free nuclear endosperm etc. (Dolchar, 1947: Kajale, 1944: Sninivasaschar, 1940: Mulay, Nair and Sastry, 1953: Nair and Parasaruman, 1954: Nair and Namibisan, 1957: Nair and Suri, 1957: Kashyap, 1956, 1958).

The Celastraceae differ from the Rhamnaceae in the presence of tenuinucellate or weakly crassinucellate ovules, absence of integumentary vascular tissue and hypostase, fusion of polar nuclei before fertilization. Solanad type one embryo: seeds simulate and their spatulate type of internal morphology (Adatia and Gavade, 1962: Martin, 1946). Hutchinson (1959) included the family Elaeagnaceae along with Rhamnaceae and Vitaceae in his order Rhamnales. Therefore the comparison of Elaeagnaceae and Rhamnaceae appears pertinent. Both of them share similar embryological features e.g. anatropous, bitemgic and crassinucellate ovules, nucellar endosperm and investing type of internal morphology of the seed (Martin, 1946: Sarma, 1963). Rhamnaceae differs from Elaeagnaceae in absence of integumentary vasculature and parietal tissue in the ovule, polar nuclear fusion before fertilization, one antipodal cell becoming prominent and persistent, presence of chalazal embryosac, haustorium and spatulate type of internal morphology of the seed (Martin loc. cit:Sarma loc. cit.)


A resume of taxonomic alignments of different authors points out that the family Vitaceae and Celastraceae (including Hippocrateaceae) are kept in the same taxonomic group. Therefore it appears, pertinent to discuss their taxonomic affinities on embryological ground. They are similar in having Polygonum type of embryo sac, nuclear endosperm and similar structure of anther wall. The weakly crassinucellate ovules with one layer of parietal tissue, outer integument forming the microphyte, the inner integument getting, absorbed by the embryo sac, absence of hypostase and Solanad type of embryo are characteristic of the Celastraceae (sensu lato). This set of embryological characters are absent from the Vitaceae. It is to be further noted that ruminate endosperm, spheroidal growth, ingrowth from seed coat and few other developmental features of seeds which are characteristic of Vitaceae are absent in the Celastraceae (sensu lato).
Palynological features

The commonly occurring 3-colporate or 3-colporoidate condition of pollen grain is found in the families such as Celastraceae, Hippocrateaceae, Stackhousiaceae, Salvadoraceae, Staphyleaceae, Aquifoliaceae, Empetraceae, Cyrillaceae and Goupiaceae. The family Siphonodontaceae is characterized by 3-porate pollen grains. The pollen grains in Corynocarpaceae are not encountered in the Celastralean families and other families enlisted above. The family Icacinaceae is, however, eurypalynous. These three families therefore, appear not related on pollen morphological ground to the families of celastralean plexus (cf. Erdtman 1952, Farzana and Bhandari, 1979).

Synthetic assessment of higher hierarchy

The Family Staphyleaceae has been placed under the order Sapindales by Engler and Diels (1936); Hutchinson (1959, 1969, 1973); Benson (1957); Cronquist (1969, 1981, 1988); Takhtajan (1980); Soo (1975), whereas it is referred to order Celastrales by Melchior (1964); Rendle (1959); Bessey (1915) and Wettstein (1935). The Staphyleaceae are included in the Sapindales by Bentham and Hooker (1862–1883). The anatomical characteristic such as anisocytic stomata, vessel end with scalariform perforation plate, clustered crystals and paratracheal wood parenchyma do not help disband the family Staphyleaceae from the other families of the Celastralean plexus. Hallier (1912) refers it to the Rosales and conceived it allied to the Cunoniaceae and Saxifragaceae.

According to Ingva (1990) the family Sapindaceae including Staphyleaceae is homogeneous in possessing similar flavonoid profile. She also confirms origin of these two from a common stock. As pointed out earlier the 3-colporate condition of the pollen grains in Staphyleaceae does not preclude the affinity with the Celastralean families, although similar condition is also noted in the families of the order Sapindales. Erdtman (1952) allies it with the Celastraceae. Foster (1933) on cytological ground inferred that they have a common origin with Aceraceae. Cronquist (1981) considers the Staphyleaceae as anomalous under the order Celastrales, as he thinks the Staphyleaceae as intermediate between the Cunoniaceae (Rosales) and the Sapindaceae and Aceraceae (Sapindales). He also refers Staphyleaceae to the order Sapindales. The Staphyleaceae is indistinctive on account of cup like intrastaminal disc. Numerous ovules, ample endosperm and straight embryo. It is also distinguishable by absence of ellargic acids not cyanogenic not saponiferous and in lacking iridoid compounds. In macromorphological features like pinnate stipulate leaves and ovules numerous in each locule render the Staphyleaceae anomalous in the order Celastrales. However, it is to be noted that the micromorphological characteristic e.g. anisocytic stomata, vessels with scalariform perforation plates, clustered crystals, paratracheal wood parenchyma and pollen grains, ovule anatropous, bitegmic, crassinuecellate, endosperm nuclear tapetum glandular, simultaneous cytokinesis in M.M.C. Pollen grains 2-celled at anthesis, fusion of polar nuclei prior to fertilization and Polygonum type of embryo sac etc. Decisively allies the Staphyleaceae with the Celastrales rather than the Sapindales. However, it should be regarded the most primitive family of the order Celastrales.

A resume of different systems of Ranalian and Englerian schools indicate that the families viz., Celastraceae, Hippocreaceae, Stackhousiaceae, Salvadoraceae, Staphyleaceae, Siphonodontaceae, Icacinaceae, Goupiaceae, Empetraceae, Cardiopteridaceae and Cyrillaceae constitute core of the Celastralean families (Shisode and Patil, 1980).

The families viz., Celastraceae (sensu stricto) Aquifoliaceae, Cyrilaceae, Staphyleaceae, Empetraceae, and Goupiaceae, show similar development in vessel specialization. The end walls of vessel in these families exhibit scalariform perforation. However, in the families Hippocreaceae, Salvadoraceae, Stackhousiaceae and Corynocarpaceae, the end walls of vessels are simple perforated and advanced over the other celastralean families.

The family Celastraceae–Hippocreaceae complex exhibit a variety of stomatal types ranging from anamocytic to anisocytic to paracytic to heliocytic, cyclocytic, etc. Few genera like Kurrimia (Bhesa) Brasiantha Xylonimus, Hedraethina however show exclusively paracytic condition. In remainder of this alliance other types noted earlier are found in different combinations, although the anamocytic type is more prevalent in this alliance. The core families of the Celastralean plexus viz., Staphyleaceae, Goupiaceae, Cyrillaceae, Aquifoliaceae, Icacinaceae, Stackhousiaceae also show anamocytic or anisocytic as dominant or codominant types. It is only Corynocarpaceae and Salvadoraceae which have paracytic stomata. The Siphonodontaceae are also marked out by the laterocytic type. The laterocytic condition is sometimes thought as “complex anisocytic” (Hartog and Bass, 1978). This resume of the stomatal features in Celastralean plexus indicates that all these families can be easily accommodated under one taxonomic entity. The various other types noted particularly in the Celastraceae (sensu lato) are derivable from one another (cf. also Hartog and Bass, loc. cit.). Majority of celastralean families show unicellular and uniseriate trichomes. The other types such as stellate, peltate scales or hairs are rarely noted in few taxa. The typology of trichomes certainly helps to lump all these families under one broad taxonomic rank.

The wood anatomical features, especially the distribution of wood parenchyma do not exclude close affinities of these families from one another as both type viz., paratracheal and apotracheal are observed in different families of the alliance as also within the same families. The common occurrence of anamocytic stomata, unicellular or uniseriate hairs, solitary and clustered crystals, wood parenchyma paratracheal, vessels being either simple or scalariform perforated do not preclude the affinities of the Rhamnaceae and Vitaceae (sensu lato). Instead these features help align all these families closely.

Bentham and Hooker (1862–1883) placed the family Stackhousiaceae under the order Celastrales in between the families Celastraceae and Rhamnaceae. Engler and Prantl (1889) however kept it under the order Sapindales in between the families Salvadoraceae and Staphyleaceae. Hutchinson (1920) followed the same treatment. The family Hippocreaceae is now said to form a transitional group between the Stackhousiaceae and Celastraceae (sensu stricto). Mauritzen (1936) Narang (1953) investigated embryology of the genus Stackhousia (Stackhousiaceae) and pointed out many similarities with the Celastraceae. In either of the families, the outer integuments form the micropyyle, whilst the inner integuments are consumed by the embryo sac, the nucellus degenerate at the 2-nucleate and 4-nucleate stage of embryo sac. The embryo sac is monosporic and eight nucleate; the endosperm is nuclear. The author therefore lends support to assign the family Stackhousiaceae to the order Celastrales. The further remarked that the family Stackhousiaceae is the closest to the Celastraceae and the Hippocrataceae.

The relationship of the family Salvadoraceae and the order Celastrales has been the subject of dispute in the past. Bentham and Hooker (1862–1883) and Bessey (1915) assigned it to the Gentianales. Rendle (1959) placed it under the order Oleales. Engler and Diels (1936) placed the Salvadoraceae in polypetalae in Celastrineae under the Sapindales. Hutchinson (1920) recommended similar taxonomic position. Gunderson (1950) considered it within the order Celastrales. Takhtajan (1980) and Cronquist (1981) followed the same treatment. Takhtajan (loc. cit.) accepted its close relationship with the Celastraceae.

Mashashwari devi (1962, 1964, 1971, 1972) studied embryology of Salvadoraceae as well as the families of Gentianales. Johri (1963) reviewed and assessed the embryological features of Salvadoraceae the Gentianales and Oleales. He opined that the inclusion of Salvadoraceae in either
of the order is not justifiable. On the contrary, in his opinion, the inclusion of Salvadoreae in the order Celastrales is best on the basis of embryology. The representative genera viz. Azima and Salvador of the Salvadoreae share the features with the Celastraceae such as two - celled pollen grains, anatropous bitegmic crassinucellate ovules, Formation of parietal tissue and nucellar type of endosperm. The placement of the Celastrales is also supported by floral anatomy (Kshetrapal, 1970). Gamopetal in case of Salvador seems to contradict this position but should be regarded as an exceptional feature for the family. This view is also impressed by Melchior (1964).

Erdtman (1952) in the light of palynological evidence opined that pollen grains of the Celastraceae are more or less similar to those in Hippocrateaceae. Pollen grains are usually three-colporate in both families. He drew attention towards the artificial division between these families as pointed out by Smith and Bailey (1914). Likewise, Erdtman (loc. cit.) pointed out pollen morphological similarly between the families Rhamnaceae and Vitaceae. He regards Rhamnaceae as a stenopalous family. Pollen grains are usually three colporate. It is also to be noted that the pollen grains in the Celastraceae and Rhamnaceae are three colporate but the former have usually more rounded pollen grains. The grains are triangular in the Rhamnaceae.

Farzana and Bahandari (1979) investigated the pollen morphology of the Indian family Rhamnaceae. They also concluded that the family Rhamnaceae plus stenopalous. They observed pollen grains usually three zonocolporate, to sub - oblate sphaeroidal and often triangular. Exine strarification is more or less reticulate and psilate. They opined that there are only minor pollen morphological differences which are not of much taxonomic significance. According to them the occurrence of similar pollen grains in the Rhamnaceae and Vitaceae is suggestive of their close affinities as reported by Erdtman (1952). They further suggest close affinities between the three families viz. Rhamnaceae, Vitaceae and Celastraceae on palynological base.

Lobreau (1971) divided the order Celastrales on the basis of pollen morphology into two groups – the first group consisting on the families viz.; Celastraceae, Hippocrateaceae, Staphyleaceae and Stackhousiaceae characterized by pollen grains with a reticulate sculpturing and simple endexine, whereas the another group comprising the families such as Iccacineae, Siphonodonataceae, Cordipteridaceae, Salvadoraceae and Aquifoliaceae characterized by the pollen with various sculpturing patterns and an irregularly cracked, and structural endexine. He considers some families of the order as doubtful in position and remarks for their exclusion from the Celastrales.

Muller (1981) recorded fossil angiosperm pollen types of different families. Based on this evidence, he gave the appearance of angiospermous families. The families viz. Celastraceae (sensus lato) Rhamnaceae and even Vitaceae appeared in the oligocene of tertiary. This evidence demonstrates that none of them originated from the other. On the contrary, this evidence warrants their origin from a common ancient stock. The Sapindales into which Celastraceae is sometimes included (Engler and Diels., 1936) appeared quite later in the upper mesocene of the tertiary. This evidence indicates that none of the Sapindales are progenitors of the Celastrales.

A resume of the basic chromosome number (x) of the three families presently under consideration brings certain things to the fore. The basic numbers in the Celastraceae and Hippocrateaceae are not by far suggestive of their relationship to each other. Much studies on other characters obviously needed for better comprehensive treatment and phylogenetic considerations. However, the close relationship between the Rhamnaceae and Vitaceae appears certainly warranted. The base numbers x = 10, 11, 12, 13 are commonly met with the genera, of both families. Other base numbers in rest of the members of these families also appear derivable from them. Thus their closer affinity may be pointed out.

Gibs (1974) while summarizing chemistry of Celastraceae and Hippocrateaceae commented that very little of the chemistry is known of the latter and hence expressed inability to assess the affinity between them. He noted (doubtfully) the absence of raphides in the Celastraceae. However, the present author noted them in Euonymus fortunei. He also doubted occurrence of raphides in the Hippocrateaceae. The present author also could not locate them in the species studied. It is interesting to note that three species of Kurrimia (now the genus Bhesa) are said to be accumulators of Aluminium. No accumulates of Aluminium are known within the other celtacestraceous members and in the Hippocrateaceae. Rhamnaceae and Vitaceae as well. Gibbs (1974) noted absence of raphides in the Rhamnaceae, present study also records their absence in the family. However, they have been noted in the members of Vitaceae. The chemical evidence then available to Gibbs hardly reflects relationship of the three in Hippocrateaceae. Pollen grains in Flouvier (1963) noted distribution of aliphatic polyols and cyclitols in the Celastraceae and Hippocrateaceae. On the chemical basis, he confirms the parentage of Hippocrateaceae with the Celastraceae. He further adds that the family Strophuliaceae has affinities with the Celastraceae and Hippocrateaceae through the intermediate family Stackhousiaceae.

Ingueva (1990) studied phytochemistry and systematics of some Sapindales and its related taxa. According to her, flavonols and proanthocyanidins form the major phenolic pigments of the group. Flavonols are particularly abundant in Celastraceae as well as in Rhamnaceae. Likewise alkaloids are also abundant in these two families. The Origin of the order, viz. Celastrales (Celastraceae), Rhamnales (Rhamnaceae) and Vitidales (Vitaceae and Leeaceae) is according to her unconfirmed. The Staphyleaceae, which are sometimes included in the order Sapindales, show closer affinities to the Celastrales, flavonols, quinones and parenthocyanidins are highly prevalent in the Rhamnaceae. Flavonols and glycoflavonols are rare but these characters according to her make the family a natural taxon. The family Rhamnaceae is however distinct in producing quinines and peptide alkaloids.

The Vitaceae and Leeaceae are dissimilar; the former shows the presence of flavons, glycoflavonols and flavonoids, whereas the latter produces highly hydroxylated compounds like myricatins and gallic acid. Both these families do not synthesize the quinones and peptide alkaloids characteristic to the Rhamnaceae. She therefore opposed grouping of the Vitaceae and Leeaceae alongwith the Rhamnaceae under the order Rhamnales.

The genus Leea is treated as a separate family—the Leeaceae between the Vitaceae (Sarmentaceae) and Meliaceae (Sussenguth, 1953), Barting, 1830). It is also supported by Melchior (1964): Cronquist (1968, 1981, 1988). Takhtajan (1969, 1980) and Wettsoon (1933) treated it as a subfamily Leeoideae of the Vitaceae. The genus Leea shows many embryological similarities with the Vitaceae. Both of them exhibit multicellular parietal archesporium, bitunicate ovules and with a cap, presence of hypostase, Polyspermous embroy sac, perichalaza, nuclear endosperm, Asterend type of embryo development, structure of seed coat, fatty reserves in endosperm etc. (Adatia et al., 1950, 1955; Mulay et al. 1953; Kashyap, 1956, 1958: Nair and Bajaj, 1967. Nair and Parasuraman, 1954, 1962: Nair and Suri 1957; Periaswamy, 1962). They also show similar floral anatomical features such as valvate sepals and petals, antipetalous, stamens, fertile introrse anthers, conjoint petal-stamen traces, gymocoeum derived from multicellular pollinatory (Kashyap, 1957: Nair 1968, Nair and Mani, 1960: Nair and Nambiseng, 1957) Both of them have tricolpate pollen grains (Erdtman, 1952). They are similar in anomocytic stomata, parenchyma of these families as well. They also exhibit plantaroodle, leaves, petiolar anatomy of divided strands, epipetalous stamens, staminal tube, inner whorl of staminodes, obdiplostemonary condition and absence of disc. 4-6 lobed ovary, development of false sepal in the

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ovary, single ovule per loculus, chalazal, ingrowth in the seed, absence of raphides in seed coat (Kashyap 1957; Nair, 1968; Nair and Mani, 1960; Nair and Namibisan, 1957).

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