

REVIEW ARTICLE

Taxonomic and phylogenetic census of the Celastrales: A synthetic review

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ABSTRACT

A comprehensive assessment of the taxonomic and phylogenetic status of the celastralean 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 lato*) 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 lato*). They categorised these genera into two tribes - Celastreae and Hippocrateae. The tribe Hippocrateae included only four genera viz., Hippocratea, Salacia, Siphonodon and Llavea, whereas the others are kept under the tribe Celastreae. The family Celastraceae (*sensu lato*), in their scheme, is kept under the order Celastrales alongwith the families such as Rhamnaceae, Vitaceae and Stackhousiaceae. The family Rhamnaceae is divided into four tribes viz., Ventilagineae, Zizyphaeae, Rhamneae and Gouanieae. Bessey (1915) included the families Rhamnaceae, Vitaceae, 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., Celastroideae, Tripterygiodeae, Cassinoideae, Goupioideae and Siphonodontoideae. 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., Rhamneae, Zizyphaeae, Ventilagineae, Colletieae and Gouanieae. Treatment by Wettstein (1935) 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 Celastraceae (*sensu lato*) 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 lato*) 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 alongwith 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) recognised the order Celastrales as containing the separate families Celastraceae and Hippocrateaceae alongwith 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- the Celastraceae and Aquifoliaceae. Likewise, his order Rhamnales contains the Rhamnaceae and Vitaceae only. He appears to have included Hippocrateaceae under the Celastraceae (*sensu lato*) and Leeaceae under the Vitaceae (*sensu lato*).

Thorne (1992) in his recent treatment included Celastraceae under his order Celastrales but divided it into five subfamilies *viz.*, Celastroideae, Tripterygiodeae, Cassinoideae, Hippocrateoideae and Siphonodontoideae. The genera Goupia and Lophopyxis are kept under their independent families - the Goupiaceae and Lophopyxidaceae respectively. Hippocrateaceae (*sensu stricto*) is accorded a subfamilial rank under the family Celastraceae (*sensu lato*). He included the family Rhamnaceae and Elaeagnaceae in his order Rhamnales. It is 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 Leoideae.

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 lato*), 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 lianas 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, while 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 Celastrae 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 and distinguished from the order Geraniales in the ovules pendulous with the dorsal raphe and micropyle upward or erect with the ventral 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 sepals 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 tendrils, antipetalous stamens, axile placentation and berried fruit. Benson (1957) exploits the characteristics of sepals, fruits and presence of tendrils to delimit these families. Rendle (1959) characterizes the order Celastrales by flowers bisexual or unisexual by abortion, regular hypogynous cyclic, four to five numerous petals free or sometimes connate 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 pellucid, punctate leaves, inflorescence leaf opposed, presence of tendrils 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 wherein 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 freely borrowed 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, two-traced condition is found in *Ziziphus caracutta*, *Z. mauritiana* and *Z. nummularia* of the Rhamnaceae. The three-lacunar, three-traced nodes are basic. The unilacunar, one-traced is derived one in all the three families investigated. Thus anatomy of nodes represents evidence more to indicate similar development and evolutionary trend in these three families.

The present author's investigation (Shisode and Patil 2000 b, 2005c, 2008a,c) and those summarized by Metcalfe and Chalk (1950) show anomocytic and anisocytic types more common in the three families. Other types such as paracytic, diacytic,

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 hexacytic 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 hypostomatic leaves; very few 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 2000 b, 2005 c, 2008 a,c).

Clustered crystals are common in the petiole of Rhamnaceae. They are totally absent in the Hippocrateaceae and present only in *Eunonymus 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) consider 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 *Eunonymus 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 petiole, 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 Tripterygium 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 the genus *Goupia* definitely aberrant within the Celastraceae and erected an independent family Goupiaceae (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 angolita*, *Z. sonorensis*, *Z. mistol* 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. rothiana* 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 *C. stylosus* on the midrib and veinlets of the abaxial foliar epidermis by Pant and Kidwai (1965). The cuticular striations on the foliar epidermis are wanting in the Celastraceae and Hippocrateaceae. Exceptionally, they are present on mid-vein cells of *Reissantia grahamii*. They are observed in fairly good number of plants of the family Rhamnaceae (Shisode and Patil 2005 C). They are observed on the upper foliar surface, mid-vein cells and the cells of veinlets *Pomaderris apetala* and *Rhamnus wightii*. They are noticed only on the upper foliar surface but not on the veins and veinlets in case of *Scutia rnyrtina*. In *Colubrina asiatica*, *Ziziphus nummularia* and *Z. rugosa* they are present on the lower foliar surface of the cells of midvein and veinlets. The occurrence of cuticular striations appears to be of systematic value. These

are also thought so in other taxa of angiosperms (Cuttler, 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 stomatal 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 and simple filiform types are common to 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 (1979) noted P-type and S-type of plastids present 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 Cerverea*, *Elachyptera*, *Hemiangium*, *Hippocratea*, *Hyleanea*, *Pristimera* and *Prionostemma*, can be characterised by broad and very high rays, mainly composed of procumbent cells, by the presence of septate fibres, tracheids and the absences 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. Loesner (1942) includes it in the Celastraceae. However, the wood anatomy of this genus evidently is in good agreement with species of *Salacia*. Another genus viz., *Campylostemon* kept under the Celastraceae by Loesner (*loc.cit.*) was returned by Lawalree (1947) to the Hippocrateaceae because its wood exactly matches that of *Hippocratea* of the Hippocrateaceae. *Kokoona* sometimes thought *Celastraceae* belonged to the Hippocrateaceae. This is, however, contradicted by its very regular concentric parenchyma bands and by the absence of septate fibres. Stenzil (1882) finds certain resemblance in petiolar anatomy of *Kokoona* to the genus *Maytenus*.

Mennega (1997) studied some more genera of the Hippocrateaceae. *Campylostemon* is thought by some taxonomists as belonging to the Celastraceae or as intermediate between the Hippocrateaceae and Celastraceae. In her opinion, the genus *Campylostemon* 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 Hippocrateaceae assigned by Cronquist (1981) and others. The division of the latter into two distinct groups, depending up on the nature of fruit also confirmed by her present wood anatomical studies. Halle (1986, 1990) also accepts these two groups the Salacidae on one hand and Hippocrateae, Halictoneae and Campylostemonae on the other. According to him, genera of the *Salacidae* with drupaceous fruits and wingless seeds are anatomically characterised by a rather thin bark of uniform thickness, narrow rays, presence of septate fibres often arranged in a parenchyma like banded pattern, and by the frequent presence of intraxylary phloem. Other genera with dry

dehiscent apocarpic fruits, an often winged seeds, have stems showing a thick bark deeply intruding to the woody cylinder, irregular or as regular deltooid intrusions, wide rays and intraxylary phloem lacking.

Zhang and Menega (1990) extended their wood anatomical observations on the basis of *Bhesa*. A comparison with other *Celastraceae* genera revealed that the combination of the salient wood anatomical features of *Bhesa* e.g. exclusively scalariform perforations, vessels mainly in radial multiples, large vessel-ray pits, non septate 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 *Kurrimia*) was also advocated (cf. Hou, 1962; Metcalfe and Chalk, 1950) and to a position in the *Saxifragaceae (sensu lato)* or as a separate family *Kurrimiaceae* closer to the *Celastraceae*. A computer search of the GUESS wood identification database with information of over 500 wood species (Wheeler *et.al.*, 1986) revealed that outside the *Celastraceae* the genus *Bhesa* matches rather closely with the tribe *Couleae* of the family *Oleaceae*.

Hallier (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 *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 on anatomical grounds. 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 antiseptalous 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 placentation 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, anatropous and bitegmic ovules, *Polygonum* type of embrosac, presence of endothecium and nucelar 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 exalbuminous, winged and exarillate seeds. They suggested disbanding of *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 nucelar endosperm 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 nucellar caps, single celled female archesporium, embryosac absorbing inner integument and seed coat formed by outer integument alone (Mauritzen, 1936; Narang, 1953). Embryologically, *Rhamnaceae* and *Vitaceae* share more common features e.g. anther wall consisting of five layers of cells, multinucleate Secretory tapetum, bitegmic crassinucellate antropous ovules with downwardly directed micropyle, thick integument, a nucellar caps, a well developed hypostase, free nuclear endosperm etc. (Dolchar, 1947; Kajale, 1944; Srinivasachar, 1940; Mulay, Nair and Sastry, 1953; Nair and Parasuraman, 1954; Nair and Nambisan, 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 arillate 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, bitegmic and crassinucellate ovules, nuclear 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.*)

The family *Rhamnaceae* and *Vitaceae* are generally placed in one taxonomic entity. They share similar embryological features such as anatropous, bitegmic, crassinucellate ovule, formation of nucellar cap, presence of hypostase *Polygonum* type of embryo sac, nuclear endosperm and *Asterad* type of embryo (Adatia *et.al.* 1950; 1953, Kashyap, 1955, 1958, Mulay *et.al.* 1953; Nair and Bajaj, 1966; Nair and Parasuraman; 1954 Nair and Suri, 1967; Souges 1957) These families exhibit striking embryological dissimilarities . Integumentary vascular strand, epistase and *Allium* type of embryo sac noticed in *Rhamnaceae*, obturator, proliferation on nucellar tissue and its disappearance during post fertilization stages, haustrial nature of embryo sac and ruminant endosperm observed in *Vitaceae* are not encountered in the *Rhamnaceae* (Adatia, *loc.cit.*; Kashyap, *loc.cit.*, Mulay, *loc.cit.*, Nair and Bajaj, *loc.cit.*, Nair and Parsuraman, *loc.cit.*, Nair and Suri, *loc.cit.*, Souges *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 micropyle, 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 ruminant endosperm, perichalazal 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 Celastraceae 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 celastreal 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 core families of the *Celastreal* plexus. Hallier (1912) refers it to the Rosales and conceived it allied to the Cunoniaceae and Saxifragaceae.

According to Inguva (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 *Celastreal* 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 Celastrales because of compound leaves; 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 ellagic 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, 3-colporate pollen grains, ovule anatropous, bitegmic, crassinucellate, 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 Ralian and Englerian schools indicate that the families *viz.*, Celastraceae, Hippocrateaceae, Stackhousiaceae, Salvadoraceae, Staphyleaceae, Siphonodontaceae, Icacinaceae, Goupiaceae, Empetraceae, Cardiopteridaceae and Cyrillaceae constitute core of the Celastreal plexus. (Shisode and Patil 2010b)

The families *viz.*, Celastraceae (*sensu stricto*) Aquifoliaceae, Cyrillaceae, Icacinaceae, 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 Hippocrateaceae, Salvadoraceae, Stackhousiaceae and Corynocarpaceae, the end walls of vessels are simple perforated and advanced over the other celastreal families.

The family Celastraceae-Hippocrateaceae complex exhibit a variety of stomatal types ranging from anomocytic to

anisocytic to paracytic to heliocytic, cyclocytic, etc. Few genera like Kurrimia (Bhesa) Brassiantha Xylonimus, Hedraintera however show exclusively paracytic condition. In remainder of this alliance other types noted earlier are found in different combinations, although the anomocytic type is more prevalent in this alliance. The core families of the Celastreal plexus *viz.*, Staphyleaceae, Goupiaceae, Cyrillaceae, Aquifoliaceae, Icacinaceae, Stackhousiaceae also show anomocytic or anisocytics 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 Celastreal 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 celastreal 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 taxonomic entity.

According to Gibbs (1974) raphides are absent in the order Celastrales including the family Rhamnaceae. Their prominence, in this opinion, is notable in the allied family Vitaceae (*sensu lato*) However, it is interesting to note that majority of these families have crystalliferous foliar epidermal cells. The crystals are either solitary or clustered. This also evidences to treat the various families of this plexus 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 anomocytic 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 (1926) followed the same treatment. The family Hippocrateaceae is said to form a transitional group between the Stackhousiaceae and Celastraceae (*sensu stricto*). Mautrizen (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 micropyle, while the inner integuments are consumed by the embryo sac; the nucellus degenerate at the 2-nucleate and 4-nucleate stage of embryo sac; the embryosac 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 Hippocrateaceae.

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 (1973) 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.

Maheshwaridevi (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 Olacales. He opined that the inclusion of Salvadoraceae in either

of the order is not justifiable. On the contrary, in his opinion, the inclusion of Salvadoraceae in the order Celastrales is best on the basis of embryology. The representative genera viz. *Azima* and *Salvadora* of the Salvadoraceae share the features with the Celastraceae such as two-celled pollen grains, anatropous bitegmic crasinucellate ovules, Formation of parietal tissue and nuclear type of endosperm. The placement of Salvadoraceae in the Celastrales is also supported by floral anatomy (Kshetrapal, 1970). Gamopetaly in case of *Salvadora* 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 available 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 similarity between the families Rhamnaceae and Vitaceae. He regards Rhamnaceae as a stenopalynous 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 is a stenopalynous one. They observed pollen grains usually three-zonicolporate, to sub-oblate sphaeroidal and often triangular. Exine stratification 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 Iccacinaceae, Siphonodontaaceae, Cordiopteridaceae, Salvadoraceae and Aquifoliaceae characterized by the pollens 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 (*sensu lato*) Rhamnaceae and even Vitaceae appeared in the oligocene of tertiary. This indicates that none of them originated from the other. On the contrary, this evidence warrants their origin from a common ancestral stock. The Sapindales into which Celastraceae is sometimes included (Engler and Diels, 1936) appeared quite later in the upper miocene of the tertiary. This evidently demonstrates 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 base numbers in the Celastraceae and Hippocrateaceae are not by far suggestive of their relationship to each other. More studies on other taxa of these families are 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 plausibly pointed out.

Gibbs (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 celastraceous 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 Rhamnaceae to the Celastrales.

Plouvier (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 Scrophulariaceae has affinities with the Celastraceae and Hippocrateaceae through the intermediate family Stackhousiaceae.

Inguva (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 orders viz., Celastrales (Celastraceae), Rhamnales (Rhamnaceae) and Vitales (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 proanthocyanidins 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 Wettstein (1935) treated it as a subfamily Leeoideae of the Vitaceae. The genus *Leea* shows many embryological similarities with the Vitaceae. Both of them exhibit multicellular microsporial archesporium, bitegmic crassinucellate ovules with a cap, presence of hypostase, Polygonum embryo sac, perichalaza, nuclear endosperm, Asterad type of embryo development, structure of seed coat, fatty reserves in endosperm etc. (Adatia *et. al.*, 1950, 1953; 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 sepal and petals, antipetalous, stamens, fertile introrse anthers, conjoint petal-stamen traces, gynoeceum derived from multicarpellary condition (Kashyap, 1957; Nair 1968, Nair and Mani, 1960; Nair and Nambisan, 1957) Both of them have tricolpate pollen grains (Erdtman, 1952). They are similar in anomocytic stomata, presence of raphides and mucilage, vessels with simple perforations, and paratracheal wood parenchyma, similar trichomes and deciduous pearl glands (Metcalfe and Chalk, 1950) In the broad medullary rays and petiolar anatomy, *Leea* is different from the other Vitaceae (Metcalfe and Chalk 1950). As stated earlier, chemically they are dissimilar (Inguva 1990) *Leea* is also different from the remainder Vitaceae in the erect habit. Terminal inflorescence, exstipulate, leaves, petiolar anatomy of divided strands, epipetalous stamens, staminal tube, inner whorl of staminodes, obdiplostemonous condition and absence of disc. 4-6 lobed ovary, development of false septa in the

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 Nambisan, 1957).

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