

CHAPTER - 7

AN EMBRYOLOGICAL APPROACH TO THE STATUS AND

ORIGIN OF COMPOSITAE

Most systems of classification of plants have been evolved on the basis of exomorphic characters placing particular reliance on the characters of the flower, the flower being considered more conservative than the vegetative organs. Even so the goal of reaching a truly natural system of classification has remained unfulfilled. The importance of embryological data as an additional evidence to that obtained from the fields of cytology, anatomy, palynology and phytochemistry in elucidating the taxonomic relationships is well known, and it has been emphasised by eminent embryologists, eg. Schnarf (1933, 1937), Just (1946), Johansen (1945, 1950), Maheshwari (1950, 1963, 1964), Lebeque (1952), Cave (1953), (1959), P^odubna-ja-Arnoldi (1964, 1976) and Palser (1975). Maheshwari (1950) listed a number of embryological features of taxonomic significance which are taken into consideration for evaluating phylogenetic relationships.

Bearing in mind that embryological evidence is only supplementary to the other criteria- cytological, anatomical, palynological and phytochemical - an attempt has been made to discuss the systematic position and phylogeny of the family Compositae on Embryological grounds.

THE SYSTEMATIC POSITION OF THE COMPOSITAE

Diverse opinions have been expressed regarding the systematic position of the family in various systems of classification by different taxonomists. Engler (1926), Engler and Diels (1936) and Pulle (1937) included Compositae in the order Campanulatae along with Campanulaceae, Goodeniaceae (including Lobelioideae), Brunoniaceae, Stylidaceae and Calyceraceae. Melchior's (1964) order of Campanulales is essentially similar to that of Engler excepting that he raised the Sphenocleaceae and Pentaphragmataceae to the family rank. Rendle's (1938) order Campanulales comprises the families Campanulaceae, Goodeniaceae, Stylidaceae and Compositae. Core's (1955) classification is similar to that of Rendle, the only difference being that he included Cucurbitaceae in his order Campanulales. Bentham and Hooker (1862-1883) included the family Compositae in the order Asterales along with valerianaceae, Dipsacaceae and Calyceraceae, while Hutchinson (1926) incorporated the family Adoxaceae also in the Asterales. Later Hutchinson (1948, 1959, 1969, 1973) revised his system and raised the taxonomic hierarchy of Compositae to that of an ordinal rank Asterales comprising the only family Asteraceae (Compositae). A similar treatment was accorded to the family by Benson (1957), Cronquist (1968), Takhtajan (1969) and Dahlgren (1975).

In Table-I the various systems of classifications are represented. For convenience the morphological features of different families also are tabulated in the last column of the table. The embryological features of Compositae and those of the other families included in the orders Campanulatae/Campanulales/Asterales are tabulated in Table II.

An analysis of the data from tables I and II clearly shows that Cucurbitaceae differs from the rest of the families of Campanulales in its morphological as well as embryological features. In Cucurbitaceae the plants chiefly are tendrillar climbers, while in the other families of Campanulales the plants are mostly herbs, shrubs or trees. Further Cucurbitaceae is characterized by the presence of glandular tapetum, 2-celled pollen grains, 3-5 carpellary ovary which is either unilocular with parietal placentation or trilocular with axile placentation, bitegmic and crassinucellate ovules with well developed parietal tissue, Polygonum type of embryo sac development (*Allium* type in *Benincasa cerifera*), three ephemeral antipodals, aggressive chalazal endosperm haustorium and Onagrad type of embryo development. The rest of the families of Campanulales are characterised by the presence of unitegmic and tenuinucellate ovules, absence of parietal tissue and Solanad or Asterad type of embryo development. Thus both morphological

and embryological evidence is not in favour of the retention of the Cucurbitaceae in Campanulales as was treated by Core (1955). Further, from table II it is very clear that the embryological differences between Cucurbitaceae and Compositae are still greater and there appears to be no possibility even to think of any relationship between these two families.

Although Hutchinson (1926) in his earlier classification included the Adoxaceae in Asterales later he (1948, 1959, 1969, 1973) removed the family from the Asterales and placed in Saxifragales. Of course, the family Adoxaceae differs in its morphological features from the rest of the families of Asterales. Adoxaceae is characterised by the head inflorescence with 4-6 merous flowers, 4-6 stamens which split at the base to form double the number and contain single-celled anthers, semi-inferior ovary with 3-5 locules, pendulous ovules and the fruit which is a drupe. In the embryological features also the family differs from the rest of the families of Asterales by the Adoxa type of embryo sac development and Geum variation of Asterad type of embryo development. Thus both morphological and embryological features support the later classification of Hutchinson (1948, 1959, 1969, 1973), in the removal of the family Adoxaceae from Asterales.

The families Campanulaceae, Goodeniaceae, and Stylida-

case which are included in Campanulatae of Engler (1926), Engler and Diels (1936) and Campanulales of Rendle (1938), Core (1955) and Melchoir (1964) differs from the Compositae not only in their morphological characters (see Table I), but also in their embryological features (see Table II). In the embryological features these families are characterised by the presence of more than one row of archesporial cells in the anther lobe, glandular anther tapetum, smooth exine of the pollen grains, constant occurrence of three antipodal cells which degenerate before fertilization, Cellular type of endosperm development with both chalazal and micropylar haustoria, presence of starch as reserve food in the endosperm and Solanad type of embryo development. Thus both morphological and embryological features are not in favour of the inclusion of Compositae either in Campanulatae of Engler (1926) and Engler and Diels (1936) or in the Campanulales of Rendle (1938), Core (1955) and Melchoir (1964).

The family Calyceraceae is included along with Compositae in Campanulatae by Engler (1926), Engler and Diels (1936), in the Campanulales by Melchoir (1964) and in the Asterales by Bentham and Hooker (1862-1883) and Hutchinsen (1926). Embryologically the family Calyceraceae is inadequately known. Even from the little available data it is clear that the family differs from Compositae in having

glandular anther tapetum, 2-celled pollen grains, monocarpellary ovary with a single pendulous ovule, 3-eph^emeral antipodal cells and formation of 4-celled linear proembryo. Morphologically also Calyceraceae differs from Compositae in the presence of variable number of perianth lobes, more or less distinct anthers, pendulous ovule and undivided stigma.

The three families, Valerianaceae, Dipsacaceae and Compositae show resemblances in certain of their embryological characters. In these three families the anther is tetrasporangiate the development of the anther wall is of the dicotyledonous type, the pollen grains are 3-celled, the ovule is anatropous unitegmic and tenuinucellate and the antipodal cells are persistent. The development of the endosperm is of the Cellular type in Dipsacaceae and Valerianaceae, while it is of both Cellular and Nuclear type in Compositae.

In spite of these resemblances with Valerianaceae and Dipsacaceae, Compositae is unique in showing certain specialised embryological characters like the presence of a single row of archesporial cells in the anther lobe, formation of periplasmodial anther tapetum, 3-celled pollen grains with thick spinous exine, occurrence of a well developed integumentary tapetum and development of Senecio variation of Asterad type of embryo development.

Similarly the family shows some outstanding morphological characters like the presence of head inflorescence with involucre of bracts, calyx which is not green but consists of pappus, corollas differentiated either into disc or ray types, anthers more or less united, ovary bicarpellary syncarpous and unilocular with single basal ovule and fruit an achene. From the above it is clear that both morphological and embryological characters are not in favour of the grouping of these three families - Dipsacaceae, Valerianaceae and Compositae in the same order Asterales. Thus on embryological grounds it appears to be proper to retain Compositae as the only family of the order Asterales. Such a view gains support from Hutchinson (1948, 1959, 1969, 1973), Benson (1957), Cronquist (1968), Thorne (1968), Takhtajan (1969) and Dahlgren (1975). Dipsacaceae and Valerianaceae should be treated as immediate allies of Compositae.

In the majority of the above systems of classification the family Compositae is divided into two sub-families and 13 tribes. However, some systematists like Link (1829), Bessey (1915), Gundersen (1950) and Britton (see Lawrence, 1951) raised the tribes to the status of independent families. Link (1829) raised some taxa of lower hierarchy to the status of families, namely Acarnaceae, Ambrosiaceae, Anthemidaceae, Calendulaceae, Coreopsidaceae, Echinopaceae, Eupatoriaceae, Helichry-

saceae, Partheniaceae and Peridiaceae. Bessey's (1915) order Asterales comprises of Helianthaceae, Ambrosiaceae, Heleniaceae, Arctotidaceae, Calendulaceae, Inulaceae, Asteraceae, Vernoniaceae, Eupatoriaceae, Anthemidaceae, Senecionidaceae, Carduaceae, Mutisiaceae and Lactucaceae. Similarly Gunderson (1950) raised the tribe Cichoreae to the status of an independent family based on the character like the presence of latex, flowers always ligulate and mostly yellow. He incorporated the family Cichor^eaceae in the Asterales along with Calyceraceae and Compositae. Britton and his students (see Lawrence, 1951) raised the Compositae to that of an order, the Carduales and divided it into 3 families - (1) Ambrosiaceae consisting of non-syngenesious genera of Heliantheae (2) Carduaceae equivalent of Tubulifloreae of other authors excepting the non-syngenesious Heliantheae and (3) Cichoreaceae the equivalent to Ligulifloreae.

Embryologically Compositae are homogenous in showing a single row of archesporial cells in the anther lobe, a dicotyledonous type of anther wall development, periplasmodial anther tapetum, 3-celled and echinate pollen grains, anatropous, unitegmic and tenuinacellate ovules, presence of integumentary tapetum and Asterad type of embryo development. In this connection it may be quoted from Crété (1963) who states "All members of the Compositae belong to

the embryogenic family of Senecio vulgaris. Further confirmation of the homogeneity of the Compositae came from the extensive study of Vernin (1952) on the development of embryo in a large number of genera and species and by the observations of Mestre (1957), Maheshwari and Roy (1952) and Venkateswarlu and Maheshwari Devi (1955a,b)*. Morphologically also the family is homogenous in showing involucre head inflorescence, inferior ovary with a single basal ovule and introrsely dehiscent anthers which are more or less connate (or at least connivent) around the style, which grows through the anther tube and pushes the pollen out into the open. The unity of Compositae can be cited on numerous bases and continues to be emphasized, most notably and recently by Fairbrothers et. al. (1975), who have found sesquiterpine lactones throughout the family.

Thus morphological, phytochemical and embryological evidence lend no support for the views of Link (1829), Bessey (1915), Gunderson (1950) and Britton (see Lawrence, 1951) to split the Compositae into small separate families by raising one or more tribes to the status and rank of separate families.

THE PHYLOGENY OF COMPOSITAE

Compositae is considered as a highly evolved family of Dicotyledons. Three different views exist regarding the

origin of the family. According to one school of taxonomists the family has been derived from the ancestral stock of the Campanulaceae, while the other school derived it from the Dipsacaceous stock. Cronquist (1955, 1968, 1977) consider it had been derived from Rubiaceae.

Based on morphological and anatomical evidence the Campanulaceous and Dipsacaceous origin of the family are discussed below separately along with Rubiaceae and Umbelliferae origin.

1. Campanulaceous Origin

Delpino (1871) based on his work on Absinthium, regarded that the Compositae is originated from Campanulaceae through Lobelioideae. Wettstein (1901-1908), Hallier (1905), Lotsey (1911), Rendle (1925) and Pulle (1937) also favored the Campanulaceous origin of Compositae.

Hutchinson in his earlier classification (1926) favored the Dipsacaceous relationship of Compositae and considered that the Order Asterales is polyphyletic in origin. In this connection it may be well to quote Hutchinson (1926) who says "(Asterales) is a polyphyletic group probably derived from several lower groups including the Umbellifloreae, Rubiales and Campanales." However, in the later years (1959, 1969, 1973) he favored the Campanulaceous origin and says "Campanulaceae seem to be the most likely

stock pointing to the evolution of that huge and wonderful family Asteraceae (Compositae) though the latter may be in small part polyphyletic". All the above systematists based their views largely on the evidence derived from the external morphology of the flower.

Kirchner (1897) based on biological studies observed close resemblances between the Campanulaceae and Compositae flower. In both the cases the flowers are markedly protandrous and show adaptation for self pollination.

Wernham (1912) based on the type of the inflorescence emphasized that Compositae is more closely related to Campanulaceae rather than to Dipsacaceae. According to him Rubiaceae, Caprifoliaceae, Valerianaceae and Dipsacaceae are characterised by an umbelliform inflorescence in which cymose branching tends to bring the flowers to one level, whereas Campanulaceae, Calyceraceae, Goodeniaceae, Stylidaceae and Compositae show a racemose type of branching. Philipson (1953) who studied the inflorescence of these families supported Wernham (op. cit.).

Solereder (1885) based on anatomical characters like the presence of inulin and laticiferous vessels expressed the opinion that Campanulaceae show resemblances to Compositae, especially to Cichoreae where laticiferous vessels are present.

Similarly based on cytological investigations Mehra

(1977) is of the opinion that Compositae are evolved from a plexes of forms grouped under Campanulaceae.

Small (1919) based on embryological characters like the occurrence of antipodal haustoria and presence of endothelium in Campanula americana, C. rotundifolia and Lobelia inflata of Campanulaceae and in many members of Compositae came to the conclusion that Compositae has its origin from Lobelioideae of Campanulaceae.

Further Rosen (1946, 1949) traced the origin of the Compositae from Lobeliaceae and Subramanyam (1951) stated that the families Goodeniaceae, Stylidaceae and Brunoniaceae have originated from the Lobeliaceae and these in their turn gave rise to the highly specialised family Compositae. Further he states "there is both taxonomical and embryological evidence in support of this".

From the table II it is clear that Campanulaceae and Compositae, though share some morphological and embryological features, they differ from each other in a number of major characters and hence the derivation of Compositae from Lobelioideae of Campanulaceae does not seem to be justified. This view was also expressed earlier by Schnarf (1929) and according Compositae are characterised by the presence of syngonesious anthers, periplasmodial anther tapetum and 3-nucleate pollen

grains. On the other hand Campanulales (Campanulaceae and Goodeniaceae) are characterised by the presence of glandular tapetum and Cellular type of endosperm with both micropylar and chalazal haustoria. Thus Schnarf (1929) on embryological grounds did not favour the derivation of Compositae from Campanulaceae.

Cr te (1951) also on the basis of endosperm and embryo development came to the conclusion that there is no possibility to derive Compositae from Campanulaceae and Lobelioideae.

Desai (1982) on the basis of morphological and embryological data said that there is no close relationship between Compositae and Campanulaceae.

2. Dipsacaceous Origin

Lindley (1846) recognised that the family Compositae is more closely related to Calyceraceae and Dipsacaceae rather than to Campanulaceae. Bentham (1873) in his masterly and classical essay on the Compositae discussed the origin of the family and concluded that Compositae is derived from Dipsacales complex. Bessey (1915) also favoured Dipsacales complex as the more likely ancestors of Compositae, rather than Campanulales.

Carlquist (1966) based on extensive anatomical studies concluded that Compositae is primitively woody and the herbaceous are derived. According to him as Campanulales also

consists mostly herbaceous plants with alternate leaves there is no likelihood of them being ancestors to Compositae. However, he believed that only Dipsacaceae is the nearest ancestor of Compositae. Carlquist (1976) is also of the opinion that trichome types like those of Asteraceae (uniseriate non-glandular plus one or more glandular types) occur in Dipsacaceae and Valerianaceae while the families Calyceraceae and Campanulaceae lack glandular hairs.

Raven (1975) reported that $X=9$ is the basic number of Hydrophyllaceae and Dipsacaceae and he claims this number as basic to Compositae as well.

Based on the course of the vascular strands of the stem Vuillemin (1884) concluded that Dipsacaceae, Valerianaceae and Caprifoliaceae show resemblances to the ancestors of Compositae. Thus he favoured Dipsacaceous origin of Compositae.

Sinnot (1914) who emphasized the systematic value of the nodal anatomy observed unilacunar node in Campanulaceae and trilacunar node in Goodeniaceae and Compositae. Thus based on nodal anatomy he favoured the Dipsacaceous ancestry of Compositae. In this connection he states "In this order (the Campanulatae) the Campanulaceae are entirely unilacunar. The Goodeniaceae and Compositae, however, are trilacunar or rather in rare cases multilacunar. The theory so generally held and maintained in the recent classifica-

tions of Engler and Hallier that the Compositae have been derived from Campanulaceae or their near allies therefore receives no support from the nodal anatomy for if our general hypothesis as to the origin of the different types of nodal structure in the Angiosperms is correct we should certainly not expect the trilacunar condition of the Compositae to have been derived from the unilacunar (and hence reduced) one which characterises Campanulaceae or Caprifoliaceae for the ancestors of the Compositae.

Vernin (1952) based on the type of endosperm and embryo development considered that Dipsacaceae, Valerianaceae and Calyceraceae show close resemblances to Compositae. Schurhoff (1926), Poddubnaja-Arnoldi (1933) also on embryological grounds concluded that the family Compositae show close resemblances to the families Dipsacaceae and Valerianaceae.

Desai (1982) favoured on embryological grounds a Dipsacaceous origin of Compositae as these two families show a large number of common characters.

3. Rubiaceous origin

Cronquist (1955, 1968, 1977), believes that the Rubiaceae rather than the Campanulaceae has many characters necessary for it to be a near ancestor of the Compositae. Yet, Rubiaceae is too far advanced to be considered ancestors of the Compositae. This family could have undergone

similar changes as it developed from a common ancestral stock (Leppik, 1977). Further evidence is presented by Koch (1930), Leonhardt (1949), Zohary (1950) Augier and Merac (1951), Takhtajan (1969) and Polyakov (1967). According to Hutchinson (1948) the guard cells and stomata in the family Rubiaceae are surrounded by specialised epidermal cells, while in Compositae they are surrounded by ordinary epidermal cells. The Dipsacaceae and Valerianaceae however, commonly have a stomatal apparatus similar to that of Compositae.

Embryologically the family Rubiaceae differs from Compositae in having glandular anther tapetum, anatropous to hemianatropous ovule, poor development of nucellus, presence of megaspore haustoria, ephemeral antipodal cells, Solanad type of embryo development and occurrence of suspensor haustoria. Morphologically the Rubiaceae are characterised by the entire, opposite leaves with stipules which are absent in Compositae. Further, as pointed out by Mabry and Bohlman (1977), chemical data do not support a relationship of the Compositae to Rubiaceae, ancestors from which Cronquist (*op. cit.*) would derive the family. These reports dispel any relation between the families Rubiaceae and Compositae.

4. Umbelliferae origin

Hegnauer (1977) considering only chemical data, tends to favour the origin of Compositae from Umbelliferae

due to the presence of similar polyacetylenes and sesquiterpene lactones. This is also essentially the view of Mabry and Bohlman (1977), who summarised the various chemical reports. Further as pointed out by the latter, chemical data do not support a relationship of the Compositae to either Calyceraceae, the family considered by some to be the most closely related on morphological grounds (cf. Bentham, 1873; Turner, 1977) or to the Rubiaceae, ancestors from which Cronquist (1977) would derive the family. The families Compositae and Umbelliferae have similar polyacetylenes and sesquiterpene lactones.

Embryologically the family Umbelliferae differs from Compositae in having a glandular anther tapetum, ovule which some times pseudocrassinucellar (cf. Foeniculum vulgare), embryogeny of the Solanad type and the occurrence of a long suspensor.

CONCLUSION

From the embryological studies by the author and also from the previous reports (See Table II) it is observed that the family Compositae differs from the Campanulaceae, Goodeniaceae and Stylidaceae in a number of embryological features such as the presence of a single row of archesporial cells in the anther lobe, periplasmodial anther tapetum, spinous exine of the pollen grains, well developed

integumentary tapetum, anomalies in the development of the embryo sac in certain genera, variation in the behaviour of the antipodal cells, persistent antipodal cells, absence of endosperm haustoria and Senecio variation of Asterad type of embryo development.

Morphologically also Compositae differs from Campanulaceae in the presence of opposite or alternate leaves, characteristic head inflorescence, presence of calyx in the form of a pappus, syngenesious condition of the anthers, bicarpellary unilocular ovary with a single ovule, the fruit is an achene. While Campanulaceae is characterized by herbaceous habit, alternate leaves, the inflorescence which is a spike or a head, ovary two to three locular with numerous ovules on axile placentation, stamens free or united and fruit is a berry.

However, the family Compositae shows some resemblances in its embryological features to Dipsacaceae. In these families the anther is tetrasporangiate, the development of the anther wall is of the Dicotyledonous type, the pollen grains are 3-celled, the ovule is anatropous unitegmic and tenuinucellate, the antipodal cells are persistent, the endosperm development is of the Cellular type (some times Nuclear in Compositae). In the development of the embryo also the two families show resemblances to each other.

In the morphological features also the family Compositae shows resemblances to Dipsacaceae in the presence of heads surrounded by involucre of bracts, calyx represented by pappus, ovary unilocular with a single ovule and fruit is an achene.

Evidence from morphological, anatomical and embryological data discussed here are in favour of the Dipsacaceous ancestry of Compositae.