VI. PHYLOGENETIC AND SYSTEMATIC CONSIDERATION OF THE TRIBE

AN ANALYSIS
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HELIANTHEAE - AN ANALYSIS

SUBTRIBE: LAGASCEAE

The representative taxa of the subtribe is *Lagascea mollis* Cav.. There is considerable disagreement regarding the systematic position of *Lagascea* Cav.. Bentham, 1873; Bentham and Hooker, 1876; Hoffmann, 1890 have given a sub tribe status for the *Lagascea* Cav.. Stuessy (1973) reduced this subtribe to a synonym, placing *Lagascea* Cav. in Verbesininae. Robinson (1981) placed it along with other members of the subtribe Helianthinae. According to Robinson (I.c.), the Helianthinae is one of the most concisely characterised subtribes, having similar morphological characters such as single stigmatic surfaces on the style branches of the disc flowers, ducts outside veins in the styles, and striations in the walls of the achenes. Also, the resin in the ducts is yellowish in all members.

The present investigation on fruit morphology and palynology supports the views of Robinson (I.c.). The achene is epappose and its wall is striate as in the typical taxa *Helianthus* L.. Exine wall is granulate and general pollen characters are similar to those of the Helianthinae.
SUBTRIBE: MELAMPODIEAE

A perusal of the classical (Lessing, 1832; De Candolle, 1836; Bentham, 1873; Bentham & Hooker, 1876; Hoffmann, 1890) and the latest revised classifications (Stuessy, 1977; Robinson, 1981) reveals that the Melampodieae is assigned a primitive position. Stuessy (l.c.) considered it as the most primitive subtribe and it may be pointed out that some taxa of this subtribe reported in the present study (Melampodium paludosum B.H.K. and Acanthospermum hispidum DC.) possess comparatively low palisade ratio values and primitive characters regarding the pollen morphology and achene morphology. These taxa have longer columns and in Melampodium L. the basal cushion in pollen is inconspicuous. Achenes are medium sized in both the taxa. The above mentioned palynological characters apparently support the assignment of primitive position of this subtribe. It may be noted that evidences from biochemical studies (Stuessy, 1979) are also in favour of this in as much as both Acanthospermum Shrank. and Melampodium L. contain predominantly primitive phenolic groups. Cytological studies (Abraham and Mathew, 1988) also support the primitiveness of the subtribe, since these two taxa possess unspecialised karyotypes (2A).

SUBTRIBE: AMBROSIEAE

The relationship of Parthenium hysterophorus L. to Ambrosiinae was recognized by Bentham & Hooker (l.c.) and Hoffmann (l.c.). But the two genera were placed technically in
the adjacent part of the subtribe Melampodieae in the above mentioned classifications. This was based primarily on the presence of fused anthers and achene-palea complexes in the two genera. In formulating the revised classification of Heliantheae, Stuessy, (l.c.) and Robinson (l.c.) have effected some intra and inter-tribal transfer of genera. One obvious intra-tribal transfer concerns the removal of the genus Parthenium L. from Bentham & Hooker's and Hoffmann's Melampodiinae to the Ambrosiinae in latest classifications. The morphology and chemistry of Parthenium L. have been assigned close affinity to the Ambrosiinae (Stuessy, l.c.). Cytological evidence shows that both Xanthium L. and Parthenium L. have the same chromosome constitution, X = 18 (Abraham and Mathew, 1988; Stuessy l.c.).

In the present investigation, palisade ratio values and stomatal index values are found to be more or less similar. Regarding pollen morphology, column is very short in Parthenium, and in Xanthium L. column is reduced and surface appears scabrate. The evidences from various parameters together with the present findings show that there are more similarities rather than differences in characters existing between Xanthium L. and Parthenium L.

This subtribe is given an advanced status by Cassini, 1829; Bentham and Hooker, l.c; Hoffmann, l.c. and Stuessy l.c. But Robinson, (l.c.) considers the tribe as primitive.
The present study on palisade ratio and palynology supports the placement in an advanced position. Scabrate type of exine wall is not found elsewhere in the Heliantheae as in Xanthium L. In Parthenium L. column is very short and basal cushion is very conspicuous. Long elongate spines with exposed spine column base may be considered to precede those with concealed spine column base and with partially and fully developed basal cushions. (Nair & Lawrence, 1985). Comparatively low palisade ratio values are observed in Ambrosieae. The present findings agree with the advanced placement of Ambrosieae.

SUBTRIBE: ZINNIEAE

The subtribe is represented by Zinnia elegans Jacq. and Zinnia linearis Benth. Bentham and Hooker l.c., Hoffmann l.c. and Stuessy l.c. placed these taxa in the subtribe Zinnieae. But Robinson, l.c. placed the taxa in the subtribe Ecliptinae. The taxa coming under this subtribe share certain common characters. The achenes are with persistent corollas, pappus of one to three awns or absent and chromosome number based primarily on X = 11 and 14 (Stuessy, l.c.).

Achenes with persistent corollas are not seen elsewhere in the subtribe. Stomatal index values are similar in these two taxa. Vessels with tails are uncommon in Zinnia L. But tailed vessels are frequently observed in Eclipta L. and Wedelia Jacq. Thus, the above mentioned aspects of the tribe are in confirmity with the views of Bentham & Hooker (l.c.) and Stuessy (l.c.).
SUBTRIBE: VERBESINEAE

Bentham and Hooker's Verbesineae is found to be heterogenous. The Verbesineae of Bentham & Hooker (l.c.) is subdivided into 3 subtribes: Helianthinae proper, verbesininae proper and Ecliptinae proper (Stuessy, l.c.). The taxa such as Blainvillea L., Eclipta L., Eleutheranthera Poit., Wedelia Jacq. and Synedrella Gaertn., are placed in the subtribe Ecliptinae. The present palynological, achene morphological, and leaf architectural studies show some sort of uniqueness in these taxa. The ray achenes when fertile, characteristically are trigonous to broadly obcompressed. Achenes of all these are epappose except Synedrella Gaertn. SEM studies of inter spinal area reveal that the surface is granulate in these taxa except in Synedrella Gaertn., where it is punctate. The 2-3 awned pappus that is found in Synedrella Gaertn. is believed to have evolved independently of similar pappus types that occur in the subtribe Coreopsidiae. In Bentham & Hooker's (l.c.) classification Synedrella Gaertn. is placed in the subtribe, Coreopsidiae. But leaf architectural studies show that major venation pattern of the taxa belonging to Coreopsidiae is of Semicraspedodromous type except that of Synedrella Gaertn., where it is Acrodromous as in the members of Robinson's (l.c.) and Stuessy's (l.c.) Ecliptinae. Chromosome numbers of the taxa belonging to Ecliptinae are primarily based on X = 15 and 16 (Stuessy, l.c.).
The taxa such as *Helianthus* L. and *Tithonia* Desf., are included in the subtribe *Helianthinae* (Stuessy, l.c., Robinson, l.c.). The name "Verbesineae" which was used for the typical subtribe of Heliantheae by Bentham & Hooker (l.c.) was renamed as *Helianthinae* (Stuessy, l.c.). This was most welcomed by Robinson (l.c.). General morphological characters like the presence of solitary heads, neuter ray florets and alternate and/or basal leaves support the placement of these taxa (Robinson, l.c.).

The present findings agree with that of Stuessy, (l.c.) and Robinson (l.c.). Achene surface is striate, exine wall is granulate and major venation is Acrodromous type. Cytological evidences prove that chromosome numbers are based primarily on \( X = 17 \) and \( 18 \) (Stuessy, l.c.).

Stuessy (l.c.) reduced the subtribe Lagasceae to synonymy and placed *Lagascea* Cav. in his Verbesininae. Robinson (l.c.) placed it along with other Helianthinae (subtribe) members. Achenes of *Lagascea* Cav. is similar to *Helianthus* L. in having epappose fruits. Pollen characters are also similar to that of *Helianthinae*.

In Stuessy's (l.c.) treatment the taxa *Spilanthes* Jacq. has been removed from Verbesininae to Galinsoginae. According to Robinson (l.c.) this transfer was inexplicable. The present seed morphological and palynological aspects of the *Spilanthes* Jacq. are in conformity with the views of Robinson (l.c.). 2-3 owned pappus is noticed in *Spilanthes* Jacq.. But in *Galinsoga* Cav.
pappus is paleaceous and in *Tridax* L. it is setose. Pollen characters are also dissimilar to that of Calinsoginae. That will be discussed later.

In Bentham and Hooker's (*I.c.*) classification *Rudbeckia* L. comes under the subtribe Verbesineae and Stuessy (*I.c.*) included this taxa in his subtribe Helianthinae, but Robinson (*I.c.*) has given it a subtribal status and created a new subtribe Rudbeckinae. The present study on achene morphology, and palynology, supports the former view since the achenes are epappose and striate as that of other Helianthinae members. Pollen with long column is noticed as in the members of Helianthinae.

**SUBTRIBE : COREOPSISIDEAE**

Most of the taxa of Bentham and Hooker's Coreopsisideae are included in the subtribe Coreopsidinae by Stuessy (*I.c.*) and Robinson (*I.c.*) except *Synedrella* Gaertn. and *Guizotia* Cass. Robinson (*I.c.*) and Stuessy (*I.c.*) included *Synedrella* Gaertn. in Ecliptinae. Robinson (*I.c.*) placed *Guizotia* Cass. in the subtribe Milleriinae.

Leaf architectural studies reveal that the major venation pattern is Semicraspedodromous except in *Synedrella* Gaertn. where it is Acrodromous as in Ecliptinae.

This subtribe is given advanced position by most of the workers namely, Bentham and Hooker (*I.c.*), Hoffmann (*I.c.*).
Stuessy (l.c.) and Robinson (l.c.). The present findings are in support of these views in having high palisade ratio values. Most of the taxa possess short, broad and tail-less, vessels as in Cosmos Cav. and Dahlia Cav.. Comparatively longer achenes are noticed in taxa belonging to this subtribe. The position of Guizotia Cass. is less certain. The genus has been placed in the subtribe, Coreopsideae in the traditional systems and by Stuessy (l.c.), Baagoe (1974) transferred the genus to the Verbesininae, but later agreed with Stuessy (Baagoe, 1977). Robinson's placement of Guizotia Cass. in the subtribe Milleriinae, however, is based mostly on the close approximation of technical characters and is made in spite of differences in habit, the strictly yellow rather than whitish flower colour and the coloured resin in the corolla ducts.

Achene morphology and leaf architecture are similar to other Coreopsideae members. Achene is epappose as in typical member Coreopsis Cav.. Major venation is semicraspedodromous type. Intramarginal vein as in other taxa of Coreopsideae is noticed in Guizotia Cass.. These findings support the placement of this taxa along with other Coreopsideae members.

**SUBTRIBE: GALINSOGEAE**

This subtribe is given advanced position in classical systems (De Candolle, 1836); Bentham (l.c.); Bentham and Hooker (l.c.); Hoffmann (1890) and revised systems (Stuessy, 1977;
Robinson, 1981). The representative members of the tribe *Tridax* L. and *Calinsoga* Ruiz. & Pav. show advanced palynological and achene morphological characters. In both the taxa, achenes are small sized. In *Calinsoga* Ruiz. & Pav. highly specialised paleaceous type of pappus is observed. In *Tridax* L. pappus is setose. In both the taxa, achenes are hairy. Corner (1976) indicates that hairs in the surface of seeds is a phyletic problem and has to be interpreted differently in each family.

Regarding the pollen, conspicuous basal cushion and short column are observed in *Calinsoga* Ruiz. & Pav.. In *Tridax* L. eventhough basal cushion is inconspicuous, columns are short. Hence, from the present study the placement of this subtribe at an advanced position may be justifiable. Cytological evidences (Stuessy, l.c., Abraham and Mathew, l.c.) also are in favour of the advanced placement of the tribe.