14. General Discussion and Cladistics of the families

The distribution of flavonoids and other chemical markers in the families screened is presented in Table 14.1. All the 18 families contained flavonoids in their leaves. Flavonols form the dominant pigments in the Sapindaceae, Hippocastanaceae, Aceraceae, Melianthaceae, Staphyleaceae, Anacardiaceae, Burseraceae, Meliaceae, Zygophyllaceae, Geraniaceae, Balsaminaceae, Celastraceae, Rhamnaceae, Vitaceae and Leeaceae. Flavonols occurred with their methoxy derivatives in most of these families. Excepting for the Balsaminaceae and Celastraceae whera kaempferol is frequent, quercetin and its derivatives predominâte. Myricetin occured in high frequency in Anacardiaceae and Leeaceae while it is found in a few members (20 % to 30 %) of the Burseraceae, Meliaceae and Rhamnaceae. In Rutaceae, Simaroubaceae, Celastraceae and Vitaceae they are reported in less than 10 % of the plants. The families Sapindaceae, Aceraceae, Hippocastanaceae, Melianthaceae, Staphyleaceae, Zygophyllaceae, Geraniaceae, Oxalidaceae and Balsaminaceae are free of myricetin. Prenylated flavonols are seen in the Rutaceae and in the genus **Dodonea** of the Sapindaceae. Similarly, acylated flavonols are seen in the Zygophyllaceae and Rhamnaceae. The Rutaceae, Anacardiaceae, Geraniaceae and Celastraceae contain 5-deoxy flavonols as minor components. Flavones form the dominant pigments in the Aceraceae, Rutaceae, Simaroubaceae and Oxalidaceae, though they are seen in a few members of the other families except Hippocastanaceae, Melianthaceae, Staphyleaceae, Geraniaceae, Balsaminaceae and Leeaceae. In all these families apigenin is the most common flavone. Luteolin is compartively rare. Methoxylation is common but 6-OMe scutellarein occurs only in the Rhamnaceae. Glycoflavones are frequent in the Oxalidaceae, Rutaceae, Simaroubaceae and to some extent in the Sapindaceae and Vitaceae. They are reported from very few members of the Rhamnaceae. Aurones in the leaves are seen in some members of the Geraniaceae and Oxalidaceae. Proanthocyanidins which are abundant in other families are not seen in the Staphyleaceae, Zygophyllaceae, Geraniaceae, Oxalidaceae and Balsaminaceae, though these compounds are comparatively rare in the Rutaceae, Meliaceae and Simaroubaceae. Coumarins are common in the Rutaceae and rare in the Meliaceae and in the Zygophyllaceae. Quinones are seen in the Simaroubaceae, Zygophyllaceae, Balsaminaceae, Rhamnaceae and Celastraceae. However, in the Celastraceae they are triterpene derivatives (quinone - methides). Syringic acid is found to be absent in the Staphyleaceae, Geraniaceae and Balsaminaceae. Both hydrolysable and condensed tannins occur in a number of families while Geraniaceae have only hydrolysable tannins and Celastraceae, Vitaceae and Rhamnaceae have condensed tannins. Bitter principles which are the derived triterpenoids are seen in the Rutaceae, Meliaceae and Simaroubaceae. Saponins are located in the Sapindaceae, Zygophyllaceae, and Rhamnaceae. Alkaloids are obtained from the Rutaceae, Meliaceae, Simaroubaceae, Zygophyllaceae, Rhamnaceae and Celastraceae. The first four contain quinazolines while maytansinoids are located in the Celastraceae and peptide alkaloids in the Rhamnaceae and Celastraceae.

Evidently the most distinguishing are the families Rutaceae, Meliaceae, Simaroubaceae and Zygophyllaceae which form a group specialising in nortriterpenoid bitter principles. These families have quinazolines in common and exhibit the tendency to methoxylate flavones and prenylate flavonoids and constitute the order Rutales. The first three families are acclaimed to be forming a closely knit group. The Zygophyllaceae which are usually placed in the Geraniales/Sapindales, are chemically very similar to the other three families mentioned above and therefore, the inclusion of this family in the Rutales seems to be logical. The Rutales appear to have evolved from the Burseraceae which elaborate primitive type of flavonoids (myricetin, hydroxyflavonols and proanthocyanidins) and possess triterpenes of euphane/tirucallane series such as sapelin A & B, which form the basic compounds in the limonoid biosynthesis (Khalid, 1983.). The Rutaceae form the climax group producing a wide range of secondary metabolites (flavones, coumarins, alkaloids, terpenoids and lignans). The quassinoids of the Simaroubaceae seem to have evolved from the ursane series of triterpenoids of the Burseraceae. The Simaroubaceae eliminate myricetin and proanthocyanidins and introduce flavones and glycoflavones as well as methoxylate flavonols. It retains the hydrolysable tannins. The Meliaceae would have evolved as a line separating from the base of the Rutaceae. This 'family is characterised by the highly methoxylated flavonols and sometimes loses the flavonoid skeleton altogether (**Aglaia** and **Dysoxylum**). The Zygophyllaceae with their triterpenoid saponins (steroidal), lignans and alkaloids also can be considered evolved from the Burseraceae. Since all these families are derived from the Burseraceae, this family also is included in the Rutales.

The Anacardiaceae, which are considered as the closest ally of the Burseraceae appear to be another line of evolution from the Burseraceae specialising in lipidic phenols and retaining the biflavones and tannins. This family has diverged from the Rutalean line of specialisation so much that Harborne (1983) rules out any possibility of relationships between the Rutaceae and the Anacardiaceae.

The Sapindaceae and their allies form another group, the Sapindales, characterised by a metabolic virtuosity as diverse as that of the Rutales. These families are credited with the advanced unisexuality and diverse type of chemical compounds. The Sapindaceae are peculiar in having saponins, prenylated flavonols and cyanolipids. The Aceraceae elaborating various oligosaccharides and the Hippocastanaceae with cyclopropane aminoacids are very much similar to the Sapindaceae in other chemical characters and thus do not deserve any separate family status. The Melianthaceae with their flavonols and tannins remain close to the Sapindaceae. The Staphyleaceae also appear to be close to the Sapindaceae - Melianthaceae group, but further comments are reserved because of the poor representation of this family in the present work. The Sapindales and Rutales are similar to each other in exhibiting similar type of flavonoid pattern (flavones, glycoflavones, flavonols, deoxy_/prenylated flavonoids) and triterpenes. This corroborates well with the morphological similarities exhibited by these orders.

The affinities existing among the Geraniaceae, Oxalidaceae and Balsaminaceae are discussed in Charpter 10. The Geraniaceae with their gallotannins, flavonols and volatile oils are at a relatively low level of chemical evolution. The Oxalidaceae, on the other hand, resorted to stable flavones and glycoflavones and eliminated tannins from their leaves. These characters would have helped this family to thrive on a hot climate. Both these families produce aurones in some members. The family Balsaminaceae is slightly distinct in producing quinones but is similar to the Geraniaceae in containing flavonols as the major phenolic pigments and to the Oxalidaceae in synthesising glycoflavones. It also attempts at a quantitative decrease in the flavonols, which is an advanced character. The quinones and zygomorphy in flowers appear to support the concept of a separate order Balsaminales, but more data are needed to arrive at a final decision. These three families forming the Geraniales-apparantly originated from the primitive members of the Rutales (Sapindales of Cronquist).

The Celastraceae with their special terpenoids, quinone–methides and alkaloids (maytansinoids) form another line of chemical evolution. The presence of guttapercha and dulcitol adds to the distinct nature of this family. The seperate status of **Hippocratea** and **Salacia** as independent families is not favoured by the chemical data. The Celastraceae form the order Celastrales.

Similarly the Rhamnaceae form another line of specialisation and thus constitute the order Rhamnales. This family produces peptide alkaloids, quinones and biflavones. These properties bring the Rhamnales near to the Euphorbiales.

The Leeaceae, in containing myricetin, gallic acid and higher frequency of methoxylated flavonols, are chemically isolated from the Vitaceae and therefore, the family status of this taxon is chemically valid. The Vitaceae are flavonol rich and are very different from the Rhamnaceae with which they are grouped with. None of the specialised compounds of the Rhamnaceae are seen in the Vitaceae or Leeaceae. These two families achieved great advancements in their morphological features such as the sympodium, climbing habit and seed characters. These characters validate the creation of the Vitidales to circumscribe these two families.

The taxonomic groupings arrived at by the present investigation are as follows :

1. **Rutales :**
   Burseraceae, Rutaceae, Peganaceae, Meliaceae, Simaroubaceae and Zygophyllaceae.

2. **Sapindales :**
   Sapindaceae (incl. Aceraceae, Hippocastanacee), Melianthaceae and Staphyleaceae (?). Position of the Anacardiaceae is uncertain. This family is intermediate between the Rutales and the Sapindales and therefore, may be kept in any of the these orders, but as a separate suborder.

3. **Geraniales :**
Geraniaceae and Oxalidaceae (incl. Averrhoaceae)

4. **Balsaminales :**
Balsaminaceae

5. **Celastrales :**
Celastraceae

6. **Rhamnales :**
Rhamnaceae

7. **Vitidales :**
Vitaceae and Leeaceae

The groupings and the phylogeny of the above taxa are graphically represented in Fig. 14.1.

CLADISTIC ANALYSIS OF THE FAMILIES :

All the 18 families are subjected to a cladistic analysis, using characters selected from morphology, anatomy, palynology, embryology and phytochemistry. Most of the characters selected are already explained in the preceding chapters. The additional characters selected are explained below :

Chapter 10 : Anatropous ovule present = 0, Anatropous ovule absent =1.

Anatropous ovule is the most common type and is characteristic of many taxa especially the more primitive groups of plants such as Ranales, Helobiales etc. All other forms of ovules are derived from this.

Character 13 : Wood non-storied = 0, Wood storied = 1.

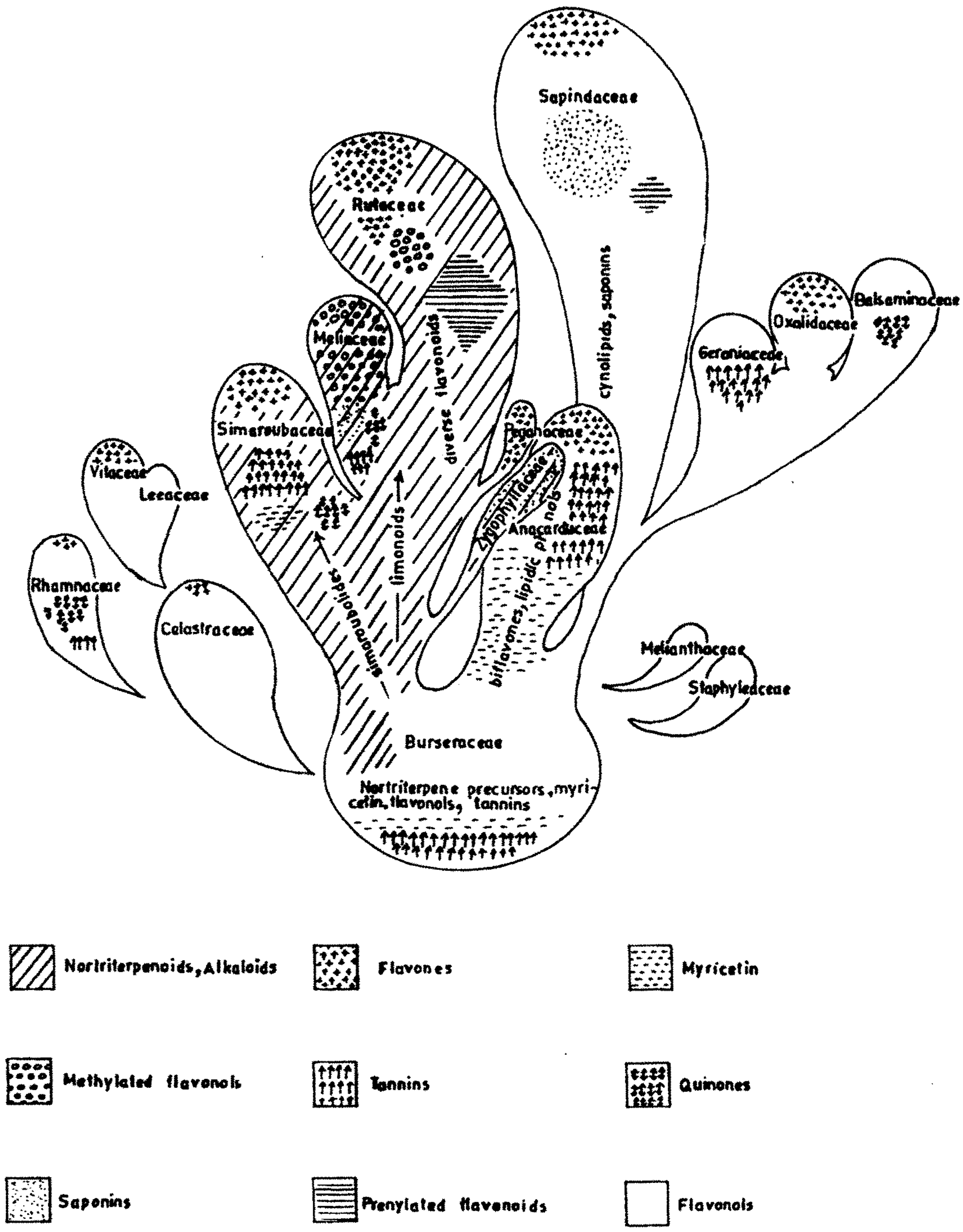

Fig. 14.1 The groupings and phylogeny of the Sapindales and related taxa

Storied structure, according to Chalk (1983), is a specialized feature associated with the most advanced group of cambial initials.

Character 14 : Wood diffuse-porous = 0, Wood ring-porous = 1.

Gilbert (1940) opines that the ring-porous type of vessel arrangement represents an evolutionary advancement from the diffuse distribution and that this feature is correlated well with other advanced anatomical features.

Character 15 : Wood parenchyma
Apotracheal = 0, Paratracheal = 1.

One of the principal trends of specialisation in axial parenchyma is from aportracheal to paratracheal. Therefore, the paratracheal condition is considered apomorphic.

Character 16 : Rays multiseriate = 0, Rays uniseriate = 1.

The most primitive type of ray tissue consists of a combination of multiseriate rays with high uniseriate wings. Uniseriate rays are evolved from this and the elimination of rays is considered to be the most advanced feature.

Character 17 : Pits bordered = 0, pits simple = 1.

The intervascular pitting is bordered in primitive woods such as conifers and early angiosperms. This is replaced by simple pits in advanced angiosperms.

Character 18 : Tracheid simple = 0, Fibre tracheids or libriform fibres = 1.

With increasing specialisation of the vessel elements the function of water transport became far less important in other kinds of cells associated, which in turn got modified for the additional mechanical support. Thus the fibre tracheids and ultimately libriform wood fibres are evolved.

Character 19 : Perforation plate scalariform = 0, Perforation plate simple = 1.

The wood of primitive angiosperms are characterised by scalariform perforation plates. During evolution these plates are replaced by the single circular or oval pore, that constitutes the simple perforation plate.

Character 20 : Embryo development Polygonum type = 0, Other types = 1.

The monosporic 8-nucleate (Polygonum) embryo sac type is considered to be primitive because (1) it is the most common pattern among the angiosperms and (2) largest number of divisions are involved in its formation and all other types of embryo sacs are evolved by reduction in gametophyte size and development.

Character 21 : Crassinucellate ovule = 0, Tenuinucellate ovule = 1.

The crassinucellate ovule is always associated with the primitive angiosperms while the tenuinucellate ovule is frequent in advanced angiosperms.

Character 22 : Copious endosperm = 0, Scanty endosperm = 1.

The current general assumption is that the primitive seed had an undifferentiated small embryo embedded in abundant endosperm. Therefore, a seed with copious endosperm is a primitive character.

Character 23 : pollen 3-colpate = 0, Pollen 3-colporate = 1.

The evolution of pollen took place from a primitive monocolpate to tricolpate and further to tricolporate and multiporate or acolpate conditions.

Character 24 : Pollen 2-celled = 0, Pollen 3-celled = 1.

The 2-celled condition of the pollen at the time of anther dehiscence is considered as primitive while the 3- or 4-celled condition is an advanced feature.

Character 25 : Exine smooth = 0, Exine ornamented = 1.

The exine of the primitive pollen is relatively unornamented. Therefore, the various ornamentations seen in pollen are considered apomorphic. The characters selected for the analysis are given in Table 14.2.

Results :

The distribution of characters in 18 families and the AD(I) values of these taxa are presented in Table 14.3.

The cladogram depicting the interrelationships and phylogeny of these families is presented in Fig. 14.2. The trunk branches into two clades A & B. The first clade A contains two groups, the first with the Aceraceae, Hippocastanaceae and Sapindaceae and the second clade with the Burseraceae, Simaroubaceae, Rutaceae, Anacardiaceae and Meliaceae. The clade B forks into two branches, one bearing the Staphyleaceae and Melianthaceae and the second branch on further branching carries the Celastraceae, Geraniaceae, Balsaminaceae, Oxalidaceae and Zygophyllaceae on one side and the Leeaceae, Rhamnaceae and Vitaceae on the other. The Sapindaceae with an AD(I) value of 25 is the most advanced family and the Aceraceae

Table - 14.2

Characters Selected for the Cladistic Analysis of the 18 Families.

Sr. No.	Characters	Plesiomorphic State = 0	Apomorphic State = 1
1.	Habit	Woody trees	Herbaceous
2.	Leaves	Alternate	Opposite
3.	"	Simple	Compound
4.	Flower	Regular	Irregular
5.	"	Bisexual	Polygamous
6.	"	Monoecious	Dioecious
7.	"	pentamerous	Tetramerous
8.	Stamens	Ten	Less than 10
9.	Carpels	Five	Less than 5
10.	Ovules per locule	Two or more	One
11.	Ovules	Anatropous	Others
12.	Fruit	Dehiscent	Indehiscent
13.	Wood	Non-storied	Storied
14.	"	Diffuse-porous	Ring-porous
15.	Wood parenchyma	Apotracheal	Paratracheal
16.	Rays	Multiseriate	uniseriate
17.	Pits	Bordered	Simple
18.	Tracheids	Simple	Fiber tracheid/ Libriform
19.	Perforation	Scalariform	Simple
20.	Embryo	Polygonum	Other types

Table : 14.2 (Contd.)

Sr. No.	Characters	Plesiomorphic State = 0	Apomorphic State = 1
21.	Embryo	Crassinucellate	Tenuinucellate
22.	Endosperm	Copious	Scanty
23.	Pollen	3 - Colpate	3 - Colporate
24.	"	2 - Celled	3 - Celled
25.	Exine	Smooth	Ornamental
26.	Flavones	Absent	Present
27.	"	Hydroxylated	Methoxylated
28.	Glycoflavones	Absent	Present
29.	Biflavones	Absent	Present
30.	Flavonols	Present	Absent
31.	Methoxylation in flavonols	Absent	Present
32.	Prenylated flavonols	Absent	Present
33.	Deoxyflavonols	Absent	Present
34.	Myricetin	Present	Absent
35.	Proanthocyanidins	Present	Absent
36.	Tannins	Present	Absent
37.	Syringic acid	Present	Absent
38.	Nortriterpenoids	Absent	Present
39.	Limonoids/Quassinoids	Absent	Present
40.	Saponins	Absent	Present
41.	Alkaloids	Present	Absent

Table : 14.3 The Distribution of Characters Selected for Cladistic Analysis of 18 Families of the Sapindales and Related Orders

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
apindaceae	0	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1	1	1	1	0	1	0	1	0	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0
Hippocastanaceae	0	1	1	0	0	1	1	1	1	1	1	1	0	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0
Aceraceae	0	1	0	0	1	1	0	1	1	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0
Melianthaceae	1	0	1	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0
Staphyleaceae	0	1	1	0	1	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0
Anacardiaceae	0	0	1	0	1	0	0	1	1	1	0	0	0	0	1	0	0	1	1	0	1	0	1	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0
Burseraceae	0	0	1	0	1	1	1	1	0	0	1	0	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0
Rutaceae	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	1	1	1	1	1	0	1	1
Meliaceae	0	0	1	0	1	1	0	0	1	0	1	1	0	0	1	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	1	0	1	0	1	1
Simaroubaceae	0	0	1	0	1	1	0	0	0	1	1	1	0	0	1	0	0	0	1	0	1	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1	1
Zygophyllaceae	1	1	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	1	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	1	1	1	0	1	0
Geraniaceae	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	0	0	0	1	0	1	1	1	0	1	0	0
Oxaliadeacea	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	1	1	0	1	0	0	1	1	1	1	0	1	1	0	0	1	1	1	0	0	0
Balsaminaceae	1	1	0	1	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	1	0	0	1	1	0	1	0	0
Celastraceae	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	1	0	0	1	1	1	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0
Rhamnaceae	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	0	0	0	1	1	1	0	1	0	1	0	1	1	1	0	1	1	0	1	1	0	0	0	0
Vitaceae	1	0	0	0	1	0	0	1	1	0	0	0	1	1	1	0	1	1	1	0	0	0	1	1	1	1	1	1	0	0	1	0	0	1	0	0	0	0	0
Leeceae	0	0	1	0	0	0	0	1	1	1	0	0	1	1	1	0	0	1	1	0	1	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0

and Melianthaceae [AD(I) value 14] are the most primitive. Most of the families have an advanced score ranging from 17-20 showing that the whole group occupies an advanced level in the evolutionary sequence. The dendrogram (Fig. 14.3) prepared based on the cladogram brings forth a number of groupings of the families. They are the following :

Group-1 : Aceraceae
Hippocastanaceae
Sapindaceae

Group-2 : Burseraceae
Simaroubaceae
Rutaceae
Anacardiaceae
Meliaceae

Group-3 : Staphyleaceae
Melianthaceae

Group-4 : Celastraceae

Group-5 : Geraniaceae,
Balsaminaceae
Oxalidaceae
Zygophyllaceae

Group-6 : Leeaceae
Rhamnaceae
Vitaceae

Discussion :

The cladogram/dendrogram introduces a few new clusters of families as well as reshuffles some of the existing

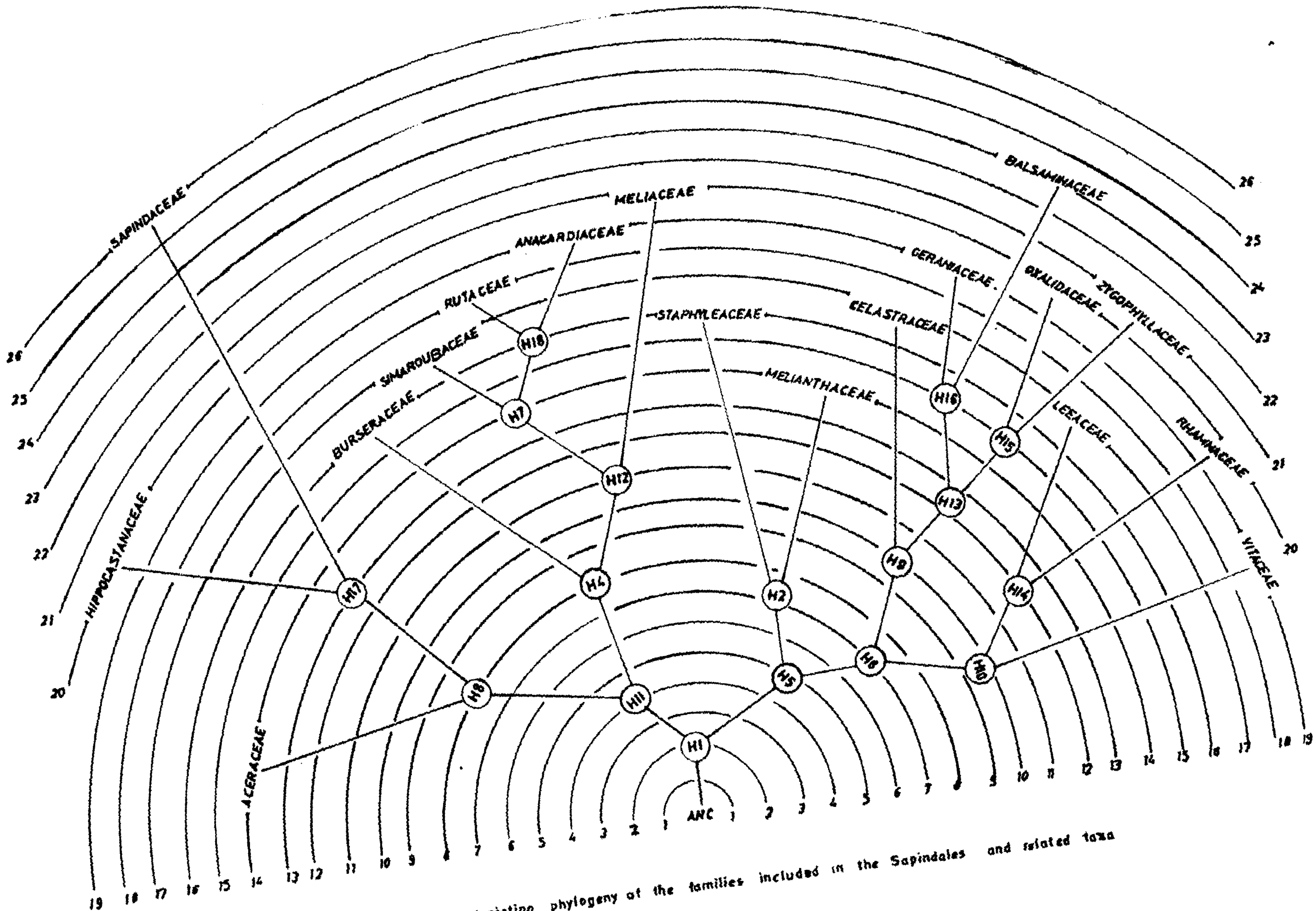

Fig.14.2 Cladogram depicting phylogeny of the families included in the Sapindales and related taxa

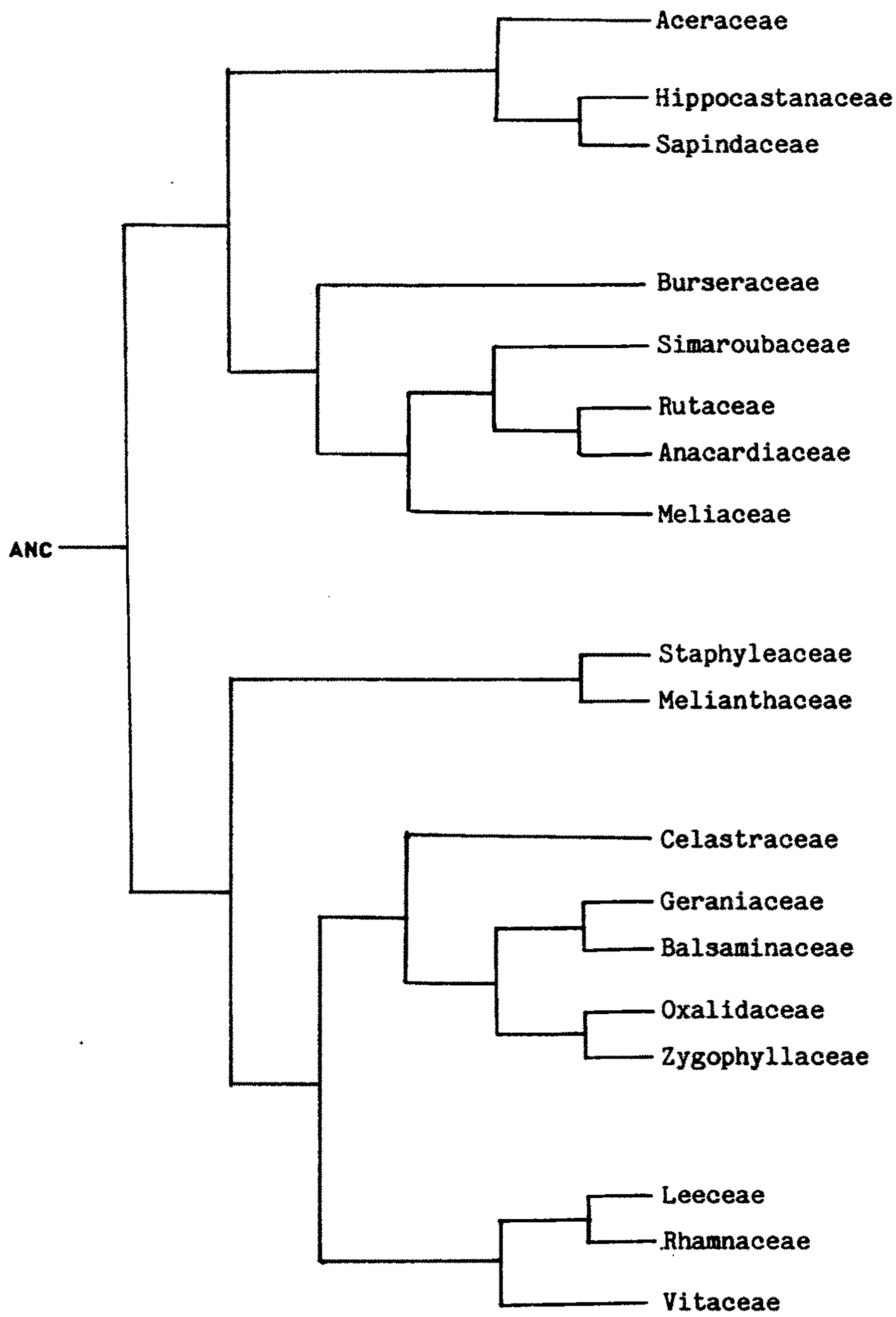

Fig. 14.3 Dendrogram showing interrelationships among the families of the Sapindales and related taxa.

groups. The first group containing the Sapindaceae, Hippocastanaceae and Aceraceae, evidently is the most natural one. Such closeness is in the favour of merging these families into one, the Sapindaceae. This constitutes the Sapindales. The second group corresponding to the Rutales, has the Rutaceae, Anacardiaceae and Simaroubaceae as the core families with the Burseraceae and Meliaceae occupying peripheral positions. Though the Staphyleaceae and Melianthaceae are considered close allies of the Sapindaceae here they orginate from the branch bearing Celastrales and Geraniales. The grouping of these two families may not be due to any close similarity between the two, but because they are apparently misfits in other groups. Tne Celastraceae can be considered constituting the order Celastrales. The Geraniaceae, Balsminaceae, Oxalidaceae and Zygophyllaceae form the Geraniales. The closeness of the Zygophyllaceae to this group than to the Rutales (in which they are grouped at times) is noteworthy. The Leeaceae, Rhamnaceae and Vitaceae form the last group, the Rhamnales.

The grouping presented above does not need any justification. The groups are the results of impartial assessment on the distribution of characters taken from many disciplines. It is also borne in mind that the cladogram may not provide a clear picture on the circumscription of the taxa but gives an insight into the relationships of the various plant groups. The decision on the status of a taxon is almost always subjective. Therefore, the Balsaminaceae and Vitaceae may be considered constituting independent orders which have evolved from the branches containing the Geraniales and the Rhamnales respectively.