CLADISTIC ANALYSIS OF THE TAXA

CHAPTER - V

CLADISTIC ANALYSIS OF THE TAXA

Cladistics is one of the two major efforts in recent decades to formalise taxonomic methods, the other effort being numerical taxonomy. In cladistics the organisms are ranked entirely on the basis of recency of common descent, that is on the basis of sequence of dichotomies in the inferred phylogeny. The resulting dendrogram is similar to that of numerical taxonomy but both are directed towards different ends. A monophyletic group should include all the descendants from the most recent common ancestor and the cases of parallelism, convergence, divergence and hybridisation are not represented in cladistic treatments. The polarity of characters as well as the selection of outgroups are mostly left to the judgement of the taxonomist. Of the many cladograms theoretically possible, the one which is most parsimonious is selected preferably by a computer. Cronquist (1987), commenting on cladism reiterates the need for a restraint on the indiscriminate usage of the method in deducing phylogeny. He suggests exercising a rational consideration in the selection of characters and advises to prepare the cladogram manually on the basis of Wagner's ground plan-divergence method (Wagner, 1980).

In the present study 32 genera of the family Scrophulariaceae as well as 13 families, belonging to the Scrophulariales and the related taxa have been subjected to cladistic treatments using characters taken from morphology and chemistry. Though Wagner's ground plan-divergence method is followed largely, a number of logical modifications are done to produce a more parsimonious tree.

Sixteen characters, taken from morphology and chemistry, have been used for the construction of the cladogram for the for the families of the Scrophulariales and 13 characters for the various genera of the Scrophulariaceae. Polarity of the morphological characters was assessed following Cronquist (1968), Hutchinson (1948) and Takhtajan (1980), whereas for the chemical characters, the known biosynthetic pathways and correlation studies were used. The selected characters and their plesiomorphic and apomorphic status are presented in table XIV & XV. The distribution of these characters in the genera as well as in the various families studied are shown in Table XVI & XVII. An advanced (apomorphic) character was given a score-I, while the primitive (plesiomorphic) character was given in score-0.

Wagner's bulls eye' chart consisting of a number of concentric semicircles having a common base point, was prepared in which each semicircle represented a single evolutionary state. These semicircles were given number 1, 2, 3 etc. The total number of apomorphic characters correspond to the total number of semicircles. The score of the taxon gave the extent of

Table XIV

THE CHARACTERS USED FOR THE CLADISTIC TREATMENT OF THE GENERA OF THE SCROPHULARIACEAE

Sr. No.	Character	Plesiomorphic Score-0	Apomorphic Score -1
1	Arrangement of leaves	Alternate	Opposite
2	Inflorescence	Racemose	Cymose
3	Nature of flower	Regular	Irregular
4	Number of stamens	4-5	2 or less
5	Capsule dehiscence	Septicidal	Loculicidal
6	Parasitic nature	Absent	Present
7	6-OH Flavones	Absent	Present
8	Glycoflavones	Absent	Present
9	Proanthocyanidins	Present	Absent
10	Quinones	Present	Absent
11	Iridoids	Absent	Present
12	Alkaloids	Present	Absent
13	Syringic acid	Present	Absent

Table XV

THE CHARACTERS USED FOR THE CLADISTIC TREATMENTS OF THE FAMILIES BELONGING TO THE SCROPHULARIALES

Sr. No.	Character	Plesiomorphic Score-0	Apomorphic Score-1
1	Habit	Woody	Herbaceous
2	Arrangement of leaves	Alternate	Opposite
3	Type of leaves	Simple	Compound
4	Nature of flower	Regular	Irregular
5	Number of ovules	Unlimited	Limited
6	Placentation	Parietal	Basal
7	Endosperm	Present	Absent
8	Flavonols	Abundance	Rare
9	Flavones	Absent	Present
10	6-OH flavones	Absent	Present
11	Glycoflavones	Absent	Present
12	Proanthocyanidins	Present	Absent
13	Iridoids	Absent	Present
14	Parasitic nature	Absent	Present
15	Tannins	Present	Absent
16	Syringic acid	Present	Absent

advancement that taxon attained and the corresponding semicircle in which it is to be placed. That is for a taxon having a total score of 17 finds a place on the 17th semicircle.

The hypothetical ancestor, having all the plesiomorphic character, formed the ground plan. The construction of cladogram followed the pattern of the formation of dichotomous keys of identification found in a flora. The length of a branch represented the total number of common character of that group. Branching occurred at the point where some members of this group acquired additional advanced characters. From this node two branches diverged one with acquired characters and the other without them. Further branching occurred with the acquisition of more characters. In the case of closely allied taxa; one taxon, say B, was derived from a close relative A, if B possessed all the characters of A, in addition to its own acquired characters. But if B did not contain all the character of A, both A and B were considered two separate branches of the same evolutionary line. A most advanced taxon occupied the farthest semicircle and that taxon with least advanced characters occupied the lowest semicircle.

Explanation of some of the characters used

Flavonols

Flavonols as the main phenolic pigment occur in large amounts in primitive woody Angiosperm. The rarity of these

compounds represent processes leading to the elimination of these compounds.

Flavones

Flavones represent one of the reduction tendencies in flavonoid evolution. They replace flavonols in advanced group of angiosperm and so are considered as an apomorphic character.

6-OH flavones

6-Hydroxylation in a flavone skeleton is associated with the highly evolved groups of Angiosperms and therefore, the 6-OH flavones are considered highly advanced.

Glycoflavones

Glycoflavones represent a primitive situation in angiosperms, but when compared to the presence of flavonols (which are primitive) the glycoflavones represent an advanced feature.

Proanthocyanidins

Proanthocyanidins are always associated with woody nature. The woody habit being primitive the production of proanthocyanidins is a plesiomorphic character and their elimination an apomorphic feature.

Iridoids

The basic pattern in evolution of repellants is one of successive shifts from one major set of compounds to another

in response to progressive increase in resistance by the predator. Thus the evolution of low mol. wt. iridoids which are bitter principles and antimicrobial in nature (which replaces the high mol.wt. tannins) is considered an advanced trait.

Tannins

Tannins form a means of protection against microbial attack or predators in woody plants. Proanthocyanidins are a group of tannins. Though there can be demarcation between primitive and not so primitive tannins their presence indicate a feature formed early in evolution. The replacement of tannins by other protective measures such as iridoids or volatile oils is an advanced character. In the Orobanchaceae the production of tannins is an adaptation to parasitism, and is secondary in nature. In this family, therefore, the tannins represent a derived feature and thus apomorphic.

Syringic acid

Syringic acid is a component of lignin and is always associated with the woody habit of the plants and hence its absence is featured as an advanced trait.

Quinones and Alkaloids

Since these compounds are associated with primitive group of plants, these are considered as plesiomorphic.

Table - XVI

THE DISTRIBUTION OF CHARACTERS WITHIN CERTAIN GENERA OF THE FAMILY SCROPHULARIACEAE

Sr. No.	Plant Name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
1.	Anticharis		+	+	+	+				+	+		+			7
2.	Verbascum									+	+		+	+		4
3.	Angelonia	+		+		+		+				+		+		6
4.	Antirrhinum	+	+	+					+	+	+	+		+		8
5.	Kickxia			+				+	+	+	+	+	+			7
6.	Linaria	+		+							+	+				4
7.	Maurandya		+	+						+	+					4
8.	Schweinfurthia		+	+				+		+	+	+		+		7
9.	Penstemon	+		+						+	+		+	+		6
10.	Russelia	+		+		+		+		+		+	+			7
11.	Scrophularia	+	+	+				+		+	+		+	+		8
12.	Sutera	+		+					+	+	+		+	+		7
13.	Mazus	+		+		+				+		+		+		6
14.	Limnophila	+	+	+		+		+		+		+	+	+		9

Table - XVI (Contd.)

Sr. No.	Plant Name	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
15.	Lindenbergia	+		+		+		+	+	+	+	+		+	9
16.	Stemodia	+		+		+		+		+	+	+		+	8
17.	Bacopa	+		+						+	+		+	+	6
18.	Dopatrium	+	+	+	+	+		+	+			+	+		9
19.	Lindernia	+		+	+	+			+	+	+		+		8
20.	Torenia	+		+					+	+			+		5
21.	Glossostigma	+	+	+	+	+				+	+		+	+	9
22.	Hemiphragma	+	+	+				+		+	+		+	+	8
23.	Mecardonia	+	+	+						+	+		+	+	7
24.	Scoparia	+	+	+				+	+	+	+			+	8
25.	Digitalis			+						+			+	+	4
26,	Picrorhiza	+		+		+				+	+		+	+	7
27.	Veronica	+			+	+	+			+	+	+	+	+	9
28.	Buchnera	+		+		+	+			+	+	+	+	+	9

Table - XVI (Contd.)

Sr. No.	Plant Name	1	2	3	4	5	6	7	8	9	10	11	12	13	Total
29.	Striga	+		+		+	+			+	+	+			7
30.	Sopubia	+		+		+	+			+	+	+	+	+	9
31.	Euphrasia	+		+		+	+				+	+		+	8
32.	Pedicularis.	+		+		+	+			+	+	+	+		8

1. Opposite leaves, 2. Cymose inflorescense, 3. Irregular flowers,
4. Two stamens, 5. Loculicidal capsule 6. Parasitic habit,
7. 6-OH flavones present, 8. Glycoflavones present, 9. Proanthocyanidins absent,
10. Quinones absent, 11. Iridoids present, 12. Alkaloids absent
13. Syringic acid absent.

Table XVII

THE DISTRIBUTION OF CHARACTERS IN THE FAMILIES INCLUDED IN THE ORDER SCROPHULARIALES

Family Name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
1. SCROPHULARIACEAE	+	+						+	+	+	+		+	+		+	10
2. PEDALIACEAE	+	+		+				+	+			+			+	+	8
3. MARTYNIACEAE	+	+		+				+	+		+	+			+	+	9
4. OROBANCHACEAE	+			+				+	+					+	+	+	7
5. GESNERIACEAE	+	+		+				+	+		+	+	+	+	+	+	11
6. LENTIBULARIACEAE	+			+		+	+	+				+	+		+	+	9
7. BUDDLEJACEAE		+						+	+	+		+	+		+		7
8. OLEACEAE		+	+		+				+	+	+	+	+		+		9
9. ACANTHACEAE	+	+		+	+				+	+	+		+		+		9
10. THUNBERGIACEAE	+	+		+	+		+	+	+		+	+			+	+	11
11. BIGNONIACEAE		+	+	+					+	+	+	+	+		+		9
12. GLOBULARIACEAE	+			+	+			+	+	+	+	+	+		+	+	11
13. MYOPORACEAE				+	+		+	+				+	+				6

1. Herbaceous, 2. Opposite leaves, 3. Compound leaves, 4. Irregular flowers, 5. Limited number of ovules, 6. Basal placentation, 7. Endosperm absent, 8. Flavonols rare, 9. Flavones present, 10. 6-OH flavones present 11. Glycoflavones present, 12. Proanthocyanidins absent, 13. Iridoids present, 14. Parasitic habit, 15. Tannins absent, 16. Syringic acid rare.

Results

(a) Genera within the Scrophulariaceae

The cladogram (Fig. II) branches at the base itself based on the presence of iridoids. Thus Scrophularia, Hemiphragma, Scoparia, Maurandya, Torenia, Anticharis, Lindernia, Digitalis, Verbascum, Bacopa, Sutera, Mecardonia, Glossostigma, Penstemon and Picrorhiza form one group which is devoid of iridoids. The second group producing iridoids contain Lindenbergia, Stemodia, Angelonia, Russelia, Dopatrium, Limnophila, Veronica, Kickxia, Mazus, Schweinfurthia, Antirrhinum, Linaria, Pedicularis, Striga, Euphrasia, Sopubia and Buchnera.

The first group proceed to level one due to the absence of proanthocyanidins where the branching occurs on the basis of 6-OH flavones. Scoparia, Hemiphragma and Scrophularia possessing 6-OH flavones form one branch which raises till level seven. At this level Scoparia gets diverged because of the presence of glycoflavones. The three plants are positioned at level eight. Dichotomy occurs in the group which do not elaborate 6-OH flavones at level one itself based on the presence of syringic acid. Thus Lindernia, Anticharis, Torenia and Maurandya, characterized by zygomorphic flowers are separated because they possess syringic acid. However, at level two, further bifurcation takes place, placing Torenia and Maurandya (lack loculicidal capsule) in a separate branch. Torenia is separated from the latter at level three due to its racemose inflorescence and is

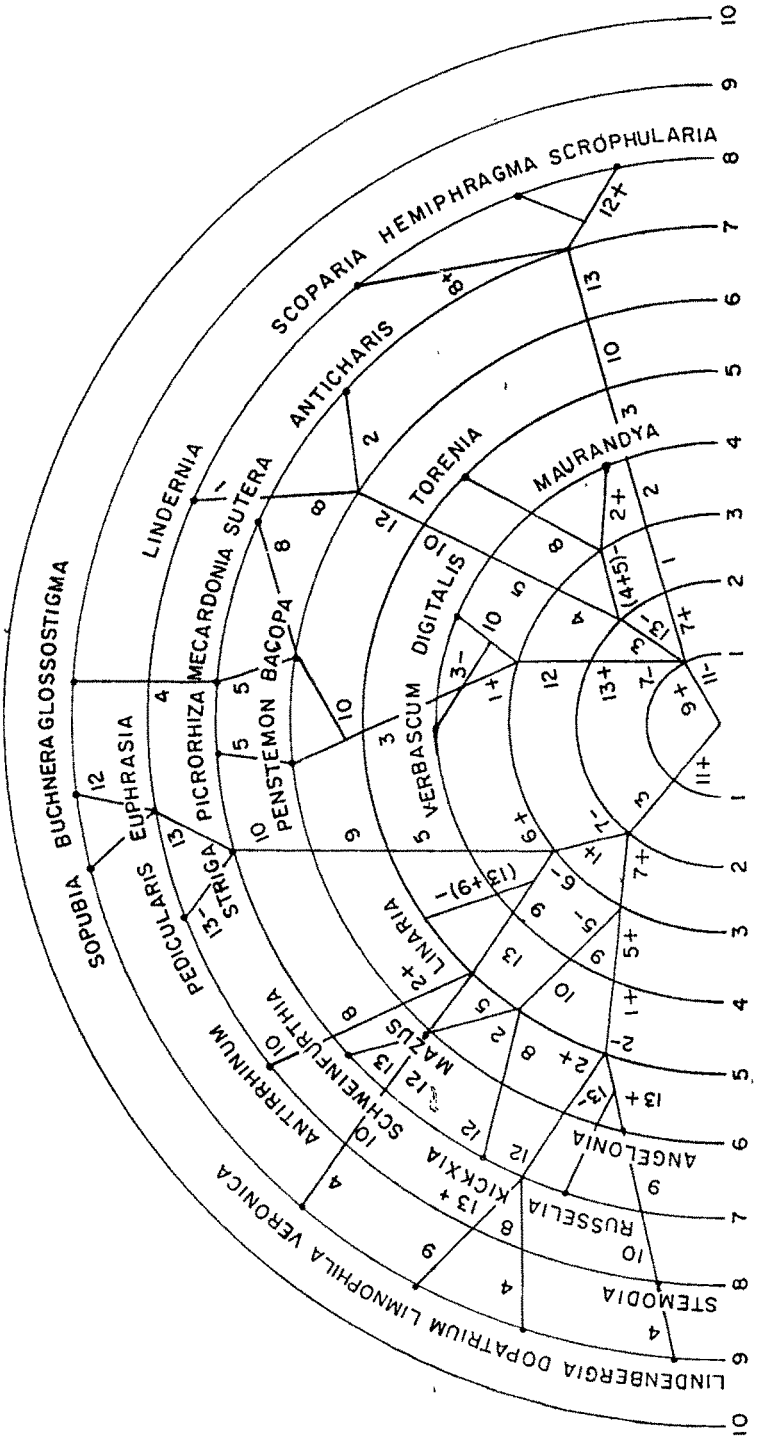

FIG: II A CLADISTIC ANALYSIS OF CERTAIN GENERA BELONGING TO THE FAMILY SCROPHULARIACEAE

placed at level five where as Maurandya at four. Lindernia and Anticharis proceed till level five where they are separated on the basis of glycoflavones. Lindernia is positioned at level eight and Anticharis at seven. The third group deviated from level one includes Verbascum, Digitalis, Bacopa, Sutera, Mecardonia, Glossostigma, Penstemon and Picrorhiza and are devoid of syringic acid and alkaloids. Dichotomy based on the arrangement of leaves takes place at level three: Digitalis and Verbascum with alternate leaves are separated and placed at level four. The remaining plants are raised till level five where branching on the basis of quinones takes place. Thus Penstemon as well as Picrorhiza possessing quinones form one branch and are placed at level six and seven respectively. In the second branch Bacopa form the base for the evolution of Sutera, Mecardonia and Glossostigma.

In the second major group, characterized by iridoids and zygomorphic flowers, dichotomy takes place at level two, based on the 6-oxygenation of flavone. Thus, Veronica, Mazus, Antirrhinum. Linaria, Pedicularis, Striga, Euphrasia, Sophubia, and Buchnera form one group which is devoid of 6-OH flavones. However, at level three the parasitic taxa are separated from the non-parasitic. The parasitic genera proceed till level seven where the genus Striga is positioned. Pedicularis and Euphrasia, derived from Striga, are placed at level eight. Sopubia and Buchnera having score nine, are derived through Euphrasia. From the non-parasitic taxa, Linaria is separated at level

three itself due to its elaboration of proanthocyanidins and syringic acids. The remaining genera are elevated till level five where branching occurs on the basis of inflorescence. Antirrhinum with cymose inflorescence is placed at level 8 where as Mazus and Veronica with racemose inflorescence is positioned at level six and nine respectively. Within the taxa having 6-oxygenated flavones, dichotomy occurs at level three on the basis of capsule. Kickxia and Schweinfurthia which are devoid of loculicidal capsule form one branch, Angelonia, Russelia, Stemodia, Lindenbergia, Dopatrium and Limnophila form the other. Kickxia and Schweinfurthia are separated at level five and are positioned at level seven. From the second branch, Dopatrium and Limnophila get bifurcated at level five due to their cymose inflorescence. However, at level seven the two plants are separated and are placed at level nine. Based on the presence of syringic acid one more division takes place at level five where by Russelia having syringic acid is placed apart at level seven. Lindenbergia positioned at level nine is derived from Angelonia through Stemodia.

b) Families within the Scrophulariales

Two groups are clearly visible in the first cladogram (Fig. III) which diverge from the base itself: one branch possessed regular flowers (Character 4) and the other with irregular flowers. The former branch proceeds to level 6 due to their common advanced characters (opposite leaves, presence

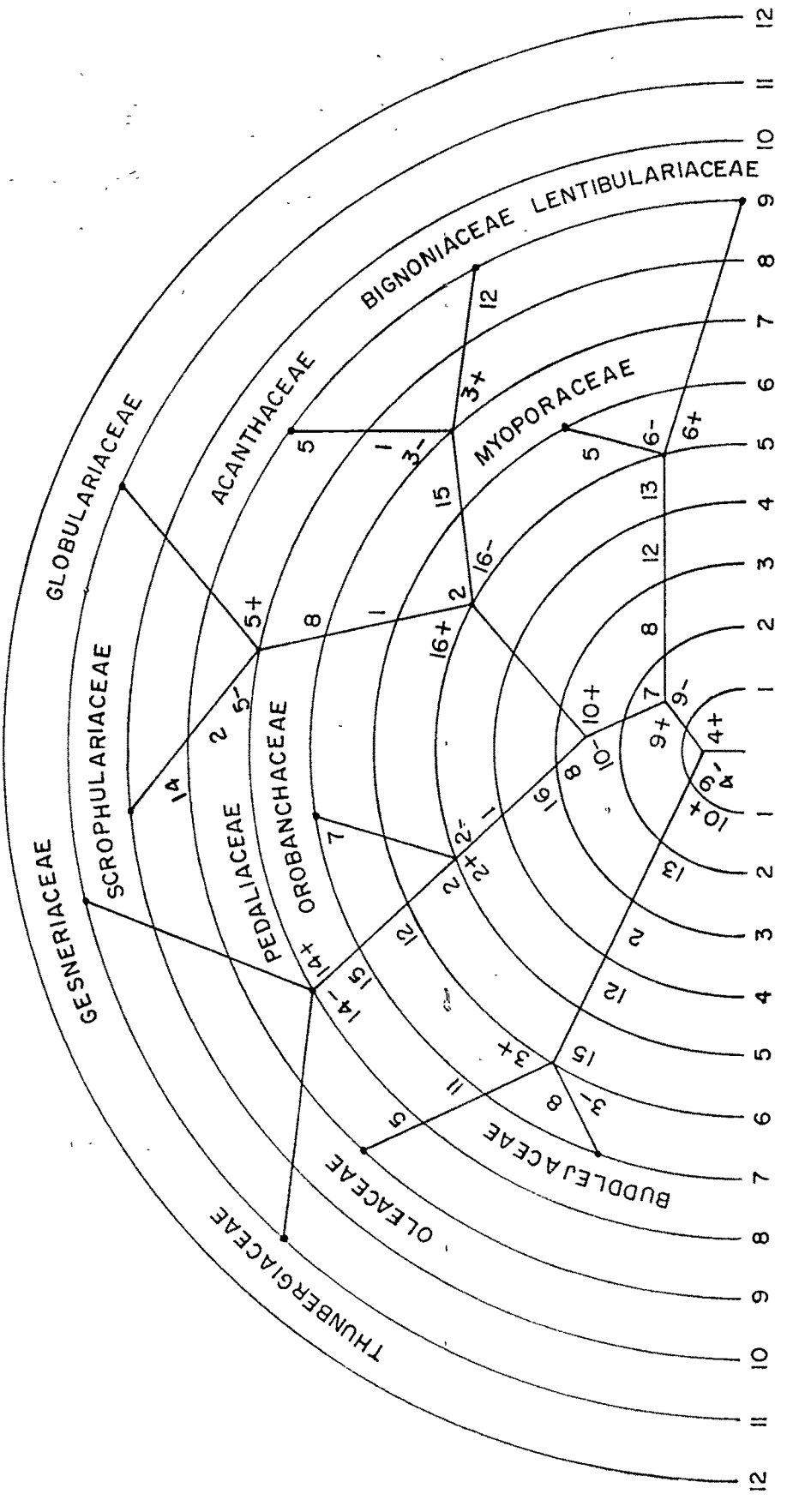

FIG: III PHLOGENY OF THE FAMILIES INCLUDED WITHIN THE ORDER SCROPHULARIALES
CLADOGRAM-I

of iridoids, flavones as also 6-OH flavones and absence proanthocyanidins and tannins) where the Buddlejaceae with simple leaves bifurcate from the Oleaceae having compound leaves. Buddlejaceae with an advanced score of 7 remain in this level while the Oleaceae proceeds further to the level 9.

The second branch indicating the major group in the order bifurcates from the level one whereby the families Myoporaceae and Lentibulariaceae which show the absence of flavones get separated forming a branch and the rest of the families with flavones proceed as another branch. The first branch proceeds to level 5 where two families separate. Myoporaceae with axile placentation terminates at 6. The Lentibulariaceae with basal placentation reaches at level 9 because of their additional apomorphic character.

The rest of the families of the second branch cluster together till level 3 where dichotomy occurs on the basis of the presence of 6-OH flavones. Amongh the families with out 6-OH flavones (Orobanchaceae, Pedaliaceae, Thunbergiaceae and Gesneriaceae), Orobanchaceae diverge from the rest at level 5 because of the nature of leaves (character 2), The rest of the families proceed further till level 8 which is the level achieved by Pedaliaceae. From Pedaliaceae, Gesneriaceae and Martyniaceae evolve as separate branches. The Thunbergiaceae is derived from the Martyniaceae.

The branch which contains 6-OH flavones include the Scrophulariaceae, Globulariaceae, Acanthaceae and Bignoniaceae, and they proceed together from level 3 to 5. At level 5 further dichotomy occurs and the families Acanthaceae and Bignoniaceae (they are rich in syringic acid) form a branch and Scrophulariaceae and the Globulariaceae form the other (rarity of syringic acid). In the first branch, the Bignoniaceae which is arborescent and characterized by compound leaves gets separated from Acanthaceae at level 7 and both the families are positioned at level 9.

The Globulariaceae with limited number of ovules are isolated from the Scrophulariaceae at level 8 and terminates at the 11th level. Scrophulariaceae finds its place at level 10.

In cladogram 2 (Fig.IV) first dichotomy is based on the presence of iridoids. Thus Orobanchaceae, Pedaliaceae, Martyniaceae and Thunbergiaceae from the first branch which is devoid of iridoids. Thunbergiaceae tops the highest level in the group keeping itself at level 11.

The absence of 6-OH flavones separates Nyoporaceae Lentibulariaceae and Gesneriaceae from the second group. Buddlejaceae, Oleaceae and Bignoniaceae form another sub group because of their predominantly arborescent nature. The terminal clustering is formed by the families Acanthaceae, Scrophulariaceae and Globulariaceae. The core families of the order Scrophulariales are aggregated in the second major group of cladogram 2.

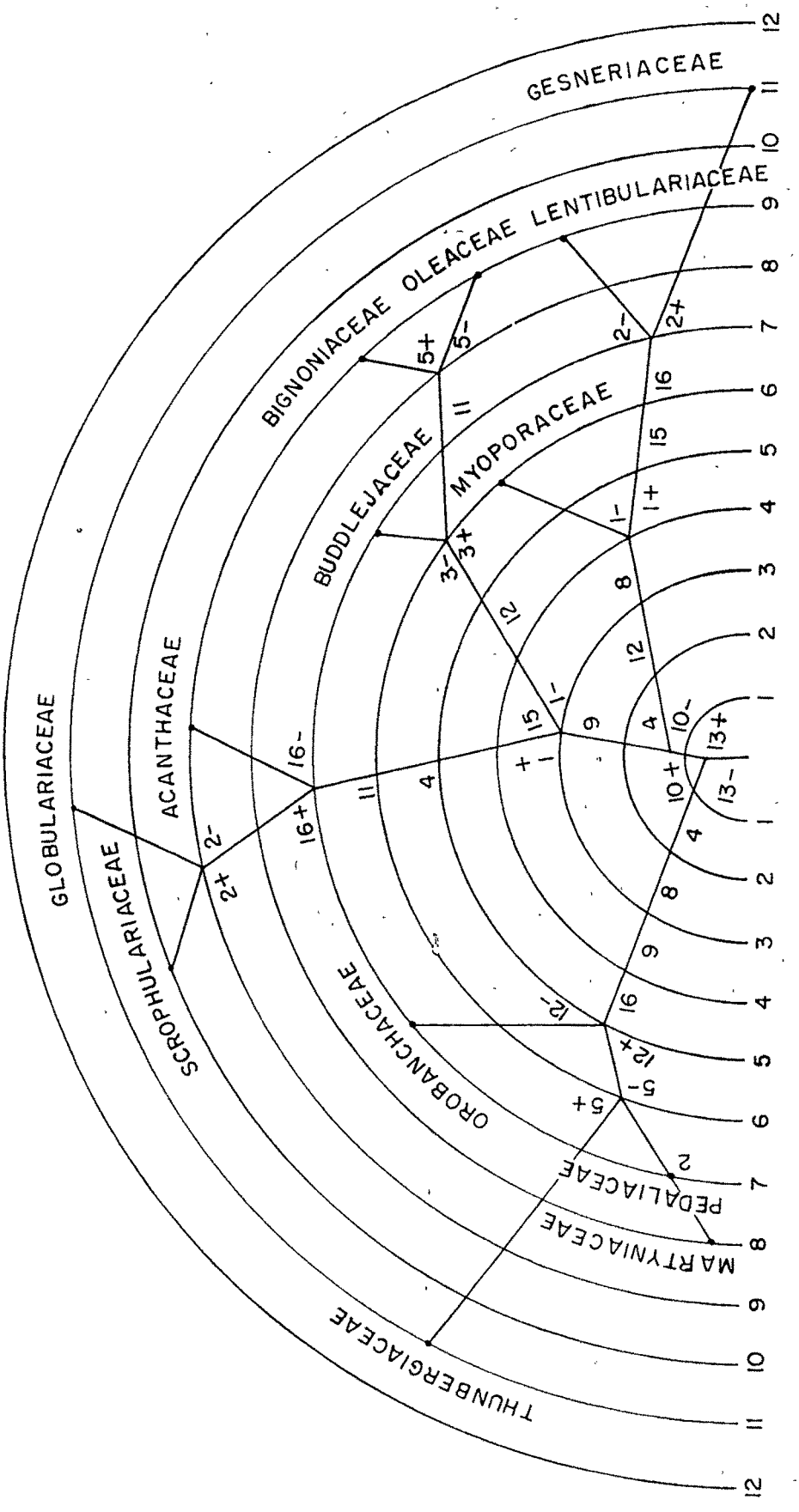

FIG: IV PHYLOGENY OF THE FAMILIES INCLUDED WITHIN THE ORDER SCROPHULARIALES
CLADOGRAM-II

A trend, almost similar to that of cladogram 1 is observed in cladogram 3 (Fig.V) wherein the major bifurcation is based on the character 9 (Presence of flavones). This separates the families Myoporaceae and Lentibulariaceae from the rest of the families for they are devoid of flavones, and keeps Oleaceae and Buddlejaceae in the second major group. Except for this difference the cladogram is similar to the cladogram 1.

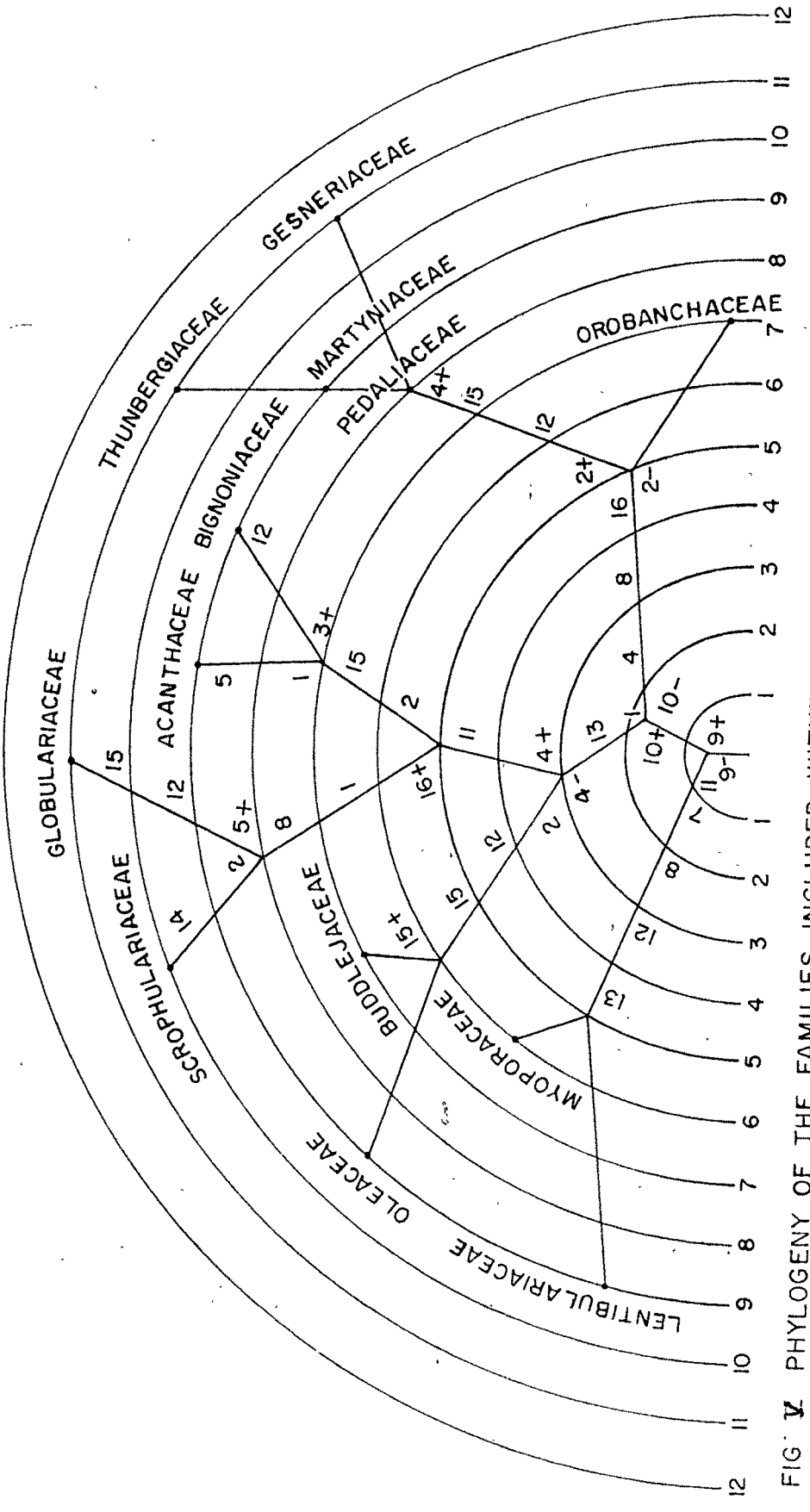

FIG. V PHYLOGENY OF THE FAMILIES INCLUDED WITHIN THE ORDER SCROPHULARIALES
CLADOGRAM - III