

INTRODUCTION

CHAPTER - I

INTRODUCTION

A taxonomic system is supposed to reflect the totality of similarities and differences among organisms. It is implicit in this concept that the more information one uses in producing a taxonomic system, the closer one reaches to the desired end. The technical and conceptual advances in the field of isolation and characterization of organic compounds thus gave a new dimension in systematics and are used as evidences in taxonomic deliberations. Chemical compounds are given equal weightage at par with the evidences from other disciplines and can be effectively used in refining the systems of classification based on morphological characters. They are significant in tracing the evolution as the evolution of many a chemical characters has proceeded in a particular direction and help in formulating a phylogenetic system of classification. In all the recent treatments (Cronquist, 1981; Takhtajan, 1980; Dahlgren, et al. 1981) phytochemical data have been incorporated effectively at various levels of hierarchy.

The subclasses of Magnoliatae (Dicotyledons) proposed by Takhtajan (1980) and later accepted by Cronquist (1981)

although seemingly natural are characterized only in generalities and hang together on the basis of all available information. When arranged in any of the several linear sequences, the subclass Magnoliidae comes first and the Asteridae the last. The most highly evolved Asteridae on the basis of accumulating chemical evidence is sought to be derived from the Rosidae rather than the Dilleniidae. Hegnauer (1964-1973) on the basis of chemical data has conceived two groups within the Asteridae separately derived from the Rosidae, one of them containing the Solanaceae and the other the Scrophulariales.

The Asteridae are sympetalous (rarely polypetalous or apetalous) dicotyledons with unitegmic, tenuinucellate ovules and with stamens usually as many as or fewer than the corolla lobes and alternate with them. Most of them have two carpels. It is a highly natural subclass and is morphologically the best defined of the six subclasses of dicots.

The highly evolved Asteridae have been a subject of chemosystematic investigation at the Phytochemistry and Taxonomy laboratories of the department of Botany of the M.S. University of Baroda. The efforts of the research group (of which, the candidate is a member) have been directed at understanding the relationships and evolutionary tendencies within the various orders and families constituting the subclass. Extensive chemical surveys involving taxa belonging to Gentianales, Rubiales, Polemoniales, Lamiales

and Scrophulariales are being carried out not only with a view to accumulating diverse chemical data on unknown plant sources but also utilizing the information to resolve various taxonomic tangles or refining the classification at various levels of hierarchy.

In the present thesis 80 plants belonging to the Scrophulariales (central family Scrophulariaceae and some allied and derived families) have been screened with respect to a number of chemical markers. 22 taxa of the Solanaceae have also been screened to assess their relationship with the Scrophulariaceae.

In this on-going research programme, more and more taxa will be screened to verify and consolidate the various taxonomic judgements tentatively offered in the present thesis. Availability of plant material as also the time allotted to the candidate have been the major constraints.

TAXONOMY OF THE SCROPHULARIACEAE

The Scrophulariaceae owe their name to the genus Scrophularia which was used by some herbalist as a cure for scrofula. The family Scrophulariaceae when first constituted by A.L. de Jussieu (1791) contained 33 genera including Buddleia, Cyrtandra and Browallia but excluded Verbascum and Celsia. The Pedicularia constituted a parallel order.

A new circumscription of the family was offered by Bentham (1835) which he revised later (1846) giving an account of all the then known species. This treatment was further modified by Bentham and Hooker in 1876 wherein, the family is divided into three series (subfamilies) viz. Pseudosolaneae (characterized by a nearly actinomorphic corolla, alternate phyllotaxy and the frequent presence of a full complement of five stamens), Antirrhinoideae (leaves atleast the lower ones opposite with centripetal or composite inflorescence; corolla with the two upper lobes exterior in bud) and Rhinanthoideae (corolla lobes variously imbricate, anterior or lateral usually the outer in bud).

The subfamily Pseudosolaneae of Bentham & Hooker has three tribes i.e. Leucophylleae, Aptosimeae and Verbasceae. The subfamily Antirrhinoideae contains six tribes, Calceolarieae, Hemimerideae, Antirrhineae, Cheloneae, Manuleae and Gratioleae and the subfamily Rhinanthoideae included the tribes Digitaleae, Gerardieae, and Euphrasieae. Three tribes have been subdivided. They are (i) tribe Gratioleae (subtribes Mimuleae, Stemodieae, Herpestideae, Vandelleae and Limoselleae) (ii) Digitaleae (subtribes Sibthorpieae, Eudigitaleae and Veroniceae) and (iii) Gerardieae (subtribes Escobedieae, Hyobanche, Buchnereae and Eugerardieae).

Based on the frame-work of the family scrophulariaceae of Bentham and Hooker (1876), Wettstein (1891) revised the classification by an appreciable reassignment of tribes and inclusion of genera hitherto assigned to other families.

The classification of the family by Engler and Diels (1914) was more or less on the pattern of Bentham and Hooker and Wettstein treatment. Hallier (1903) abandoned aestivation as the basis for delimiting the subfamilies and enlarged the family circumscription to include the Plantaginaceae, Lentibulariaceae, Orobanchaceae and Selagineae. He, however, transferred Paulownia and Wightia to the Bignoniaceae; Brookea and Rehmannia to the Gesneriaceae and Zenkeria to the Acanthaceae.

A primary division of the family based upon staminal characters was proposed by Van Tieghem (1903). Bellini (1907) divided the Personatae (i.e. Scrophulariaceae) into two subfamilies, the Scrophulariaceae (not parasitic) and Rhinanthaceae (parasitic or semi-parasitic). The subdivisions of these families were based on the nature of stamens and nectaries. The recognition of the tribe Collinsieae, a taxon, characterized by the origin of the nectary from the aborted fifth stamen, is one of the salient feature of this classification. Bellini included the Orobanchaceae within the second subfamily Rhinanthaceae.

The conspectus of the tribes and genera of the Scrophulariaceae published by Rouy (1909) is essentially a combination of the Bentham's, Bentham and Hooker's and Wettstein's treatment of the family.

The reclassification of the family on a phylogenetic basis was done by Pennell (1935). He divided the Scrophulariaceae into two subfamilies, the Antirrhinoideae and the Rhinanthoideae distinguished from each other by the relative position of the corolla lobes.

Varghese (1967) classified the scrophulariaceae into six groups, which can be divided into fifteen series and 34 types based on the development of endosperm as well as the construction and structure of endosperm haustoria.

Kooiman (1970) questioned the validity of the subfamilial classification but divided the family into four groups based on the distribution of iridoid glycosides.

- Group I Taxa devoid of iridoid glycosides (most Gratioleae, the Calceolaria, most Digitaleae, Sphenandra and Nemesia)
- Group II Taxa containing aucuboside and/or catalpol (Verbasceae Scrophularieae, Collinsieae, Hemiphragmeae, Buchnereae, Veroniceae, Rhinanthaeae, Sutera, Limosella, Mazus, Zaluzianskya, Angelonia, Diascia, Erinus and Rehmannia).

- Group III Taxa containing antirrhinoside (Antirrhineae).
 Group IV The selaginoideae with unidentified glycosides.
 Group V Remaining taxa with unidentified glycosides
 (Leucocarpus, Halleria, Alonsoa etc.)

The Orobanchaceae have been included in the Scrophulariaceae not only by Hallier (1903) and Bellini (1907) but also by Dahlgren et al. (1981). Apart from the Orobanchaceae, Dahlgren et al. included Nelsonoideae (of Acanthaceae) to widen his scrophulariaceae.

Subfamilial Divisions

Bentham and Hooker (1876) and also Wettstein (1891) maintained that the subfamily Pseudosolaneae with its nearly actinomorphic corolla, alternate phyllotaxy and the frequent presence of full complement of five stamens formed a link between the Scrophulariaceae and the Solanaceae. The validity of this view was questioned by Robertson (1891) who considered the apparently Solanaceous character of the Pseudosolaneae as a derived trait from the zygomorphic group. Later Robyns (1931) proved that the Solanaceous zygomorphy is quite different from that of the Scrophulariaceae, in that, in the Salpiglossideae (of Solanaceae) the aestivation is plicate, the anterior stamen is lost or reduced, the carpels oblique and the vascular bundles bicollateral, whereas in the verbasceae (Pseudosolaneae), the aestivation is imbricate, the

posterior stamen is lost or reduced, the carpels are median and the vascular bundles are collateral. Moreover, the Verbascum type of seeds, characterized by the presence of longitudinal and transverse endosperm ridges and local proliferation of cells in the inner layers of the testa apparently is not found in the Solanaceae.

These data strengthen the theory that the actinomorphic corolla and the frequent occurrence of five stamens in Verbasceae is a derived character and not a primitive feature. This is further evidenced by the united stigmas and the relatively complex seeds of this taxon.

Since, the supposed affinity between Pseudosolaneae and Solanaceae is disproved, Pennell advocates the dissolution of this subfamily (Pennell, 1935). The Scrophulariaceae, then, are divided into two subfamilies, the Antirrhinoideae (Scrophularioideae) and the Rhinanthoideae. The Verbasceae, Leucophylleae and Aptosimeae, the three tribes included in Pseudosolaneae are now to be placed in the Antirrhinoideae. Since the Verbasceae have been shown to possess characteristics which are derived rather than primitive, Pennell placed this group in a relatively advanced position. This prompted taxonomists to consider the tribes Cheloneae or Gratiroleae as an alternative tribe that could be treated as phylogenetically primitive within the Antirrhinoideae. Pennell accepted the tribe Gratiroleae as the most primitive taxa due to their five distinct sepals, the usually open throated zygomorphic

corolla, approximate two celled anthers, distinct stigmas, septicidal capsular dehiscence and the ovoid seeds with simple reticulate seed coats. Thieret (1967) agreed with Pennell in considering the Gratioleae as the primitive tribe. The tribe Antirrhineae with its variety of seed shapes, modified corolla and varying forms of capsule dehiscence is considered as an advanced taxon (Pennell, 1935).

The Rhinanthoideae, due to their specialised parasitic habit and elaborate zygomorphy appear to be the derived group of the family Scrophulariaceae. Within Rhinanthoideae the tribe Euphrasieae is considered as the 'apex' of the family. To cite Pennell "there can be no question of its correct position at the end of the Rhinanthoid subfamily and so at the summit of evolution in the Scrophulariaceae".

Jirawongse (1964) studied the occurrence of aucuboside in a fairly large number of the members of the Scrophulariaceae and found that the presence of absence of aucuboside is rather strongly correlated with Pennell's classification. Moreover data from embryology (Arekal *et al.* 1971) floral anatomy (Arati and Datta, 1975) and secondary xylem (Arati and Datta, 1975) are in favour of this system of classification.

The controversies existing among the taxonomists regarding the circumscription of the family and the placement of various genera within the family are as follows:

The tribe Leucophylleae (Sensu Benth and Hooker, 1876) because of its possible relationship with Myoporaceae in anatomical and palynological characters has been transferred from Scrophulariaceae to the former family (Metcalf and Chalk, 1950; Flyr, 1970; Niezgode and Tomb, 1975).

The African tribe Selagineae given family status long back was first reduced to a tribe in the Scrophulariaceae by Baillon (1888) and later accepted by Wettstein (1891) and Hallier (1903). Previous to (and ever since) Baillon's work, the Selagineae were regarded as a distinct family related either to the Myoporaceae and Verbenaceae (Bentham and Hooker 1876; Choisy 1848; Endlicher, 1836-40; Lindley, 1836; Hutchinson, 1926; Rolfe, 1883; Van Tieghem, 1891; Wernham, 1912; Mukherjee, 1975) or to the Scrophulariaceae (Marloth, 1932; Rendle, 1925). Rouy (1909) transfer the genera belonging to the selagineae to the Myoporaceae whereas Cronquist (1981) merges this family with his Globulariaceae.

A number of genera have been shifted to and fro from the family Scrophulariaceae and to the closely allied families. Based on palynological studies, the genus Capraria placed in Gratiroleae (Thieret, 1954) was shifted to Myoporaceae (Niezgode and Tomb, 1975). The genus Oftia historically placed in the Myoporaceae is considered atypical in the family with regard to its morphology, palynology and anatomy (Dahlgren and Rao, 1971). T.E.M. studies of pollen agrees its

better placement in Scrophulariaceae (Niezgode and Tomb, 1975). Chemical studies prompted Swaitek et al. (1976) to shift Lathraea from Orobanchaceae to the Scrophulariaceae. Because of the 'U' shaped placenta which are common in Bignoniaceae and absent in Scrophulariaceae, genera Schlegelia is transferred from the Scrophulariaceae to the Bignoniaceae. (Leinfellner [] , 1973). The genus Paulownia is referred to the Bignoniaceae by Hallier (1903), Campbell (1930), Pennell (1920) and Li (1947). However Steenis (1949), Fernald (1950) and Gleason (1952) advocated its retention in the Scrophulariaceae. Later in 1982 Padhye further corroborated its transfer to the Bignoniaceae.

The circumscription of the tribes within the family is also under dispute. Some of the controversial tribes of this family are discussed below.

Verbasceae

The Verbasceae (Sensu Wettstein, 1891) contain five genera including Leucophyllum and Eremogeton. The separation of these two genera into the tribe Leucophylleae (Sensu Benth and Hooker, 1876) is accepted by Thieret (1967). However, Thieret, judging from the nature of seeds claimed close relation of Verbascum with Russelia and Scrophularia (tribe Cheloneae).

Cheloneae

The Cheloneae are an assemblage of genera whose principal common characteristic is the cymose disposition of the flower. Thieret (1967) observed heterogeneity in this taxon. From this tribe Synapsis, Paulownia and Wightia were transferred to the Bignoniaceae (Urban, 1926; Campbell, 1930; Hallier 1903) and Brookea and Uroskinera to the Gesneriaceae (Hallier, 1903).

Leucocarpus, Berendtiella and Hemichaena were transferred to the tribe Gratiroleae (Pennell, 1935) because of their characteristic similarities with Mimulus. The distinctive characteristics of Collinsia and Gonella necessitated their grouping in a separate tribe Collinsieae as proposed by Bellini (1907).

The genus Russelia is somewhat enigmatic in the relationship within this tribe. The outstanding characteristic of the genus is the presence of densely packed long hairs within the loculicidal capsule. This character is not observed anywhere else in the family, thus prompting Thieret (1967) to propose a unigeneric tribe, Russelieae. The systematic position of Scrophularia, which possesses similarities in gross external and internal seed structural characters as well as in the microscopic structure of the testae with Verbascum (Thieret, 1967; Bachmann, 1882; Hartl,

1959) is debated. Schmid (1906) found the development of the endosperm and haustoria and the behaviour of the tapetal layers to be very similar in these two genera. Other points of resemblance between them include hairy filaments, reniform anthers with wholly confluent sacs and the septicidal, many seed capsule. Interestingly Endlicher (1836-40) included the genus Scrophularia with Verbascum in the Verbasceae.

Gratioleae

This taxon comprises a large assemblage of obviously related genera. This tribe is characterized by a uniformity of seed types that is found in no other tribes of the Scrophulariaceae (Thieret, 1967).

The genus Scoparia placed in the Digitaleae by Bentham and Hooker, and retained there by Wettstein is dissimilar to the other members of the tribe in the nature of its exterior posterior corolla lobes. This genus was transferred to the Gratioleae (along with Capraria) due to their frequently four angled stems, delicate, relatively long pedicels, their axillary flowers and especially by their possession of glands on the calyx, pedicel etc. (Pennell, 1935). The seeds of this genus are of the Bacopa type characteristic of many Gratioleae (Thieret, 1967). The plant has a type of axial parenchyma different from those observed in other members of Digitaleae, but similar to those noticed in the members of Gratioleae (Arati and Datta, 1977) Embryologically too Scoparia resembles

Gratiroleae members (Arekal, Rajeshwari and Swamy, 1971).

A similar treatment is given to the genus Sutera (Pennell, 1935). The taxon is shifted from the tribe Manuleae to the Gratiroleae which is further supported by wood anatomical studies (Arati and Datta, 1977).

It is interesting to note that in Lindenbergia the placentation at the basal region of the ovary is axile while at the upper region it is typically parietal. After a study of the aestivation of the corolla, the stamens and other characteristics Brühl (1920) assigned the genus to the Rhinanthoideae either near Euphrasia or near the head of the subfamily. Kooiman (1970) after studying the iridoids within the family Scrophulariaceae opines that the genus Lindenbergia fits well in the tribe Antirrhineae. The genus was critically studied by Hartl (1957) and Prijanto (1969) and referred it to the tribe Gratiroleae.

The inclusion of Torenia in Lindernia, partially or entirely has been considered by several authors (Philcox, 1968). The calyx has been used as the main character in separating these two genera. In Lindernia, the calyx is either deeply or shallowly lobed and where the lobes are shallow the resulting calyx tube has regular and equal lobes bearing five distinct nerves and is not distinctly winged. The calyx of Torenia is never deeply lobed and has 3-4 teeth and prominent wings. Based on phytochemical studies Diaz (1977) could characterize

the four sections of South American Lindernia. His observation of a combination of apigenin and luteolin in Torenia section Nortenia which is otherwise absent in Lindernia convinced him of their separation. However the characteristic similarity in seed character observed in Lindernia crustacea and Torenia spp. strengthen their close relationship (Thieret, 1967).

Antirrhineae

This tribe, considered as one of the most highly evolved of all the Scrophulariaceae in the antirrhinoid division, is characterized by loculicidal, transverse or porous dehiscence of the capsule. The inclusion of Antirrhinum and Linaria in the same subtribe Linarineae by Rothmaler (1954) and others is objected to on the basis of seed coat characters and pollen morphology and warranted a subtribal segregation (Elisen, and Tomb, 1983; Elisen, 1986).

Digitaleae

This tribe is characterized by (referring to Wettstein's Key) plants having the upper corolla lobes internal in bud and non-parasitic plants. However the distinctiveness in characters in the genera Digitalis and Veronica will emphasize the creation of tribes Digitaleae and Veroniceae (Rouy, 1909; and Pennell, 1921).

According to Pennell (1935) most of the genera in Wettstein's Digitaleae pertain to the Veroniceae and the Digitaleae is a small taxon comprising mainly Digitalis. He has excluded the genus Sibthorpia from the tribe.

General characters of the family

The Scrophulariaceae contain about 190 genera and 4000 species of cosmopolitan distribution, but most abundant in temperate regions and tropical mountains. A predominantly herbaceous family, rarely lianous (Maurandya) or tree-like (Halleria) has some parasitic or saprophytic genera, and are often provided with hairs that have a basal cystolith. Leaves alternate or opposite (whorled in Veronicastrum and heterophylly in Veronica and Limnophila species). Flowers in various types of determinate or indeterminate inflorescence. Bracts and bracteoles present. Calyx 4-5 lobed (four sepals in Veronica, Scoparia, Calceolaria and Euphrasia), imbricate or valvate. Corolla sympetalous, zygomorphic (almost actinomorphic in Scoparia and Verbascum species), 4-8 lobed (four petals in Scoparia, Veronica and Veronicastrum), obsolete corolla in Lindernia ciliata and Veronica, large and bell shaped in Digitalis, spreading in Veronica sp. and spurred or saccate in Linaria sp.) with usually four (five in Verbascum thapsus) stamens, (with one anther lobe of each stamen reduced/ sterile in Striga and Sopubia) or two, (half of each of the two stamens sterile in Calceolaria);

Anthers tetrasporangiate and dithecal. An annular disk commonly present at the base of the ovary. Gynoecium of two median carpels united to form a compound superior ovary (gynoecium showing all stages from tricarpellary to bicarpellary condition in Scoparia dulcis), with numerous ovules in each locule on axile placenta (parietal in Dopatrium ; axile placentation at the base and parietal at the upper region in Lindenbergia). Style terminal with simple or two lobed usually wet stigma. Fruit various often a septicidal capsule rarely a berry (Leucocarpus, Halleria) or a schizocarp (Hebenstretia). Seeds numerous angular or winged. Endosperm oily.

Pollen morphology

Within the family the pollen grains exhibit considerable variation in size and shape. Pollen grains binucleate or trinucleate, 2-7 aperturate and tricolporate (Varghese, 1967). Compared to the eurypalynous families associated with the Scrophulariaceae such as Acanthaceae (Raj 1961) and the Bignoniaceae (Suryakanta, 1973; Gentry and Tomb, 1979), the total number of morphotype is not high and the character differences are not great (Elisens, 1986).

Embryology

Microspore development is normal. The tapetum is of 'secretory type'. Polyspory in Veronica anagallis and in situ germination of pollen grains in Dopatrium are other points of interest.

Embryosac development conforms to polygonum type. Both chalazal and micropylar haustoria are noticed. Embryo development is either crucifer or onagrad type.

Seed coat morphology

The Scrophulariaceae have a wide variety of seed shape, size and testal pattern. Minute seeds are characteristic feature of the family. Seeds may be cristate, tetracostate, foveolate, tumid, tuberculate, circumalate or medusiform.

Anatomy

Stomata commonly anomocytic, rarely anisocytic (Kumar et al., 1982). The node is uniformly unilacunar (Varghese, 1967). In wood, a very specialized erect type of ray cells is common in most of the species. Storied wood, another notable character also is observed in the family (Arati and Dutta, 1977). Wood parenchyma and internal phloem wanting.

Chemistry

The family is characteristically rich in orobanchin and iridoids. Apart from this, various type of flavones, flavonols, flavonanones, aurones, chalcones, alkaloids, terpenoids, sterols, quinones, saponins and cardiac glycosides are reported from this family.

About half of the total species of the family belong to the genera Pedicularis (500), Calceolaria (300), Verbascum (300), Veronica (300), Penstemon (380), Castilleja (150), Linaria (150), and Scrophularia (150). In India the family is represented by 56 genera and 258 species (Hooker, 1884).

The family has been placed in Tubiflorae (Caruel, 1881; Wernham, 1911-12; Hallier, 1912; Wettstein, 1935; Rendle, 1938; Skotsberg, 1940; Pulle, 1952, and Melchior, 1964). Personales (Don, 1835; Martius, 1935; Endlicher, 1836-40; Grisebach, 1854; Drude, 1887; Soo, 1953; Boivin, 1956; Crete, 1959; Hutchinson 1969) Scrophulariales (Bessey, 1915; Gates, 1940; Benson 1957; Cronquist 1968; Takhtajan, 1969; Dahlgren et al. 1981) Polemoniales (Gunderson, 1950) or Bignoniales (Lindley, 1853). In all these groupings the family Scrophulariaceae has usually been associated with its related families like Pedaliaceae, Orobanchaceae, Gesneriaceae, Lentibulariaceae, Acanthaceae, Bignoniaceae, Buddlejaceae, Oleaceae, Myoporaceae, Globulariaceae and Solanaceae.

Pedicularidaceae, Rhinanthaceae, Personatae, Antirrhinaceae, Melampyraceae, Aragoaceae, Chelonaceae, Veronicaceae, Sibthorpiaceae, Limosellaceae, Personaceae, Verbasceae, Ellisophyllaceae and Helleriaceae are the family names used for the segregates from the Scrophulariaceae.

TAXONOMY OF ALLIED FAMILIES

PEDALIACEAE

The family Pedaliaceae consists of 20 genera and 80 species occurring chiefly in the tropics. The largest genus Sesamum is with about 20 species.

Morphologically the family is similar to the Scrophulariaceae. But the herbage is slimy because of the

specialized multicilaginous trichomes.

The plants belonging to this family exhibit a very wide variety of vegetative and reproductive characters. Some of these interesting features are (1) the extra floral nectaries in Sesamum and Pedaliium (2) the inferior condition of the ovary in Trapella (3) the nature of the placentation and the peculiar types of fruits with their variable spinous appendages in Pedaliium, Martynia and Trapella. The Pedaliaceae show embryological similarity with the members of the Scrophulariaceae (Kulkarni, 1968).

On the basis of parietal placentation, characteristic fruit and terminal racemose inflorescence, Engler and Prantl (1897) segregated Martynia along with Craniolaria and Proboscidea of Pedaliaceae into a distinct family Martyniaceae. Bessey (1915), Rendle (1925), Wettstein (1935) and Hutchinson (1959) supported this view. Das, Rao and Rao (1966) observed differences in phenolic acid distribution between the two groups. Martynia also shows variation on the epidermal structure as well as the structure and ontogeny of stomata (Inamdar, 1969). The different type of trichomes observed in Martynia annua are quite different from those of Pedaliium murex and Sesamum indicum. Moreover, multicilage glands, oil glands and pearl glands present in the species of Pedaliium and Sesamum are totally absent in M. annua. Arrested development of stomata are seen in M. annua only. These characters further corroborate the view that these two taxa have evolved separately.

However, several other taxonomists like Hallier (1905) did not support this treatment and followed Bentham and Hooker in retaining these genera within the Pedaliaceae. The genetical study by Srinivasan (1942) has shown that the genus Martynia is related to the genus Sesamum. Pawar and Kulkarni (1971) did extensive wood anatomical studies in these genera and couldn't observe much of variation between the two families thereby advocating its retention within the Pedaliaceae. Cronquist (1981) merged Martyniaceae in Pedaliaceae and gave it a sub-familial status.

Other segregates of the family are Josephiniaceae, Sesamaceae, and Trapellaceae. Taxonomists agree in the placement of Pedaliaceae in Tubiflorae or equivalent orders like Personales, Scrophulariales or Polemoniales.

Burnett (1835) included his 'Pedalidae' in Acanthaceae. But for Den Outer et al. (1983) the family shows more similarity in wood anatomical structures to the Bignoniaceae rather than the Acanthaceae or the Scrophulariaceae.

OROBANCHACEAE

The family consists of annual or perennial herbaceous root parasites, often fleshy and without chlorophyll. Leaves often reduced to scales. In morphological characters it almost resembles the Scrophulariaceae, but for the unilocular ovary and parietal placentation.

The family consists of about 17 genera and 150 species best developed in subtropical and temperate regions. About two-third of the species belong to the single genus orobanche.

Agardh (1858) described the Orobanchaceae as parasitic Gesneriaceae. This gains support because of the unilocular ovary observed in both these families. The genera of Gesneriaceae are however, strictly autotrophic. The Scrophulariaceae, on the other hand, exhibit various degree of parasitism, mainly in the tribes Gerardieae and Rhinanthaeae (Euphrasieae). A gradual gradation from partial parasitism to total parasitism is observed in Gerardieae from Gerardia flava to G. aphylla. The south African genera Harveya and Hyobanche are completely parasitic. Heinricher's (1897-1902) intensive morphological and physiological studies on the Euphrasieae indicate a very close relationship between Orobanchaceae and Scrophulariaceae. This is further confirmed by the embryological studies of Nagendran et al. (1980). Dahlgren et al. (1981) included Orobanchaceae in his Scrophulariaceae.

Embryologists especially Boeshore (1920), Glisic (1929) and Tiagi (1956) supported the attempts to unite the Orobanchaceae with the Scrophulariaceae. Tiagi's studies on Striga convinced him that there was no embryological differences between Striga and the Orobanchaceae members. Tiagi, however, pointed out the differences in placentation which is axile in Scrophulariaceae and parietal in the Orobanchaceae. On the other hand Cr  t   (1955) warned against too hasty a fusion of the Scrophulariaceae and the Orobanchaceae.

The affinities between Scrophulariaceae and Orobanchaceae have been clearly discussed by Job (1969). Loss of photosynthetic capacity and increased host dependence, fleshiness of stem, opposite to alternate phyllotaxis, longevity, the shift from secondary lateral haustoria to primary terminal ones, anther evolution, septation of ovary, placentation, reduction of the embryo, number of seeds and the need for a host stimulant in germination are the traits looked into to assess the relationship. According to Job, a line of demarcation between the two families was ambiguous and made the placement of Lathraea, Hybbanche, Harveya, and Buchnera very difficult.

The genus Pseudo-orbanche based on Alectra orobanchoides Benth. formulated by Rouy (1909), seemed to emphasize the affinity between scrophulariaceae and Orobanchaceae. At present the justification of orobanchaceae as a separate family has been seriously disputed. One is tempted to dismiss this familial separation since a nearly complete continuity of morphological features exist. The systematic significance of parasitism within Scrophulariaceae remain an open question.

GESNERIACEAE

The family Gesneriaceae consists of about 120 genera and 2500 species with pantropical distribution. Cyrtandra is the largest genus with variously estimated 200 to 600 species. This is followed by Columnea with 150 to 200 species.

Based on the position of the ovary the family is divided into two distinct subfamilies, Cyrtandroideae with superior ovary and Gesnerioideae with a more or less inferior ovary.

Hutchinson (1920) found it difficult to distinguish Gesneriaceae from the Bignoniaceae and the Scrophulariaceae. In pollen morphology too, the three families resemble very much (Erdtman, 1952). But according to Cronquist (1981) the Gesneriaceae are closely allied to the Scrophulariaceae. The best distinction is in the unilocular ovary, parietal placentation and the frequently more or less inferior ovary in the Gesneriaceae. The Orobanchaceae are sometimes regarded as a parasitic degenerated group of the Gesneriaceae. Hence, the family is placed near Scrophulariaceae by taxonomists.

Belseriaceae, Cyrtandraceae, Didymocarpaceae, Ramondiaceae, Replicataceae are the segregates from the family.

LENTIBULARIACEAE

Plants of this family are insectivorous herbs found in aquatic or wet habitats. The Lentibulariaceae consist of 5 genera and nearly 200 species of cosmopolitan distribution. Utricularia (Bladderwort) with about 150 species form the largest genus followed by Pinguicula (Butterwort) with 35 species.

The Lentibulariaceae resemble the Scrophulariaceae in the zygomorphic flower, reduction in the number of stamens, the median position of the carpel and the capsular fruit. But they are distinguished by the unilocular ovary with free central

placentation and insectivorous habit.

The free central placentation found in the family prompted Kamienski (1897) and Wettstein (1935) to trace a possible relationship between the Lentibulariaceae and the Primulaceae. At present there seems, however, to be no doubt that its nearest relation are to be found among the Scrophulariaceae. The derivation of unilocular ovary with its free central placentation from the condition in Scrophulariaceae is brought out clearly by Wernham (1912). Well-developed endosperm which is characteristic of the Scrophulariaceae is present in majority of the members of the Lentibulariaceae. The relation is further confirmed by the palynological (Erdtman, 1952) and embryological studies (Reayat Khan, 1954). Added to this Wieffering (1966) visualised a chemical affinity between the Scrophulariaceae and the Lentibulariaceae in the presence of iridoids. Significantly in both these families aucubin seems most often to be accompanied or replaced by catalpol and other aucubin-like glycosides.

It is now generally agreed that the Lentibulariaceae are derived from the Scrophulariaceae. Pinguiculaceae and Utriculaceae are the segregates from the family.

BUDDLEJACEAE

Unlike Scrophulariaceae plants belonging to the Buddlejaceae are usually shrubs or trees with regular tetramerous flowers; however, a trend towards zygomorphy is

observed in some of its members such as Sanango. Apart from these characters the family share morphological characters with the Scrophulariaceae.

The family Buddlejaceae consists of about 10 genera and 150 species, mainly tropical and subtropical. Buddleja is the largest genus with about 100 species.

Morphological and anatomical characters prompted Melchior (1964) to separate the Buddlejaceae from the Loganiaceae. Rendle (1938) suggested that the toothed leaves and falsely tetramerous flowers of these taxa indicated an affinity with the scrophulariaceae. An additional chemical support to this view was lent by Harborne (1966) and Bate-Smith (1966) based on the presence of aucubins, Daniel and Sabnis (1979) supported the elevation of the family, but called for its retention within Gentianates along with Loganiaceae and Oleaceae. The Serological studies of Piechura (cf. Cronquist, 1981) highlighted the strong affinities between the Buddlejaceae and the Scrophulariaceae. This is further endorsed by the palynological similarities (Cronquist, 1981). Sanango stands as a transitional genera.

OLEACEAE

Plants belonging to this family usually are arborescent with cosmopolitan distribution. The family consists of about 300 genera and 600 species with Jasminum (200) and Chionanthus (150) as the dominant genera. The plants are morphologically similar to members of the Scrophulariaceae but for the 4-lobed corolla which is essentially regular.

The affinities of the Oleaceae are debatable. The treatment of the family in Ligusterales by Tournay and Lawalree (cf. Cronquist, 1981) along with Menyanthaceae is contradicted by Cronquist (1981). He opined in favour of the inclusion of the family in Scrophulariales since the plants are similar to the members of Buddlejaceae.

Traditionally the family has been placed in Gentianales where they are anomalous in embryological features, in having only two stamens and in not having internal phloem. However, the chemical features such as the abundant presence of flavonols and steady representation of iridoids strongly favour its retention with Gentianales itself (Daniel and Sabnis, 1987). Thus the placement of the family either in Gentianales or Scrophulariales is difficult and therefore appears to form a link between the two orders. The serological studies on these families further strengthen this view (Piechura, cf. Cronquist 1981).

Bolivariaceae, Forestieraceae, Fraxinaceae, Jasminaceae Liliaceae, Nyctanthaceae, Syringaceae, Turbinaceae are the segregates from the family.

ACANTHACEAE

The plants of the family are having very diverse habitats and include some mangrove species also. The

Acanthaceae diverge from the Scrophulariaceae primarily in their explosively dehiscent fruit and specialized funiculus. Furthermore, the loss of endosperm and development of cystoliths are other distinguishing characters.

Widespread in tropical regions, the family Acanthaceae consists of about 250 genera and 2500 species. More than half of the species belong to only 7 genera. They are Justicia (300), Ruellia (250), Barleria (250), Strobilanthes (200), Thunbergia (200), Dicliptera (180) and Aphelandra (150).

There are differences of opinion regarding the circumscription of the family. Benthams and Hooker (1862-83) divided the Acanthaceae into tribes such as Thunbergieae, Nelsonieae, Ruellieae, Acanthoeae and Justicieae, Lindau (1895) divided the family into Thunbergioideae, Mendoncioideae, Nelsonioideae and Acanthoideae. On morphological grounds, Mohan Ram and Wadhi (1965) elevated the sub family Thunbergioideae to a distinct family and was ably supported by Chaubal (1966) and Sahi and Dixit (1969). However, this contention was contradicted by Cronquist (1981), who found Mendoncioideae more distinctive in the family and elevated the same to a separate family Mendonciaceae.

Bremekamp (1953) advocated the transfer of the subfamily Nelsonioideae from the Acanthaceae to the Scrophulariaceae due to the similarities in the albuminous seeds and the loculicidal

capsule of the Nelsonioideae to the tribe Rhinanthae of the latter family. Palynological evidences (Chaubal, 1966; Raj, 1961) supported Bremekamp's view but embryological (Mohan Ram and Wadhi, 1965; Johri and Singh, 1959) and morpho-anatomical characters (Ahmed, 1974a) are not in favour.

Cronquist (1981) opined that the traditional line between the Scrophulariaceae and Acanthaceae is purely arbitrary, but it seems as good as any other and the connecting forms are not numerous enough to warrant uniting the two families.

The Nelsonioideae and Thunbergioideae represent way-station along the route between the two families Acanthaceae and Scrophulariaceae.

BIGNONIACEAE

Members of the family Bignoniaceae are predominantly woody in nature. More than 100 genera and perhaps 800 species are included in this family which is best developed in tropical regions. Tabebuia with about 100 species is the largest genus.

The family is similar to Scrophulariaceae in their floral traits. However there is difference in habit and seed characters. The Bignoniaceae are characterized by winged and non-endosperms seeds as against many, small and endospermous seeds of the Scrophulariaceae.

Solanaceae is divided into two subfamilies Curvembryae and Rectembryae (Endlicher, 1841) which in due course of time are renamed as the Solanoideae and Cestroideae respectively. The subfamily Solanoideae is characterized by primitive floral vasculature, accrescent calyx, actinomorphic corolla, five stamens inserted low in the corolla tubes, small stigmas, baccate fruits, compressed seeds, an embryo uniform in diameter, a chromosome base number 12 and stenopalynous type of pollen.

The subfamily Cestroideae is characterized by reduced vasculature, calyx not accrescent, corolla often zygomorphic, four or fewer stamens inserted high in the corolla tube, elaborate stigmas, capsular fruits, prismatic seeds, cotyledons frequently wider than the rest of the embryo, chromosome number various but seldom 12 and eurypalynous type of pollen.

The tribe Salpiglossideae having zygomorphic corolla was elevated to a family by Hutchinson (1969) who considered it as an intermediate taxon between the Solanaceae and the Scrophulariaceae. Serological tests, however, favour the retention of this tribe within Solanaceae itself (Cronquist, 1981).

The family is placed in different orders by different taxonomists. Thus Endlicher (1836-40); Hallier (1912); Wettstein (1935); Rendle (1938); Melchior (1954) and others in Tubiflorae; Bentham and Hooker (1876); Bessey (1915);

Gates (1940); Benson (1957); et al. in Polemoniales; Lindley (1853); Boivin (1956); Thorne (1968), Hutchinson (1969); Cronquist (1981); Dahlgren et al. (1981) in Solanales; Grisebach (1854) and Soo (1953) in Personatae and Takhtajan (1969) in Scrophulariales.

Certain genera of Solanaceae are related to various members of the Boraginaceae, Gesneriaceae and Nolanaceae, and it seems that the family is not a simple monophyletic family. They seem to occupy a middle place in the Tubiflorae between those with actinomorphic and zygomorphic corolla.

Atropaceae, Cestraceae, Duckeandraceae, Goetzeaceae, Narcaceae, Retziaceae, Salpiglossideaceae and Sclerophyllaceae are some of the segregates from the family Solanaceae.

Although scattered data from various disciplines including chemistry are available for the family Scrophulariaceae and its allies, these are not sufficient to set at rest various controversies regarding the taxonomic limits of the Scrophulariaceae and the taxa within as also the relationship of the central Scrophulariaceae with the peripheral allied families. These gaps in our detailed knowledge of the taxa is sought to be partially filled in this project with the chemical investigation of 72 plants of the Scrophulariaceae involving flavonoids, phenolic acids, quinones, alkaloids,

tannins, saponins and iridoids. The distribution pattern of the chemical characters in conjunction with data from various disciplines is used in solving certain taxonomic controversies within the family, in assessing the inter-relationships of the Scrophulariaceae with other supposedly related families and in deducing the phylogeny of various taxa. Members of the Pedaliaceae (2), Orobanchaceae (2) Gesneriaceae (1) and Lentibulariaceae (3) were screened for comparison to assess their affinity with the Scrophulariaceae. All the families grouped in the order Scrophulariales (Cronquist, 1981) viz. the Scrophulariaceae, Acanthaceae, Bignoniaceae, Pedaliaceae, Orobanchaceae, Lentibulariaceae, Gesneriaceae, Buddlejaceae, Oleaceae, Globulariaceae and Myoporaceae have been subjected to a cladistic treatment, to understand their probable ancestry and relationships. Some Solanaceous members (22) were also analysed to ascertain the position of the solanaceae vis-a-vis the Scrophulariaceae. The main objectives of the present project are as follows:

- 1) Understanding the chemical complexity within the family scrophulariaceae.
- 2) Assessment of the taxonomic validity of the subfamily Pseudosolaneae, which is considered as a connecting link between Scrophulariaceae and Solanaceae.
- 3) Assessment of the identification of the two widely accepted subfamilies Antirrhinoideae and Rhinanthoideae of the Scrophulariaceae (Pennell, 1935) and their evolutionary status mainly on chemical grounds.

- 4) Attempt to understand the evolutionary trends operating in various tribes within each of the subfamilies and to evaluate the evolutionary levels achieved by the tribes as well as genera.
- 5) Reassessment of the systematic position of non-parasitic tribe Digitaleae and the parasitic tribes Gerardieae and Euphrasieae in the subfamily Rhinanthoideae.
- 6) Validity of the creation of the monogeneric tribe Russelleae and its separation from the tribe Cheloneae as proposed by Thieret (1967).
- 7) Validity of the subtribal divisions of the Gratiroleae and Digitaleae as done by Bentham and Hooker (1876).
- 8) Assessment of the generic status of
 - (a) Lindernia and Torenia.
 - (b) Linaria and Kickxia.
- 9) Evaluation of the subtribal segregation of Antirrhinum and Linaria within the tribe Antirrhineae.
- 10) Examination of the proposed relationship of Scrophularia (tribe cheloneae) with Verbascum (tribe Verbasceae).
- 11) Shifting of the genus Scoparia from the Digitaleae (Rhinanthoideae) to the Gratiroleae (Antirrhinoideae).
- 12) Understanding the taxonomic placement of the genus Lindenbergia.
- 13) To assess the relevance of shifting the genus Sutera from the Manuleae to the Gratiroleae.
- 14) To examine the chemical nature of the family Solanaceae and its probable relationship with the Scrophulariaceae.

- 15) To trace out the relation of the tribe Salpiglossideae of Solanaceae (which is often considered as ancestral to the Scrophulariaceae) with the Pseudosolaneae (Scrophulariaceae)
- 16) Brief understanding of the chemical nature of the Pedaliaceae, Orobanchaceae, Gesneriaceae and Lentibulariaceae and their relationship with the Scrophulariaceae.
- 17) To assess the validity of the separation of Martyniaceae from the Pedaliaceae.
- 18) To assess the relationship of the families Buddlejaceae, Oleaceae, Acanthaceae, Bignoniaceae, Globulariaceae and Myoporaceae with the Scrophulariaceae by analysing the previous chemical report.
- 19) To trace out the probable evolutionary trends within Scrophulariales with the help of cladistic analysis.