

FOLIAR ANATOMY OF SCROPHULARIACEAE AND ACANTHACEAE

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ABSTRACT

The survey comprises representatives of the two families of the Order Tubiflorae, viz. Scrophulariaceae and Acanthaceae. In the former, the node is uniformly unilacunar. The number of strands entering the petiole may be one, three or even more. Two distinct types of venation patterns are recognizable. The leaves have been classified under two groups on the basis of distribution of tracheidal elements which have been further sub-divided into those possessing dense, medium, and feeble venation. The family is characterized by uniformly anomocytic stomata but a few forms such as *Russelia coccinea* and *R. sarmentosa* also possess anisocytic ones. The trichomes are of non-glandular and glandular types. Crystals, resembling cystoliths, occur in *Lindenbergia macrostachya*. Three species of the genus *Anticharis* investigated showed bundle sheath cells around the veins. The investigated members of the Acanthaceae also possess an uniformly unilacunar node and three types of venation. The stomata are uniformly diacytic. Trichomes of both glandular and non-glandular types have been seen. In Barlerieae the unicellular, non-glandular trichomes occur in tufts. Characteristic cystoliths, either single or in groups of two, have been recorded for most of the taxa investigated. This shows that the foliar characters are indicative of certain trends in these families and thus serve as valuable adjuncts to other criteria, in part confirming the accepted arrangements and in part conflicting with them.

INTRODUCTION

The family Scrophulariaceae was established by A. L. DE JUSSIEU in the year 1789 and has since been placed in different orders like the Polemoniales (GUNDERSON, 1959), Tubiflorae (LAWRENCE, 1951), and Personales (HUTCHINSON, 1959). On the basis of morphological studies, particularly the floral organization, anatomy and embryology of some taxa of the family, its systematic affinity has been indicated with Bignoniaceae, Acanthaceae, Verbenaceae, Solanaceae, Lentibulariaceae, Gesneriaceae and Orobanchaceae. The overall weight of evidence, however, tends to suggest that Orobanchaceae is its nearest relative.

With regard to the taxonomic assignment of the taxa within the family, a far-reaching suggestion was put forward by BREMEKAMP (1953) who transferred the subfamily Nelsonioideae of the Acanthaceae to the subfamily Rhinanthoideae of the Scrophulariaceae. RAJ (1961) and CHAUBAL (1966) supported this arrangement on palynological grounds. However, JOHRI AND SINGH (1959), MOHAN RAM AND MASAND (1963) and MOHAN RAM AND WADHI (1965) have repeatedly contradicted this approach on the basis of embryological studies of a number of acanthaceous taxa. Furthermore, VARGHESE (1967) who investigated the floral anatomy of several species of the family has suggested that *Calceolaria* should be recognized as a separate subfamily in consideration of its peculiar endothecium and the inferior ovary.

In the earlier publications of the series, KUMAR AND PALIWAL (1975; 1977a, b; 1978; 1980a, b), have outlined the variations in the leaf anatomy and the nodal anatomy of these two families. The present article aims at indicating the impact of these charac-

ters for supporting or rejecting the assignment of the taxa studied within the respective families, as well as their interrelationships.

A. SCROPHULARIACEAE

HUCHEDE (1907) was the first to analyse the tissue organization in a number of species of this family exhibiting both herbaceous and shrubby habit. Later, SOLEREDER (1908) reported the presence of tanniferous sacs which occur either singly or in groups in the mesophyll cells of the leaves of several taxa. ADAMSON (1910) attempted a comparative analysis of the leaf anatomy of certain veronicas as a follow-up of the work referred to earlier.

SINNOTT (1914) in his detailed review made a mention of some taxa of this family and indicated that they possess a unilacunar node. However, in *Nemesia*, he reported that the unilacunar condition is brought about only later since three distinct gaps fuse into one and leading to the broad, arch-like leaf trace. VARGHESE (1963, 1966) has investigated the foliar venation of a few representatives of the various tribes of the family and showed that their venation pattern can be of taxonomic value only when used along with other characters. Moreover, some minute characters of the leaves—like the accumulation of the tracheids and the presence or absence of tracheidal nodules, taken singly, appear to have significant value for separating the species from each other. This trend, however, needed further investigation and confirmation in a wider number of representatives.

The present study covers 91 species of the family in respect to the above features, the subfamilies, tribes, and subtribes having been grouped according to MELCHIOR (1964). In the earlier publications of the series, we have outlined details of the various features examined.

NODE

The node is uniformly unilacunar providing a constant feature. The strands entering the petiole may be one, three, or even more. Two major categories of venation are recognizable : (i) pinnate, camptodromous, brochidodromous, for the leaves having entire margins and (ii) semicraspedodromous for those with serrate margins. The areoles measure from 0.4 to 20.5 mm² with quadrangular to polygonal outline. These are well organized, oriented, with simple, linear, curved, or branched (once, twice or thrice vein endings).

BUNDLE SHEATH

Three species of the genus *Anticharis* show the presence of bundle sheath cells. The cells composing the sheath are thin-walled and rectangular in outline. Besides this feature, species of some genera like *Anticharis*, *Barsia*, *Cordylanthus*, *Euphrasia* and *Pedicularis* possess accumulation of tracheids, localized at the apices, and vein endings. At places, some cells situated towards the inner side of the group become converted into nodules while others continue to remain thin-walled. The feature referred to above (tracheidal accumulation) has made it possible to place the genera into two major groups: with accumulation and without accumulation. Further division into feeble, medium, and dense venation categories is also suggestive which helps in arriving at probable affinities.

EPIDERMIS

A survey of the dermal features has shown that the characters which can be successfully employed for distinguishing various species from each other include the configuration of the epidermal cell walls, diverse types of trichomes, and stomata dispersed all over the leaf surfaces. Information based on the lower epidermis only has been presented. In general, the cells of the lower epidermis are polygonal to irregular in outline with arched to highly sinuous walls. The frequency of the cells is also quite variable. Ornamentations in the form of depositions occur on the ridges of the epidermal cell walls in *Mazus japonicus* and cuticular striations in all the species of *Penstemon* and *Scrophularia chinensis*. Anomocytic stomata are more common whereas those of anisocytic type were observed in *Russelia coccinea* and *R. sarmentosa*. The stomatal index for the taxa investigated ranges from 6.06 to 75.00. As many as five types of trichomes have been observed, i.e. unicellular, uniseriate multicellular, branched multicellular, glandular type with unicellular and multicellular uniseriate stalk. Of these unicellular trichomes occur in the maximum number of species.

From the present study, the correlation between copious tracheidal accumulation and xeromorphic features becomes strengthened. This is also borne out by the observations that predominantly the species with medium or feeble venation possess marked accumulation of tracheidal elements at vein endings in the areoles, at the apices and at the margins. The leaves with dense venation pattern are either without the accumulation or, if it is present at all, it is very scanty, whereas in aquatic forms, like *Limosella aquatica*, the areoles are quite large but without accumulation.

SYSTEMATIC CONSIDERATIONS

Both on embryological and palynological grounds, the family has been associated with Acanthaceae, Bignoniaceae, Solanaceae, and Verbenaceae by ERDIMAN (1952), FAROOQ (1962), KHAN (1954), and KRISHNA-IYENGAR (1947). On the basis of anatomical features it shows resemblances with Bignoniaceae in having similar type of unicellular and branched multicellular trichomes as well as cuticular striations. Identical trichomes occur in members of the family Verbenaceae also. The hydathode-like structure of Bignoniaceae can also be compared with the so-called 'hydathodes' of Scrophulariaceae. The anatomical characters of Scrophulariaceae do not go much with Acanthaceae as they share only the presence of unilacunar node, while in the rest of the characters, such as stomatal ontogeny and organization, types of trichomes, cystoliths, etc. differ markedly. Solanaceae is yet another family which resembles the scrophulariaceous taxa in the occurrence of cuticular striations (see AHMAD, 1972) in which the stomatal types are the same. There is also great similarity in the non-glandular and glandular trichomes. Thus, its proximity to Scrophulariaceae much more than any other family of the order, as proposed by MELCHIOR (1964), is substantiated. With Lentibulariaceae it does not show much resemblance excepting the presence of identical hydathodes.

VARGHESE (1967) described the floral anatomy of *Calceolaria pinnata* and derived to give it a subfamily rank. His statement does not get support on anatomical grounds and we believe that it can still be maintained in the tribe Calceolarieae.

DUTTA AND DEB'S (1975) inclusion of *Scoparia dulcis* under Gratiolleae is, however, upheld. But the transposition of *Sutera* under Gratiolleae is not borne out. The separation of *Calceolaria mexicana* and *Russelia equiestiformis* as proposed by these authors is also negated on features like single-stranded condition and non-accumulation of tracheids.

PENNELL's plan for considering Gratioleae most primitive, Antirrhineae fairly advanced, and Rhinanthaeae most highly evolved, gets full support on characters of venation.

On the whole, therefore, the features which characterize the family Scrophulariaceae (from the leaf anatomical point of view) are : unilacunar node, one, three or several strands entering the petiole, two types of venation patterns pinnate (camptodromous, brochidodromous), and semicraspedodromous, well-organized areoles with vein endings ornamented in forms having tracheidal accumulations, anomocytic type of stomata, and branched multicellular type of trichomes. These form a good basis, worthy of consideration, in any taxonomic grouping.

B. ACANTHACEAE

Recently, AHMAD (1974a-d; 1975) has exhaustively described the characters of 102 species belonging to 39 genera, arranged according to LINDAU (1895), and included subfamilies Nelsonioideae, Mendoncioideae, Thunbergioideae, and Acanthoideae. According to him, the family is characterized by diacytic stomata which differentiates it from all other families of the order Tubiflorae except the Verbenaceae and Labiatae. Furthermore, the epidermal cells, the glandular hairs, and the lithocysts (referred to as cystoliths by AHMAD) are of variable shapes and sizes and these have bearing in systematic considerations. SINGH AND JAIN (1975) have also recorded 40 type of trichomes on the floral appendages of 41 species of the Acanthaceae and studied their distribution.

LEAF MORPHOLOGY

The leaves of most of the species are simple with small or long petiole, a few forms being sessile. The lamina shows considerable range in size whereas shape varies from linear to oblong, ovate, obovate with entire, serrate and wavy margin. The apex may be acute, obtuse, or acuminate. The presence of spines at the tips of entire and serrate margins in forms like *Acanthus ilicifolius*, species of *Barleria*, *Blepharis indica*, and *Lepidagathis cuspidata* denotes xerophytic nature of leaves.

NODAL ORGANISATION

A survey of several representatives belonging to the two subfamilies, *viz.*, Thunbergioideae and Acanthoideae has revealed that the node is uniformly unilacunar.

VENATION PATTERNS

Three types of venation pattern have been recorded—pinnate (camptodromous brochidodromous), semicraspedodromous, and campylodromous. The areoles are well organized and their areas range from 28.00 to 30.66 mm² and the areole may vary from quadrangular to polygonal, with simple, linear, curved or branched (once or twice) vein endings.

EPIDERMIS

The epidermal cells possess straight to variously arched to sinuous walls. The stomata are uniformly diacytic which have proved extremely useful in distinguishing its representatives from members of the related families, especially the Scrophulariaceae and Solanaceae.

Trichomes can be easily divided into 4 major categories : non-glandular—unicellular (single or in tufts), multicellular; glandular—glandular head with subsessile

stalk and glandular with multicellular stalk. Both unicellular and multicellular, non-glandular trichomes generally possess pointed apices and various kinds of ornamentations. Cystoliths are present in all the forms except two subfamilies—the Nelsonioideae and Thunbergioideae and the subtribe Acanthinæ (except for two species of *Thunbergia*, viz. *T. coccinea* and *T. grandiflora* var. *laevis*). The number of cystoliths ranges from 0.69 to 16.59 per mm² and these may be simple or of variable shapes and sizes (round, elongated with blunt or pointed extremities); two or several of these may also be placed together to form chains.

SYSTEMATIC CONSIDERATIONS

On the basis of foliar anatomy, the transfer of Nelsonioideae (of LINDAU) to Scrophulariaceae, as suggested by BREMEKAMP (1953, 1965), RAJ (1961), and CHAUBAL (1966), is not supported by our observations on *Elytraria acaulis* and *Nelsonia campestris*. On the other hand, these taxa show close affinity to *Thunbergia* (Thunbergioideae), since they possess diacytic stomata, characteristic of Acanthaceae (in Scrophulariaceae the stomata are anomocytic and, occasionally, anisocytic). We would, therefore, tend to agree with JOHRI AND SINGH (1959), MOHAN RAM AND MASAND (1963), NAFDAY (1964, 1965), PALIWAL (1966, 1967, 1969), and AHMAD (1974a).

With regard to the controversy whether the subfamily Thunbergioideae should be regarded as a tribe of Acanthaceae as proposed by BENTHAM AND HOOKER (1876) and HUTCHINSON (1926), or raised to the family rank as assigned by MAURITON (1934), BREMEKAMP (1953, 1965), MOHAN RAM AND WADHI (1965) and CHAUBAL (1966), it is indicated that the species of *Thunbergia* examined in the present work show similarity with Nelsonioideae and Acanthoideae in possessing unilacunar node, but differ from Acanthoideae in the absence of cystoliths (except for *T. coccinea* and *T. grandiflora* var. *laevis* which has cystoliths). Besides, the venation pattern is midway between the Nelsonioideae and Acanthoideae. Furthermore, the non-glandular hairs of *Thunbergia* are broadly similar to those of the other Acanthaceae coupled with the diacytic stomata. Taking into account all the above points, a subfamily status for Thunbergioideae, like Nelsonioideae and Mendoncioideae (within Acanthaceae) appears to be the best course to follow.

Reverting to LINDAU's subfamily Acanthoideae, one finds that it is a large group and shows considerable diversity. He had, therefore, himself proposed its division into two groups, viz. Contortae and Imbricatae, on the basis of aestivation of the corolla lobes. Evidently, this was in contrast to BENTHAM AND HOOKER's (1876) earlier attempt to divide the family Acanthaceae into five tribes out of which three, namely Ruellieae, Acantheae, Justiceae, together corresponded to LINDAU's Acanthoideae. However, BREMEKAMP's Acanthaceae corresponded to LINDAU's subfamily Acanthoideae alone. Present investigation supports this division since the cystoliths are present in Ruellioideae and absent in the Acanthoideae. Thus delimited, BREMEKAMP's Acanthaceae is broken up into subfamilies Acanthoideae and Ruellioideae which are subdivided into five and seven tribes, respectively.

BREMEKAMP (1944) also remarks that as delimited at present the genus *Strobilanthus* Blume betrays its artificiality by its wide range of variability. Using pollen morphology and some megascopic characters, he has split it into several genera. We have examined twelve species of *Strobilanthus* representing six new genera of BREMEKAMP. The anatomical characters of these species do not show any striking dissimilarities which would help

us to support this attempt. Among the common features are : single-stranded vasculature in the petiole and camptodromous, brochidodromous and semicraspedodromous nature of the foliar venation. In most of the species the non-glandular hairs on the lower epidermis are restricted to the costal and marginal areas having hair bases of two to several polygonal cells and a broad pore. The cystoliths are simple or sometimes even curved. We are, therefore, inclined to disagree with the delimitation as suggested by BREMEKAMP (from an artificial status to natural one).

A word may be stated with regard to *Barleria* and *Lepidagathis* which have been grouped in different subtribes, under the tribe Justicieae, by BENTHAM AND HOOKER (1876). On the other hand, LINDAU (1895) places these in the tribe Barlerieae. BREMEKAMP (1953, 1965) assigns them to independent tribes Ruellieae and Lepidagathidae, respectively. CHAUBAL (1966) also believes that the removal of *Lepidagathis* from LINDAU's Barlerieae to a separate tribe is justified on the basis of pollen morphology. According to the present analysis, the most important character—distinguishing *Barleria* from *Lepidagathis* and other genera of the Acanthaceae, is the occurrence of double cystoliths in the former. Also, the non-glandular hairs of *Barleria* are of a characteristic (ornamental) type. Epidermal characters thus appear to support the above attempts to place *Barleria* and *Lepidagathis* into separate tribes. Similarly, the present findings support DE (1967) for the separation of *Acanthus* and *Grossandra* on the basis of presence of cystoliths and absence of glandular hairs in the latter and their absence in the former. Furthermore, BENTHAM AND HOOKER's inclusion of *Grossandra* with *Barleria* into Barlerieae can be justified on the basis of presence of cystoliths in both. However, the type of cystoliths—double and in chains—are characteristic of *Barleria* (not seen in *Grossandra*). Besides, the sinuous course of the venation of *Grossandra* is also a distinct feature. With regard to *Adhatoda vasica*, whose independent status *vis-a-vis* *Justicia* has been variously debated, it can be put forth that the accumulation of tracheids does not seem to support this contention. Moreover, its cystoliths are also simple and not very long. We, therefore, conclude that *Adhatoda* should be treated as a separate genus.

Thus, the features which characterize the family Acanthaceae are : unilacunar node, a single prominent strand entering the lamina, pinnate (camptodromous, brochidodromous), and semi-craspedodromous venation patterns, diamesogenous type of stomata, presence of both glandular and non-glandular trichomes, unicellular non-glandular trichomes with ornamentation and in tufts (Barlerieae), and cystoliths of characteristic shapes and arrangement.

It can, therefore, be concluded that on foliar anatomical grounds, the families Scrophulariaceae and Acanthaceae are quite distinct from each other and there is no justification for removing the tribe Nelsonioideae from Acanthaceae to Scrophulariaceae.

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