

FOLIAR VENATION AS AN AID TO THE SYSTEMATICS OF SCROPHULARIACEAE, I. THE TRIBES DIGITALEAE, GERARDIEAE AND EUPHRASIEAE (SERIES RHINANTHEAE)

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ABSTRACT

On the basis of the number of strands entering the petiole or the base of the lamina, the eighteen investigated species of the Series Rhinanthae (family Scrophulariaceae) can be broadly classified into three categories—single, tri-, and pentastranded. Leaves with a single strand are more numerous, followed by the tri- and penta-stranded conditions. Differences have been noticed in the venation organization not only within the tribes but also in the various species of some genera such as *Veronica* and *Pedicularis*. It is invariably pinnate in all the representatives which can be further grouped into camptodromous types. Variations have also been recorded regarding the size and structure of the areoles and nature of vein-endings. A comparative analysis has been presented of these characters in the families Acanthaceae and Scrophulariaceae—especially the series Rhinanthae—to ascertain its value in the systematics of these families which have long been debated in the literature.

INTRODUCTION

VON ETTINGHAUSEN (1861), as a result of his pioneering work, ascribed important venation characters to be used in studying the taxonomy of fossil leaf forms. Later, FOSTER (1950a, b), in a series of papers dealing with foliar venation emphasized the use of diagnostic characters of venation of living taxa. Leaf venation has also been proposed as a tool for interpreting palaeoclimatic vegetation. MANZE (1968) considered the abundance of fine veins in relation to numerous environmental variables such as sun *versus* shade, north *versus* south facing, height, and moisture. He correlated density of fine venation with relative humidity and found that leaves of a species may exhibit quite different densities of fine venation dependent upon certain environmental factors.

This report is a part of the studies on the leaf anatomy of some scrophulariaceous genera carried out at this laboratory. The family has been chosen because of the controversy that centers around the various sub-families included in the Scrophulariaceae as well as on the various taxa included in them. In an attempt to rationalize these ideas, BREMEKAMP (1953) transferred sub-family Nelsonioideae of the family Acanthaceae to sub-family Rhinanthoideae of Scrophulariaceae on the basis of the presence of a well-developed endosperm. According to him, in both *Elytraria* (Nelsonioideae) and Rhinanthae, the early segmentation of endosperm corresponded to the *Pedicularis* type. However, in its later growth both differ fundamentally. JOHRI AND SINGH (1959), MOHAN RAM AND MASAND (1963), and MOHAN RAM AND WADHI (1965) held that the morphology and embryology of *Elytraria* agree in general with the other members of Acanthaceae and therefore, the transfer of *Elytraria* to the Rhinanthae is not warranted. Contrarily, RAJ (1961) and CHAUBAL (1966) supported the viewpoint of BREMEKAMP on the basis of palynological characters. NAFDAY (1964-65) also reached the same conclusion from anatomical investigations of the

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genus. PALIWAL (1966, 1967), investigated the ontogeny of stomata in *Elytraria* and several other members of the Acanthaceae and found a close resemblance among them. AHMAD (1972) indicated that all genera which belong to the Nelsonioideae are characterized by diacytic stomata, panduriform glandular hairs, and the absence of cystoliths. According to him these and other epidermal features are similar to those of the Acanthaceae in general and show an important difference from those of the Scrophulariaceae (Rhinantheae included). KUMAR AND PALIWAL (1975) also support this contention.

The present study deals with the foliar venation of 18 species of the family and has been undertaken to supplement our knowledge of the vasculature of the representatives of the Rhinanthaeae. For the descriptive terminology of leaf form and venation patterns, suggestions made by VARGHESE (1969) have been combined with the more recent, comprehensive and handy systems proposed by HICKEY (1973) and DILCHER (1974). Attempts have been made to see as to how far the foliar venation can help us in tracing the systematic position.

MATERIAL AND METHODS

The leaves employed for the present study were obtained from Meerut College, Botany Department Herbarium, Delhi University Botany Department Herbarium, and Botanical Survey of India, Dehra Dun. Table 1 shows the various taxa studied and localities of collection :

Table 1

Tribe	Name of the species	Locality
Digitaleae	<i>Hemiphragma heterophyllum</i> Wall.	Kedarnath, Uttar Pradesh
	<i>Scoparia dulcis</i> L.	Pachmarhi, Madhya Pradesh
	<i>Picrorhiza kurrooa</i> Royle	Tunganath area
	<i>Wulfenia amherstiana</i> Benth.	Rawalpindi, Pakistan
	<i>Veronica agrestis</i> Linn.	Azadpur, Delhi
	<i>V. anagallis</i> Linn.	Lucknow, Uttar Pradesh
	<i>V. serpyllifolia</i> Linn.	Timarpur, Delhi Chhota Simla, Himachal Pradesh
Gerardieae	<i>Buchnera hispida</i> Ham.	Pachmarhi, Madhya Pradesh
	<i>Striga lutea</i> Lour.	Chakrata, Uttar Pradesh
	<i>S. euphrasioides</i> Benth.	Pachmarhi, Madhya Pradesh
	<i>Ramphicarpa longiflora</i> (Benth.) Benth.	Hastinapur, Delhi
	<i>Centranthera hispida</i> Br.	Purandhar, Maharashtra
	* <i>Leptorhabdos benthamiana</i> Walp.	Ranikhet, Uttar Pradesh
	<i>Leptorhabdos parviflora</i> (Benth.) Benth.	Ranikhet, Uttar Pradesh
<i>Sopubia delphinifolia</i> (Linn.) G. Don	Kashmir	
Euphrasiaeae	<i>Euphrasia officinalis</i> Linn.	Purandhar, Maharashtra
	<i>Pedicularis carnosus</i> Wall.	Badrinath, Uttar Pradesh
	<i>P. zeylanica</i> Benth.	Mussoorie, Chakrata, Uttar Pradesh
		Bharatpur, Rajasthan

*According to some recent workers this species is synonymous to *L. parviflora*.

Dried leaves were soaked in hot water for about half an hour. These were transferred to a 2.5 per cent aqueous solution of NaOH at 37-40°C in an oven till all the pigments got bleached out. The leaves were then rinsed thoroughly with distilled water to remove alkali and brought in a mixture of saturated aqueous solution of chloral hydrate and hydrogen peroxide (1 : 1). When these became transparent, they were again brought to water through a graded series of chloral hydrate solution. They were washed thoroughly with distilled water and dehydrated in an usual manner by passing through alcoholic series. Staining was carried out in safranin dissolved in a mixture of absolute alcohol and xylene. The preparations were mounted in piccolyte.

OBSERVATIONS

Tribe—DIGITALAE

Considerable variation exists in the size of the leaves. They are all symmetrical and microphyllous* except that of *Veronica serpyllifolia* (Table 2). Their form is variable with acute or obtuse apex and a broad narrow base. The margin is toothed except in *V. serpyllifolia* with serrate, acute or obtuse type of dentations extended to the complete margin or upper half of the blade. The attachment wherever present is normal. The strands entering the petiole may be three or five except *V. anagallis* and *V. serpyllifolia* where a single-stranded condition has been recorded.

The venation is of pinnate camptodromous, brochidodromous, semicraspedodromous type. The primary or 1° vein is weak or moderate and follows a straight or markedly curved course (Table 3). Secondary or 2° veins have acute or moderate divergence except in *V. serpyllifolia*, being curved abruptly and these are usually fine or moderate in thickness. The inter-secondary vein if present is composite or simple. The tertiary or 3° vein shows a variable pattern. It may be in alternate, opposite or right angle type of relationship to the midrib, with a variable arrangement (Text-fig. 1 A-D).

The areoles are imperfect or well-developed, polygonal, usually large except in *Wulfenia amherstiana* (Text-fig. 3D) with a random or oriented arrangement. The veinlets are branched (once, twice or thrice) except in the leaves of *Veronica anagallis* (Table 4 ; Text-fig. 3 A-G). The ratio between the size of lamina and areole is variable (Table 4).

Tribe—GERARDIEAE

The leaves show considerable variation in their size and are symmetrical, nanophyllous or microphyllous except in *Leptorhabdos benthamiana* (Table 2). They also vary in form with acute or obtuse apex and cuneate base except those of *Ramphicarpa longiflora*. The margin is variable with serrate, acute dentation and an acute apex lobe which may be obtuse or extended to the upper half of the blade. The attachment—whenever existing—is normal.

Usually only one (Table 4) strand enters the petiole. In some cases, however, a smaller one also joins from below. The leaves show pinnate type of venation with variation in details (Table 3). The primary or 1° vein is moderate or stout and markedly curved. Secondary or 2° veins are moderate or diverged at right angle except in *Sopubia delphinifolia*, curved abruptly and fine or moderate in thickness. The intersecondary vein if present is simple or composite. Tertiary or 3° veins shows a variable pattern and relationship to the midrib with close or distant type of arrangement except in *Striga euphrasioides* (Text-fig. 2A-E).

*Terminology after DILCHER (1974):

The areoles are well organized except in *S. euphrasioides* (Table 4 ; Text-fig. 4A). These are polygonal or quadrangular, very large with oriented arrangement except in *S. euphrasioides*. The penultimate veinlet is linear and branched except in *R. longiflora* (Text-fig. 3H, I ; 4 A-E) or simply branched (not linear) once, twice, or even thrice. The size of the lamina and areoles has been given in Table 5.

Tribe—EUPHRASIEAE

The leaves are symmetrical and microphyllous with a variable form and size, obtuse apex and acute to cuneate or obtuse base (Table 2). The margin is toothed or lobed with variable dentation extended to the entire margin. The attachment, wherever present, is normal. The number of strands entering the petiole is one (another joining it from below).

The venation is pinnate, semicraspedodromous (Table 3). The primary or 1° vein is moderate in size and curved. The secondary or 2° vein has wide divergence, curved abruptly or uniformly, moderate or fine in thickness. The intersecondary vein if present is simple. The tertiary or 3° vein shows considerable variation in pattern, relationship to the midrib and arrangement. Marked accumulation of tracheidal elements was noticed at the tips or the margin (Text-fig. 2F-H).

The areoles are well-developed, polygonal or quadrangular, very large with random or oriented arrangement (Table 4). The veinlets are linear and straight except in *Euphrasia officinalis* (Text-fig. 4 G-I) and branched once or twice. The ratio of size of lamina and areole is variable (Table 5).

DISCUSSION

On the basis of the number of strands entering the petiole, the 18 species of the Scrophulariaceae investigated in the present work can be broadly classified into three categories—single-, tri-, and penta-stranded. Leaves with a solitary strand are more numerous followed by tri- and penta-stranded conditions. Variation exists not only within the tribe but many a time also within the same genus as for instance in *Veronica* and *Pedicularis* species.

The venation in all cases is of the pinnate type. It can be grouped further into two types—camptodromous brochidodromous and semicraspedodromous, depending upon the differentiation of the secondaries in relation to the primary. Within the types variations have been recorded with regard to the size of the areoles, nature of vein-endings, and their tips per areole. The areole size differs even in the same genus, except in *Pedicularis* and *Veronica* but here also the ratio of areole and lamina size tends to be variable. In general no direct correlation could be established between the size of the areoles and number of vein-endings and their tips per areole (Tables 3-4).

A survey of the literature reveals that LEVIN (1929) attached great systematic importance to vein islet areas or size of areole based upon his study of the genera *Barosma*, *Cassia*, *Digitalis* and *Erythroxylon*. Later, HALL AND MELVILLE (1951, 1954) opined that the veinlet termination number, either alone or in conjunction with other histological characters is of taxonomic value particularly in genera having only a small number of species.

The present investigation which is based on a limited number of species tends to suggest that the size of areole and veinlet termination number vary among the genera within a limited range (may even be ascribed as specific for a species) except in *Veronica* and *Pedicularis* species. Thus, these features can be regarded to be of taxonomic significance more so in conjunction with other characters of leaf anatomy.

Table 2—Morphological characters of the leaf

Name of the species	Lamina length (cm)	Lamina area	Balance	Form	Apex	Base	Margin	Dentation	Extent of dentation	Attachment
<i>Hemiphragma heterophyllum</i>	1.1	microphyll	symmetrical	very wide, ovate	obtuse	cordate	toothed	serrate (obtuse)	on complete margin	absent
<i>Scoparia dulcis</i>	1.5	"	"	narrow, oblong	acute	acuneate	toothed	serrate (acute)	on upper margin	normal
<i>Picrohiza kurroa</i>	2.5	"	"	oblanceolate	obtuse	acuneate	toothed	serrate (acute)	on upper margin	absent
<i>Wulfenia ambersiana</i>	1.5	"	"	narrow, oblong	obtuse	acuneate	toothed	serrate (acute)	on entire margin	normal
<i>Veronica agrestis</i>	1.5	"	"	narrow, ovate	obtuse	truncate	toothed	serrate (obtuse)	on entire margin	normal
<i>V. anagallis</i>	1.5	"	"	narrow, ovate	acute	truncate	toothed	serrate (acute)	on entire margin	normal
<i>V. serpyllifolia</i>	1.3	nanophyll	"	very wide, ovate	obtuse	rounded	entire	normal
<i>Buchnera hispida</i>	1.4	microphyll	"	narrow, obovate	obtuse	acuneate	toothed	serrate (acute)	on upper margin	normal
<i>Striga lutea</i>	1.5	nanophyll	"	oblanceolate	acute	acuneate	entire	absent
<i>S. euphrasoides</i>	7.4	microphyll	"	narrow, oblong	acute	acuneate	"
<i>Raphicarpa longiflora</i>	3.0	nanophyll	"	pinnatisect	acute	normal	lobed	apex lobed, obtuse	..	absent
<i>Centranthera hispida</i>	2.5	microphyll	"	oblanceolate	obtuse	acuneate	dentated	apex lobed obtuse	..	normal
<i>Leptorhabdos benthamiana</i>	1.0	leptophyll	"	special shape needle-like	acute	acuneate	entire	absent
<i>L. parviflora</i>	2.5	microphyll	"	special shape	acute	acuneate	lobed apex	apex lobed acute	..	absent
<i>Sopubia delphinifolia</i>	2.0	microphyll	"	"	"	"	"	serrate acute	..	absent
<i>Euphrasia officinalis</i>	1.0	microphyll	"	very wide, ovate	obtuse	obtuse	toothed	"	entire margin	absent
<i>Pedicularis carnosia</i>	1.5	"	"	narrow, oblong	obtuse	acute (acuneate)	lobed	serrate obtuse	"	absent
<i>P. zeylanica</i>	1.0	"	"	obovate	obtuse	"	lobed	apex lobed obtuse	..	normal

Table 3—Venation patterns

Name of the species	Type of venation	Primary 1°			Secondary 2°		Tertiary 3°			
		Size	Course	Divergence	Course	Relative thickness	Inter-secondary	Pattern	Relationship to course to the midrib	Arrangement
Tribe Digitalaceae										
<i>Hemiphragma heterophyllum</i>	pinnate camptodromous brochidodromous	weak	straight	acute	curved abruptly	fine	..	percurrent, retrecorflexed	at right angle	alternate opposite
<i>Scoparia dulcis</i>	pinnate, semi-craspedodromous	moderate	"	"	"	moderate	..	"	alternate, opposite	approximately at right angle
<i>Picrohiza kurrooa</i>	"	"	markedly curved	moderate	"	"	composite	percurrent, recurved	"	"
<i>Wulfenia amherstiana</i>	"	"	"	"	"	"	..	percurrent, sinuous	"	"
<i>Veronica agrestis</i>	pinnate, semi-craspedodromous	weak	straight	"	"	fine	composite	"	approximately at right angle	close
<i>V. anagallis</i>	"	weak	"	"	"	"	..	percurrent, retrecorflexed	"	"
<i>V. serpyllifolia</i>	pinnate, camptodromous, brochidodromous	moderate	"	wide	"	"	simple	percurrent, sinuous	"	distant
Tribe Gerardiaceae										
<i>Buchnera hispida</i>	pinnate, camptodromous, brochidodromous	"	"	moderate	"	"	"	"	"	close
<i>Striga lutea</i>	pinnate moderate, camptodromous, brochidodromous	stout	markedly curved	right angle	"	moderate	composite	"	longitudinally	distant

<i>S. euphrasioides</i>	pinnate camptodromous, brochidodromous	moderate	straight	"	"	"	..	percurrent, straight	longitudinally parallel	alternate oppo- site in about equal propor- tion
<i>Ramphicarpa longiflora</i>	pinnate camptodromous, brochidodromous	stout	markedly curved	"	"	fine	..	percurrent, simple	"	distant
<i>Centranthera hispidula</i>	"	moderate	"	moderate	"	"	..	percurrent, sinuous	approximately at right angle	"
<i>Leptorhabdos benhamiana</i>	"	stout	"	right angle	"	"	approximately parallel	"
<i>L. parviflora</i>	pinnate, semicraspedo- dromous	"	straight	moderate	"	"	..	percurrent, retreflexed	approximately at right angles	"
<i>Sopubia delphinifolia</i>	pinnate semicraspedo- dromous	"	"	wide	"	moderate	..	percurrent, convex	"	distant
Tribe Euphrasieae										
<i>Euphrasia officinalis</i>	pinnate, semicraspedo- dromous	moderate	curved	wide	"	"	simple	..	approximately at right angle	predominately alternate joining with an offset
<i>Pedicularis car nosa</i>	pinnate semicraspedo- dromous	"	"	"	curved uniformly	fine	"	random, reticulate	approximately oblique	close
<i>P. zeylanica</i>	"	"	"	"	curved abruptly	moderate	..	percurrent, retreflexed	approximately parallel	distant

Table 4—Variation in the organization of the areoles

Name of the species	Development	Arrangement	Shape	Size	Veinlet
Tribe Digitaleae					
<i>Hemiphragma heterophyllum</i>	imperfect	random	polygonal	very large	branched once
<i>Scoparia dulcis</i>	"	"	"	large	"
<i>Picrohiza kurroa</i>	well-developed	oriented	"	very large	branched twice
<i>Wulfenia amherstiana</i>	imperfect	random	"	medium	"
<i>Veronica agrestis</i>	well-developed	oriented	"	very large	branched thrice
<i>V. anagallis</i>	"	"	"	"	linear, curved
<i>V. serpyllifolia</i>	"	"	"	"	branched once
Tribe Gerardiaceae					
<i>Buchnera hispida</i>	"	"	"	"	linear, curved and branched once
<i>Striga lutea</i>	"	"	quadrangular	"	linear and branched once
<i>S. euphrasioides</i>	imperfect	random	polygonal	"	branched twice
<i>Ramphicarpa longiflora</i>	well developed	oriented	quadrangular	"	linear
<i>Centranthera hispida</i>	"	"	polygonal	"	linear, branched once or twice
<i>Leptorhabdos benthamiana</i>	"	"	"	"	"
<i>L. parviflora</i>	"	"	"	large	branched once, twice or thrice
<i>Sopubia delphinifolia</i>	"	"	quadrangular	very large	linear, branched once
Tribe Euphrasieae					
<i>Euphrasia officinalis</i>	"	"	polygonal	very large	"
<i>Pedicularia carnosa</i>	"	"	quadrangular	"	linear, straight branched once and twice
<i>P. zeylanica</i>	"	random	polygonal	"	linear, straight branched once and twice

Table 5—Details of foliar venation

Name of the species	Lamina size sq. mm.	Areole size sq. mm.	Ratio of areole lamina size	Vein ending per areole	No. of strands entering the petiole
Tribe Digitalaceae					
<i>Hemiphragma heterophyllum</i>	90	0.8	0.009	0.9	Tri-stranded
<i>Scoparia dulcis</i>	60	0.3	0.005	0.8	Tri-stranded at the base of lamina
<i>Picrorhiza kurrooa</i>	211	0.5	0.002	0.9	5-stranded
<i>Wulfenia amherstiana</i>	150	0.2	0.001	0.7	Tri-stranded
<i>Veronica agrestis</i>	120	0.6	0.005	0.6	Penta-stranded
<i>V. angallis</i>	59	0.6	0.01	0.4	Single-stranded
<i>V. serpyllifolia</i>	24	0.3	0.01	0.4	Single-stranded
Tribe Gerardiaceae					
<i>Buchnera hispida</i>	69	0.7	0.01	0.8	Tri-stranded
<i>Striga lutea</i>	13	1.0	0.07	0.5	Single-stranded
<i>S. euphrasioides</i>	24	0.7	0.03	0.5	Single-stranded
<i>Ramphicarpa longiflora</i>	5	0.3	0.06	0.0	Tri-stranded
<i>Centranthera hispida</i>	62	0.5	0.008	0.4	Penta-stranded
<i>Leptorhabdos benthamiana</i>	45	0.1	0.2	1.3	Single-stranded, one joins from below
<i>L. parviflora</i>	25	0.3	0.01	0.6	Single-stranded, one joins from below
<i>Sopubia delphinifolia</i>	25	v. long			Single-stranded
Tribe Euphrasieae					
<i>Euphrasia officinalis</i>	67	1.0	0.01	0.9	Penta-stranded
<i>Pedicularis carnosae</i>	62	0.4	0.006	0.5	Tri-stranded
<i>P. zeylanica</i>	37	0.4	0.01	1.4	Single-stranded, one joins from below

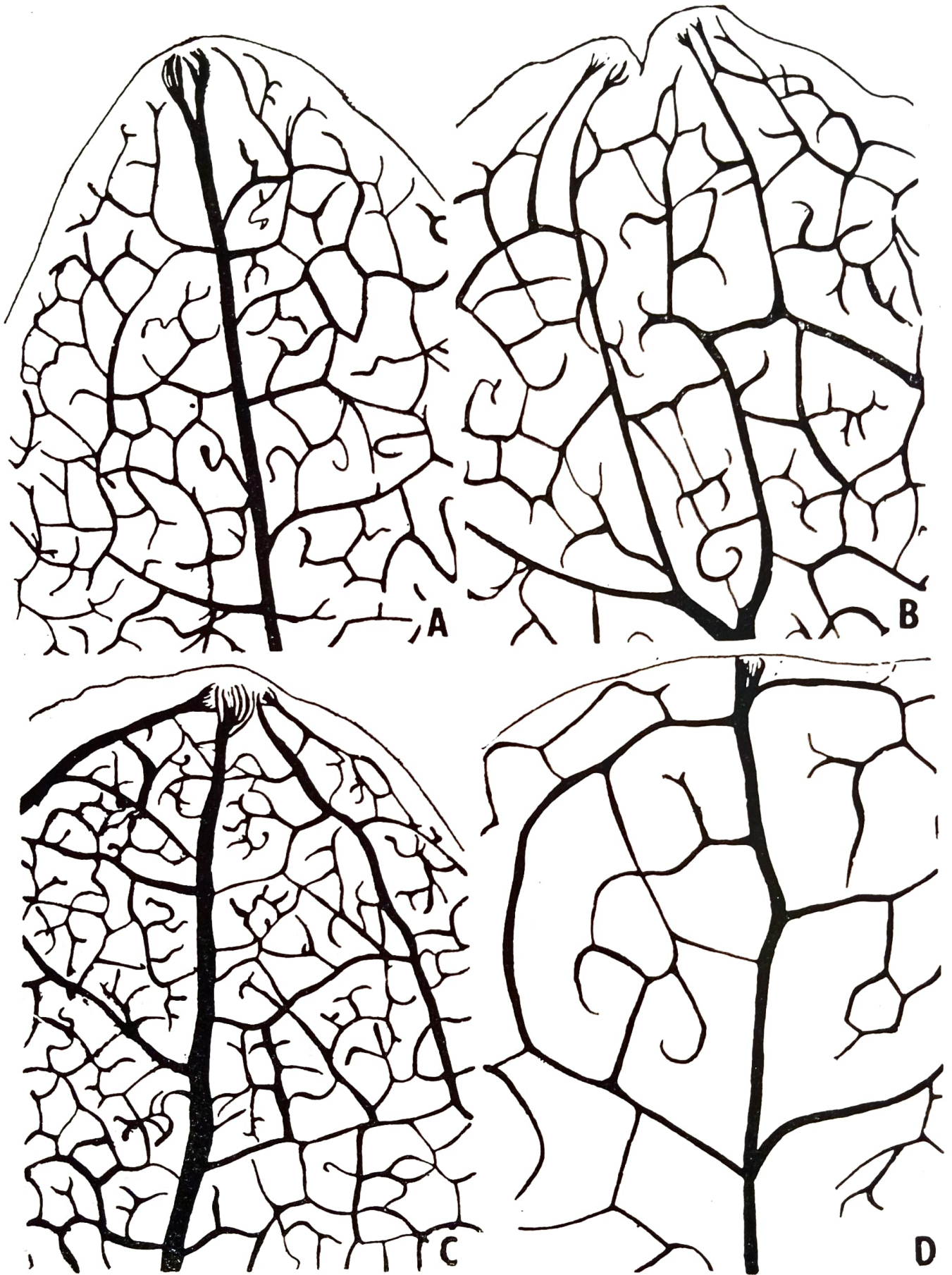


Fig. 1A-D. Apices of the cleared leaves showing simple organization of vascular elements. A. *Scoparia dulcis*, $\times 80$. B. *Picrorhiza kurrooa*, $\times 60$. C. *Wulfenia amherstiana*, $\times 60$. D. *Veronica serpyllifolia*, $\times 60$.

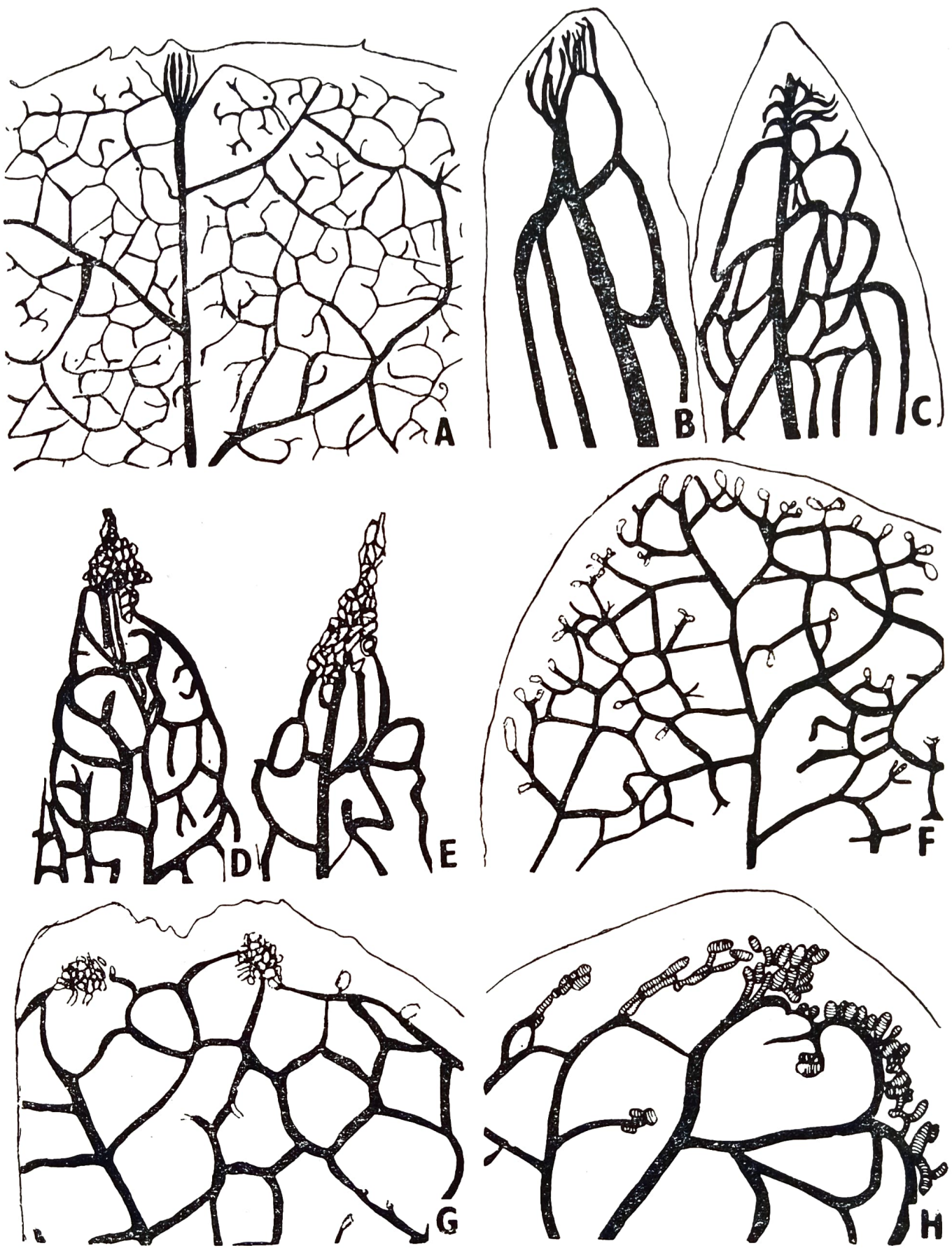


Fig. 2A-I. Apices of the cleared leaves showing accumulation of tracheidal elements. A. *Buchnera hispida*, $\times 80$. B. *Ramphicarpa longiflora*, $\times 100$. C. *Striga euphrasioides*, $\times 80$. D. *Leptorhabdos benthamiana*, $\times 100$. E. *L. parviflora*, $\times 100$. F. *Euphrasia officinalis*, $\times 100$. G. *Pedicularis carnosa*, $\times 100$. H. *P. zeylanica*, $\times 100$.



Fig. 3A-I. Venation patterns and types of areole organization in the series Rhinanthaeae. A. *Hemiphragma heterophyllum*, $\times 80$. B. *Scoparia dulcis*, $\times 80$. C. *Picrorhiza kurrooa*, $\times 80$; D. *Wulfenia amherstiana*, $\times 80$. E. *Veronica agrestis*, $\times 80$. F. *V. serpyllifolia*, $\times 80$. G. *V. anagallis*, $\times 80$. H. *Buchnera hispida*, $\times 80$. I. *Striga lutea*, $\times 80$.



Fig. 4A-I. Venation pattern and the organization of arcoles in the series Rhinanthaeae (Contd.).
 A. *Striga euphrasioides*, $\times 80$. B. *Ramphicarpha longiflora*, $\times 80$. C. *Centranthera hispida*, $\times 80$. D. *Leptorhabdos benthaniana*, $\times 80$. E. *L. parviflora*, $\times 80$. F. *Sopubia delphinifolia*; $\times 80$. G. *Euphrasia officinalis*; $\times 80$. H. *Pedicularis carnosa*, $\times 80$. I. *P. zeylanica*, $\times 100$.

The accumulation of tracheids has been recorded in some members of the series Rhinanthae. In *Pedicularis carnosus*, *P. zeylanica* and *Leptorhabdos* sp. tracheidal accumulation has been noticed at the apical region of the lobes, while this is present in the marginal lobes in *E. officinalis*. Since *Pedicularis* and *Euphrasia* grow in physiologically xerophytic conditions due to high altitude, tracheidal accumulation may be considered an adaptation.

A point that deserves special mention with regard to the venation of members of Rhinanthae is that the number of the strands entering the petiole shows a great variation, i.e. starting from single- (8 species) to tri- (6 species) to penta-stranded (4 species) conditions. Members of the Nelsonioideae, on the other hand, are single-stranded uniformly—a characteristic feature of the other taxa of the family Acanthaceae as well, investigated by us (unpublished data). Several taxa, such as *Hemiphragma heterophyllum*, *Striga lutea*, and *R. longiflora* show similarity to *Elytraria acaulis* and *Nelsonia campestris* of the tribe Nelsonioideae (family Acanthaceae) in their gross or major venation. Furthermore, the accumulation of tracheidal elements recorded here for members of the tribe Rhinanthae has rarely, if at all, been noticed in acanthaceous taxa.

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