

LEAF ARCHITECTURAL STUDIES IN THE ASTERACEAE-I

K. RAVINDRANATH AND J.A. INAMDAR

*Department of Biosciences, Sardar Patel University,
Vallabh Vidyanagar 388 120,
Gujarat, India.*

Abstract

Leaf architectural studies have been made in 22 genera and 25 species belonging to 8 tribes of the Asteraceae. Leaves are oblong, ovate or elliptic. Base acute, obtuse or lobate. Apex acute, acuminate, attenuate or lobate. Margin is lobed, wavy or serrate. Average size of the fully mature foliage leaves vary from species to species. Major venation pattern conforms to pinnate-craspedodromous, pinnate-camptodromous with festooned brochidodromous secondaries, acrodromous and palinactinodromous types. Marginal ultimate venation is either incomplete, looped or fimbriate. Number of primary veins vary according to the type of venation pattern. The number of secondaries on one side of the primary vary from species to species and even within the same species. Highest vein order is noticed up to 5^o. Areoles are formed by tertiary and higher order veins. Bundle sheath is noticed in some species. Loop formation, isolated free vein endings and isolated tracheids are observed. Tracheids are uni-, bi- or multi-seriate. Secretory cavities are observed at the margins of *Tagetes patula*. Qualitative features and numerical data on leaf architecture are compiled.

Introduction

Radford et al. (1974) have pointed out that leaves are generally neglected organs in taxonomic and comparative morphological studies due to the lack of detailed classification of their features. The arrangement of veins in the lamina is an important component of the study of leaf architecture. Ettingshausen (1861) proposed the venation pattern terminologies for angiosperms which were systematized and made precise by Hickey (1973). Melville (1976) gave venation pattern terminologies for both monocots and dicots. In an attempt to study the vasculature of leaves, Foster (1950) published data on the feathery venation that is characteristic of Quinaceae. Foster (1950, 1961, 1966, 1970, 1971) also made a detailed survey of leaves with dichotomous venation. In recent past attempts have been made to study the leaf architecture of some dicotyledonous families (Sehgal & Paliwal, 1974; Jain, 1975; Singh et al., 1978; Tyagi & Kumar, 1978; Inamdar & Murthy, 1978; Inamdar & Shenoy, 1981a, 1981b; Avita et al., 1981 etc.). Banerjee & Deshpande (1973) and Banerjee (1978) made a cursory reference to the foliar venation of

Table 1. Qualitative leaf features of Asteraceae

S. No.	Name of taxon	Shape	Base	Apex	Margin	Texture	Primary vein size	Intersecondary vein	Comp. site	Predominant tertiary vein origin angle	Marginal venation	Major venation pattern
1	<i>Acanthospermum hispidum</i> D.C.	Elliptic	Acute	Serrate	Coriaceous	Stout	Moderate	Simple	R-A, A-A	Incomplete	Semi-Craspedodromous	
2	<i>Ageratum conyzoides</i> L.	Ovate	Acute	Serrate	Coriaceous	Moderate	Moderate	Simple	A-A, R-R	Complete	Semi-Craspedodromous	
3	<i>Blainvella rhomboides</i> Cass.	Elliptic	Acute	Serrate	Coriaceous	Stout	Moderate	Simple	R-R, R-A	Incomplete	Semi-Craspedodromous	
4	<i>Bidens biternata</i> (Lour.) Merr & Sherff	Ovate	Acute	Serrate	Coriaceous	Stout	Moderate	Simple	R-R, R-A	Incomplete	Semi-Craspedodromous	
5	<i>Chrysanthemum indicum</i> L.	Ovate	Acute	Serrate	Coriaceous	Stout	Moderate	Simple	R-R, R-A	Incomplete	Semi-Craspedodromous	
6	<i>Dhala pinnata</i> Cav.	Ovate	Acute	Serrate	Coriaceous	Stout	Moderate	Simple	R-R, R-A	Incomplete	Semi-Craspedodromous	
7	<i>Eclipta alba</i> L.	Elliptic	Acute	Serrate	Coriaceous	Stout	Moderate	Simple	R-R, R-A	Incomplete	Semi-Craspedodromous	
8	<i>Emilia sonchifolia</i> Link.	Ovate	Acute	Serrate	Coriaceous	Stout	Moderate	Simple	R-R, R-A	Incomplete	Semi-Craspedodromous	
9	<i>Engeron asteroides</i> Roxb.	Ovate	Acute	Serrate	Coriaceous	Stout	Moderate	Simple	R-R, R-A	Incomplete	Semi-Craspedodromous	
10	<i>Guizotia abyssinica</i> Cass.	Oblong	Acute	Serrate	Coriaceous	Stout	Moderate	Simple	R-R, R-A	Incomplete	Semi-Craspedodromous	

11	<i>Helianthus annuus</i> L.	Ovate	Obtuse	"	"	Stout	"	A-A, A-R	"	Mixed craspedodromous
12	<i>Helianthus</i> sps.	"	"	Acuminate	"	Weak	"	R-R, R-A	"	"
13	<i>Myriactis wallitchii</i> Less.	Elliptic	Acute	"	"	Moderate	"	R-R, O-A, R-A	Looped	"
14	<i>Parthenium hysterophorus</i> L.	Ovate	"	"	Lobed	Massive	"	R-R, R-A	Incomplete	"
15	<i>Sonchus oleraceus</i> L.	Oblong	Lobate	Obtuse	Serrate	Moderate	"	A-A	"	Semi Craspedodromous
16	<i>Splianthus acumell</i> Murr.	Ovate	Obtuse	Acute	"	"	"	R-R, R-A, A-A	"	"
17	<i>Siegesbeckia orientalis</i> L.	"	Acute	"	Crenate	"	"	A-A, R-R	"	"
18	<i>Solidago virga-aurea</i> Linn.	Oblong	"	Alter-nate	Serrate	Stout	"	R-O, A-K	"	"
19	<i>Sclerocarpus africanus</i> Jacq.	Ovate	Obtuse	Acute	"	Moderate	"	R-R, R-A	"	Acrodromous
20	<i>Tagetes patula</i> L.	Elliptic	Acute	"	"	Massive	Absent	R-R, R-A	"	Festooned brochidodromous
21	<i>Tagetes</i> sp.	"	Obtuse	Obtuse	Smooth	Moderate	Simple	R-R, R-A, A-A	Looped	Acrodromous
22	<i>Tridax procumbens</i> Linn.	Ovate	"	Acute	Serrate	Weak	Composite	R-R, R-A	Incomplete	Festooned brochidodromous
23	<i>Vernonia anthelmintica</i>	"	Acute	"	"	"	"	R-R, R-A	"	Semi Craspedodromous
24	<i>Vernonia cineria</i> Murr.	Elliptic	"	Obtuse	"	Moderate	Simple	R-A, R-R	"	"
25	<i>Vernonia divergens</i> L.	"	"	Acuminate	Smooth	Massive	Composite	R-A	"	Festooned brochidodromous

the family Asteraceae. The present work has been undertaken on the leaf architecture of 25 species as no detailed report exists. Terminologies as defined by Hickey (1973) and Hickey & Wolfe (1975) are followed.

Material and Methods

Material of twenty-five species (Table I) was collected from the University campus. Leaves were cleared following the method of Rao et. al. (1980). Direct photographs of cleared leaves were taken on an enlarger. The size of the leaves was measured on a graph paper. The average of 5 readings of different leaves were taken for all studies and were tabulated.

Observations

Leaves are simple or compound. The leaf shape may be ovate, oblong or elliptic. Base is acute, obtuse or lobate. Apex is acute, acuminate, attenuate or obtuse. Margin is lobed, wavy or serrate (Fig. 5). The texture of the leaf is coriaceous or membranaceous. Secretory cavities are present at the margin of *Tagetes patula* (Fig. 6).

Major venation pattern is either pinnate-craspedodromous, pinnate-camptodromous with festooned brochidodromous secondaries, acrodromous or palinactinodromous. On the basis of the relative thickness of the veins, they can be classified into several size classes. The primary vein is the thickest which originates from the base of the lamina and traverses towards its apex. The thickness of the primary vein gradually decreases from base towards the apex. Primary vein gives rise to secondaries on either side which are thinner than the primary. They originate either in opposite, sub-opposite or alternate fashion. Their number and the angle of divergence vary from species to species and even within the same species. Secondaries after originating from primary pass towards the margin. They may or may not terminate at the margin. Depending upon the number of primaries and the arrangement of secondaries major venation pattern can be classified into several types and subtypes. In pinnate-craspedodromous type (Fig. 1) single primary vein gives off secondaries which divide dichotomously, with one arm terminating at the margin and the other joining with superadjacent secondary. In pinnate-camptodromous with festooned brochidodromous type (Fig. 2) single primary vein gives rise to secondaries which do not terminate at the margin, but join with superadjacent secondaries and forms prominent loops. Secondaries having a set of secondary loops outside the main brochidodromous loops and forms festooned brochidodromous type. In acrodromous type (Fig. 3) 3-4 primary veins originate from a single point and pass towards the apex in a convergent fashion. In palinactinodromous type (Fig. 4) more than one primary vein originates from one or two points and pass towards the apex in a divergent manner.

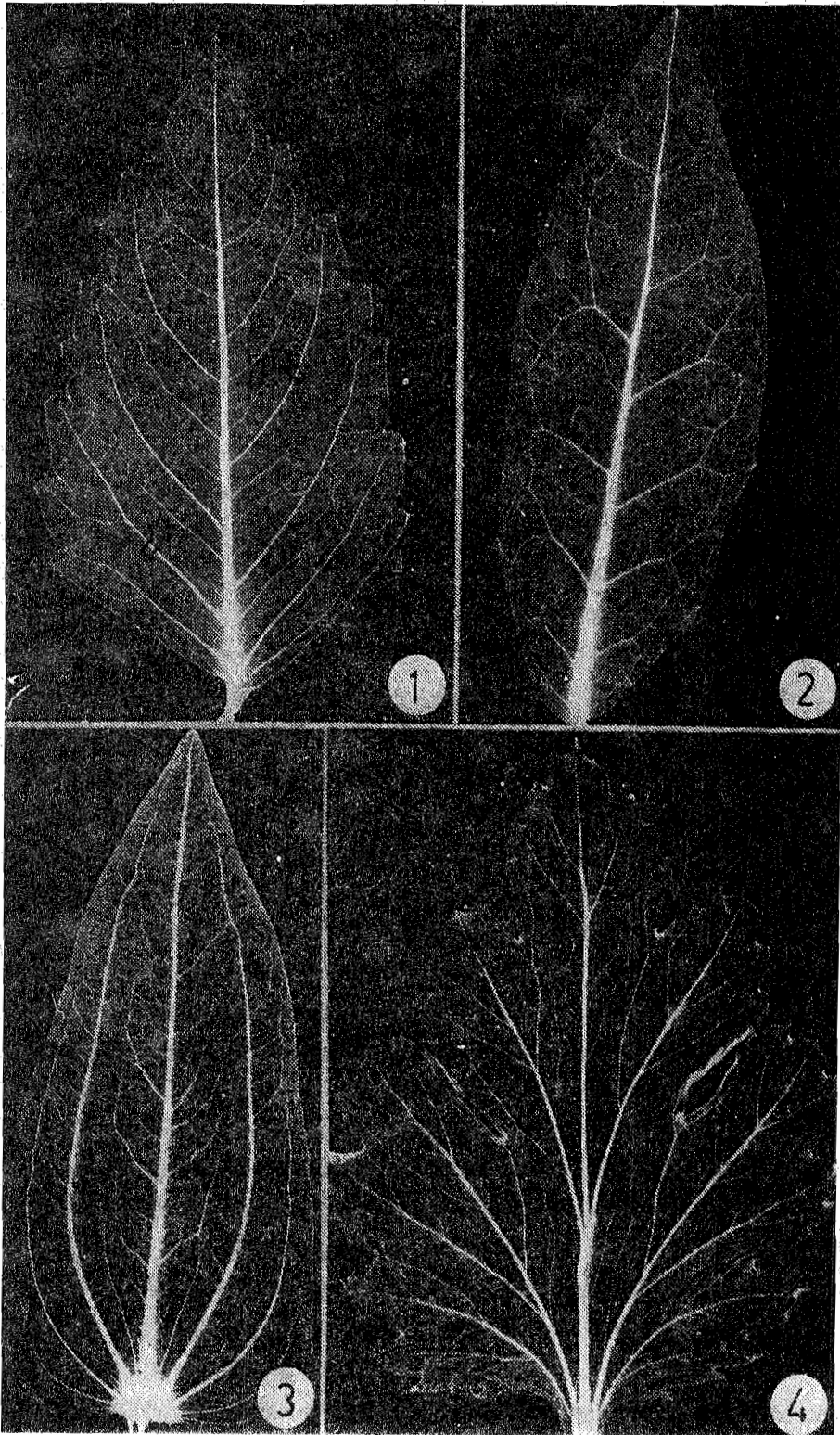


Fig. 1-4. Photographs showing the venation patterns of cleared leaves.

1. *Dahlia pinnata* x 1.5

3. *Tagetes* sps. x 1.5

2. *Vernonia divergens* x 2

4. *Chrysanthemum indicum* x 1.4

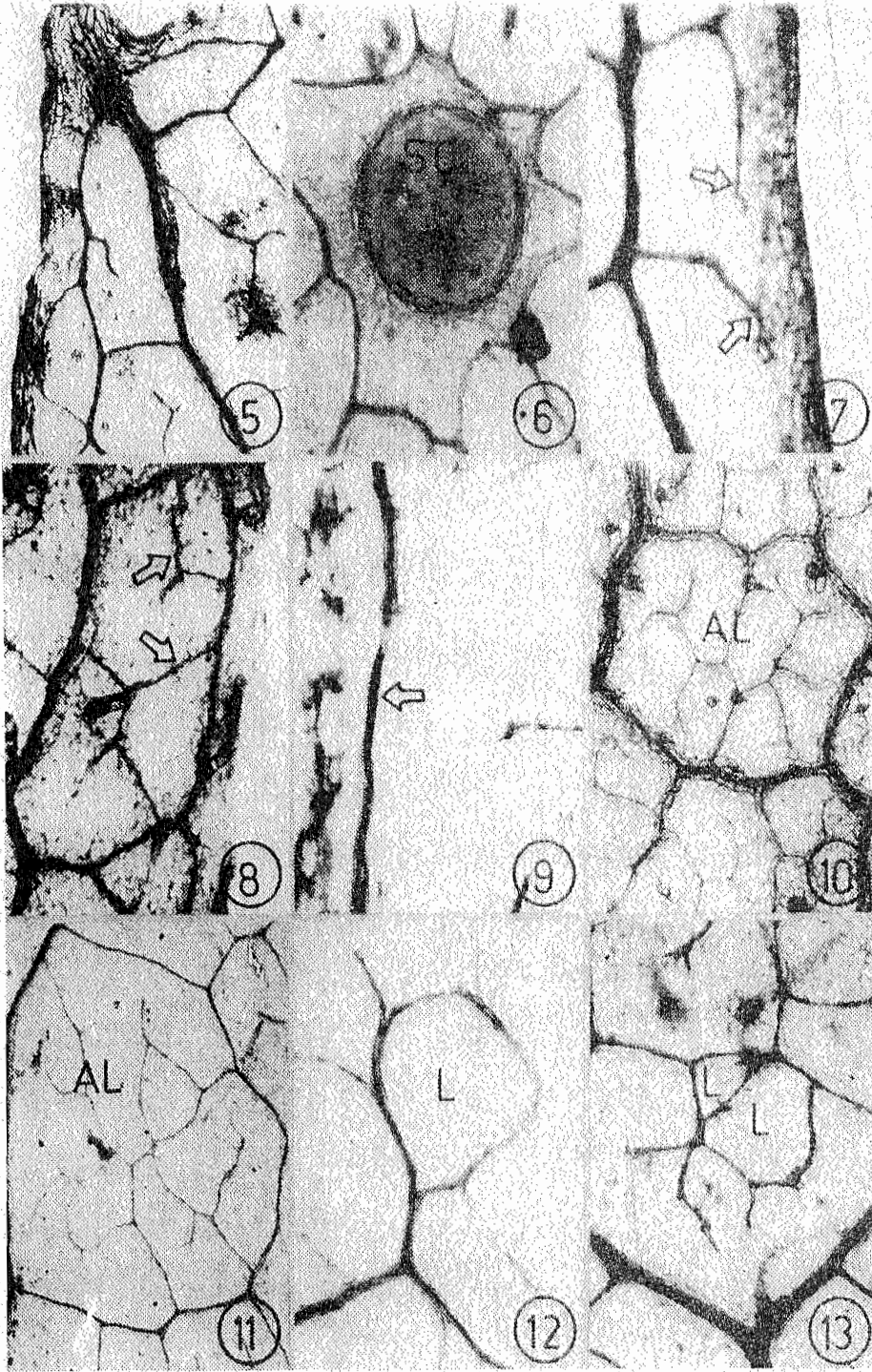


Fig. 5-13. Photomicrographs showing various aspects of leaf architecture.

- | | |
|------------------------------------|---------------------------------------|
| 5. <i>Dahlia pinnata</i> x 40 | 10. <i>Tagetes</i> sps. x 40 |
| 6. <i>Tagetes patula</i> x 100 | 11. <i>Tagetes patula</i> x 40 |
| 7. <i>Vernonia divergens</i> x 100 | 12. <i>Vernonia divergens</i> x 92 |
| 8. <i>Myriactis wallichii</i> x 40 | 13. <i>Solidago virga-aurea</i> x 100 |
| 9. <i>Bidens biternata</i> x 120 | |

(AL: areole, L: loop, SC: secretory cavity)

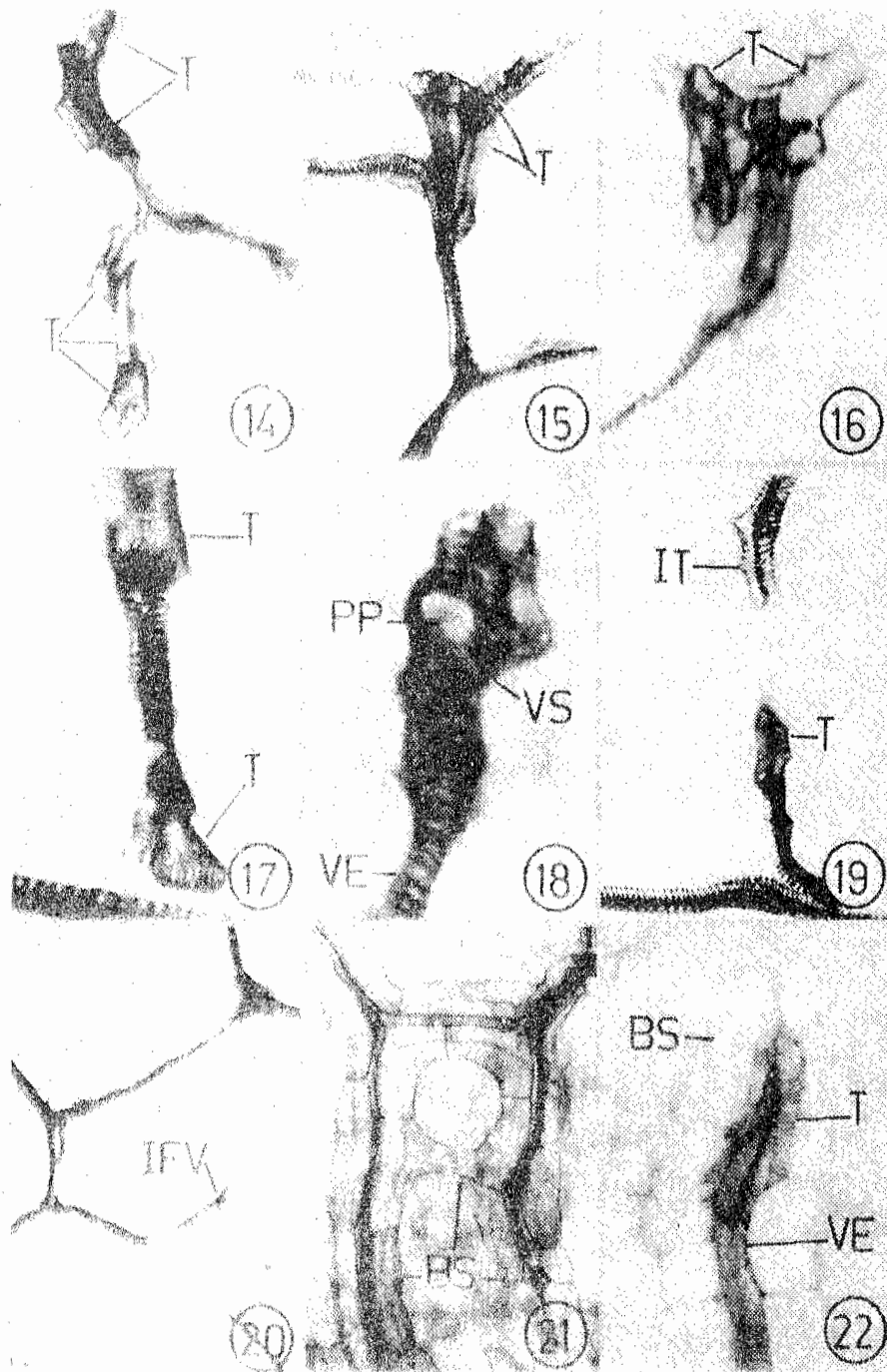


Fig. 14-22. Photomicrographs showing various aspects of leaf architecture.

- | | |
|---------------------------------------|--|
| 14. <i>Solidago virga-aurea</i> x 350 | 19. <i>Solidago virga-aurea</i> x 400 |
| 15. <i>Solidago virga-aurea</i> x 350 | 20. <i>Solidago virga-aurea</i> x 160 |
| 16. <i>Solidago virga-aurea</i> x 600 | 21. <i>Tagetes</i> sps. x 208 |
| 17. <i>Solidago virga-aurea</i> x 640 | 22. <i>Pyrrhuloxia hysterothorus</i> x 500 |
| 18. <i>Solidago virga-aurea</i> x 920 | |

(T: tracheid, PP: perforation plate, VS: Vessel, VE: Vein ending, IT: isolated tracheid, IFV: Isolated free vein ending, BS: Bundle sheath)

Intersecondary veins (Fig. 1 at arrows) are present between two secondaries which are thinner than the secondaries and originate from primary vein.

Minor veins which are of the next category of veins originating from the secondaries or tertiaries form the minor venation pattern. Highest vein order is observed up to 5⁰. The orientation of the higher order veins is random. In all the cases the higher order veins are uniseriate. Vein endings may or may not have terminal tracheids.

Marginal ultimate venation is either incomplete (Fig. 7 at arrows), looped (Fig. 8 at arrows) or fimbriate (Fig. 9 at arrows). The higher order veins after their ramification fuse to form a fimbriate vein which runs just inside the margin. Fimbriate vein is observed in *Bidens biternata* and *Dahlia pinnata*. In *Chrysanthemum indicum*, *Emilia sonchifolia*, *Myriactis wallichii* and *Tagetes* sp. marginal ultimate venation is looped. In the remaining species marginal ultimate venation is incomplete.

Areoles of different sizes (Figs. 10, 11) are formed by the tertiaries and higher order veins. They are mostly irregular in shape. The number of vein endings which cross the areoles vary from species to species and even within the same species. Vein endings may be simple or branched. In branched vein endings both the arms may be equal or unequal.

Loop formation (Figs. 12, 13) is formed by the union of two ultimate vein endings (*Vernonia divergens*) or two terminal tracheids (*Solidago virga-aurea*).

Tracheids on the vein endings show increase in cell diameter. Tracheids are uniseriate (Fig. 13), biseriare (Fig. 14), multiseriate (Fig. 15) or grouped (Fig. 16). Tracheids may be long or short. Normally, they occur on the vein endings, but sometimes in the middle of the vein (Fig. 17). In case of *Solidago virga-aurea* a vessel like element (Fig. 18) is present at the vein ending.

In *Solidago virga-aurea* isolated tracheid (Fig. 19), isolated free vein endings (Fig. 20) are observed which are lying free in the mesophyll tissue.

All the veins including tracheids are ornamented by parenchymatous bundle sheath. Bundle sheath is quite prominent in *Parthenium hysterophorus* (Fig. 21) and *Tagetes* sp. (Fig. 22).

Discussion

According to Banerjee & Deshpande (1973), Banerjee (1978) the venation pattern is craspedodromous in *Launea*, *Sonchus* and *Amberboa*. These authors considered that

Table 2: Numerical data on the venation patterns of Asteraceae

No.	Name of the taxa	Leaf area in mm ²	No. of 2° vein along one side of the primary	Angle between p & 2° veins	No. of areoles (veinlets) for mm ²	No. of veinlets entering into 1 areole	No. of vein endings terminations for areole	Average size of the areole for mm ²	Absolute areole no. in thousands	Absolute vein ending termination no. in thousands	Highest vein order	No. of primary veins
1	<i>Acanthospermum hispidum</i> DC.	390	3-4	30°-35°	4	5-6	6-10	0.25	1.56	2.145	5°	1
2	<i>Ageratum conyzoides</i> L.	1465	4	30°-35°	1	4	8	1	1.47	11.72	4°	1
3	<i>Blainvella rhomboides</i> Cass	572	4-5	30°-40°	1	6	12	1	0.572	6.864	5°	1
4	<i>Bidens biternata</i> (Lour) Merrd Sherff.	165	4-6	50°-55°	2	3	6	0.5	0.33	0.99	4°	1
5	<i>Chrysanthemum indicum</i> L.	955	4-6	28°-30°	1	4	1	1	0.955	0.955	4°	5
6	<i>Dahlia pinnata</i> Cav.	1390	5-7	35°-55°	1	4-6	10-14	1	1.39	16.68	5°	1
7	<i>Eclipta alba</i> L.	370	4-6	40°-45°	1	3-5	8-12	1	0.37	3.7	4°	1
8	<i>Emilia sonchifolia</i> Linn.	355	3-4	35°-45°	1	3	2	1	0.355	0.71	5°	1
9	<i>Erigeron asteroides</i> Roxb.	165	4-5	55°-60°	2	3-5	4-6	0.5	0.33	0.825	4°	1
10	<i>Guizotia abyssinica</i> Cass.	1613	5-7	40°	1	6-8	7	1	1.613	11.3	3°	1
11	<i>Helianthus annuus</i> L.	2640	6-8	50°-60°	3	8-10	10-12	0.33	7.92	29.04	5°	1
12	<i>Helianthus</i> sps.	1940	5-6	60°-65°	1	4-8	6	1	1.94	11.64	4°	1
13	<i>Myriactis wallichii</i> Less.	500	3-4	45°-55°	1.5	2	3	0.7	0.75	1.5	4°	1
14	<i>Parthenium hysterophorus</i> L.	340	4-5	40°-50°	3	6	16	0.33	1.02	5.44	4°	1
15	<i>Sonchus oleraceus</i> L.	774	2-3	25°-30°	1	3	5	1	0.774	3.87	5°	1
16	<i>Spilanthes acmella</i> Murr.	510	4-6	40°-45°	1	4	5	1	0.51	2.55	4°	1
17	<i>Siegesbeckia orientalis</i> L.	2265	6-8	70°-90°	1	4-8	10-12	1	2.26	24.91	5°	1
18	<i>Solidago virga-aurea</i> Linn.	1116	4-6	46°	1.5	5	5	0.7	1.67	5.9	5°	1
19	<i>Sclerocarpus africanus</i> Jacq.	575	3-5	60°-90°	1	4-5	10	1	0.575	5.75	4°	1
20	<i>Tagetes patula</i> L.	360	10-12	40°-50°	1	4-6	4-10	1	0.36	2.52	3°	1
21	<i>Tagetes</i> sps.	800	2	30°-35°	1	4-5	4-6	1	0.8	4	4°	1
22	<i>Triadax procumbens</i> Linn.	620	4-6	45°-50°	1	4-5	6-8	1	0.62	4.34	4°	1
23	<i>Vernonia anthelmintica</i> Murr.	875	7-8	52°-60°	1	3	7	1	0.88	6.12	4°	1
24	<i>Vernonia cinerea</i> Murr.	530	4-6	50°-55°	1	4	10	1	0.53	5.3	4°	1
25	<i>Vernonia divergens</i> L.	1165	6-7	60°-65°	1	4	6	1	1.165	7	4°	1

Launea which exhibits extreme open type of venation pattern be selected as starting plant. The present observation reveals that the Asteraceae exhibits diverse type of venation patterns, i.e. pinnate-craspedodromous, pinnate-camptodromous with festooned brochidodromous secondaries, acrodromous and palinactinodromous. It therefore becomes rather difficult to consider *Launea* as a starting plant since open craspedodromous venation is exhibited by several members of the Asteraceae (Hickey & Wolfe, 1975).

The characters such as number of secondaries, size of areoles, the number of vein endings entering into the areole vary from species to species and even within the same species. The veins which are surrounded by parenchymatous bundle sheath are termed as ornamented by Kakkar & Paliwal (1972). Such ornamentations are observed in some members of the Asteraceae. Gupta (1961) reported that the vein-islet number and veinlet termination number are inversely proportional to the area of the lamina. Nicely (1965) observed the significant variations within the same leaf as regards the size and shape of the areoles and number of vein endings in each vein-islet. The present observations also supports this.

Vein endings may be simple or branched, with or without terminal tracheids. Tracheids are uni-, bi- or multi-seriate. Kasapligil (1951) reported the occurrence of isolated veins in dicotyledonous leaves. Later Foster & Arnott (1960) in *Circaeaster* and Herbest (1972) in *Euphorbia* have noticed the presence of isolated veins. Isolated free vein endings and isolated tracheids are observed in *Solidago virga-aurea*.

Acknowledgement

K. Ravindranath thanks the University Grants Commission, India for financial assistance.

References

- Avita (Sr.), N.V. Rao and J.A. Inamdar. 1981. Studies on the leaf architecture of the Ranunculaceae. *Flora*, 171: 280-292.
- Banerjee, G. 1978. Foliar venation and leaf histology of certain members of Compositae II members with combination craspedodromous. *Amberboa ramosa* Roxb. Wagnev (Syn: *Voluntarella ramosa* Roxb.). *J. Indian bot. Soc.*, 57: 338-342.
- Banerjee, G. 1978. Foliar venation of *Sonchus arvensis*. *Curr. Sci.*, 47: 26-27.
- Banerjee, G. and B.D. Deshpande. 1973. Foliar venation and leaf histology of certain members of Compositae. *Flora*, 162: 529-532.
- Elttingshausen, C.R. Von. 1861. *Die Blattskelete der dicotyledonen*. Vienna.

- Foster, A.S. 1950. Venation pattern in the leaves of Angiosperms, with special reference to the Quinaeaceae. Proc. Seventh Bot. Cong., Stockholm, 380-381.
- Foster, A.S. 1961. The phylogenetic significance of dichotomous venation in Angiosperms. Rec. Adv. Bot., 2: 971-975.
- Foster, A.S. 1966. Morphology of anastomoses in the dichotomous venation of *Circaeaster*. Amer. J. Bot. 53: 588-599.
- Foster, A.S. 1968. Further morphological studies on anastomoses in the dichotomous venation of *Circaeaster*. J. Arnold. Arb., 49: 52-67.
- Foster, A.S. 1970. Types of blind vein endings in the dichotomous venation of *Circaeaster*. J. Arnold. Arb., 51: 70-80.
- Foster, A.S. 1971. Additional studies on the morphology of blind vein endings in the leaf of *Circaeaster agrestis*. Amer. J. Bot., 58: 263-272.
- Foster, A.S. and H.J. Arnott, 1960. Morphology and dichotomous vasculature of the leaf of *Kingdonia uniflora*. Amer. J. Bot., 47: 684-698.
- Gupta, B. 1961. Correlation of tissues in leaves I. Absolute vein-islet numbers and absolute vein-islet termination numbers. Ann. Bot., 25: 65-70.
- Herbst, D. 1972. Ontogeny of foliar venation in *Euphorbia forbesii*. Amer. J. Bot., 59: 843-850.
- Hickey, L.G. 1973. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot., 60: 17-33.
- Hickey, L.G. and J.A. Wolfe. 1975. The bases of angiosperm phylogeny - vegetative morphology. Ann. Misso. Bot. Gard., 62: 538-589.
- Inamdar, J.A. and G.S.R. Murthy. 1978. Leaf architecture in some Solanaceae. Flora, 167: 265-272.
- Inamdar, J.A. and K.N. Shenoy. 1981a. Leaf architecture in some Convolvulaceae. Phytion (Austria), 21: 115-125.
- Inamdar, J.A. and K.N. Shenoy. 1981b. Leaf architecture of *Merremia* Dennst. ex. Hall. f. *Flora* (in press).
- Jain, D.K. 1978. Studies in Bignoniaceae III. Leaf architecture. J. Indian Bot. Soc., 57: 369-386.
- Kakkar, L. and G.S. Paliwal. 1972. Studies on the leaf anatomy of *Euphorbia* VI. The bundle sheath. Biology of land plants. Eds. V. Puri et. al., Sarita prakashan, Meerut (India) 71-77.
- Kasapliligil, B. 1951. Morphological and ontogenetic studies of *Umbeleularia californica* Nutt. and *Laurus nobilis* L., Univ. Calif. Pub. Bot. 25: 115-240.
- Melville, R. 1976. The terminology of leaf architecture. Taxon. 25: 549-561.

- Nicely, K.A. 1965. A monographic study of Calycanthaceae: *Castanea*, 30: 38-81.
- Pray, T.R. 1963. Origin of vein endings in angiosperm leaves. *Phytomorphology*, 13: 60-81.
- Radford, A.E., W.C. Dickison, J.R. Massey and C.L. Bell. 1974. *Vascular plant systematics*. Harper & Row Publishers, New York.
- Rao, V.S., K.N. Shenoy, J.A. Inamdar, 1980. Clearing and staining technique for leaf architectural studies. *Microscopica acta*, 83: 307-310.
- Sehgal, L. and G.S. Paliwal. 1974. Studies on the leaf anatomy of *Euphorbia* II. Venation patterns. *Bot. J. Linn. Soc.*, 68: 173-208.
- Singh, V., D.K. Jain, and Meena Sharma, 1978. Leaf architecture in Berberidaceae and its bearing on circumscription of the family. *J. Indian Bot. Soc.*, 57: 272-281.
- Tyagi, S. and V. Kumar. 1978. Venation pattern in the tribe Ocimoideae (Labiatae). *J. Indian Bot. Soc.*, Abst., V. 17.