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Leaf venation architecture in some Apiaceae

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ABSTRACT

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Foliar venation architectural characteristics of sixteen species belonging to twelve genera of family Apiaceae have been investigated. The leaves are simple, ternate, pinnately trifoliate, pinnately compound or decompound. The major venation conforms to actinodromous pattern but in *Bupleurum*, it is parallelodromous. Detailed observations have been made on major and minor venation of the leaves along with marginal ultimate venation, areoles, veinlets and vein terminations. The marginal ultimate venation is mostly fimbriate and the highest vein order resolved is up to 3°-6°. Quantitative parameters like the number of secondary veins, areoles and veinlets per unit area have been analyzed. Several of these features are of diagnostic value and accordingly a key is presented for delimiting the taxa studied.

Key-words: Apiaceae, leaf venation architecture, actinodromous, taxonomy.

INTRODUCTION

Leaf venation architectural characteristics are genetically implied and hence they are reliable taxonomic tool (Roth-Nebelsick et al. 2001). Their importance in elucidation of taxonomic kinship both in the extant and extinct plants needs no emphasis (Hickey 1973, 1979, Subba Rao & Shanmukha Rao 1992, Shanmukha Rao & Srinivas Rao 2015). Recent studies also emphasized usefulness of venation studies in palaeoecology, palaeoclimatology, agriculture, urban ecology, science and industry (Sack & Scoffoni 2013). The studies on the leaf architecture in Apiaceae are almost non-existing and only passing remarks have been made about its major venation patterns (Hickey & Wolfe 1975). The present data regarding Apiaceae are entirely new and are recorded for the first time.

MATERIAL AND METHODS

Sixteen species belonging to twelve genera have been investigated and the material was collected either locally or obtained from different sources (Table 1). The leaves were fixed in Carnoy's fixative consisting of alcohol and glacial acetic acid (3:1) (Johansen 1940). After one week, the fixative was replaced by 70% alcohol for preservation of the material. The fixed leaves were cleared following a modified procedure of Thakur (1988) to suit the present investigation. Accordingly, the leaves were kept in 5% KOH solution at 25° for 4-5 hours. Thereafter, the material was washed in water and stained with safranin or aniline blue and mounted in glycerine. But in case of coriaceous leaves of *Bupleurum*, the material was transferred to acetic acid, H_2O_2 and lactophenol in 1:1:1 ratio for 6 to 12 hours. The terminology used in the description of venation pattern is after Hickey (1973, 1979) and Ellis et al.

Table 1. Mature foliar characteristics in Apiaceae

S. No.	Name of the taxon	Locality	Marginal ultimate venation	No.of 1⁰ veins	No.of 2⁰ veins	Angle of divergence Between 1⁰ & 2⁰	Predominant tertiary vein origin angle	Highest vein order	No. of areoles per sq. mm.	No. of veinlets per sq.mm.	No. of veinlets entering the areoles	Venation pattern
Sub-family : Hydrocotyloideae												
Tribe : Hydrocotyleae												
1	*Centella asiatica* (L.) Urban	Hyderabad	Looped	7-8	2-3	Acute-obtuse	OR, OO, AR	5^0	3.2	4.8	3	Actinodromous
2	*Hyderocotyle javanica* Thunb.	B.S.I., Coimbatore	Fimbriate	5	3-4	Acute-obtuse	AO, OO, OA	5^0	0.4	0.8	-	Actinodromous
3	*Hydrocotyle rotundifolia* Roxb.	Pune	Looped	5-7	2-3	Acute	AO, RR, OO	4^0	1.8	1.2	1	Actinodromous
Sub-family : Apioideae												
Tribe : Dauceae												
4	*Daucus carota* L.	Hyderabad	Fimbriate	3	2-3	Acute	A	5^0	4.2	2.4	1.6	Actinodromous
Tribe : Coriandreae												
5	*Corindrum sativum* L.	Hyderabad	Fimbriate	3	2-3	Acute	OA, AA	6^0	3	5.2	3.2	Actinodromous
Tribe : Apieae												
6	*Ammi majus* L.	Lucknow	Fimbriate	3	2-4	Acute	OR, RA	4^0	3	5.8	2.4	Actinodromous
7	*Anethum graveolens* L.	Lucknow	Fimbriate	3	1-2	Acute	A	4^0	6	0.2	0.2	Actinodromous
8	*Apium graveolens* L.	Lucknow	Looped	3	2-3	Acute-obtuse	RA, OA	4^0	3	3.6	1.4	Actinodromous
9	*Bupleurum distichophyllum* Wight & Arn.	B.S.I., Coimbatore	Fimbriate	5	Numerous	Right angle	A	3^0	-	-	-	Parallelodromous
10	*Bupleurum mucronatum* Wight & Arn.	B.S.I., Coimbatore	Fimbriate	7	Numerous	Right angle	AO, OO	4^0	-	-	-	Parallelodromous
11	*Foeniculum vulgare* Miller	Lucknow	Fimbriate	3	2-3	Acute	A, OA	3^0	0.6	0.6	-	Actinodromous
12	*Pimpinella candolleana* Wight & Arn.	B.S.I., Coimbatore	Fimbriate	7	4-5	Acute-obtuse	OA, OR, OO	4^0	4	3	2.6	Actinodromous
13	*Pimpinella heyneana* (Wall. DC) Kurz	B.S.I., Coimbatore	Fimbriate	3	4-5	Acute	RR, OO, AO	6^0	6.2	5.4	4.2	Actinodromous
14	*Pimpinella monoica* Dalz.	B.S.I., Coimbatore	Fimbriate	5	3-4	Acute	AO, OO	4^0	1	2.8	2	Actinodromous
15	*Trachyspermum ammi* (L.) Sprague	Lucknow	Fimbriate	3	2-3	Acute	OA, OO	3^0	2.4	3	0.2	Actinodromous
16	*Heracleum rigens* DC.	B.S.I., Coimbatore	Fimbriate	3	2-3	Acute-obtuse	OO, OA	5^0	2.8	7.6	6.4	Actinodromous

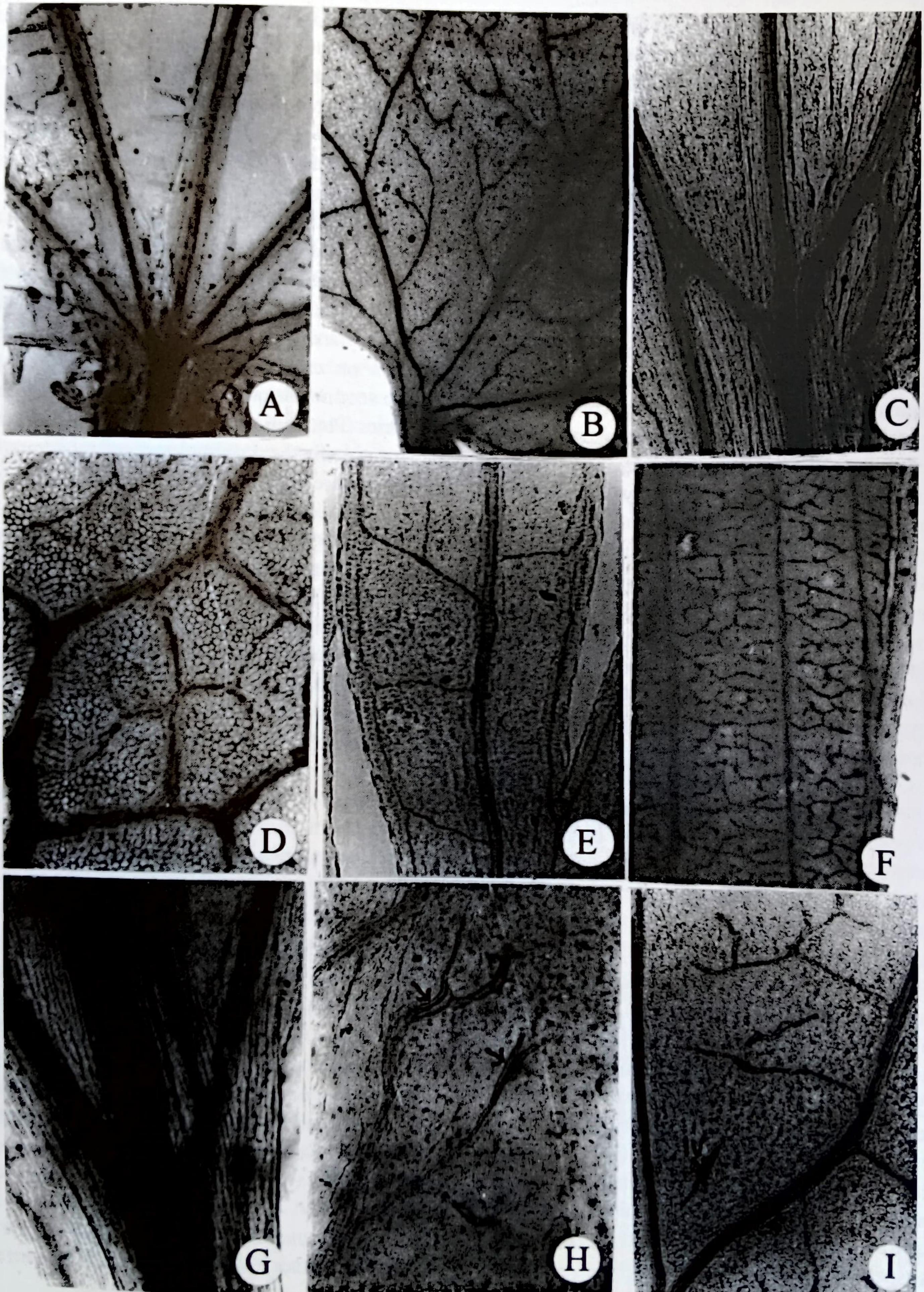
(2009) and the same for vein terminations is after Tucker (1964).

RESULTS AND DISCUSSION

Leaves of the Apiaceae presently studied are either simple (entire or lobed), ternate, pinnately trifoliate, pinnately compound or decompound. But the leaves of most of the species studied show a trend of simple to pinnately dissected nature in the proximal region but they become more and more dissected, i.e. decompound in nature in the distal region of the plant body. This is also in tune with the earlier literature

Plate 1

A-I. Leaf venation in Apiaceae. **A.** *Hydrocotyle javanica*, actinodromous venation with prominent mid primary veins, x20. **B.** *Apium graveolens*, actinodromous venation, x36. **C.** *Coriandrum sativum*, actinodromous venation showing three primaries, x100. **D.** *Heracleum rigens*, pentagonal areoles with veinlets, x63. **E.** *Anethum graveolens*, marginal ultimate venation fimbriate, x83. **F.** *Bupleurum mucronatum*, parallelodromous venation, x23. **G.** *Pimpinella heyneana*, suprabasal actinodromous venation, x100. **H.** *Daucus carota*, juxtaposed (shown with arrow) and superposed tracheids, x94. **I.** *Coriandrum sativum*, branched veinlets; isolated vein ending present, x63. **IV:** Isolated vein ending.


A
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(Mukherjee & Constance 1993). The simple leaves are orbicular, reniform, cordate, flabelliform, ovate, linear or lanceolate whereas the ultimate segments of the compound leaves vary from ovate, oblong, linear, and lanceolate to filiform. Variation is also observed in the base, apex and margin of different taxa studied. The texture of the leaf is mostly membranous but coriaceous in *Bupleurum*.

Venation Patterns: Hickey (1979) classified the venation patterns in dicotyledons into six types. Of these only two patterns are presently observed, i.e. actinodromous (= three or more primary veins diverging radially from a single point) (Plate 1, figures A-C, G) and parallelodromous (= two or more primary veins originating at the leaf base and running parallel to the apex where they converge) (Plate 1, figure F). Of these, actinodromous is the most common pattern and mostly of basal type except in *Pimpinella heyneana* where it is suprabasal [= initial point of radiation located some distance above the leaf base] (Plate 1, figure G). This character is useful to distinguish this taxon from rest of the species studied. *Bupleurum* is unique among the Apiaceae by the possession of simple and entire leaves and majority of the species show parallel venation (Neves & Watson 2004). This taxon is remarkable as it shows parallelodromous venation (Plate 1, figure F). Thus, this taxon stands apart from rest of the Apiaceae studied. In general, the network of veins in the mature leaves of Apiaceae is distinguished by the overall decrease of all grades of veins/areoles/veinlets in comparison to those of the other dicotyledonous taxa (Shanmukha Rao & Leela 1990, Saibaba & Shanmukha Rao 1990, Vijayalakshmi Sarma et al. 1992, Subba Rao & Shanmukha Rao 1992, Shanmukha Rao & Narmada 1994). This is possibly due to two reasons: (i) Presence of often decompound leaves producing fine thread like laminar segments. This may not possibly be conducive for the formation of extensive network of venation resulting in the limited formation of all grades of veins. (ii) Predominant occurrence of these taxa in temperate zones and their shorter life span. Study of foliar architecture in similar taxa would be highly interesting and may shed light on this aspect.

Major venation: Primary vein (1°): Its thickness is variable among the actinodromous primaries as the mid primary is considerably thicker than others (Plate 1, figures A, G) but all primaries are of the same thickness in *Daucus carota, Foeniculum vulgare, Bupleurum mucronatum, B. distichophyllum, Heracleum rigens, Anethum graveolens, Trachyspermum ammi* and *Apium graveolens* (Plate 1, figures B, F). The number of primaries are either three (Plate 1, figures B-C, G) or five and above (Plate 1, figure A) and useful to segregate the taxa studied (Table 1). **Secondary veins (2°):** They are meagre and range from 1-5 except in *Bupleurum mucronatum* and B. *distichophyllum* where secondaries are numerous between parallel primaries (Plate 1, figure F). The angle of divergence is narrow acute in the proximal part and moderate, wide acute to obtuse in the distal end in all taxa studied except in *Bupleurum* where the secondaries arise at right angles or nearly so to the primaries (Plate 1, figure F). They are exceptionally thick in *Coriandrum sativum* and *Pimpinella heyneana* and moderate in rest of the taxa studied. Further, their course is straight or curved but always curved towards distal end in all the taxa studied. **Tertiary veins (3°):** They are ramified, reticulate or percurrent. The tertiary vein origin angle is mostly obtuse-acute or obtuse-obtuse and rarely as right angle-acute, right angle-right angle, acute-obtuse or right angle-acute. They are the highest vein order in *Bupleurum distichophyllum, Foeniculum vulgare* and *Trachyspermum ammi* (Table 1) and constitute areoles or veinlets. They form the mid-vein of leaf lobes in *Anethum graveolens*.

Minor venation: Quaternary veins (4°): They are always thin and mostly orthogonal and some are randomly oriented. They represent the highest vein order in seven taxa (Table 1). **Quinternary veins (5°):** These veins represent the highest order of venation in *Hydrocotyle javanica, Centella asiatica, Daucus carota* and *Heracleum rigens* (Table 1) and constitute the veinlets. They form areoles in *Pimpinella heyneana*. They are always thin and their course is mostly orthogonal. **6° veins:** *Coriandrum sativum* and *Pimpinella heyneana* have 6° veins as the highest vein order. This character is diagnostic to delimit them from the rest of the members. These veins are thin and their course is orthogonal. **Areoles:** Areoles are present in all the taxa and formed by 1°- 5° veins. They are perfect or imperfect with variable shapes (polygonal, hexagonal, pentagular, rectangular, trianglular) (Plate 1, figure D) and some are incompletely closed. They are randomly oriented and their size class range from large to medium. **Veinlets:** They are common and represented by 3°- 6° veins. They are simple (linear and curved) or branched (once or rarely twice). Presently, the veinlets with vein terminations are observed (Plate 1, figures E, I). **Vein terminations:** Foliar veinlet terminations are classified by Tucker (1964) into six types. Presently, two types, i.e. conventional and dilated type of tracheids are encountered in the leaves and the tracheids are of uniseriate or biseriate in nature. Further, the conventional tracheids are either simple (linear/curved) or branched mostly once and occasionally twice, either symmetrically or asymmetrically (Plate 1, figures B, H-I). On the other hand, the dilated tracheids are present only in *Bupleurum mucronatum* and *B. distichophyllum*. **Isolated vein endings:** The tracheoidal elements sometimes lying free in the areoles have been described as free isolated or free vein endings. Kasapligil (1951) reported these isolated veins in mature leaves of dicotyledons. Isolated free vein endings and isolated tracheids are reported in *Ricinus* (Foster & Arnott 1960), *Euphorbia forbesii* (Herbst (1972), Apocynaceae (Mohan & Inamdar 1982) and *Ipomoea* (Shanmukha Rao & Leela 1990). In the present work, presence or absence of isolated vein endings is a diagnostic character. The isolated vein endings are observed in *Ammi majus* and *Coriandrum sativum* (Plate 1, figure I) and they are absent in rest of the taxa studied.

Comparison of cotyledonary and mature foliar venation: Though investigations have been initiated on the foliar venation architectural aspects of many dicotyledons, comparative accounts vis-à-vis their cotyledonary leaves are almost a rarity. Keeping this in view an attempt has been made in this direction in the Apiaceae. In terms of gross morphological features, all the cotyledonary leaves of the Apiaceae studied are always simple (long or ovate) but the mature ones are either pinnately trifoliate, ternate, pinnately lobed, pinnately compound or decompound and occasionally simple (entire or lobed). The cotyledons reveal mostly acrodromous venation and sometimes brochidodromous (Sita Ratnam & Shanmukha Rao 2015), but the mature leaves are always actinodromous (but rarely parallelodromous in *Bupleurum*) irrespective of different types of leaves present in the umbellifers.

Cotyledonary leaves show 1-3 primary veins but they go up to 3 - 8 in mature leaves. The highest vein order is generally 3°- 4° in cotyledonary leaves but 3°- 5° in the mature leaves except in *Coriandrum sativum* and *Pimpinella heyneana* where it is 6°. However, the marginal ultimate venation in both cotyledonary as well as mature leaves almost similar and it is either looped or fimbriate excepting in *Apium graveolens* showing fimbriate in cotyledons but looped in mature leaves. The number of areoles as well as the veinlets is more in mature leaves (Table 1) than in cotyledonary leaves (Sita Ratnam & Shanmukha Rao 2015).

Taxonomic importance: Taxonomically significant foliar architectural characteristics in Apiaceae are as follows: Venation pattern, number of primary veins, highest vein order, marginal ultimate venation and veinlets frequency/mm^2. Accordingly, the following key is prepared for the delineation of taxa studied.

1. Venation parallelodromous
2. Primary veins 7; leaf lanceolate with mucronate apex.......................*Bupleurum mucronatum*
2. Primary veins 5; leaf linear with acute apex .... *Bupleurum distichophyllum*
1. Venation actinodromous
3. Primaries suprabasal (primary veins originating some distance above the leaf base).................. ....*Pimpinella heyneana*
3. Primaries basal (primary veins originating from the leaf base)
4. Highest vein order 6°........*Coriandrum sativum*
4. Highest vein order less than 6°
5. Highest vein order 3°

6. Number of veinlets per mm^2 less than 1.......................................*Foeniculum vulgare*
6. Number of veinlets per mm^2 more than 2...................................*Trachyspermum ammi*
5. Highest vein order 4° or 5°
7. Highest vein order 4°
8. Marginal ultimate venation looped
9. Number of primary veins 3.......*Apium graveolens*
9. Number of primary veins 5 – 7.......................... .... *Hydrocotyle rotundifolia*
8. Marginal ultimate venation fimbriate
10. Number of primary veins 3
11. Number of veinlets per mm^2 less than 1.......................................*Anethum graveolens*
11. Number of veinlets per mm^2 more than 5...*Ammi majus*
10. Number of primary veins more than 3
12. Number of primaries 5 ..... *Pimpinella monoica*
12. Number of primaries 7 ..*Pimpinella candolleana*
7. Highest vein order 5°
13. Marginal ultimate venation looped .... *Centella asiatica*
13. Marginal ultimate venation fimbriate
14. Primary veins 5 .... *Hydrocotyle javanica*
14. Primary veins 3
15. Number of veinlets per mm^2 less than 3.. *Daucus carota*
15. Number of veinlets per mm^2 more than 7................................. .... *Heracleum rigens*

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