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Source: *American Journal of Botany*, Vol. 60, No. 1 (Jan., 1973), pp. 17-33
Published by: Botanical Society of America
Stable URL: http://www.jstor.org/stable/2441319
Accessed: 10/12/2009 19:12

Amer. J. Bot. 60(1): 17–33. 1973.

CLASSIFICATION OF THE ARCHITECTURE OF DICOTYLEDONOUS LEAVES[1]

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ABSTRACT

A classification of the architectural features of dicot leaves—i.e., the placement and form of those elements constituting the outward expression of leaf structure, including shape, marginal configuration, venation, and gland position—has been developed as the result of an extensive survey of both living and fossil leaves. This system partially incorporates modifications of two earlier classifications: that of Turrill for leaf shape and that of Von Ettingshausen for venation pattern. After categorization of such features as shape of the whole leaf and of the apex and base, leaves are separated into a number of classes depending on the course of their principal venation. Identification of order of venation, which is fundamental to the application of the classification, is determined by size of a vein at its point of origin and to a lesser extent by its behavior in relation to that of other orders. The classification concludes by describing features of the areoles, i.e., the smallest areas of leaf tissue surrounded by veins which form a contiguous field over most of the leaf. Because most taxa of dicots possess consistent patterns of leaf architecture, this rigorous method of describing the features of leaves is of immediate usefulness in both modern and fossil taxonomic studies. In addition, as a result of this method, it is anticipated that leaves will play an increasingly important part in phylogenetic and ecological studies.

LEAVES are generally neglected in taxonomic and comparative morphologic studies due in large part to the lack of a detailed, standardized, unambiguous classification of their features. Students of modern plants have been content, in most cases, with brief descriptions of leaf outline, margin, and major vein configuration. Most paleobotanists, for whom leaves represent the majority of angiosperm remains, have also neglected to go much beyond the use of comparatively superficial leaf features in their identifications. This has resulted in a prohibitively high percentage of incorrect generic assignments, especially with leaves older than the mid-Tertiary (Pacltová, 1961; Wolfe, 1966, 1968, 1969; Doyle, 1969; Dilcher and Dolph, 1970).

The purpose of this report is to present an inclusive, coherent classification of the architecture of dicotyledonous leaves. Many of the features to be enumerated are also found in the monocots, but no specific attempt has been made to extend the classification to them. The proposed system is based in part on portions of previous classifications and has been modified and expanded as the result of four years of research with the collections of the U. S. National Herbarium. The initiative for developing such a scheme resulted from my research on an early Tertiary flora, which will be reported elsewhere (Hickey, in press).

In this and in subsequent reports I will use the term "leaf architecture" to denote the placement and form of those elements constituting the outward expression of leaf structure, including venation pattern, marginal configuration, leaf shape, and gland position. This term is appropriate because the elements of leaves are organized into certain definite structural patterns capable of description, thus conforming to the definition of architecture as "formation or construction whether the result of conscious act or of growth or of random disposition of parts" (Webster's New International Dictionary, third edition). Architecture is the aspect of morphology which applies to the spatial configuration and coordination of those elements making up part of a plant without regard to histology, function, origin, or homology. The term was used in this sense by Devadas and Beck (1971) and the specific term "leaf architecture" by Hickey (1971a) and Delevoryas and Gould (1971).

Botanical terms describing specific aspects of leaves are in ample supply, largely because of the influence of early systematists such as Linnaeus, Bentham, Lindley, and Asa Gray. Unfortunately these terms frequently have ambiguous, overlapping, or imprecise meanings and are not organized into any coherent system. The available descriptive terminology is mainly concerned with the shape of the leaf and its extremities and the most obvious aspects of its major vein patterns.

[1] Received for publication 28 December 1971.
Research conducted, in part, while an NAS-NRC-Smithsonian Visiting Postdoctoral Research Associate. Grateful acknowledgment is made of the advice and critical comment of Dr. Edward S. Ayensu, Dr. James A. Doyle, Dr. William L. Stern, and Dr. Jack A. Wolfe.

The method of classifying leaf shape employed here is based on a scheme developed by W. B. Turrill at the Royal Botanic Gardens, Kew, about 1925. First publication of the method was by Lee (1948), followed by more complete summaries by Stearn (1956) and Krussmann (1960). The system represents a considerable improvement in terminology because it establishes precisely defined shape categories for leaves, based on the position of the axis of greatest width on the long axis of the leaf and the ratio of length to width (l/w ratio). Apical and basal shapes were also given more precise formulation. The only other shape classification in use is that of the Systematics Association Committee for Descriptive Terminology (1962). This system also defines shape classes using l/w ratio and position of the axis of greatest width but includes other criteria such as the shape of the margins, thus arriving at a more elaborate and less generalized classification than the Turrill system.

Constantin von Ettingshausen made the first comprehensive effort to systematize the description of leaf architecture with his classification of venation patterns in 1861 (Foster, 1952). His categorization proceeds in logical fashion from the configuration of the primary veins to that of the areolation. Although it is over-elaborate and mixes features having taxonomic utility with others having no significance, I have found it a useful starting point for the venational classification proposed here. Unfortunately Von Ettingshausen's system never came into widespread use, although the paleobotanists Lesquereux (1878), Berry (1916), and Hollick (1936) used a few of his terms to describe the configuration of the lower orders of venation.

Later, Kerner (1895) formulated a classification, treating only the primary and secondary vein pattern. Although this system appears to be at least partly derived from that of Von Ettingshausen, the approach used is somewhat different from the original and, regrettably, Kerner employed some of the same or closely similar terms for different patterns of venation. A modern application of Kerner's terminology can be seen in Krussmann's "Handbuch der Laubegehölze" (1960). Another derivative system was outlined by Takhtajan (1963).

One important example of a totally independent classification of some elements of leaf architecture is found in Lam's (1925) monograph on the Sapotaceae of the East Indies. Lam's recognition of a number of taxonomically significant characteristics of secondary and tertiary venation, such as their angular relationships, curvature, paths both inside the leaf and near its margins, branching patterns, and vein junctions, was important in influencing my choice of such features in the present system. Both Goebel (1905) and Troll (1938) developed classifications dealing principally with the developmental morphology of venation, but neither of these had any important influence on the terminology used here.

The ability to catalogue and describe leaf characters precisely will add considerably to the usefulness of leaves as taxonomic features for botanists and paleobotanists alike. In addition, a more sophisticated knowledge of leaf architecture has permitted a start to be made in discerning phylogenetic trends from leaves (Hickey, 1971b), which may have important bearing on the study of modern and fossil groups. Finally, the existence of a body of carefully defined terms for leaf architecture may facilitate the study of environmental effects on leaves.

MATERIALS AND METHODS—In developing this classification the leaf architecture of 1212 genera in 135 families of dicotyledons was surveyed, using uncleared leaves in the U. S. National Herbarium. A cleared leaf collection, now amounting to 473 species in 223 genera and 70 families, was made for this study in order to examine finer details such as areolation patterns and higher order venation which are not visible in uncleared material. These clearings were made by the method of Foster (1952) with modifications by Wolfe (personal communications) and myself. These modifications include the clearing of some leaves (fresh or herbaceous) in commercial bleach solutions (approximately 5% sodium hypochlorite) instead of 5% sodium hydroxide; the use of plastic screening to weight the leaves during clearing; of toluene rather than xylene as the solvent for the mounting medium; and the use of a hard-rubber photographic roller to flatten the petiole and midvein of the leaf during mounting.

In constructing this classification, an effort was made to include a large number of taxonomically significant lower order features which can be observed in uncleared leaves and which are most apt to be preserved in fossil leaves.

The architecture of fossil angiosperm leaves of all ages, from the Early Cretaceous to the Pleistocene, was surveyed by examining substantial portions of the U. S. National Museum collections[2] and all cards in the Type Catalogue of North American Fossil Plants maintained at Princeton University by Professor Erling Dorf. (This catalogue includes illustrations of virtually all described fossil species of North American angiosperms.)

Fossil and modern leaf architecture were com-

[2] Among specific collections examined, including those of the author, are: the Potomac Flora (Lower Cretaceous); the Raritan, Dakota, and Lance Floras (Upper Cretaceous); the Fort Union, Raton, Denver, and lower Golden Valley Floras (Paleocene); the upper Golden Valley, Wind River, Yellowstone Park, Kisinger Lakes, Wilcox, Green River, Claibourne, and Jackson Floras (Eocene); the Florissant Flora (Oligocene); and the Latah Flora (Miocene).

pared by means of high contrast photographs (taken on Dupont Ortho A Litho or Kodalith Pan plate films) or camera lucida drawings of the fossils and high resolution photographs of modern leaves (made from Wratten M glass plate negatives of the whole, cleared leaf taken with the anti-halation backing toward the camera lens).

A leaf architectural classification could include an almost infinite number of features. The taxonomic utility of those features chosen for this system was evaluated by assembling data sheets showing their distribution among various taxa. These features were then used in the identification of fossil leaves in the early Tertiary, Golden Valley Flora (Hickey, in press) and to separate various taxa of modern leaves from the ordinal to the specific level, thus providing a continuous test of the components of this classification during its formulation. An early Tertiary flora provided an important impetus for this study because its high content of extinct forms and the large number of generic misidentifications secured by superficial and traditional matching techniques both necessitated the development of a more precise approach. Examples of the use of this classification in the identification process as well as actual photographs of leaves displaying the features described will appear in the report on the Golden Valley Flora (Hickey, in press).

SCOPE AND BASIS OF THE CLASSIFICATION—The essential justification for the classification presented here is the fact that the various taxa of dicots have leaves possessing consistent and recognizable patterns of architectural organization. Most members of the Theaceae, for example, exhibit serrations of a characteristic shape, with glandular setae; have pinnate, camptodromous venation with elongated intercostal areas and large, loosely organized irregular areolation. Character sets of families or genera sometimes overlap, as in the case of the lauraceous genera, making a positive assignment impossible. Sets of characters proving significant for recognizing one taxon may be completely different from those distinguishing another, although in general areolation and marginal features are rather reliable (cf. Wolfe, 1968).

Some families and genera contain several basic patterns of leaf architecture. This is particularly true of "artificial" or paraphyletic families such as the Euphorbiaceae. In other families variation from the basic pattern appears in those genera or species in environments more extreme than the mean to which the family is adapted. For example, most of the Theaceae live in paratropical and subtropical forests where the majority of them possess the characteristic glandular serrate margins mentioned above. Species living in drier, more open areas (*Laplacea* and *Ternstroemia*), in high montane settings (*Eurya*), or in the lowland tropics (some *Gordonia* and *Shima* sps.) show a trend first toward loss of the serrations and finally to the loss of marginal glands. As a general rule, the small, coriaceous, entire-margined leaves of xeric, arctic, or alpine environments show relatively few of the characters needed for taxonomic identification.

The outline below begins by describing features of the whole lamina, such as directions within it and its form. For the sake of simplicity simple leaves and leaflets are treated together as laminae. Arrangement of the elements of compound leaves is not discussed in this summary since they have been adequately described elsewhere, e.g., Lawrence (1951) and Federov, Kirpichnikov, and Artushenko (1956). After considering the shape of the parts of the leaf and position of glands, the system proceeds to an examination of vein configuration, starting with the primary and secondary veins which determine the major vein classes, such as pinnate, acrodromous, or actinodromous (see below). Proceeding as in the Von Ettingshausen classification, the present system describes the traits of progressively higher orders of venation, terminating with those of areolation. In view of the rudimentary state of our present knowledge of leaf architecture, the system set forth here should not be regarded as a final formulation but rather as open-ended and subject to modification as more information accumulates.

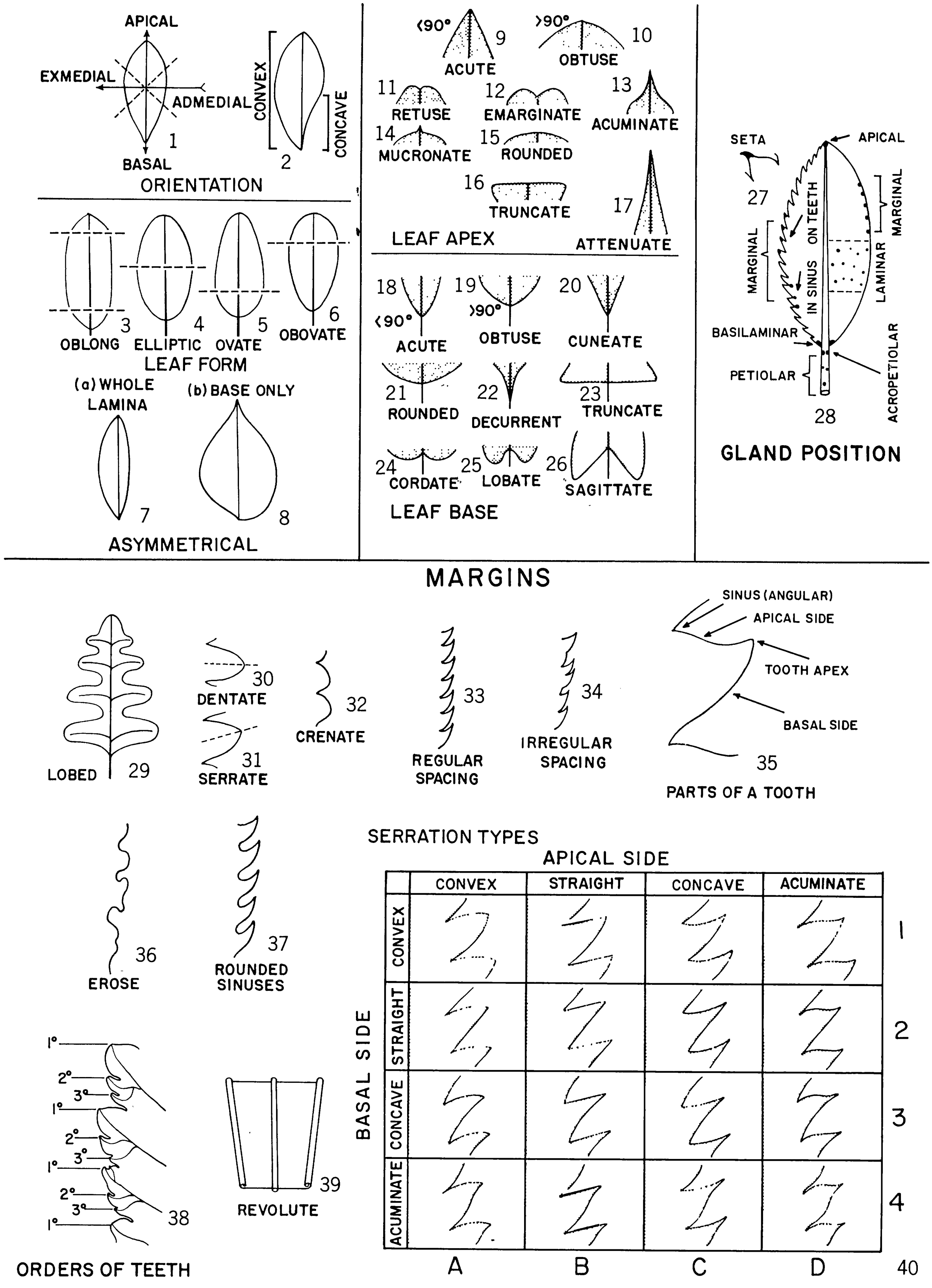
All terms listed in the following outline are illustrated and defined, except where their meaning is obvious. Although I have set limits based on observed breaks in morphological features in describing some characters, such as size of primary veins and of areolation, in many cases it is not possible to avoid being somewhat arbitrary. Thus, although most acute leaf apices can be distinguished from most acuminate ones, there will be a number which fall in a transitional zone; the same sort of transition is present between the imperfect actinodromous venation class and the pinnate class where the lowest pair of secondary veins is set at an angle different from those above. Such difficulties are inevitable in imposing a classification on natural features and in no way detract from the utility of doing so.

OUTLINE OF LEAF ARCHITECTURAL CLASSIFICATION

I. Orientation—The basic axes of orientation in the leaf are indicated in Fig. 1 (as modified after Wolfe, written communication, 1968):

A. Apical—toward the apex (upward).

B. Basal—toward the base (downward).


APICAL
EXMEDIAL
ADMEDIAL
BASAL
CONVEX
CONCAVE
1
2
ORIENTATION
3
OBLONG
4
ELLIPTIC
5
OVATE
6
OBOVATE
LEAF FORM
(a) WHOLE LAMINA
(b) BASE ONLY
7
8
ASYMMETRICAL
<90°
9
ACUTE
>90°
10
OBTUSE
11
RETUSE
12
EMARGINATE
13
ACUMINATE
14
MUCRONATE
15
ROUNDED
16
TRUNCATE
17
ATTENUATE
LEAF APEX
18
<90°
ACUTE
19
>90°
OBTUSE
20
CUNEATE
21
ROUNDED
22
DECURRENT
23
TRUNCATE
24
CORDATE
25
LOBATE
26
SAGITTATE
LEAF BASE
SETA
27
APICAL
MARGINAL
ON TEETH
IN SINUS
MARGINAL
LAMINAR
BASILAMINAR
PETIOLAR
ACROPETIOLAR
28
GLAND POSITION
MARGINS
LOBED
29
30
DENTATE
31
SERRATE
32
CRENATE
33
REGULAR SPACING
34
IRREGULAR SPACING
SINUS (ANGULAR)
APICAL SIDE
TOOTH APEX
BASAL SIDE
35
PARTS OF A TOOTH
36
EROSE
37
ROUNDED SINUSES
1°
2°
3°
38
ORDERS OF TEETH
39
REVOLUTE
SERRATION TYPES
APICAL SIDE
CONVEX
STRAIGHT
CONCAVE
ACUMINATE
BASAL SIDE
CONVEX
STRAIGHT
CONCAVE
ACUMINATE
1
2
3
4
A
B
C
D
40

C. Exmedial—away from the leaf axis. Not synonymous with abaxial which implies the presence of a physical axis such as a stem, rather than an axis of symmetry.
D. Admedial—toward the leaf axis. Not synonymous with adaxial which term rejected for reasons given above.

The curvature of leaf elements (margin or part thereof, sides of a serration, venation) is referred to as (Fig. 2):

E. Convex—curved away from the center of the leaf, or its axis, or (for venation in the actinodromous class) the point of origin of the primary veins.
F. Concave—curved toward the center of the leaf, etc.

II. Shape.
  A. Lamina.
    1. Balance.
      a. Whole lamina.
        1) symmetrical (Fig. 1).
        2) asymmetrical (Fig. 7).
      b. Base only.
        1) symmetrical (Fig. 1).
        2) asymmetrical (Fig. 8).
    2. Form (modified after Stearn, 1956).
      a. Oblong—widest portion constituting a zone through the middle of the long axis of the leaf, margins parallel or nearly so within this zone (Fig. 3). The length-width (l/w) ratios given for the subclasses are lower limits except for the last.

1) linear	l/w ratio	10:1 or more
2) lorate	l/w ratio	6:1
3) narrow oblong	l/w ratio	3:1
4) oblong	l/w ratio	2:1
5) wide oblong	l/w ratio	1.5:1
6) very wide oblong	l/w ratio	1.2:1 or less

      b. Elliptic—axis of greatest width perpendicular to the approximate midpoint of the leaf axis (Fig. 4). Margins in this and succeeding classes convex or some combination of convex and concave.

1) very narrow elliptic	l/w ratio	6:1 or more
2) narrow elliptic	l/w ratio	3:1
3) elliptic	l/w ratio	2:1
4) wide elliptic	l/w ratio	1.5:1
5) suborbiculate	l/w ratio	1.2:1
6) orbiculate	l/w ratio	1:1
7) oblate	l/w ratio	0.75:1 or less

      c. Ovate—axis of greatest width intersecting the leaf axis basal to the midpoint of the latter axis (Fig. 5).

1) lanceolate	l/w ratio	3:1 or more
2) narrow ovate	l/w ratio	2:1
3) ovate	l/w ratio	1.5:1
4) wide ovate	l/w ratio	1.2:1
5) very wide ovate	l/w ratio	1:1 or less

      d. Obovate—axis of greatest width intersecting the long axis of the leaf apical to the midpoint of the latter axis (Fig. 6).

1) narrow oblanceolate	l/w ratio	6:1 or more
2) oblanceolate	l/w ratio	3:1
3) narrow obovate	l/w ratio	2:1
4) wide obovate	l/w ratio	1.2:1
5) very wide obovate	l/w ratio	1:1 or less

←
Fig. 1–40. Leaf architectural features—orientation and form of whole leaf, shape of apex and base, gland position, and marginal configuration.

e. Special shapes (including needle or awl shaped, reniform, deltoid, spatulate, etc.).

B. Apex—that portion of the leaf bounded by approximately the upper 25% of the leaf margin.
1. Acute—straight to convex margins forming an angle of less than 90° (Fig. 9).
2. Acuminate—tip acute, margins markedly concave, either long or short acuminate (Fig. 13).
3. Attenuate—margins straight or only slightly concave, gradually tapering to a narrow acute apex (Fig. 17).
4. Obtuse—straight to convex margins forming an angle of more than 90° (Fig. 10).
5. Rounded—margins forming a smooth arc across the apex (Fig. 15).
6. Mucronate—apex terminating in a sharp point which is a continuation of the midvein (Fig. 14).
7. Retuse—apex slightly notched as if by removal of the termination of the midvein; internal angle of the sinus generally less than 25° (Fig. 11).
8. Emarginate—apex broadly notched by the embayment of the leaf tissue (Fig. 12).
9. Truncate—Apex terminating abruptly as if cut, margin perpendicular to the midvein or nearly so (Fig. 16).
10. Other.

C. Base—that portion of the leaf bounded by approximately the lower 25% of the margin.
1. Acute—margins forming an angle of less than 90°.
   a. normal—base with curved margins terminating at the petiole without appreciable change in direction (Fig. 18).
   b. cuneate—margins straight, or nearly so, and forming a "wedge" of less than 90° (Fig. 20).
   c. decurrent—margin extending downward along the petiole at a low angle to it (Fig. 22).
2. Obtuse—margins forming an angle of greater than 90° (Fig. 19).
   a. normal—(as above).
   b. cuneate—margins straight or nearly so and forming a "wedge" of greater than 90° (rare).
   c. decurrent—(as above).
3. Rounded—margins forming a smooth arc across the base (Fig. 21).
4. Truncate—terminating abruptly as if cut, margin perpendicular to the midvein or nearly so (Fig. 23).
5. Cordate—leaf base embayed in a sinus whose sides are straight or convex (Fig. 24).
6. Auriculate to Lobate—small to large rounded projections whose inner margins (those toward the petiole) are in part concave (Fig. 25).
7. Saggitate—with two large pointed lobes whose apices are directed downward, i.e., at an angle of 45° or less from the leaf axis (Fig. 26).
8. Hastate—with two large pointed lobes whose apices are directed outward, i.e., at an angle of greater than 45° from the leaf axis (not illustrated).
9. Peltate—petiole attached inside the leaf margin (not illustrated).
10. Other.

III. Margin.

A. Entire—margin forming a smooth line or arc without noticeable projections or indentations.

B. Lobed—margin indented ¼ or more of the distance to the midvein or (where this is lacking) to the long axis of the leaf (Fig. 29).

C. Toothed—margin having projections with pointed apices, indented less than ¼ of the distance to the midvein or long axis of the leaf (Fig. 30, 31, 33–35, 37, 38).
1. Dentate (Fig. 30)—dentations are pointed with axes approximately perpendicular to the trend of the margin; as with leaf apices these can be acute (Fig. 9), obtuse (Fig. 10), acuminate (Fig. 13), attenuate (Fig. 17), or mucronate (Fig. 14) (definitions as under apices, above).
2. Serrate (Fig. 31)—serrations are pointed with their axes inclined (i.e., at an oblique angle) to the trend (tangent) of the margin.

a. Apical angle.
 1) Acute—angle formed by the two sides less than 90° (typical).
 2) Obtuse—angle formed by the two sides greater than 90° (rare).
b. Serration type—determined by the shape of the basal side (shown on the vertical or lettered lines of Fig. 40) vs. the shape of the apical side (shown on the horizontal or numbered lines of Fig. 40). Families and genera often exhibit a high degree of consistency in their possession of one or two types of serration. See Fig. 35 for orientation. The configurations used for each side are given in Table 1.

D. Crenate (Fig. 32)—crenations are smoothly rounded, without a pointed apex.
E. Erose (Fig. 36)—irregular, as if chewed.
F. Revolute or enrolled (Fig. 39)—margin turned under or rolled upon itself like a scroll—applies to both entire and non-entire margins.
G. Sinuses—incisions between marginal projections of any sort—lobes, dentations, serrations, or crenations.
 1. Rounded (Fig. 37)—margins of sinus meeting in a smooth curve.
 2. Angular (Fig. 35)—margins of sinus meeting at a point.
H. Spacing—interval between corresponding points on the teeth or crenations.
 1. Regular (Fig. 33)—interval varying by no more than 25%.
 2. Irregular (Fig. 34)—interval varying by more than 25%.
I. Series—teeth separated into size groups.
 1. Simple (Fig. 33)—teeth all of one size.
 2. Compound (Fig. 38)—teeth in two or more definite size groups—double serrations, etc.

IV. Texture.
 A. Membranaceous—thin and semi-transparent, like a fine membrane.
 B. Chartaceous—opaque and like writing paper.
 C. Coriaceous—leathery, thick, stiff.
 D. Other.

V. Gland Position (includes nectaries, hydathodes, tanniniferous glands, etc.).
 A. Petiolar (Fig. 28)—on the tissue of the petiole; includes *acropetiolar* (Fig. 28)—at the top of the petiole.
 B. Basilaminar (Fig. 28)—on the foliar tissue at the base of the blade.
 C. Laminar (Fig. 28)—generally distributed on the foliar tissue.
 D. Apical (Fig. 28)—on the leaf apex.
 E. Marginal—distributed on the margin or marginal processes.
  1. At the margin in entire marginal leaves (Fig. 28).
  2. On the teeth.
   a. As a glandular thickening (Fig. 28).
   b. As a glandular seta or bristle (Fig. 27).
  3. In the sinus (Fig. 28).

VI. Petiole(ule).
 A. Normal—without noticeable thickenings or other processes.
 B. Inflated—thickened, includes pulvini.
 C. Winged—with a narrow strip of blade tissue on each side.
 D. Absent—blade sessile, arising directly from the axis of attachment, without an intervening bladeless area of the leaf.

VII. Venation.
 A. Type (for definitions of vein orders see p. 25).
  1. Pinnate—with a single primary vein (midvein) serving as the origin for the higher order venation.
   a. Craspedodromous[3]—secondary veins terminating at the margin.
    1) Simple—all of the secondary veins and their branches terminating at the margin (Fig. 41).

[3] From the Greek *kraspedon*, edge, border; and *dromos*, a running, course.

2) Semicraspedodromous—secondary veins branching just within the margin, one of the branches terminating at the margin, the other joining the superadjacent secondary (Fig. 42).

3) Mixed—some of the secondary veins terminating at the margin and an approximately equal number of (usually intervening) secondaries otherwise (Fig. 43).

b. Camptodromous—secondary veins not terminating at the margin.

1) Brochidodromous[4]—secondaries joined together in a series of prominent arches (Fig. 46).

2) Eucamptodromous—secondaries upturned and gradually diminishing apically inside the margin, connected to the superadjacent secondaries by a series of cross veins without forming prominent marginal loops (Fig. 47).

3) Reticulodromous—secondaries losing their identity toward the leaf margin by repeated branching into a vein reticulum (Fig. 48).

4) Kladodromous[5]—secondaries freely ramified toward the margin (Fig. 49).

c. Hyphodromous—all but the primary vein absent, rudimentary, or concealed within a coriaceous or fleshy mesophyll (Fig. 44).

2. Parallelodromous—two or more primary veins originating beside each other at the leaf base and running parallel to the apex where they converge (Fig. 45).

3. Campylodromous[6]—several primary veins or their branches, originating at, or close to, a single point and running in strongly developed, recurved arches before converging toward the leaf apex. Vein pattern convergent above and below (Fig. 58).

4. Acrodromous—two or more primary or strongly developed secondary veins running in convergent arches toward the leaf apex. Arches not recurved at base (Fig. 59–62).

a. Position.

1) Basal—acrodromous veins originating at the base of the leaf (Fig. 59, 61).

2) Suprabasal—acrodromous veins originating some distance above the leaf base (Fig. 60, 62).

b. Development.

1) Perfect—acrodromous veins well developed, running at least ⅔ of the distance to the leaf apex (Fig. 59, 60).

2) Imperfect—acrodromous veins running less than ⅔ of the distance to the leaf apex (Fig. 61, 62).

5. Actinodromous—three or more primary veins diverging radially from a single point (Fig. 50–56) or

6. Palinactinodromous—primaries having one or more subsidiary points of radiation above the lowest point, e.g., *Platanus* (Fig. 57).

(The following categories apply to 5 and 6 above.)

a. Position of the first point of primary vein radiation.

1) Basal (Fig. 50, 52, 54, 55) initial point of radiation at the leaf base.

2) Suprabasal (Fig. 51, 53, 57) initial point of radiation located some distance above the leaf base.

b. Development.

1) Perfect—ramifications of the lateral actinodromous veins covering at least ⅔ of the blade area (Fig. 50–53).

a) Marginal—actinodromous veins reaching the margin (Fig. 50, 51).

b) Reticulate—actinodromous veins not reaching the margin (Fig. 52, 53).

2) Imperfect—veins originating on the lateral actinodromous primary veins covering less than ⅔ of the blade area.

a) Marginal (Fig. 54).

b) Reticulate (Fig. 55).

3) Flabellate—several to many equally fine basal veins diverge radially at low angles and branch apically (Fig. 56).

[4] *brochos* Gr., a noose.
[5] *klados* Gr., a branch.
[6] *campylos* Gr., a bend or curve.

Orders of venation—In most leaves venation is clearly differentiated into a number of size classes. Veins of a particular size class also display some degree of uniformity in their courses and patterns of distribution in relation to other classes and to the marginal features of the leaf. In practice the objective designation of vein order is more complex than easily observed differences in thickness, course, and pattern among size classes would seem to indicate. However, the recognition of vein orders is essential in describing leaf architecture.

The primary venation of the leaf serves as the starting point for the identification of the various vein orders. Veins of the primary order are the thickest veins of the leaf and occur singly or as a medial vein accompanied by others (lateral primaries) of roughly equal thickness. These emerge from the petiole of the leaf, or the medial and lateral primaries may give rise to additional lateral primary veins above the base. Recognition of these branches as primary veins is based on the criterion that the branch be roughly equal in thickness to its primary source when both are measured just above the point of branching. The next set of branches of markedly smaller size than their primary source are the secondary veins, while the next finer set arising from both primary and secondary veins are designated the tertiary veins and so on, until reaching the ultimate vein order present in the leaf.

The primary rule for the determination of the order of a vein is its relative size at its point of origin. Where a lateral vein branch is approximately equal in width, measured just above the point of branching, to the continuation of the source vein just above the point of branching, both branches are of the same order; where the lateral vein branch is markedly finer than the continuation of its source, that branch is of a higher order. This rule is applied when tracing a vein of any order distally from its point of origin.

Subsidiary to size at the point of branching in the recognition of vein order is a consideration of the behavior of a vein in relation to veins of other orders and to marginal features of the leaf blade. It is necessary to consider this additional criterion when dealing with orders having a wide range of sizes or where the boundaries between size classes are not particularly sharp. Three of the most common situations where designation of vein order is difficult involve:

a) suprabasal lateral primary veins—i.e., primary veins originating as lateral branches of a primary vein above the base of the leaf
b) branches of secondary veins
c) intersecondary veins.

TABLE 1. *Serration Types*

	Marginal configuration	*basal*		*apical*
1)	Convex—Fig. 40 lines	A	&	1
2)	Straight—Fig. 40 lines	B	&	2
3)	Concave—Fig. 40 lines	C	&	3
4)	Acuminate—Fig. 40 lines	D	&	4

Lateral primary veins frequently occur as suprabasal branches of a primary vein. In most examples, the thickness of these veins at their point of branching will be the same, or very nearly the same, as the continuation of their source. In other cases the lateral primary branches will be somewhat thinner than their primary source but still considerably thicker than the next thinner set of veins, i.e., the secondaries. Here a number of features permit the recognition of these lateral branches as primary veins. The primary branches will give rise to secondary veins whose size and behavior is no different from secondaries arising on primary veins which originate at the base of the leaf. The primary branch may form the midvein of a leaf lobe as do the other primaries; and in all other ways its behavior will be comparable to that of the other members of its order (Fig. 57). However, if the thickness of a branch of the primary vein is the same as that of the typical secondary veins, it is regarded as a secondary despite some differences in its behavior (usually angle of origin) in relation to them.

Branches of the secondary veins ("outer secondary nerves" of Von Ettingshausen, a-2° of Fig. 41) are frequently of the same thickness at their points of branching as the continuation of the secondary veins from which they arise. In cases where the branches are slightly thinner there is no difficulty in classifying them as secondaries because of their geometric relationships. However, in series where the size of these branches gradually diminishes toward that of the third order their behavior also gradually alters until by both criteria they have become indistinguishable from the tertiaries.

Intersecondary veins are intermediate in thickness between second and third order veins and most often occur interspersed between the secondaries of pinnate leaves (e, Fig. 63). Although their length is shorter than that of the secondary veins their course is parallel, or nearly so, to them, and they more closely resemble the secondaries in their relationship to other orders of veins.

Other difficulties in designating vein order arise as the tendency toward dichotomous branching increases in the higher vein orders. However, the behavior of the resultant branches frequently serves to distinguish separate vein orders. In other cases the higher order venation of a leaf merges into a reticulum in which designation or vein order is impossible (Fig. 79, 80).

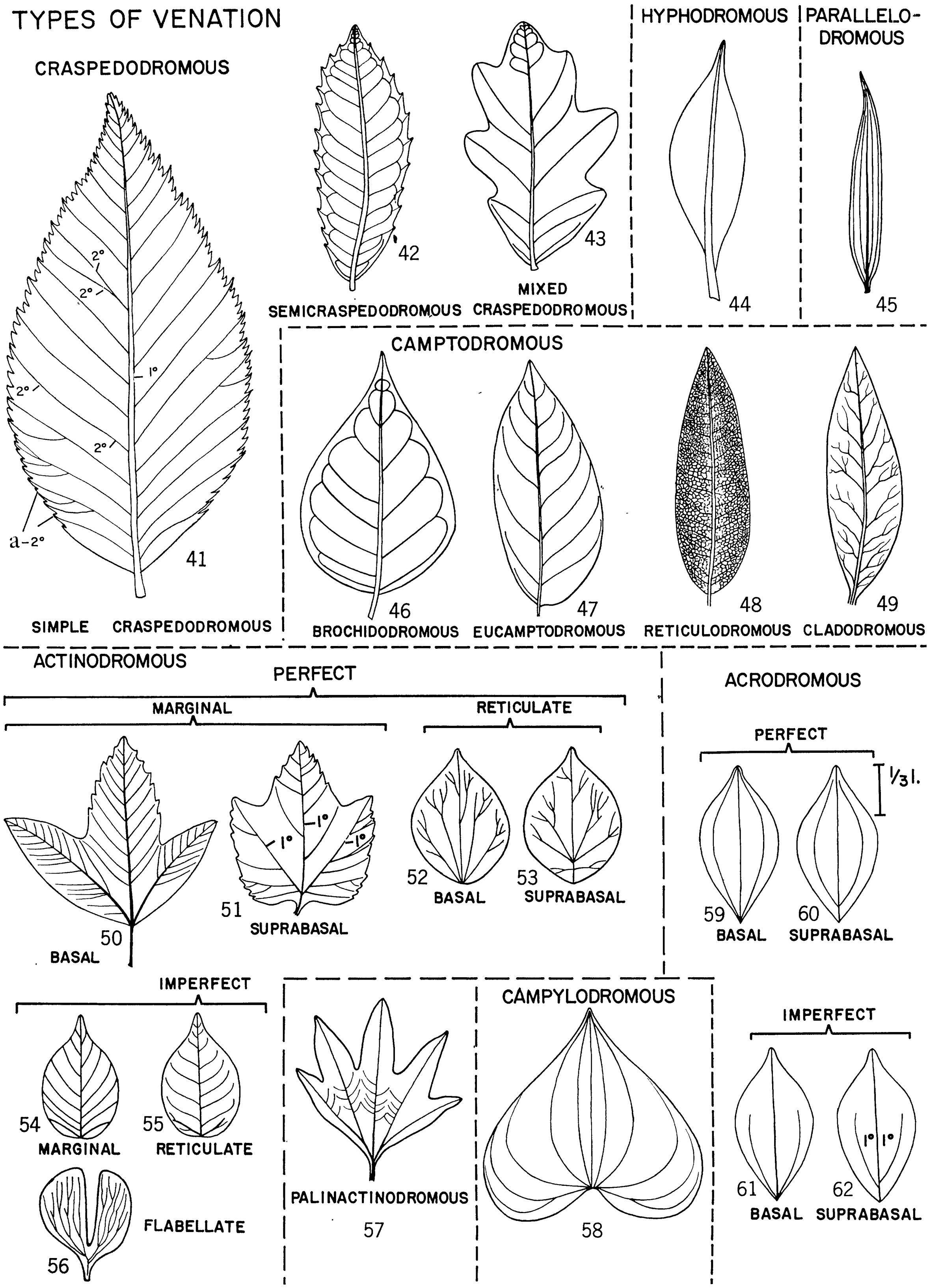


Fig. 41–62. Leaf architectural features (continued)—types of venation.

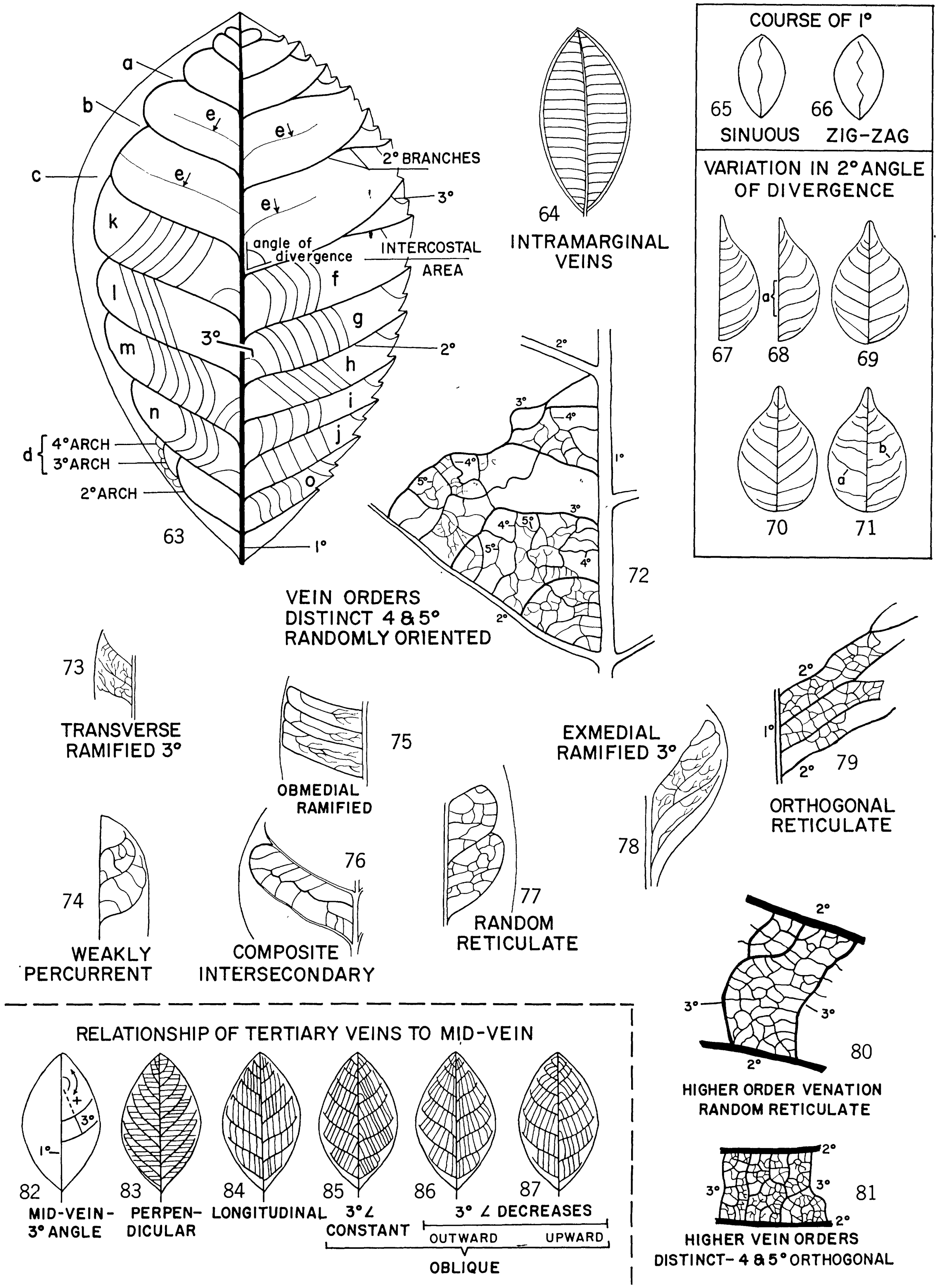


Fig. 63–87. Leaf architectural features (continued)—orders of venation and vein configuration.

1. Primary Veins (1°)—the thickest vein(s) of the leaf, occurring either singly as the midvein, or as a series of veins of relatively equal thickness emerging from the petiole (Fig. 50, 52), or as branches of the medial or lateral primary veins above the base of the blade (suprabasal primaries). In the latter case, both the primary branch and the continuation of its primary source are of the same relative thickness measured just above the point of branching.
   a. Size—determined midway between the leaf apex and base as to the ratio of vein width (vw) to leaf width (LW) vw/LW × 100% = Size.
      1) Massive > 4% (Fig. 44).
      2) Stout 2–4% (Fig. 42).
      3) Moderate 1.25–2% (Fig. 43, 46, 47).
      4) Weak < 1.25% (Fig. 59).
   b. Course.
      1) Straight (Fig. 46)—lacking noticeable curvature or change in course.
         a) Unbranched (Fig. 63)—lacking ramifications of primary rank.
         b) Branched (Fig. 51)—with one or more primary ramifications.
      2) Markedly curved (Fig. 42)—bent noticeably into a smooth arc.
      3) Sinuous—repeated smooth changes in direction of curvature (Fig. 65).
      4) Zig-zag—repeated angular changes in direction (Fig. 66).
2. Secondary Veins (2°)—the next smaller size class of veins (which arise from the primaries) and their branches (Fig. 63) of relatively equal thickness measured just above the point of branching.
   a. Angle of divergence—measured between the branch and the continuation of the source vein above the point of branching (Fig. 63).
      1) acute—angle less than 80°.
         a) narrow < 45°.
         b) moderate 45–65°.
         c) wide 65–80°.
      2) right angle or approximately so, 80–100°.
      3) obtuse > 100°.
   b. Variations in angle of divergence.
      1) divergence angle nearly uniform (Fig. 63). The general case, departures from which are often taxonomically useful features.
      2) upper secondary veins more obtuse than lower (Fig. 67).
      3) upper secondary veins more acute than lower (Fig. 68).
      4) only lowest pair of secondary veins more acute than pairs above it (Fig. 69).
      5) lower and upper secondary veins more obtuse than middle sets (Fig. 70).
      6) divergence angle more acute on one side of the leaf than on the other (Fig. 47).
      7) divergence angle varies irregularly (Fig. 71).
   c. Relative thickness of secondary veins—a measure of the width of the middle secondary veins compared to those of the primary and tertiary orders. Such relative estimates of thickness for this and succeeding vein orders are essentially a measure of the proportional reduction in width from one vein order to the next. This is a useful character only in cases of marked departure from the width expected in the proportional reduction series.
      1) thick—proportionately wide in relation to the primary and tertiary orders or to the secondaries in other leaves of similar size.
      2) moderate—the general case.
      3) fine to hairlike—proportionately narrow in relation to the primary and tertiary vein orders or to the secondaries in other leaves of similar size.
   d. Course—more than one of the following terms may apply:
      1) straight (Fig. 41)—without noticeable deviation in course.
      2) recurved (lower secondaries in Fig. 41)—arching basally for a portion of its course.
      3) curved—bending in an arc.
         a) uniformly (Fig. 54)—arc smooth or gradually increasing in degree of curvature.
         b) abruptly—sharp local increase in degree of curvature (Fig. 46).
      4) sinuous—repeated smooth changes in direction of curvature (Fig. 71a).

TABLE 2. *Analysis of tertiary vein origin*

		Angle of 3° origin on the Exmedial (Lower) Side of the 2°'s		
		Acute	Right	Obtuse
Angle of 3° origin on the Admedial (Upper) Side of the 2°'s	Acute	AA (Fig. 63f)	RA (Fig. 63i)	OA (Fig. 63l)
	Right	AR (Fig. 63g)	RR (Fig. 63j)	OR (Fig. 63m)
	Obtuse	AO (Fig. 63h)	RO (Fig. 63k)	OO (Fig. 63n)

5) zig-zag—repeated angular changes in direction (Fig. 71b).
6) unbranched (Fig. 68)—without second order ramifications.
7) branched (Fig. 63)—with one or more secondary ramifications.
8) provided with outer secondary veins (Fig. 41a)—a series of secondary branches arising on the exmedial side of the secondary vein.

e. Behavior of loop-forming branches (if any).
1) joining superadjacent secondary at acute angle (Fig. 63a).
2) joining superadjacent secondary at right angle (Fig. 63b).
3) joining superadjacent secondary at obtuse angle (Fig. 63c).
4) enclosed by secondary arches. 3° or 4° arches (Fig. 63d).
5) forming an intramarginal vein (Fig. 64).

f. Intersecondary Veins—thickness intermediate between that of the second and third order veins; generally originating from the medial primary vein, interspersed among the secondary veins, and having a course parallel, or nearly so, to them.
They are of two types:
1) simple—consisting of a single vein segment (Fig. 63e).
2) composite—made up of coalesced tertiary vein segments for over 50% of its length (Fig. 76).

g. Intramarginal Vein—a vein closely paralleling the leaf margins and into which the secondary veins are fused. Probably the result of the fusion and straightening of the exmedial brochidodromous secondary arch segments into what appears to be an independent vein (Fig. 64).

h. Intercostal Areas—those portions of the leaf blade lying between the secondary veins (Foster, 1950).

3. Tertiary Veins (3°)—the next finest branches of the secondary veins and those branches of equal thickness from the primaries.
a. Angle of Origin—(defined above). When the predominant angle of tertiary origin on the exmedial (lower) side of the secondary veins is compared with that on the admedial (upper) side of the secondary veins, the combinations shown on Table 2 are possible. This trait is of diagnostic value. As a rule, in those tertiary veins which originate on the admedial side of the secondary veins and curve to join the primary forming the midvein, the angle of tertiary vein origin on the midvein equals the angle of tertiary vein origin on the exmedial side of the secondary veins of the leaf. Departure from this rule is a taxonomically significant feature.
b. Pattern.
1) Ramified—tertiary veins branching into higher orders without rejoining the secondary veins (although their higher order derivatives may do so).
a) exmedial—branching oriented toward the margin, rare (Fig. 78).
b) admedial—branching oriented toward the leaf axis (Fig. 75). [Not obmedial as in Fig.]
c) transverse—branching oriented across intercostal area—the commonest case (Fig. 73).
2) Reticulate—tertiary veins anastomosing with other tertiary veins or with the secondary veins.
a) random reticulate—angles of anastomoses vary (Fig. 77).
b) orthogonal reticulate—angles of anastomoses predominantly right angles (Fig. 79).
3) Percurrent—tertiaries from the opposite secondaries joining.
a) course.

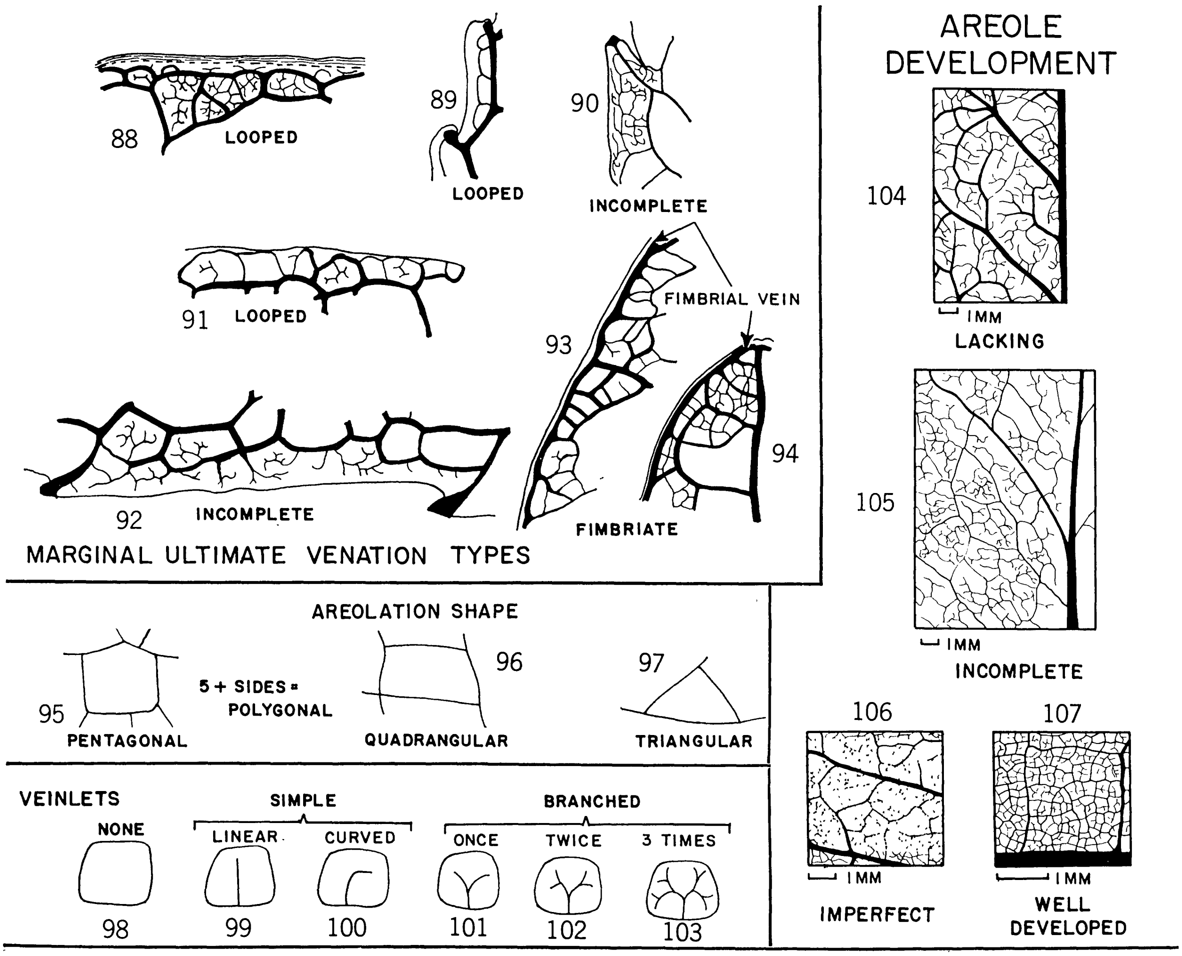


Fig. 88–107. Leaf architectural features (continued)—ultimate venation and areolation.

(1) simple—unbranched (Fig. 63).
(2) forked—giving rise to third order ramifications (Fig. 76).
(3) straight—passing across the intercostal area without a noticeable change in course (Fig. 63h, 1).
(4) convex—middle portion of the vein curving away from the center of the leaf (Fig. 63f).
(5) concave—middle portion of the vein curving toward the center of the leaf (Fig. 63n).
(6) sinuous—repeatedly changing direction of curvature (Fig. 74).
(7) retroflexed—forming a single *S* shaped curve concave apically and convex basally (Fig. 63o).
(8) recurved—curving inward from point of origin on the adaxial side of a secondary vein to terminate on the midvein of the leaf (Fig. 63).

b) relationship to midvein (Fig. 82).
(1) approximately at right angles (Fig. 83).
(2) longitudinal—approximately parallel (Fig. 84).
(3) oblique—trending in an obtuse or, rarely, an acute angle to the midvein.
(a) tertiary angle with midvein remaining approximately constant (Fig. 85).
(b) angle decreasing exmedially (Fig. 86).
(c) angle decreasing apically (Fig. 87).

c) arrangement.
   (1) predominantly alternate—joining each other with an offset i.e., an abrupt angular discontinuity such as a branch (Fig. 76, 81).
   (2) predominantly opposite—joining each other smoothly i.e., in a straight or curved path (Fig. 63).
   (3) alternate and opposite in about equal proportions.
   (4) distant—interval between veins 0.5 cm or greater.
   (5) close—interval between veins less than 0.5 cm.

4. Higher order venation—the next finer order of veins originating from the tertiaries and those of equal size from lower order veins is known as the quaternary (4°) venation and the veins originating from these and those of equal size from lower orders are the quinternaries (5°), etc.
   a. Resolution.
      1) Higher order venation forming a reticulum in which vein orders cannot be distinguished (Fig. 80).
      2) Vein orders distinct (Fig. 72, 81).
   b. Quaternary veins.
      1) Size—a relative measure of the width of the quaternary veins compared to those of the third and fifth orders. Such relative estimates of thickness for this and the fifth order veins (below) are essentially a measure of the proportional reduction in width from one vein order to the next. Notable only is any marked departure from the width expected for the fourth order (fifth order, below) veins as part of a proportional reduction series.
         a) thick—wider than expected.
         b) thin—narrower than expected.
      2) Course.
         a) relatively randomly oriented (Fig. 72).
         b) orthogonal—arising at right angles (Fig. 81). Their subsequent courses may or may not be at right angles.
   c. Quinternary veins [analyzed as in b 1 above].
      1) Size (as above).
         a) thick.
         b) thin.
      2) Course [analyzed as in b 2 above].
         a) random (Fig. 72) (as above).
         b) orthogonal (Fig. 81) (as above).
   d. Highest vein order of leaf: 3°, 4°, 5°, 6°, 7°.
   e. Highest vein order showing excurrent branching: 2°, 3°, 4°, 5°, 6°.
   f. Marginal ultimate venation.
      1) Incomplete—freely ending veinlets directly adjacent to the margin (Fig. 90, 92).
      2) Looped—the major portion of the marginal ultimate venation recurved to form loops (Fig. 88, 89, 91).
      3) Fimbriate—higher vein orders fused into a vein running just inside of the margin (fimbrial vein) (Fig. 93, 94).

5. Veinlets—the freely ending ultimate veins of the leaf and veins of the same order which occasionally cross areoles (see below) to become connected distally.
   a. Veinlets none (Fig. 98).
   b. Simple—without branches.
      1) Linear (Fig. 99).
      2) Curved (Fig. 100).
   c. Branched—giving rise to ramifications by dichotomizing.
      1) Once (Fig. 101).
      2) Twice (Fig. 102).
      3) Three times (Fig. 103), etc.

6. Areoles—the smallest areas of the leaf tissue surrounded by veins which taken together form a contiguous field over most of the area of the leaf. Thus, smaller areas occasionally formed when veinlets cross their areoles are excluded. Any order of venation in a leaf from the primary to the highest order below that of the freely ending veinlets can form one or more sides of an areole. However only the order represented by the veinlets will intrude, or occasionally cross, the islets formed by the non-freely ending veins. The appearance and characteristics of the areoles are termed areolation.
   a. Development.
      1) Well developed—meshes of relatively consistent size and shape (Fig. 107).
      2) Imperfect—meshes of irregular shape, more or less variable in size (Fig. 106).
      3) Incompletely closed meshes—one or more sides of the mesh not bounded by a vein, giving rise to anomalously large meshes of highly irregular shape (Fig. 105).
      4) Areolation lacking—as in hyphodromous or succulent leaves. Very rarely (Fig. 104) venation simply ramifying into the intercostal spaces with no coherent shape, size or pattern to the areas surrounded by veins.
   b. Arrangement.
      1) Random—areoles showing no preferred orientation (Fig. 106).
      2) Oriented—areoles having a similar alignment or pattern of arrangement within particular blocks or domains (Fig. 107).
   c. Shape.
      1) Triangular (Fig. 97).
      2) Quadrangular (Fig. 96).
      3) Pentagonal (Fig. 95).
      4) Polygonal—with more than 5 sides.
      5) Rounded.
      6) Irregular.
   d. Size—the size classes of areoles chosen appear to represent, at least partially, naturally occurring groups.
      1) Very large > 2 mm.
      2) Large 2–1 mm.
      3) Medium 1–0.3 mm.
      4) Small < 0.3 mm.

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