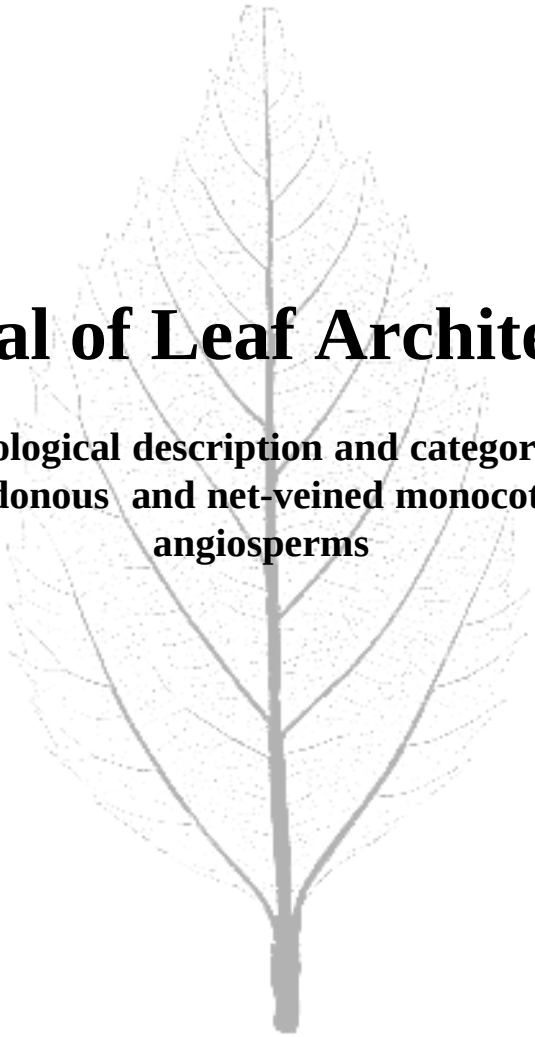
Manual of Leaf Architecture

Morphological description and categorization of dicotyledonous and net-veined monocotyledonous angiosperms



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Names and addresses of the Leaf Architecture Working Group in alphabetical order:

Amanda Ash
Department of Paleobiology
Smithsonian Institution NHB
10th St. & Constitution Ave, N.W.
Washington, DC 20560-0121
Telephone: 202 357-4030
Fax: 202 786-2832
Email: ash.amanda@nmnh.si.edu

Beth Ellis
1276 Cavan St.
Boulder, CO 80303
Telephone: 303 666-9534
Email: Beth@displaytech.com

Leo J. Hickey
Division of Paleobotany
Peabody Museum of Natural History
Yale University
170 Whitney Avenue, P.O. Box 208118
New Haven, CT 06520-8118
Telephone: 203 432-5006
Fax: 203 432-3134
Email: leo.hickey@yale.edu

Kirk Johnson
Department of Earth and Space Sciences
Denver Museum of Natural History
2001 Colorado Boulevard
Denver, CO 80205-5798
Telephone: 303 370-6448
Fax: 303 331-6492
Email: kjohnson@dmnh.org

Peter Wilf
University of Michigan
Museum of Paleontology
1109 Geddes Road
Ann Arbor, MI 48109-1079
Telephone: 734 763-9373
Fax: 734 936-1380
Email: pwilf@umich.edu

Scott Wing
Department of Paleobiology
Smithsonian Institution NHB
10th St. & Constitution Ave, N.W.
Washington, DC 20560-0121
Telephone: 202 357-2649
Fax: 202 786-2832
Email: wing.scott@nmnh.si.edu

INTRODUCTION

Since the time of Linnaeus the identification and reconstruction of relationships between plants have been based largely on features of the reproductive organs. Although flower and fruit characters have proved very useful in both botany and paleobotany, there are situations in which these organs are not available for study. For example, leaf compression and impression fossils are the most common macroscopic remains of plants, but they are generally not attached to other plant organs. Because of their abundance and dense stratigraphic occurrence, fossil leaves can provide an enormous amount of information about the composition and diversity of past floras - if they can be used to recognize species reliably and assign them to higher taxa. Tropical botanists also find themselves confronted with the need to identify and classify plants using vegetative characters because so many long-lived tropical plants flower infrequently and irregularly. In spite of the success of Linnaeus's sexual system and its descendants, there is a great need to be able to identify and classify dispersed leaves. The overall purpose of this manual is to help you do that.

The problem of working with isolated leaves is a long-standing one in paleobotany. Lacking both an accepted system of terms for describing leaf form, and a knowledge of the systematic distribution of leaf features among living angiosperms, and in many cases faced with poorly preserved fossils, most early workers focused on overall characters of leaf shape and size that ultimately have not proven very useful in recognizing species or higher taxa. Names of living genera were widely applied to fossils so that there are, for example, many taxonomically valid fossil species of *Ficus*, *Populus*, and *Aralia* based on poorly preserved leaves with only vague similarities to the living members of these genera. Late nineteenth and early twentieth century angiosperm paleobotanists left a legacy of poorly defined taxa with botanically misleading names.

In the last half of the twentieth century two new approaches have helped rectify this problem. One has been to study multiple organs, including leaves, thought to represent the same plant species, either because they are preserved in attachment or because they occur together at many localities. This approach allows traditional characters of flowers and fruits to be used in defining extinct taxa and determining their relationships (e.g., Manchester 1986). Studying characters of multiple organs of the same plant allows fossil taxa to be described more comprehensively and systematic relationships to be established with greater certainty than can be gained from leaves alone. However, there are many types of fossil leaves that have not been found attached to or consistently associated with other organs. The second approach has been to identify systematically informative leaf features (Hickey and Wolfe 1975, Wolfe 1989, Hickey and Taylor 1991) that allow species to be recognized on the basis of dispersed leaves; these features may also permit the fossil to be assigned to a family or higher taxonomic category. This approach has been used principally in dicotyledonous angiosperms with complex vein systems. Among living dicots, foliar characters may or may not offer conclusive evidence of the generic or higher-level affinities of a plant, but generally they do allow even closely related species to be distinguished (e.g., Merrill 1978).

The main goal of this manual is to define and illustrate for the reader an unambiguous and standard set of terms for describing leaf form and venation, particularly of dicots. This manual also provides a template and set of instructions that show how descriptive information can be entered into a standardized database of fossil and extant leaves. The Leaf Architecture Working Group (LAWG) adopted and in some cases added or modified the definitions and terms found in this manual and developed its format.

The purpose of any terminology or method for quantifying leaf form is to allow objective description of and comparisons among different types of leaves. Many sets of terms and methods have been devised for describing leaves (e.g., Ettingshausen 1861; Melville 1937, 1976; Dale et al. 1971; Hickey 1973, 1977, 1979; Mouton 1966, 1967; Dickinson et al. 1987; Jensen 1990; Ray 1992). These will not be reviewed here. Terms for the description of leaf form and venation are largely from the leaf architectural system of Hickey (1973, 1977, 1979). The terms and drawings illustrating leaf cuticle features have been taken without modification from Dilcher (1974). These terminologies have been adopted because they are in wide use among botanists and paleobotanists, including the members of the LAWG. Although fully quantitative methods for describing leaf shape exist and are presumably more objective than the qualitative and semi-quantitative terms described here, they have several disadvantages. Quantification of leaf shape through, for example, Fourier or landmark methods is still time consuming when compared with semi-quantitative characterization. It is also difficult to apply these techniques to typically incomplete fossil specimens. Further, we wished this system to be applicable across all types of dicot and net-veined monocot leaves, thus eliminating methods that require recognition of homologous points or vein patterns. Finally, we decided against a fully quantitative approach because many of the most systematically valuable features of leaves are in the venation, and quantification of vein networks is even more time-consuming than quantification of leaf shape.

THE MORPHOTYPE CONCEPT

A morphotype is an informal taxonomic category independent of the Linnaean system of nomenclature. The morphotype system outlined in this manual was first used by Johnson (1989), who created explicitly defined categories of fossil leaves based on architectural features that could be used for stratigraphic and paleoecological studies without having to resolve the botanical and nomenclatural status of each leaf type.

Although many or most leaf morphotypes are probably equivalent to biological species, morphotypes are more narrowly circumscribed by their form and should not be considered as exact species equivalents. For example, some plants produce multiple leaf types with few or no intermediates, as in the long-shoot versus short-shoot leaves of *Cercidiphyllum japonicum*. The short-shoot leaves are orb-shaped and have cordate bases, while the long-shoot leaves are ovate and have rounded bases. If such distinct morphological types were found in a group of fossil leaves, they would be assigned to different morphotypes, even if the fossils shared important venational features and living relatives were known to produce similarly dimorphic foliage. If, instead, the fossil leaves showed a gradational series with intermediate morphology between the two end-members, they would all be included in the same morphotype. In some cases these variable morphotypes may represent more than one species or even more than one genus. In families with very small leaves, for example, there may be so few architectural features that multiple genera produce nearly identical leaves.

Because morphotypes may represent different taxonomic levels with different biological significance, they should not be used uncritically to assess floral diversity, composition, or paleoclimate. An additional level of analysis, synthesis, and comparison with living relatives is directed at recognizing the taxonomic level represented by a morphotype and assessing which morphotypes might represent the same biological species. Following this, morphotypes can be formally described and classified, and used in biostratigraphic, paleoclimatic, or other forms of analysis.

THE LEAF ARCHITECTURE WORKING GROUP (LAWG) DATABASE

This manual is a companion to a database developed by the LAWG and is intended to help researchers describe fossil leaves in a consistent way and to make it easier to compare leaves described by different researchers working on floras from different ages or regions. The database is a FileMaker®Pro application with 57 fields to contain information about each given morphotype. A blank database form is shown in Figure 5. The first section of the entry form has 13 fields for recording basic information about the morphotype and the fossils on which it is based. This includes fields for the higher taxonomic category, the describer, the localities at which the morphotype has been found, and specimen numbers. The next 43 fields in the form are for descriptors of the morphotype. Each field corresponds to a character of the size or shape of the leaf blade, the course of the venation, the form of the margin, and the leaf cuticle. Each field is provided with a pull-down list of character states that the character might have. These character state lists are based on our collective experience with living and fossil dicot leaves, but the lists are not exhaustive. The data-entry format of the fields will permit you to enter character states not on the pull-down lists, but clearly the comparability of descriptions by different workers, and therefore the usefulness of searching this database, will be enhanced if the defined terms are used whenever possible. If you would like additional characters or character states to be added to this manual and the database, please contact Scott Wing at the address listed on the third page of this manual. The final field in the form is formatted to hold digital images which should include both a low magnification image to show leaf shape and a higher magnification image to show details of venation and/or marginal teeth. The digital version of the FileMaker®Pro entry form is on the CD that contains this manual.

This manual is organized in the same order as the database form. Characters, the field names from the database, are numbered and in gray boxes. Choices of character states from the pull-down lists are in boldfaced type. Definitions of terms used in the manual are in italics. For an explanation and illustration of any character or character state simply go to the section of the manual that corresponds to its number (see p. 10). The figures in the manual are numbered to link them to the character names, thus figures 14.1 – 14.4 illustrate character states of the character "leaf attachment," which is the 14th field in the database. The figures used in the introductory section, and in the definitions of terms rather than characters, are numbered sequentially through the manual. Wherever possible we have tried to illustrate character states with real specimens rather than idealized drawings. Almost all of the specimens used in illustrations are from the United States Geological Survey/National Museum of Natural History cleared leaf collection. Slide numbers of the cleared leaves are available in a spreadsheet file, and the original black and white images of the figured specimens are stored in .jpg format on the CD with the digital version of this manual. The images were recorded with a digital camera.

HOW TO "MORPHOTYPE" A FOSSIL FLORA

1. Number each specimen with a locality number and prepare it in the lab so that the features of the leaf are as visible as possible. It is useful to place each specimen in a cardboard tray so that labels remain with the specimen. The CD containing the digital version of this manual also contains files that describe how to collect, prepare and label plant fossils.
2. Select a two-letter morphotype prefix for the material being morphotyped based on the stratigraphic unit and research area (e.g., HC for Hell Creek Formation of Montana or RS for Rock Springs, Wyoming). A master register of prefixes is kept by Kirk Johnson, whose address appears on the LAWG author list, although it is not necessary to register them in order to use the system. A copy of the register is on the CD with the digital version of this manual.

3. Begin to sort the leaves into groups based on shared leaf-architectural characteristics. As each group is defined, select the best specimen (most complete and well preserved) of that group to be the "holomorphotype." Assign a unique morphotype number to the holomorphotype (e.g., HC1) and sequester the type where it is accessible for comparison. This specimen should be assigned a museum specimen number and its status as the holomorphotype noted on the specimen tag. It is also useful to maintain a running list or spreadsheet that records the information about the individual holomorphotypes. One major distinction between holotype specimens (the formal name-bearing specimen in Linnean taxonomy) and holomorphotype specimens (the informal number-bearing specimen in this system) is that holotypes are permanent whereas holomorphytpes may be replaced with better specimens or sunk into other morphotypes.

   Proceed to identify all of the remaining specimens that can be referred to the morphotype based on the holomorphotype and label them accordingly. It is usually best to start with the best-preserved and most abundant morphotypes and work toward the poorly preserved and less common types. In practice, as work proceeds on a fossil flora, some of what were originally recognized as sharply delineated morphotypes will be shown to belong to a continuum, while others will remain as discrete entities.

4. The initial sorting of a collection is usually done on the basis of toothed versus entire margins, primary and secondary vein patterns, and the presence and types of lobes. These characters are *usually* stable within morphotypes. The least reliable characters are leaf size and shape. Once the fossils are grouped into broad categories, it is much easier to separate them by higher-order venation pattern and tooth type [see Hickey 1973, 1979 and Hickey and Wolfe, 1975]. To highlight the characters that define your groups, it is helpful to sketch and/or photograph the holomorphotype and note diagnostic features and the range of variation. It is useful to print photos or scanned slides as full page images that can be mounted on the wall of your work area. This allows increased familiarity with the various morphotypes. In one varition on this technique, Kirk Johnson makes two sets of holomorphotype images. The first set is mounted on the wall in numerical order and the second set is placed in folders in the following categories: pinnate toothed leaves; pinnate entire leaves; palmate toothed leaves; palmate entire leaves; palmately lobed leaves; pinnately lobed leaves; fruits, seeds and cones; gymnosperm leaves; ferns and fern allies. This allows a large number of images to be searched visually or by major architectural group.

5. Describe the morphotype using the holomorphotype as the basic reference. Expand the circumscription, when necessary, using additional specimens that show clear overlap in their morphological characters with the holomorphotype specimen. Use the fossil-leaf database and this manual as a guide in this process.

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Basic Terminology

admedial - toward the midline of the lamina (Fig. 4).

apex - usually the upper ~25% of the lamina (see Character 24).

apical (distal) - toward the apex (Fig. 4).

basal (proximal) - toward the base (Fig. 4).

base - usually the lower ~25% of the lamina (see Character 23).

concave - curving toward the center of the lamina or tooth (Fig. 3).

convex - curving away from the center of the lamina or tooth (Fig. 3).

costal vein - primary and secondary veins that extend from the base of the leaf or from a primary toward the leaf margin.

exmedial - away from the midline of the lamina (Fig. 4).

intercostal area - the region bounded by two costal veins.

lamina (blade) - the expanded, flat part of a leaf or leaflet (Fig. 1).

margin - the edge of the lamina (Fig. 1).

midvein - medial primary, in pinnate leaves this is the only primary.

node - the place where a leaf is (or was) attached to the axis (stem) (Figs. 1, 2).

petiole - the stalk of the leaf (Figs. 1, 2).

petiolule - the stalk of a leaflet in a compound leaf (Fig. 2).

primary vein - the widest vein of the leaf and any others of like width and/or course. Primaries usually originate at or just above the petiole. Symbolized 1° (Fig. 1, see Section III).

rachis - the prolongation of the petiole of a pinnately compound leaf upon which leaflets are attached (Fig. 2).

secondary - the next narrower class of veins after the primary, originating from the primary or primaries. Symbolized 2° (Fig. 1, see Section III).

sessile - a leaf or leaflet that is lacking a petiole or petiolule (Fig. 15.2a).

tertiary vein - the next narrower class of veins after the secondaries, originating from the secondaries or primaries. Symbolized 3° (see Section III).

vein course - the path of the vein.

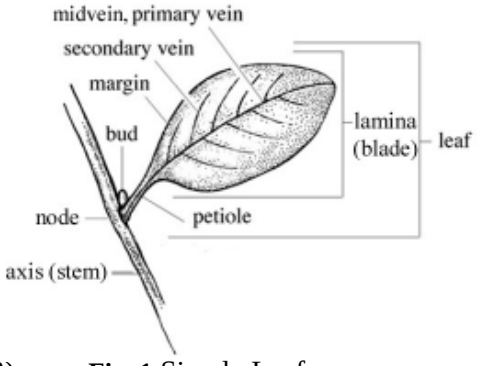


Fig. 1 Simple Leaf

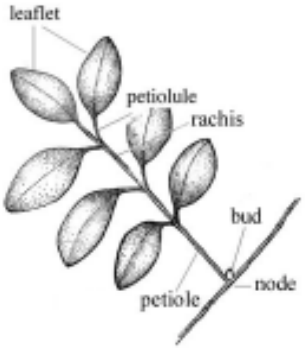


Fig. 2 Pinnately Compound Leaf

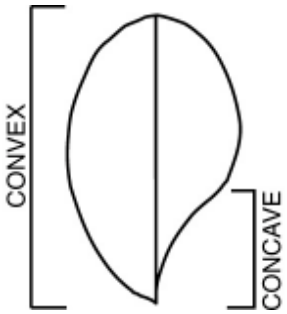


Fig. 3

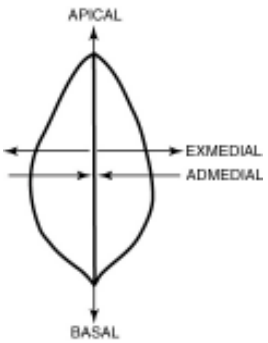


Fig. 4

LIST OF FIELDS (CHARACTERS) and OPTIONS ON PULL-DOWN LISTS (CHARACTER STATES)

1. **MORPHOTYPE NAME** – text field
2. **MORPHOTYPE #** – text field
3. **MAJOR PLANT GROUP** – DIC, MON, CON, CYC, PTE, SPE, LYC, BRY
4. **ORGAN TYPE** – leaf, root, axis, reproductive, seed, fruit
5. **MORPHOTYPER** – text field
6. **TYPE LOCALITY #** – text field
7. **RECORD DATE** – fills automatically
8. **PLANT FAMILY** – pull-down list is too long to reproduce here (>400 family names)
9. **CIC (COMPENDIUM INDEX CATEGORY)** – see categories at back of booklet
10. **LOCS. (OTHER LOCALITIES)** - text field
11. **TYPE SPECIMEN #** – text field
12. **MQI** – 1, 2, 3, 4, 5
13. **DIAGNOSTIC FEATURES OF MORPHOTYPE** - text field
14. **LEAF ATTACHMENT** - alternate, decussate, opposite, whorled
15. **LEAF ORGANIZATION** – palmately compound, pinnately compound, simple, ternate, bipinnate, tripinnate
16. **PETIOLE FEATURES** – text field, but striations, pulvinate and base swollen available on pull-down list
17. **LAMINAR SIZE** - leptophyll, nanophyll, microphyll, notophyll, mesophyll, macrophyll, megaphyll
18. **LAMINAR SHAPE** – elliptic, oblong, obovate, ovate, special
19. **LAMINAR SYMMETRY** – asymmetrical, base asymmetrical, symmetrical
20. **LAMINAR L:W RATIO** - text field
21. **BASE ANGLE** – acute, obtuse, wide obtuse, circular
22. **APEX ANGLE** – acute, obtuse, wide obtuse
23. **BASE SHAPE** – complex, concave, concavo-convex, convex, cordate, cuneate, decurrent, hastate, lobate, rounded, sagittate, truncate
24. **POSITION OF PETIOLAR ATTACHMENT** - marginal, peltate-central, peltate-eccentric
25. **APEX SHAPE** – acuminate, complex, convex, emarginate, lobed, retuse, rounded, straight, truncate
26. **MARGIN TYPE** – crenate, dentate, entire, erose, revolute, serrate
27. **LOBATION** – unlobed, bilobed, palmately lobed, pinnately lobed.
28. **1° VEIN CATEGORY** – basal acrodromous, basal actinodromous, campylodromous, flabellate, palinactinodromous, parallelodromous, pinnate, suprabasal acrodromous, suprabasal actinodromous
29. **2º VEIN CATEGORY** – basal acrodromous, brochidodromous, cladodromous, craspedodromous, eucamptodromous, festooned brochidodromous, festooned semicraspedodromous, interior, intramarginal vein, reticulodromous, semicraspedodromous, suprabasal acrodromous, weak brochidodromous
30. **AGROPHIC VEINS** – compound, none, simple
31. **# OF BASAL VEINS** – enter a number
32. **2º VEIN SPACING** – decreasing toward base, increasing toward base, irregular, uniform
33. **2º VEIN ANGLE** – abruptly increasing toward base,more acute on one side, one pair acute basal secondaries, smoothly decreasing toward base, smoothly increasing toward base, two pair acute basal secondaries, uniform
34. **INTER-2º VEINS** – absent, strong, weak
35. **3º VEIN CATEGORY** – alternate percurrent, dichotomizing, mixed opp/alt, opposite percurrent, random reticulate, regular polygonal reticulate
36. **3º VEIN COURSE** – admedially ramified, convex, exmedially ramified, sinuous, straight
37. **3º (VEIN) ANGLE TO 1º** - acute, obtuse, perpendicular
38. **3º VEIN ANGLE VARIABILITY** – decreasing medially, inconsistent, increasing basally, increasing exmedially, uniform
39. **4º VEIN CATEGORY** – alternate percurrent, dichotomizing, opposite percurrent, regular polygonal reticulate
40. **5º VEIN CATEGORY** – dichotomizing, regular polygonal reticulate
41. **AREOLATION** – lacking, moderately developed, paxillate, poorly developed, well-developed, 3 to 4 sided, 5 or more sided
42. **F.E.V.S** – absent, unbranched, 1-branched, 2 or more branched
43. **HIGHEST ORDER** - text field
44. **HIGHEST EXCURRENT** - text field
45. **MARGINAL ULTIMATE (VENATION)** – fimbrial vein, incomplete loops, looped
46. **LEAF RANK** - 1r, 2r, 3r, 4r
47. **# OF ORDERS (OF TEETH)** - 1, 2, 3
48. **TEETH/CM** - text field
49. **(TOOTH) SPACING** - regular, irregular
50. **(TOOTH) SHAPE** – cv/cv, cv/st, cv/cc, cv/fl, cv/rt, st/cv, st/st, st/cc, st/fl, st/rt, cc/cv, cc/st, cc/cc, cc/fl, cc/rt, fl/cv, fl/st, fl/cc, fl/fl, fl/rt, rt/cv, rt/st, rt/cc, rt/fl, rt/rt
51. **SINUS (SHAPE)** – angular, rounded
52. **(TOOTH) APEX** – foraminate, mucronate, non-specific glandular, papillate, setaceous, simple, spherulate, spinose
53. **TOOTH VENATION** - text field
54. **LEAF TEXTURE** – chartaceous w/ cuticle, chartaceous w/o cuticle, coriaceous w/ cuticle, coriaceous w/o cuticle, membranaceous w/ cuticle, membranaceous w/o cuticle, not apparent
55. **STOMATA** – actinocytic, amphianisocytic, amphibrachyparacytic, amphibrachyparatetracytic, amphicyclocytic, amphidiacytic, amphiparacytic, amphiparatetracytic, amphipericytic, anisocytic, anomocytic, anomotetracytic, axillocytic, brachyparacytic, brachyparahexacytic, brachyparatetracytic, coaxillocytic, copericytic, copolocytic, cyclocytic, desmocytic, diacytic, hemiparacytic, hexacytic, paracytic, parahexacytic, paratetracytic, pericytic, polocytic, polycytic, staurocytic, tetracytic
56. **(CUTICULAR) FEATURES** – hair bases, multicellular hairs, papillae, peltate hairs, simple hairs, stellate hairs, striations, thickened areas, trichomes, unicellular hairs
57. **PHOTO**

Fig. 5

GENERAL INFORMATION

Morphotype Name | Morphotype #

Major Plant Group | Organ Type | Morphotyper | Type loc. # | Record date

Plant Family | CIC

Type spec. # | MQI

LOCS.

Diagnostic features of morphotype:

LEAF

Leaf Attachment		Laminar Symmetry		Laminar L:W Ratio	
Leaf Organization		Base Angle		Apex Angle	
Petiole Features		Base Shape			
Laminar Size		Petiolar Attach.			
Laminar Shape		Apex Shape			
		Margin Type		Lobation	

1° to 2°

1° Vein Category			
2° Vein Category		2° Vein Spacing	
Agrophic Veins		2° Vein Angle	
# of Basal Veins		Inter-2° Veins	

3° to 5°

3° Vein Category		3° Vein Angle Variability	
3° Vein Course		4° Vein Category	
3° Angle to 1°		5° Vein Category	

FINER VEINS

Areolation		Highest Excurrent	
F.E.V.s		Marginal Ultimate	
Highest Order		Leaf Rank	

PHOTO

TEETH

of Orders

Teeth/cm

Spacing

Shape

Sinus

Apex

Tooth Venation

CUTICLE

Leaf Texture

Stomata

Features

Section I: Catalog information

The first section in the database contains basic information about the morphotype and where it was found.

1. MORPHOTYPE NAME

Scientific binomial (valid or invalid) or nickname.

2. MORPHOTYPE

Number assigned to the morphotype. This number consists of a two letter prefix, which is usually an abbreviation for a stratigraphic unit or research area, followed by a number. (For example: "FU37" would be the 37th morphotype designated for the Fort Union formation.)

3. MAJOR PLANT GROUP

DIC (dicotyledon)
MON (monocotyledon)
CON (conifer)
CYC (cycadophyte) - cycads and bennettitales
PTE (pteridophyte) - ferns
SPE (sphenophyte) - horsetails
LYC (lycophyte) - lycopods
BRY (bryophyte) - mosses and liverworts

4. ORGAN TYPE

Leaf
Root
Axis
Reproductive organ
Seed
Fruit

5. MORPHOTYPER

The name of the person describing the morphotype.

6. TYPE LOC.

Museum or personal locality number where the holomorphotype was found. Use identifying initials for institution or collection.

7. RECORD DATE

The date the morphotype record was created.

8. PLANT FAMILY

There is a pull-down menu with a list of plant family names.

9. CIC

Compendium Index Categories. These categories are used in the North American Paleobotany Compendium Index of Fossil Plants at Yale University to sort the major plant groups into morphological groups. CICs exist for all dicot leaves and may be used as a device to sort a fossil flora. (This database has room for up to 4 CIC entries per morphotype.) Look up this number by using the key in Appendix A.

10. LOCS.

List all localities where the morphotype is found.

11. TYPE SPEC.

Museum specimen number of the holomorphotype.

12. MQI

Morphotype Quality Index - this is determined from the following table:

MQI#	**0**	more than 10 extremely well preserved and complete specimens with cuticular data
	1	more than 10 extremely well preserved and complete specimens that lack cuticular data
	2	2 to 10 well preserved complete or partial specimens
	3	one well preserved complete or partial specimen
	4	one complete, or few to many partial but poorly preserved specimens
	5	one partial and poorly preserved specimen

Extremely well preserved means that the fossil has at least fifth order veins.
Well preserved means that the fossil has at least fourth order veins.
Poorly preserved means that the fossil has less than fourth order veins.
Complete means that the fossil has an apex, base and greater than 1/2 the margin.

13. DIAGNOSTIC FEATURES OF THE MORPHOTYPE

This field is used to state the characteristics of the morphotype that distinguish it from other leaves at the same locality or in the same formation. This field is also useful for describing features that don't conform to the categories in the form.

Section II: Leaf

Description of the shape, size and organization of the leaf.

14. LEAF ATTACHMENT

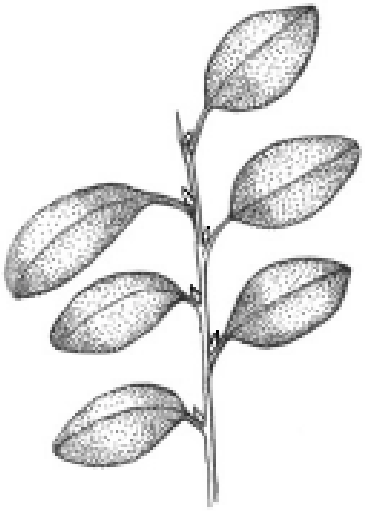


Fig. 14.1
alternate - one leaf at each node.

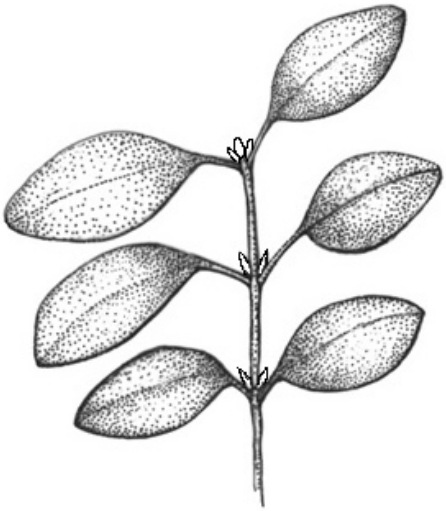


Fig. 14.2
opposite - two leaves at each node.

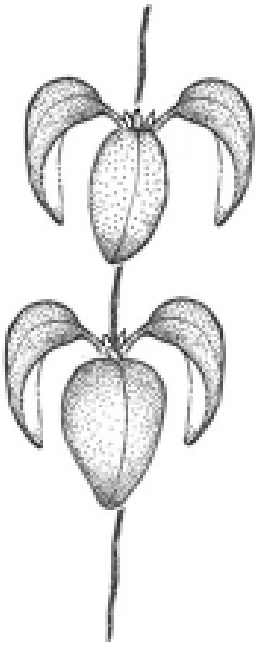


Fig. 14.3
whorled - three or more leaves at each node.

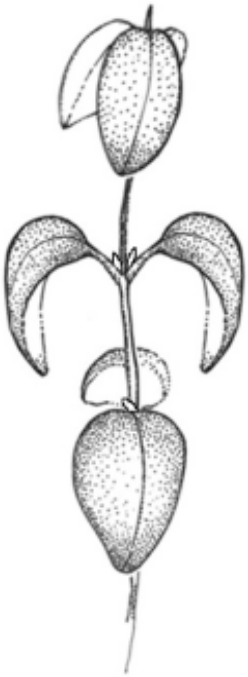


Fig. 14.4
decussate - each leaf attached at 90° from those above and below (can be opposite, as shown, or alternate).

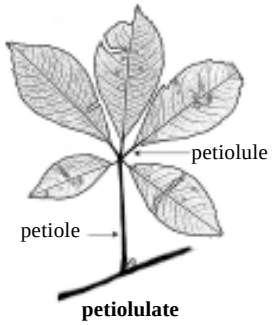
15. LEAF ORGANIZATION

Fig. 15.1

simple - consisting of a single lamina.

sessile

Fig. 15.2a



petiolulate
***Chorisia insignis* (Bombacaceae)**

Fig. 15.2b

palmately compound - a leaf with separate subunits (leaflets) attached at the apex of a petiole.

Fig. 15.3

ternate (trifoliate) - a compound leaf with three leaflets.

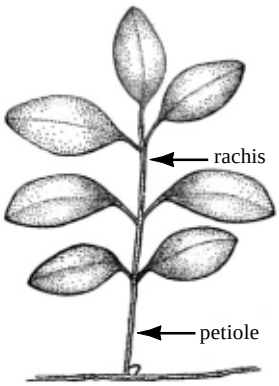


Fig. 15.4
odd-pinnate

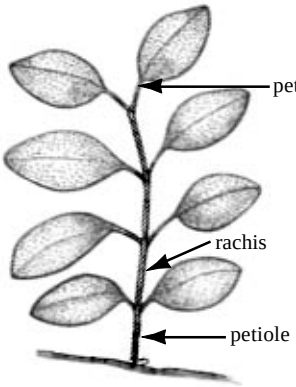


Fig. 15.5
even-pinnate

pinnately compound - a leaf with leaflets arranged along a rachis.

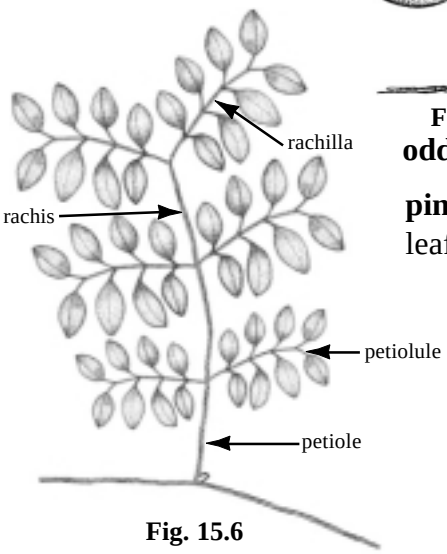


Fig. 15.6

bipinnate (twice pinnately compound) - compound leaf dissected twice with leaflets arranged along rachillae that are attched to the rachis.

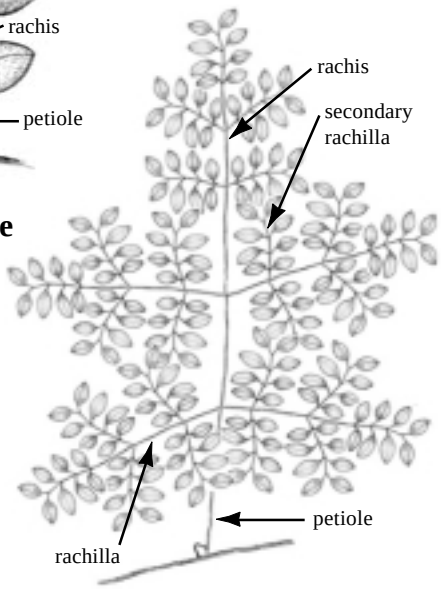
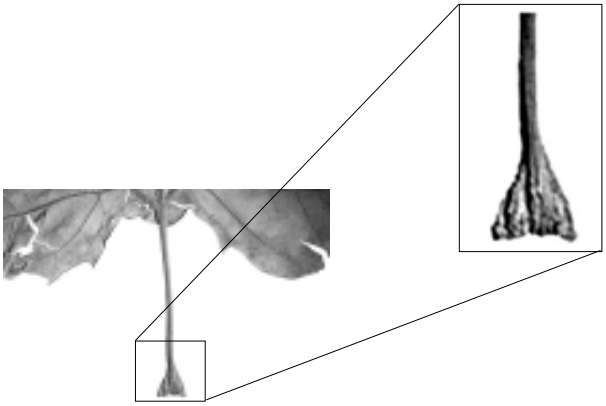


Fig. 15.7

tripinnate (thrice pinnately compound) - a compound leaf with leaflets attached to secondary rachillae that are in turn attached to rachillae, which are borne on the rachis.

16. PETIOLE FEATURES

Note distinctive features of the petiole (e.g., width, length, base swollen, base inflated, sessile or other).



Platanus occidentalis **(Platanaceae)**

Fig. 16.1

base swollen - petiole thickens at the base where it attaches to the node.

Dalbergia brownei **(Leguminosae)**

Fig. 16.2

pulvinate - having an abruptly swollen portion near the node around which the leaf can flex (e.g. legumes).

17. LAMINAR SIZE

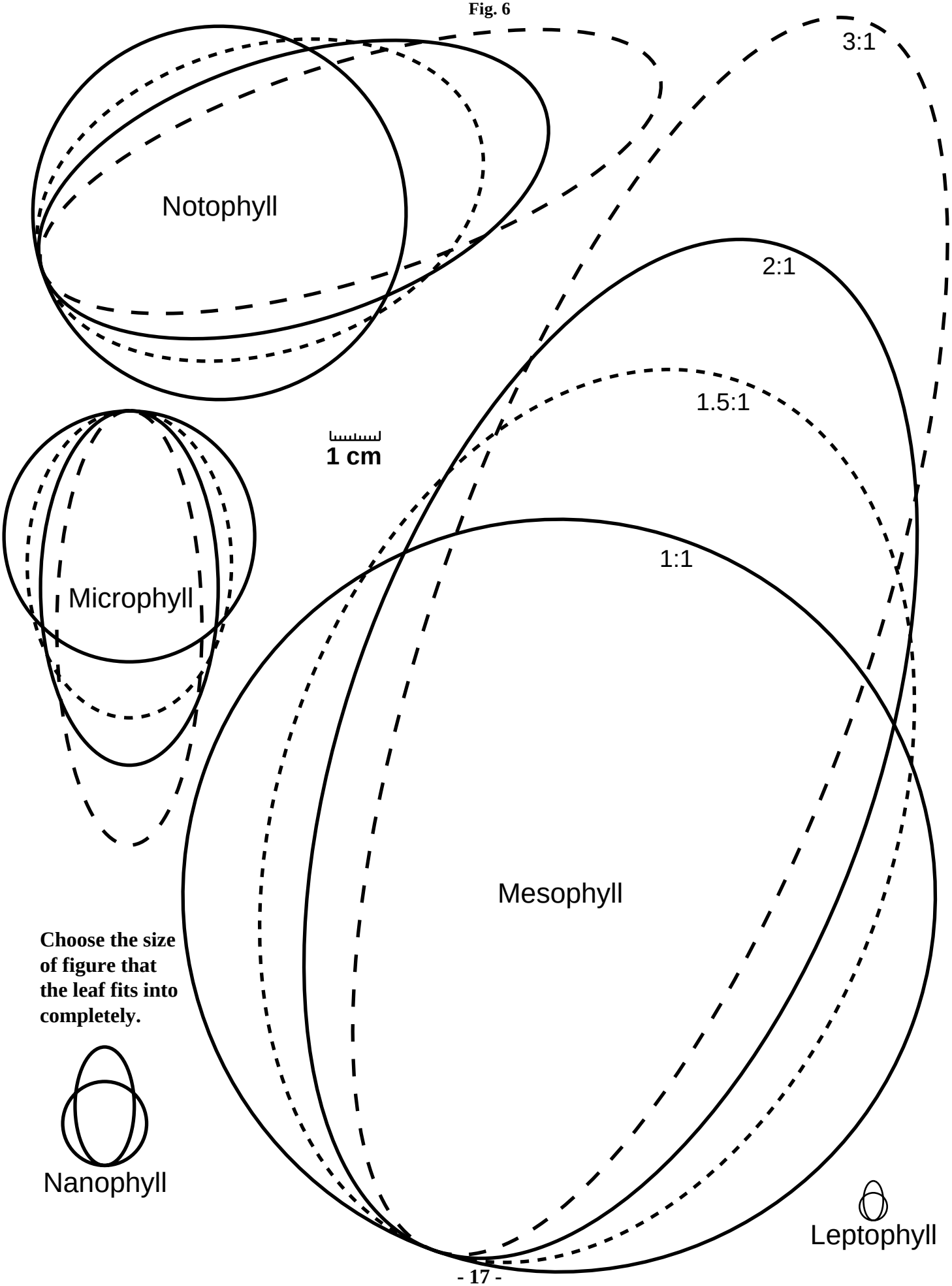
The laminar size is determined by measuring the area of the leaf. An approximation can be made by measuring the length and width of the leaf in millimeters and multiplying the length x width x 2/3. Outlines of the maximum size of 5 of the smallest laminar classes appear in Fig. 6. You can Xerox this on a transparency, place it over the fossil and choose the blade size into which the leaf fits completely. Use the template for incomplete leaves.

The following chart shows the ranges of areas for the different leaf classes (Webb 1955).

Blade class	Area of leaf in mm^2
leptophyll	< 25
nanophyll	25 - 225
microphyll	225 - 2,025
notophyll	2,025 - 4,500
mesophyll	4,500 - 18,225
macrophyll	18,225 - 164,025
megaphyll	>164,025

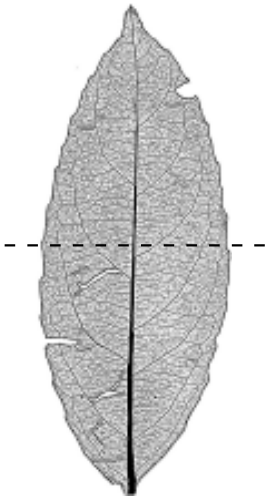
The two entries in the database field should contain the minimum and maximum size categories observed for the morphotype.

Fig. 6

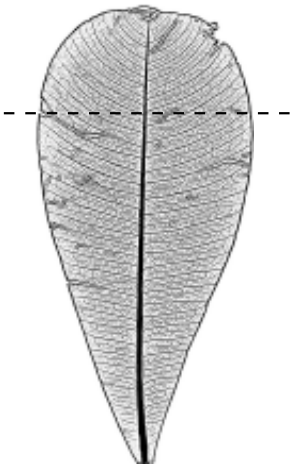

3:1
Notophyll
2:1
1.5:1
1 cm
1:1
Microphyll
Mesophyll
Choose the size of figure that the leaf fits into completely.
Nanophyll
Leptophyll

18. LAMINAR SHAPE

The simplest way to describe the overall shape of the lamina is to locate the axis or, in some cases, the zone of greatest width that lies perpendicular to the axis of greatest length (long axis):

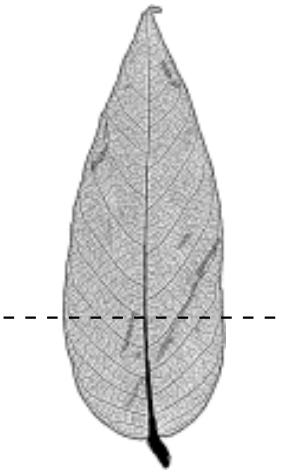


Cheiloclinium anomolum **(Celastraceae)**
Fig. 18.1



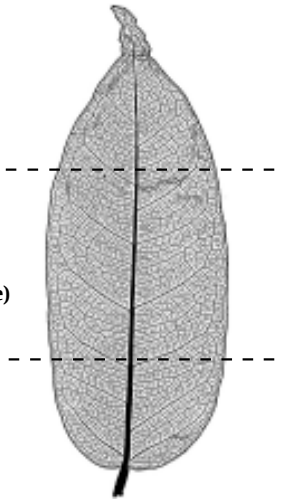
Alstonia congensis **(Apocynaceae)**
Fig. 18.2

obovate - widest part of the leaf is on an axis in the apical 2/5 of the leaf.



Parinari insularium **(Chrysobalanaceae)**
Fig. 18.3

ovate - widest part of the leaf is on an axis in the basal 2/5 of the leaf.

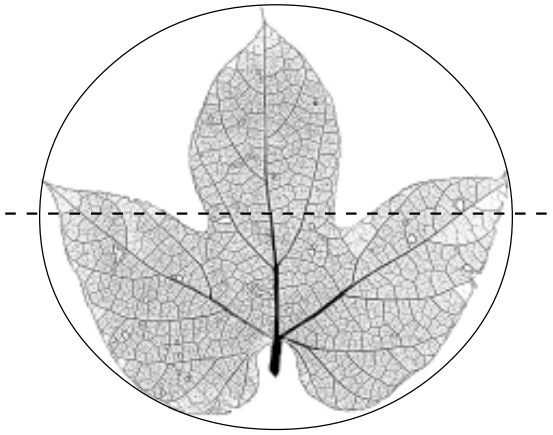


Ficus citrifolia **(Moraceae)**
Fig. 18.4

elliptic - the widest part of the leaf is on an axis in the middle fifth of the long axis of the leaf.

oblong - widest part of the leaf is a zone in the middle 1/3 of the long axis where the opposite margins are roughly parallel.

In lobed leaves the blade shape is determined from an ellipse drawn around the apices of the lobes. The widest part of the ellipse is then considered as in unlobed leaves (Fig. 18.5).



Dioscoreophyllum strigosum **(Menispermaceae)**
Fig. 18.5

special - leaf is not described by any of the shapes illustrated here (such as a needle or awl).

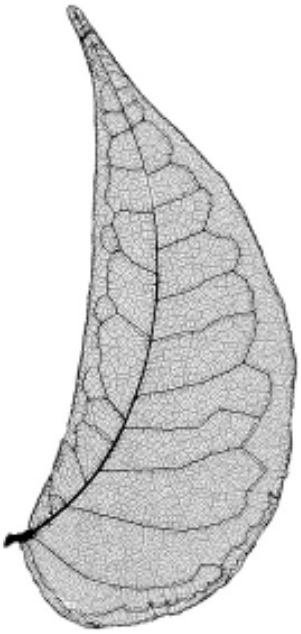
elliptic

19. LAMINAR SYMMETRY

Maytenus aquifolium **(Celastraceae)**

Fig. 19.1

symmetrical - lamina approximately the same shape on either side of the midvein.



Daniellia ogea **(Leguminosae)**

whole lamina

Fig. 19.2

asymmetrical - lamina different size or shape on either side of the midvein.

Fraxinus floribunda **(Oleaceae)**

base only

Fig. 19.3

base asymmetrical - base of the lamina of markedly different shape on either side of the midline.

20. LAMINAR L:W RATIO

Measure the length of the lamina (L - see Fig. 7) and divide this number by the width of the lamina. Report the full range of ratios (e.g., 3:1 - 6:1).

DEFINITIONS

Midvein length, l_m = distance from proximal most to the distal most point of the midvein (Figs. 7a-7d).

Apical extension length, l_a = distance on a perpendicular from the distal most point of the midvein to the distal most extension of leaf tissue (Figs. 7c, 7d). Can equal zero (Figs. 7a, 7b).

Basal extension length, l_b = distance on a perpendicular from the proximal most point of the midvein to the proximal most extension of leaf tissue (Figs. 7b, 7d). Can equal zero (Figs. 7a, 7c).

Leaf Length, $L = l_m + l_a + l_b$

Mucronate – apex terminating in a sharp point that is the continuation of the midvein. Character goes in diagnostic features field if observed.

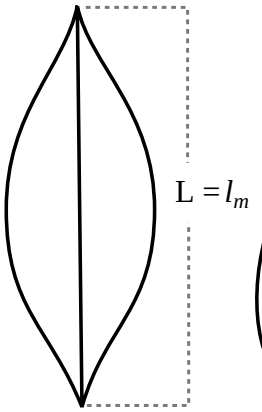


Fig. 7a

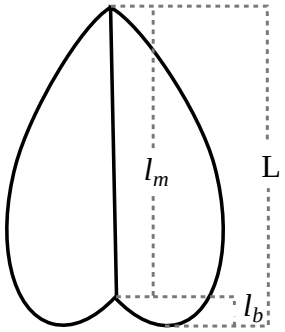


Fig. 7b

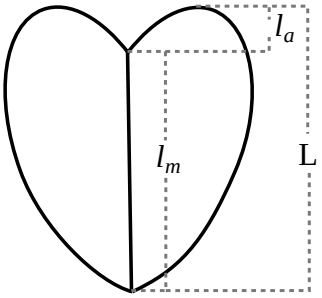


Fig. 7c

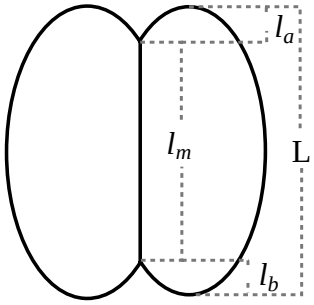
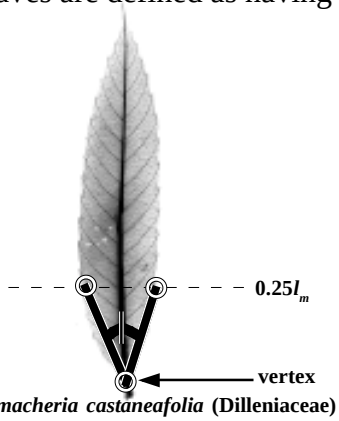


Fig. 7d

21. BASE ANGLE

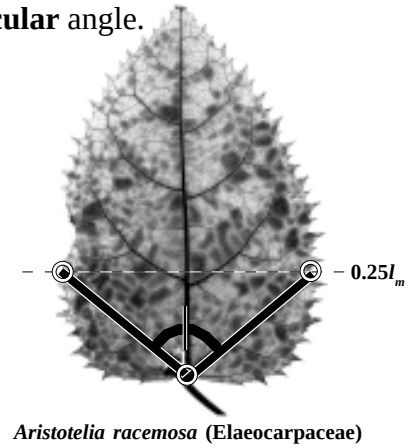
The vertex of the base angle lies in the center of the petiole at the point where the basal most laminar tissue touches the petiole. *Base angle* is the angle from the vertex to the points where a line perpendicular to the midvein at $0.25l_m$ from the base intersects the margin (Fig. 21.1, 21.2). In leaves with a basal extension (l_b>0), the base angle should be measured from the same vertex point to the basal most points of the leaf on each side (Fig. 21.3). The base angle is always measured on the apical side of the rays even in leaves where the angle is greater than 180°. Peltate leaves are defined as having a **circular** angle.



Schumacheria castaneafolia **(Dilleniaceae)**

Fig. 21.1

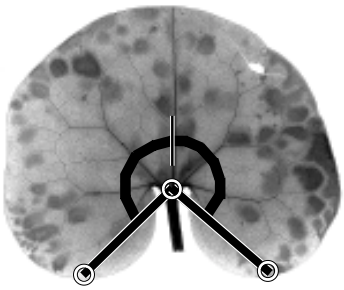
acute - base angle <90°.



Aristotelia racemosa **(Elaeocarpaceae)**

Fig. 21.2

obtuse - base angle >90°.



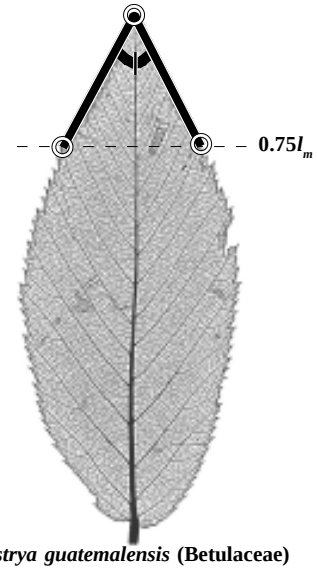
Asarum europaeum **(Aristolochiaceae)**

Fig. 21.3

wide obtuse - a special case of obtuse such that the base angle is >180°.

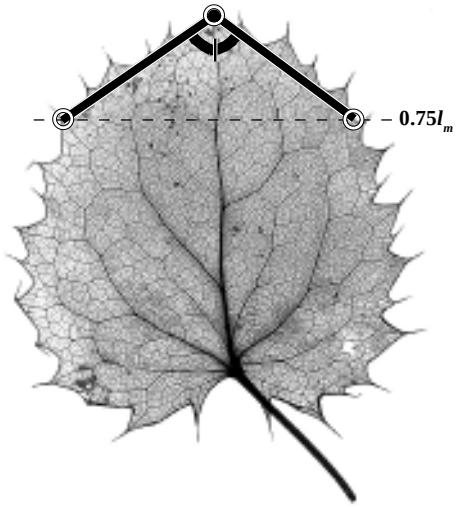
22. APEX ANGLE

Apex angle is the angle from the apical termination of the midvein to the pair of points where a line perpendicular to the midvein and $0.75l_m$ from the base intersects the margin (Fig. 22.1, 22.2). In leaves with an odd number of lobes, measure the apex angle as in unlobed leaves (Fig. 22.4, Fig. 22.5). In leaves with an apical extension (l_a>0) the apex angle should be measured using the termination of the midvein as the vertex, and the apices of the lobes on either side (Fig. 22.3). The apical angle is always measured on the basal side of the rays, even in leaves where the angle is greater than 180°.



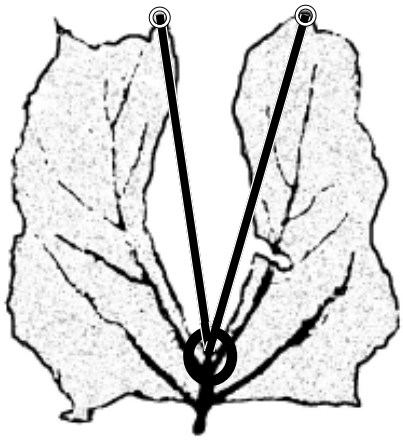
Ostrya guatemalensis **(Betulaceae)**
Fig. 22.1

acute – apex angle < 90°.



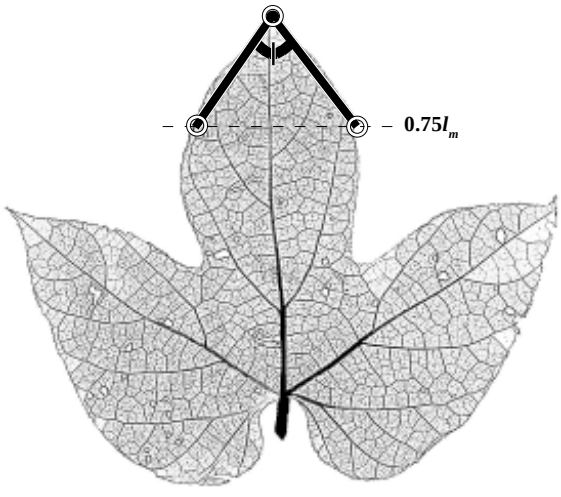
Mahoberberis neubertii **(Berberidaceae)**
Fig. 22.2

obtuse – apex angle 90 - 180°.

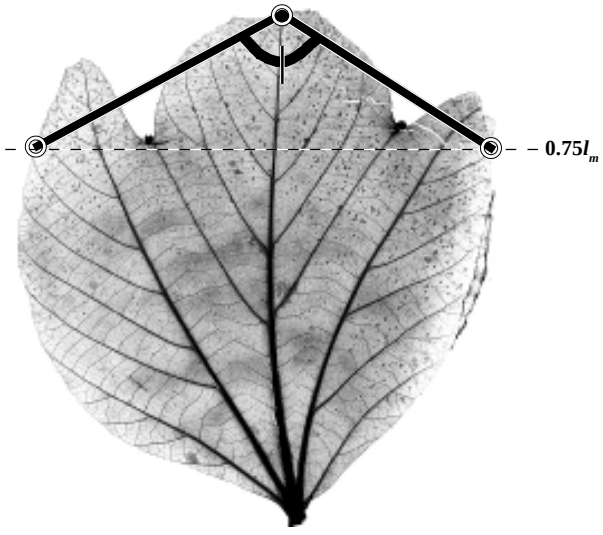


Liriodendrites bradacii
Fig. 22.3

wide obtuse - a special case of obtuse such that the apex angle is >180°.



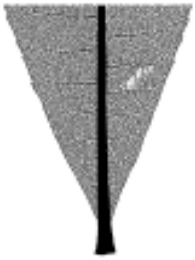
Dioscoreophyllum strigosum **(Menispermaceae)**
Fig. 22.4
odd-lobed acute apex



Aleurites montana **(Euphorbiaceae)**
Fig. 22.5
odd-lobed obtuse apex

23. BASE SHAPE

These states apply to the basal 25% of the lamina (0 - 0.25L as in Fig. 7).



Carya leiodermis **(Juglandaceae)**

Fig. 23.1

cuneate (straight) - the margin between the base and 0.25L has no significant curvature (l_b = 0).

Prunus manshurica **(Rosaceae)**

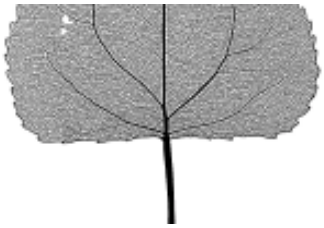
Fig. 23.2

convex - the margin between the base and 0.25L curves away from the center of the leaf (l_b = 0).

Carissa opaca **(Apocynaceae)**

Fig. 23.3

rounded - subtype of convex in which the margin forms a smooth arc across the base (l_b = 0).



Populus dimorpha **(Salicaceae)**

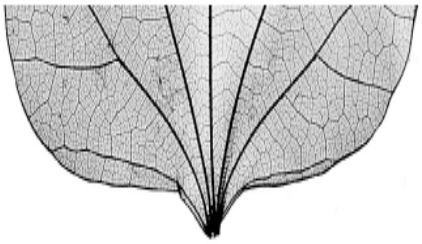
Fig. 23.4

truncate - subtype of convex in which the base terminates abruptly as if cut, with margin perpendicular to the midvein or nearly so (l_b = 0).

Sassafras variifolium **(Lauraceae)**

Fig. 23.5

concave - the margin between the base and 0.25L curves toward the center of the leaf (l_b = 0).



Diploclisia chinensis **(Menispermaceae)**

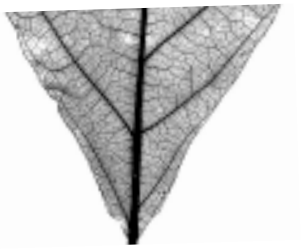
Fig. 23.6

concavo-convex - the margin between the base and 0.25L is concave basally and convex apically (l_b = 0).

Alstonia plumosa **(Apocynaceae)**

Fig. 23.7

decurrent - subtype of either concave or concavo-convex in which the laminar tissue extends basally along the petiole at a gradually decreasing angle (l_b = 0).

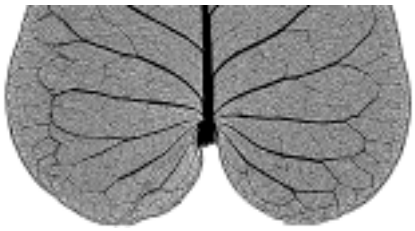


Adelia triloba **(Euphorbiaceae)**

Fig. 23.8

complex - there are more than two inflection points in the curve of the margin between the base and 0.25L (l_b = 0).

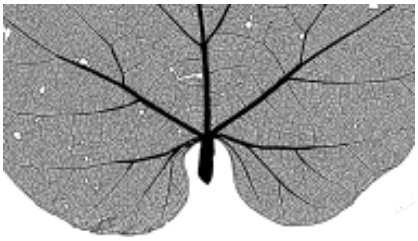
23. BASE SHAPE CONTINUED



Phyllanthus poumensis **(Euphorbiaceae)**

Fig. 23.9

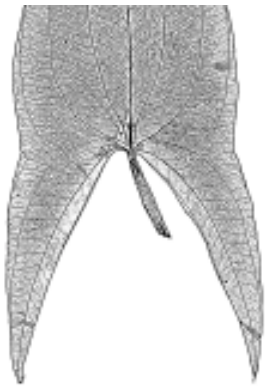
cordate - the leaf base is embayed in a sinus with straight or convex sides ($l_b > 0$).



Dioscoreophyllum strigosum **(Menispermaceae)**

Fig. 23.10

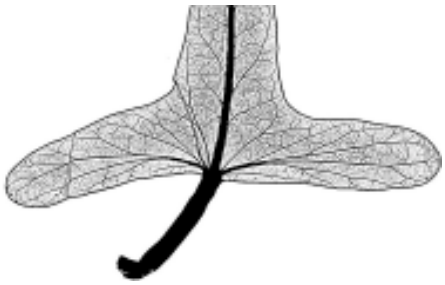
lobate - rounded projections with inner margins (those towards the petiole) concave in part ($l_b > 0$).



Sagittaria sp. **(Alismataceae)**

Fig. 23.11

sagittate - narrow pointed lobes with apices directed basally, i.e. at an angle 125° or greater from the leaf axis ($l_b > 0$).



Araujia angustifolia **(Asclepiadaceae)**

Fig. 23.12

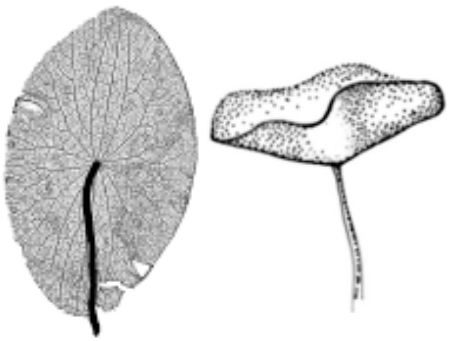
hastate - two narow pointed lobes that have apices directed exmedially, i.e. at 90°-125° from the leaf axis ($l_b \sim 0$).

24. POSITION OF PETIOLAR ATTACHMENT

Luniana piperoides **(Flacourtiaceaee)**

Fig. 24.1

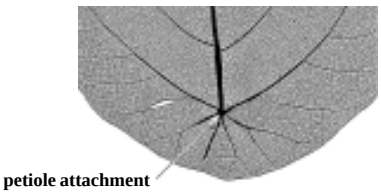
marginal - petiolar insertion at the margin of the leaf.



Brasenia schreiberi **(Cabombaceae)**

Fig. 24.2

peltate central - petiole attached within the boundaries of the leaf margin and near the center of the leaf (l_b>0).



Macaranga bicolor **(Euphorbiaceae)**

Fig. 24.3

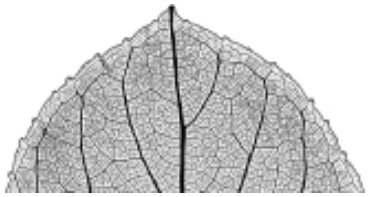
peltate eccentric - petiole attached near the edge but inside the boundaries of the leaf margin (l_b>0).

25. APEX SHAPE

These states apply to the apical 25% of the lamina (0.75L - 1L as in Fig. 7).

Agonis flexuosa **(Myrtaceae)**
Fig. 25.1

straight – the margin between the apex and 0.75L has no significant curvature ($l_a = 0$).



Saurauia calyptrata **(Actinidiaceae)**
Fig. 25.2

convex – the margin between the apex and 0.75L curves away from the center of the leaf ($l_a = 0$).

Ozora obovata **(Anacardiaceae)**
Fig. 25.3

rounded – a subtype of convex in which the margin forms a smooth arc across the apex ($l_a = 0$).

Oxalis sp. **(Oxalidaceae)**
Fig. 25.4

truncate – the apex terminates abruptly as if cut, with margin perpendicular to midvein or nearly so ($l_a = 0$).

Neouvaria acuminatissima **(Annonaceae)**
Fig. 25.5

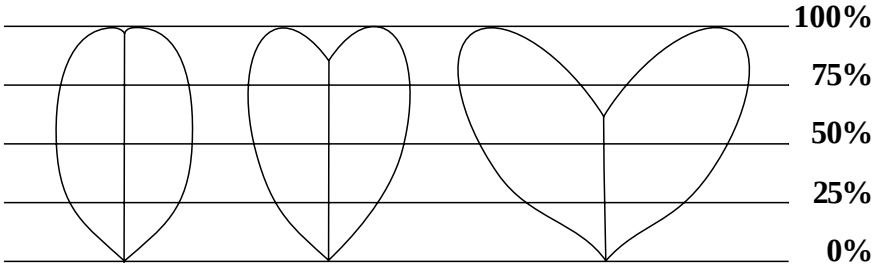
acuminate – the margin between the apex and 0.75L is concave, curving toward the center of the leaf, or is convex basally and concave apically ($l_a = 0$). This category includes most drip tips.

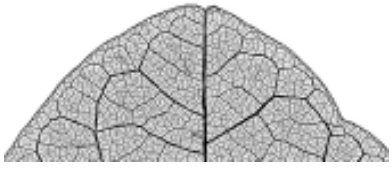
Banksia verticillata **(Proteaceae)**
Fig. 25.6

complex – there are more than two inflection points in the curve of the margin between the apex and 0.75L ($l_a = 0$).

If $l_a > 0$, then the leaf is retuse, emarginate, or lobed.

Fig. 25.7



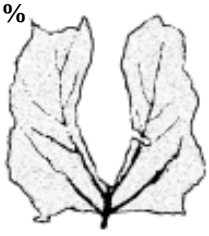


Fitzlania heteropetala **(Annonaceae)**
Fig. 25.8

retuse – the length of l_m is 95-99% of $l_m + l_a$ ($l_a > 0$).

Lundia spruceana **(Bignoniaceae)**
Fig. 25.9

emarginate – the length of l_m is 75-95% of $l_m + l_a$ ($l_a > 0$).



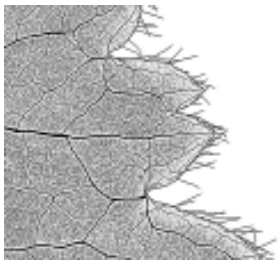
Liriodendrites bradacii
Fig. 25.10

lobed – the length of l_m is <75% of $l_m + l_a$ ($l_a > 0$).

26. MARGIN TYPE

DEFINITIONS

TEETH are marginal projections with sinuses indented less than 1/4 of the distance to the midvein or long axis of the leaf. Teeth can be either dentate, serrate or crenate.
Note: If there is a single tooth of any size, the leaf is considered to be toothed.



Waldsteinia idahoensis **(Rosaceae)**
Fig. 26.1

dentate - teeth pointed with their axes perpendicular to the trend of the leaf margin.

Fagus grandifolia **(Fagaceae)**
Fig. 26.2

serrate - teeth pointed with their axes inclined to the trend of the leaf margin.

Tripterygium wilfordi **(Celastraceae)**
Fig. 26.3

crenate - teeth smoothly rounded without a pointed apex.

Rhododendron amagianum **(Ericaceae)**
Fig. 26.4

entire - margin is smooth, without teeth.

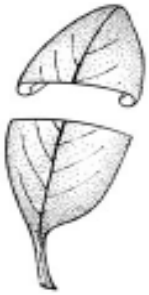


Fig. 26.5

revolute - margins are turned under or rolled up like a scroll.

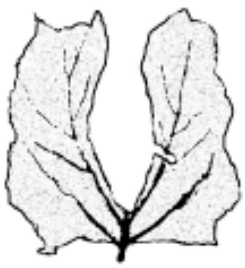
Cornus coreana **(Cornaceae)**
Fig. 26.6

erose - margins are irregular as if chewed.

27. LOBATION

LOBES are marginal indentations that reach 1/4 or more of the distance to the midvein, measured parallel to the axis of symmetry of the lobe.

Gouania longispicata **(Rhamnaceae)**
Fig. 27.1
unlobed



Liriodendrites bradacii
Fig. 27.2
bilobed

Dioscoreophyllum strigosum **(Menispermaceae)**
Fig. 27.3
palmately lobed

Stenocarpus sinuatus **(Proteaceae)**
Fig. 27.4
pinnately lobed

Section III: Vein Orders

The first step in describing the pattern of venation in a leaf is to recognize discrete categories or ***orders*** of veins that have similar widths and courses. Most angiosperm leaves have between four and seven orders of venation. The first step in describing venation is to recognize the first three orders of veins. In general, the primary and secondary veins are the major structural veins of the leaf, while the tertiary veins are the largest veins that fill the field of the leaf. The primary vein or veins are somewhat analogous to the main trunk or trunks of a tree--they are the widest veins, they usually taper along their length, and they generally run from at, or near, the base of the leaf to the margin. Secondary veins are analogous to the major limbs of a tree. They are the next set in width after the primary(s), they also usually taper along their course, and they ordinarily run from either the base of the leaf or from a primary vein toward the margin. For tertiary and higher order veins the analogy with the branching system of a tree breaks down. Tertiary veins are usually considerably narrower than the secondary set and have courses that connect primary and secondary veins to one another in a similar fashion throughout the leaf. Tertiaries are usually the widest veins that form a more or less organized "field" over the great majority of the leaf area. Generally it is fairly easy to recognize the primaries and tertiaries, but sometimes the secondaries consist of several subsets with different widths and courses. Nevertheless, all the subsets of veins between the primaries and the tertiaries are considered to be secondaries.

After the three lowest vein orders have been demarcated, the observer can proceed to discriminating the higher orders of venation (4-7) present in the leaf. Each of these higher vein orders can be highly variable among species and higher taxa in its degree of distinctness from both the next higher, and the next lower vein order. Good diagnostic features for distinguishing higher vein orders from one another are excurrent origin from their source veins and a distinctly narrower gauge. If they arise dichotomously or appear to be of the same, or nearly the same, width as their parent vein, they are of the same order as the source vein.

Obviously the simultaneous use of two criteria for the determination of vein order introduces a degree of ambiguity into the process because some veins may have the width typical of one vein order but the course typical of a different vein order. However, recognizing orders based solely on their width or solely on their course leads to illogical situations where veins that appear to have different functions and developmental origins are assigned to the same order. Assigning veins to orders also has a somewhat arbitrary aspect because variation in width and course is not discrete - for example, a vein may be intermediate in width between the primary vein and the secondary veins. However, there do appear to be natural breaks in the variation in width and course, so that most veins can be assigned to an order unambiguously. In our experience, vein orders can usually be defined in a repeatable manner for a given leaf by different observers who follow a consistent set of rules.

Leaves with veins that form a high number of discrete orders or that have regular courses, are considered to be more organized or "higher rank" leaves. The concept of leaf rank is discussed and illustrated in Character 46. Figures 8 and 9 demonstrate designation of vein orders for two leaves.

Below we provide a set of instructions for recognizing vein orders.

Vein orders continued

General rule: All vein orders should be recognized in sequence from lowest to highest. The sole and rare exception is that some leaves with extremely acrodromous primary veins may lack secondaries (Fig. 28.6). To recognize the primary, secondary and tertiary veins, take the following steps.

1. Find the widest vein(s) in the leaf; this is the primary vein. Most leaves have a single primary vein and are called pinnate (if so, go to step 3). If more than one vein originates at or near the base of the leaf, then proceed to step 2 to determine if the leaf has one or more primary veins.

2. After recognizing the widest single vein of the leaf as a primary (generally the midvein), other primaries are recognized by being 74% or more of the width of the the widest primary (at the point of origin of the widest primary). These veins are basal or nearly basal. If these veins enter lateral lobes or run in strong arches towards the apex, they are generally easily recognized as primaries. But if the lateral primaries curve toward the midline apically (Fig. 28.6) or branch toward the margin (Fig. 28.3), they may be hard to distinguish from secondaries. In pinnatifid leaves, primaries may be difficult to distinguish from costal secondary veins.

   If there is more than one primary vein (based on vein width) other veins originating at the base may be considered primaries if their course and function is similar to that of the previously defined primaries, even if their width falls into the range of 25-75% of the widest primary vein. The width of these may fall within the width range of the secondary or tertiary veins. If these veins are narrower than 25% of the widest primary vein, they are not considered primaries.

3. Find the widest veins that fill the field of the leaf; these are the tertiary veins (refer to Character 35, 3° Vein Category). Proceed to step 4. (Watch out for rare exceptions such as Clusiaceae where secondary veins fill the field of the leaves.)

4. Having recognized the limits of the primary and tertiary vein sets, identify the intermediate set. These veins are secondary veins and may consist of costals (the rib forming veins that originate on the primary and run to the margin), interior secondaries, intersecondaries, outer secondaries, and intramarginal veins (refer to Character 29, 2° Vein Category). The secondaries will fall within a smooth continuum of width and behavior. Proceed to step 5. As noted above and illustrated in Figure 37.1, secondaries may be absent rarely.

5. Once you have recognized the first three orders of venation, proceed in sequence to determine the higher orders venation using the criteria of vein width and course.

Figures 8 and 9 on the following page show examples of vein orders.

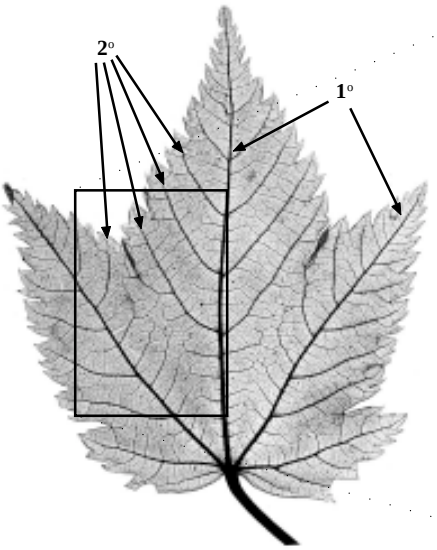


Fig. 8a

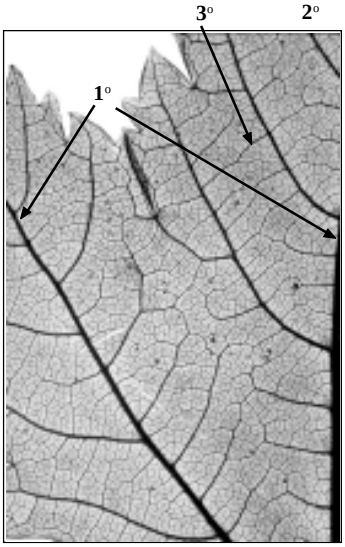


Fig. 8b

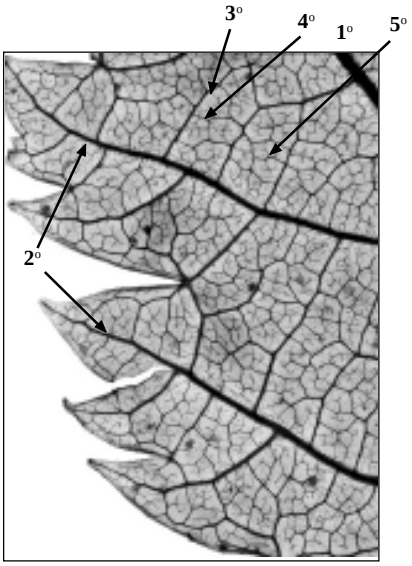


Fig. 8c

***Acer argutum* (Aceraceae)**

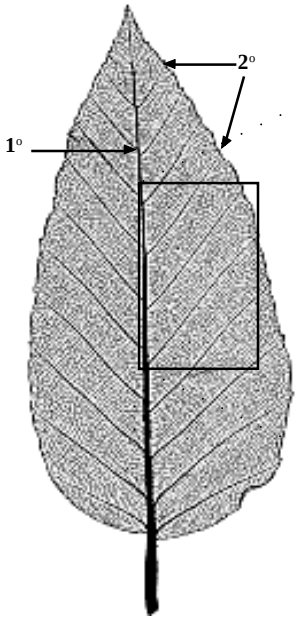


Fig. 9a

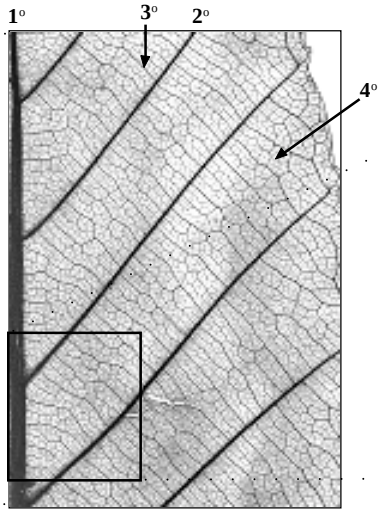


Fig. 9b

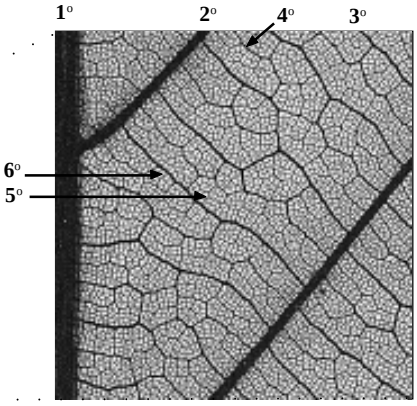


Fig. 9c

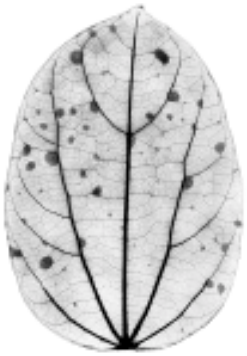
***Fagus longipetiolara* (Fagaceae)**

28. 1° VEIN CATEGORY

Ostrya guatemalensis **(Betulaceae)**

Fig. 28.1

pinnate - with a single primary vein.



Arcangelisia lemniscata **(Menispermaceae)**

basal

Fig. 28.2

actinodromous - three or more primary veins diverging radially from a single point.

Givotia rottleriformis **(Euphorbiaceae)**

suprabasal

Fig. 28.3

Platanus racemosa **(Platanaceae)**

Fig. 28.4

palinactinodromous - primaries diverging in a series of dichotomous branchings, either closely or more distantly spaced.

Paranomus saeptrum **(Proteaceae)**

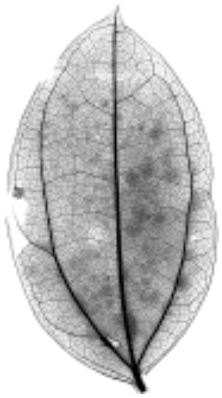
Fig. 28.5

flabellate - several to many equally fine basal veins diverge radially at low angles and branch apically.

Miconia sp. **(Melastomataceae)**

basal

Fig. 28.6



Endlicheria bracteolata **(Lauraceae)**

suprabasal

Fig. 28.7

acrodromous -three or more primaries running in convergent arches toward the leaf apex.

Fig. 28.8

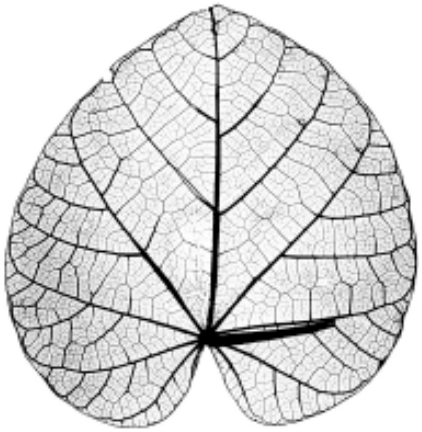
parallelodromous - 2 or more parallel primary veins originate beside each other at the leaf base and converge apically.

Fig. 28.9

campylodromous - several primary veins or their branches, originating at or near a single point and running in strongly recurved arches that converge apically.

Maianthemum dilatatum **(Liliaceae)**

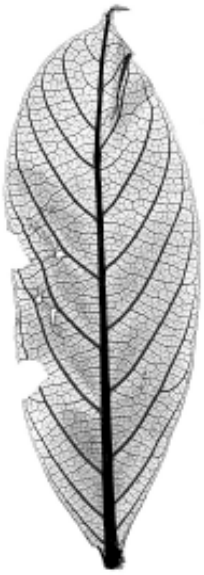
29. 2° VEIN CATEGORY



Hildegardia barteri **(Sterculiaceae)**

Fig. 29.1

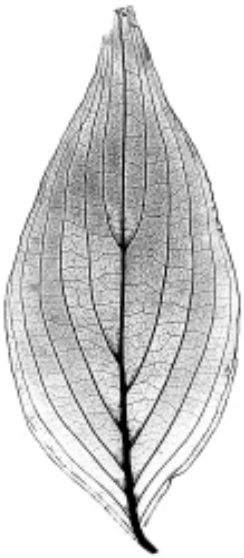
brochidodromous - secondaries joined together in a series of prominent arches.



Cryptocarya infectoria **(Lauraceae)**

Fig. 29.2

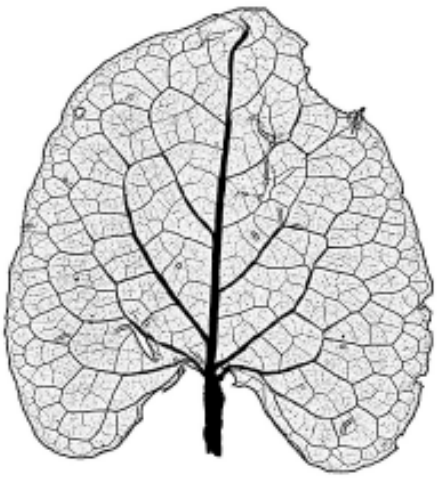
weak brochidodromous - secondaries joined together in a series of arches.



Cornus officinalis **(Cornaceae)**

Fig. 29.3

eucamptodromous - secondaries upturned and gradually diminishing apically inside the margin, connected to the superadjacent secondaries by a series of 3° cross veins without forming any 2° marginal loops.



Antigon cinerascens **(Polygonaceae)**

Fig. 29.4

festooned brochidodromous - having one or more additional sets of loops outside of the main brochidodromous loop.

Protorhus buxifolia **(Anacardiaceae)**

Fig. 29.5

cladodromous - secondaries freely branching toward the margin.

Diospyros malabarica **(Ebenaceae)**

Fig. 29.6

reticulodromous - secondaries branching into a reticulum toward the margin.

29. 2° VEIN CATEGORY CONTINUED

Celtis davidiana **(Ulmaceae)**
Fig. 29.7

craspedodromous - secondaries terminating at the margin (ordinarily in toothed leaves).

Salix monticola **(Salicaceae)**
Fig. 29.8

semicraspedodromous - secondary veins branching just within the margin, one of the branches terminating at the margin and the other joining the superadjacent secondary (ordinarily in toothed leaves).

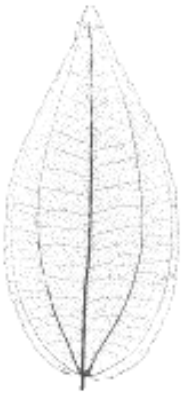
Archibaccharis subsessilis **(Compositae)**
Fig. 29.9

festooned semicraspedodromous - semicraspedodromous venation with one or more additional sets of loops outside the branch that joins the superadjacent 2^{o} (ordinarily in toothed leaves).

Leuconotis eugeniafolia **(Apocynaceae)**
Fig. 29.10

intramarginal vein - secondaries end in a strong vein closely paralleling the leaf margin.

acrodromous - two or more secondaries running in convergent arches toward the leaf apex.



Omphalopus sp.
(Melastomataceae)
basal
Fig. 29.11

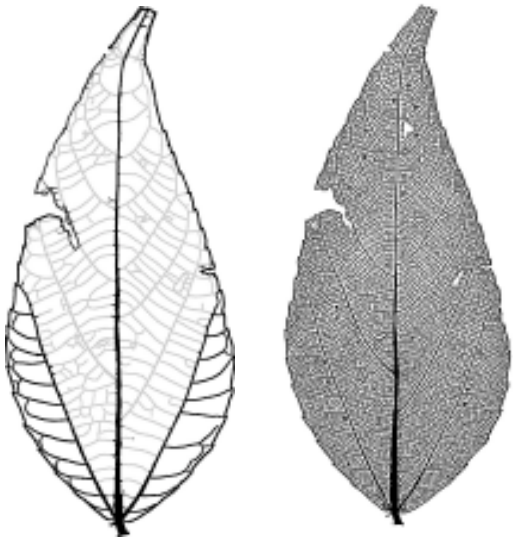
Miconia brenesii
(Melastomataceae)
suprabasal
Fig. 29.12

Acer flabellatum var. yunnanensis **(Aceraceae)**
Fig. 29.13

interior - 2° crossing between primary veins or 2° veins that do not reach the margin - typically arched or straight.

30. AGROPHIC VEINS

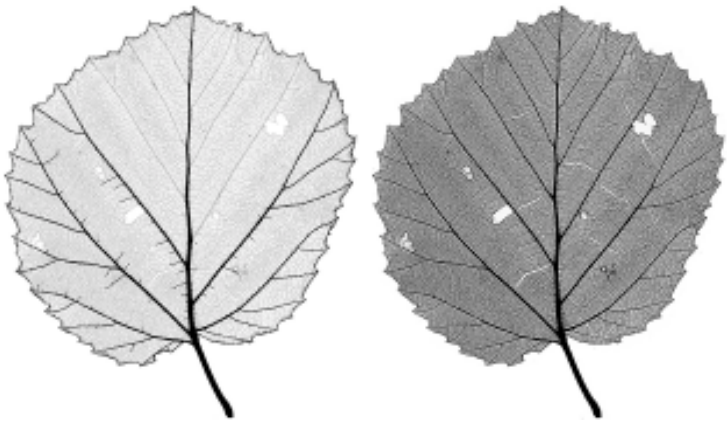
Agrophic - a comb-like complex of veins comprised of a lateral 1° or 2° backbone with 2 or more exmedial 2° veins that travel roughly parallel courses towards the margin. These veins may be straight or looped. Agrophic veins are similar to pectinal veins defined by Spicer (1986).



Alchornea parviflora **(Euphorbiaceae)**

Fig. 30.1

simple agrophic - one or a pair of agrophic veins.



Parrotiopsis jacquemontia **(Hamamelidaceae)**

Fig. 30.2

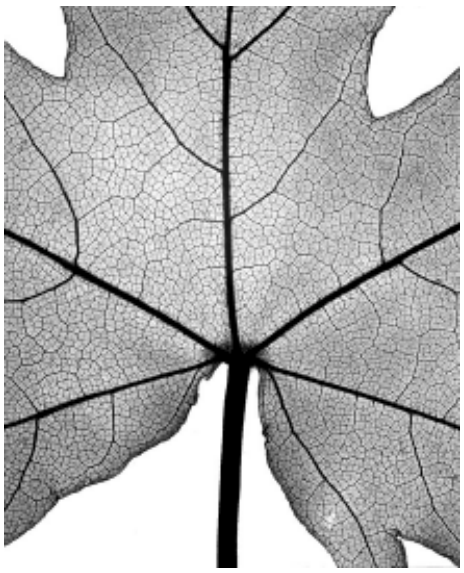
compound agrophic - more than one pair of agrophic veins.

31. # OF BASAL VEINS

The number of 1°, 2°, and 3° veins originating at or near the the base of the leaf/top of the petiole.

Acer miyabei **(Aceraceae)**

Fig. 31.1

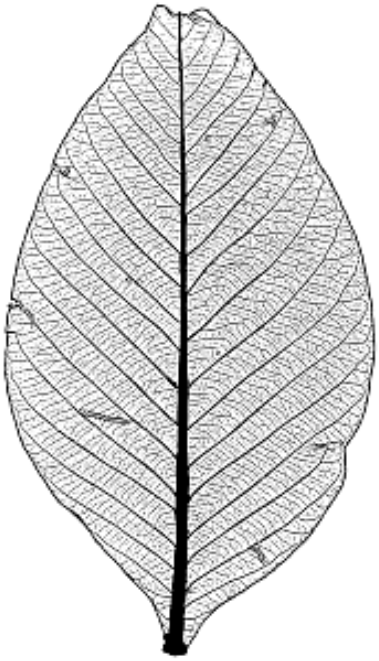


Acer miyabei **(Aceraceae)**

Fig. 31.2

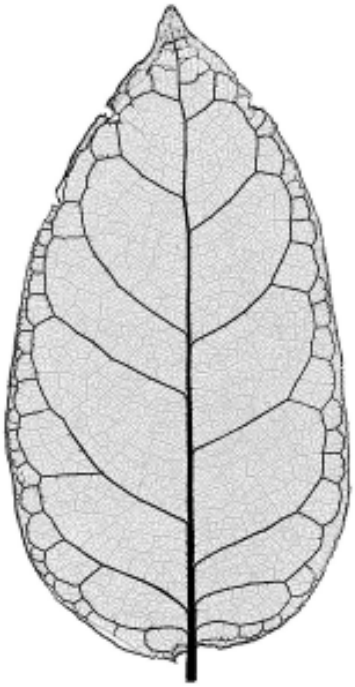
8 basal veins

32. 2° VEIN SPACING



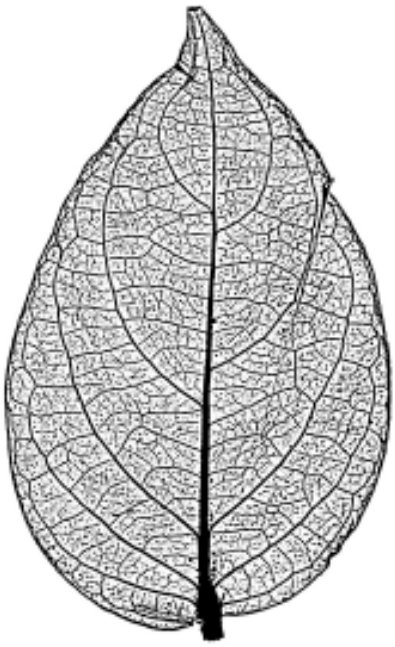
Vitex limonifolia **(Verbenaceae)**

Fig. 32.1 uniform



Keamadecia sinuata **(Proteaceae)**

Fig. 32.2 irregular



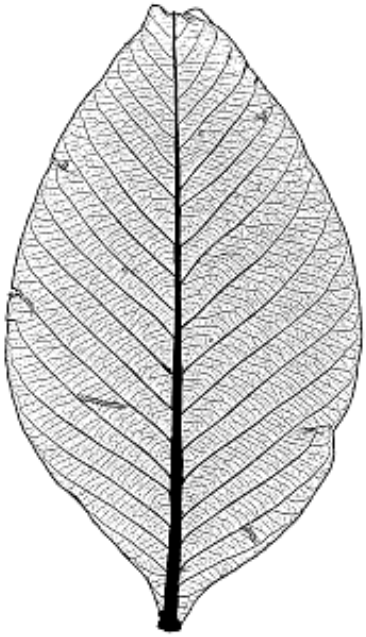
Glochidion bracteatum **(Euphorbiaceae)**

Fig. 32.3 decreasing toward base

Apeiba tibourbou **(Tilliaceae)**

Fig. 32.4 increasing toward base

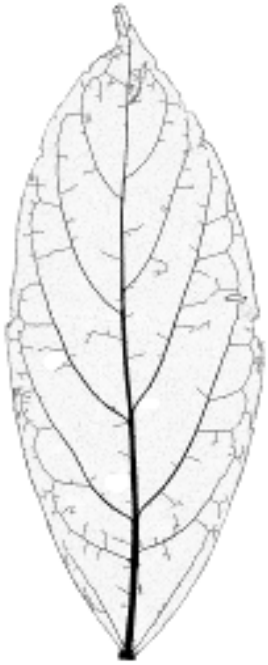
33. 2° VEIN ANGLE



Vitex limonifolia **(Verbenaceae)**

Fig. 33.1

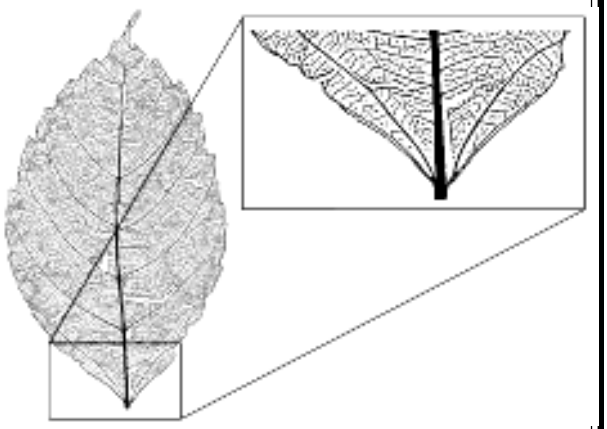
uniform



Cola nitida **(Sterculiaceae)**

Fig. 33.2

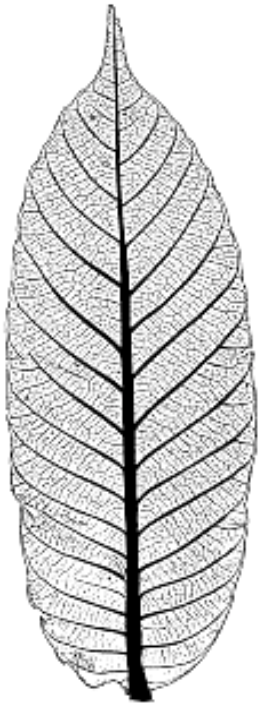
one pair acute basal secondaries



Leea sambucina **(Leeaceae)**

Fig. 33.3

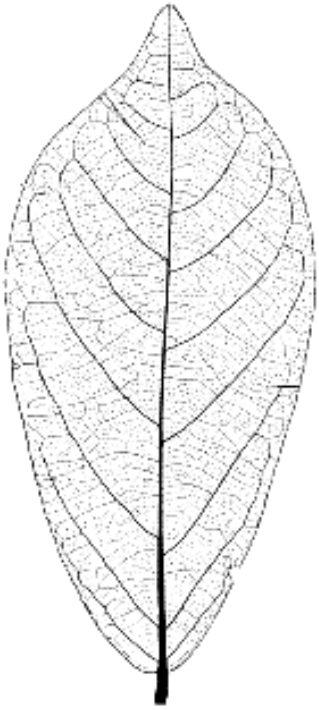
two pair acute basal secondaries



Pseudolmedia laevis **(Moraceae)**

Fig. 33.4

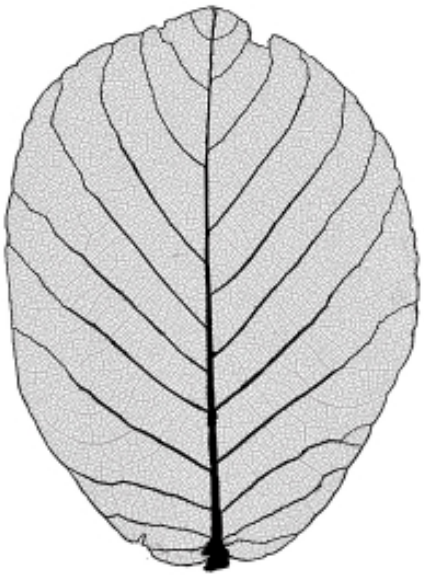
smoothly increasing toward base



Popowia congensis **(Annonaceae)**

Fig. 33.5

smoothly decreasing toward base



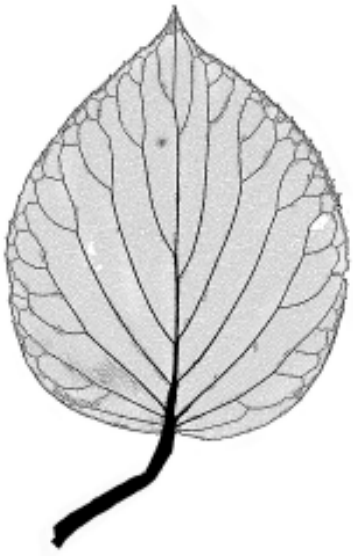
Bridelia mollis **(Euphorbiaceae)**

Fig. 33.6

abruptly increasing toward base

34. INTER-2° VEINS

Intersecondary veins have a width and course similar to the 2°s, but they are usually thinner than the costal 2°s and do not reach the margin.



Schizophragma integrifolia **(Hydrangeaceae)**

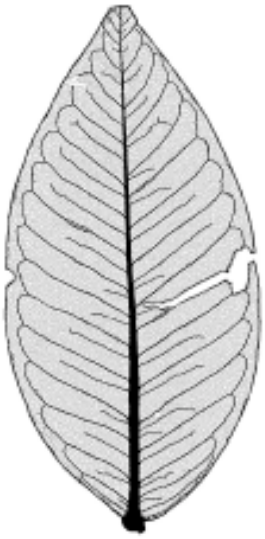
Fig. 34.1

absent intersecondaries

Diospyros guianensis **(Ebenaceae)**

Fig. 34.2

weak intersecondaries



Klainedoxa gabonensis **(Ixonanthaceae)**

Fig. 34.3

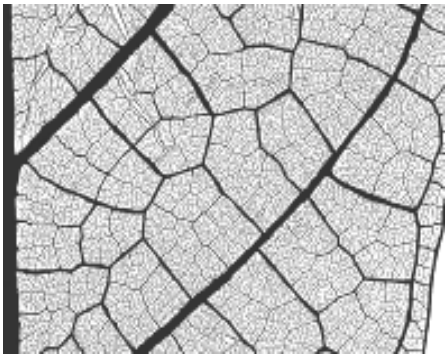
strong intersecondaries

35. 3° VEIN CATEGORY

Actinidia latifolia **(Actinidiaceae)**

Fig. 35.1

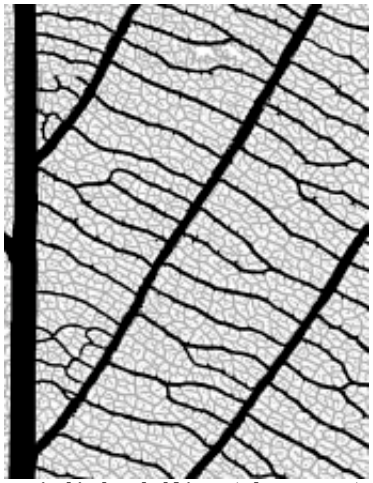
opposite percurrent - tertiaries cross between adjacent secondaries in parallel paths without branching.



Semicarpus rostrata **(Anacardiaceae)**

Fig. 35.2

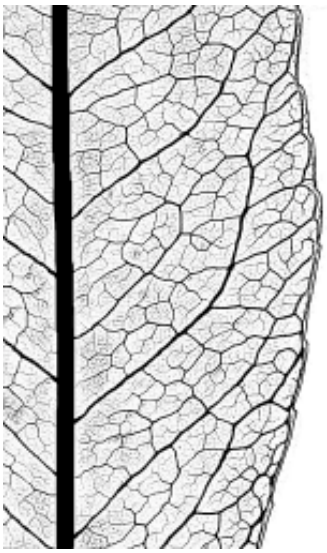
alternate percurrent - tertiaries cross between secondaries with an offset (an abrupt angular discontinuity).



Karwinskia humboldtiana **(Rhamnaceae)**

Fig. 35.3

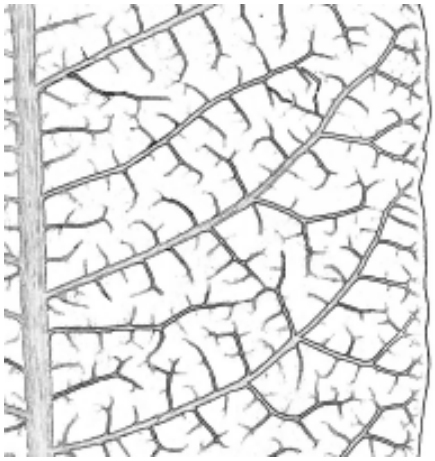
mixed opp/alt -tertiaries have both opposite percurrent and alternate percurrent courses.



Gleditsia officianalis **(Leguminosae)**

Fig. 35.4

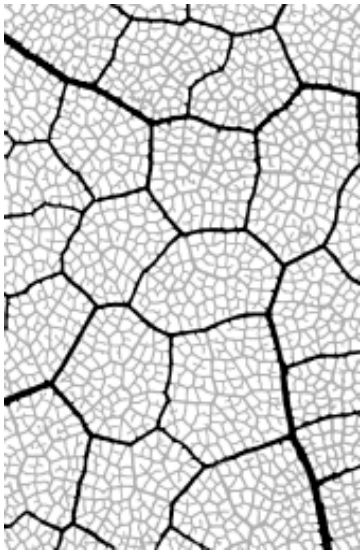
random reticulate - tertiaries anastomose (rejoin) with other 3° veins or 2° veins at random angles.



Rhus vernicifolia **(Anacardiaceae)**

Fig. 35.5

dichotomizing - tertiaries branch freely.



Acer saccharum **(Aceraceae)**

Fig. 35.6

regular polygonal reticulate - tertiaries anastomose with other 3° veins to form polygons of similar size and shape.

36. 3° VEIN COURSE

Figures 36.1-36.3 refer only to opposite percurrent tertiary veins.

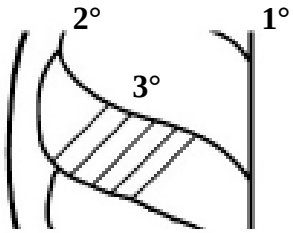


Fig. 36.1

straight - passing across the intercostal area without a noticeable change in course.

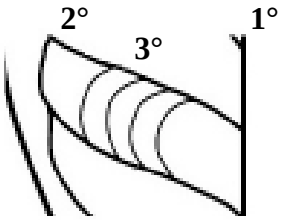


Fig. 36.2

convex - middle portion of the vein curving away from the center of the leaf.

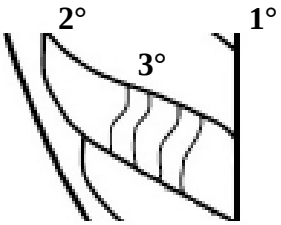
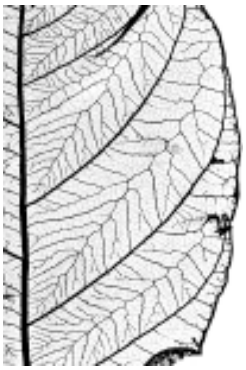


Fig. 36.3

sinuous - changing direction of curvature.

ramified - tertiary veins branch into higher orders without rejoining secondaries.



Sadrinelia gilletii **(Anacardiaceae)**

Fig. 36.4

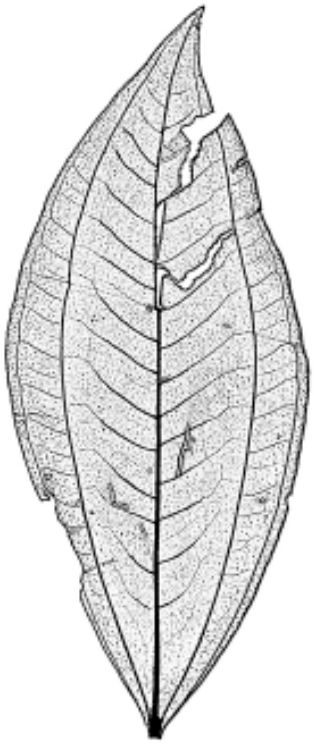
admedially ramified - branching oriented toward the primary or midline.

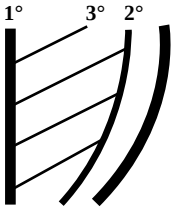
Ascarina rubricaulis **(Chloranthaceae)**

Fig. 36.5

exmedially ramified - branching oriented toward the leaf margin.

37. 3° (VEIN) ANGLE TO 1°

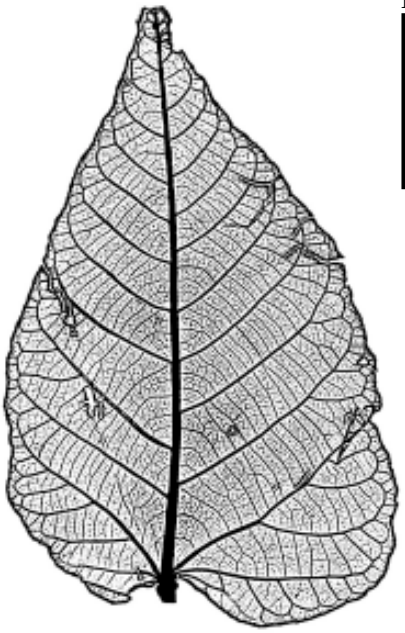


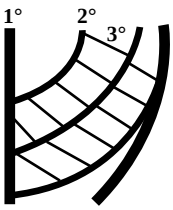


Tristemma incompletum **(Melastomataceae)**

Fig. 37.1

acute

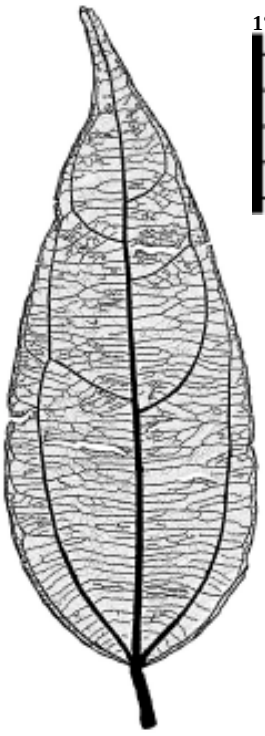


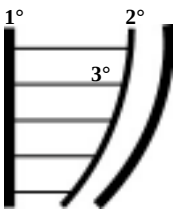


Croton urucurana **(Euphorbiaceae)**

Fig. 37.2

obtuse





Lunania piperoides **(Flacourtiaceae)**

Fig. 37.3

perpendicular

38. 3° VEIN ANGLE VARIABILITY

The tertiary angle is measured with respect to the primary vein.

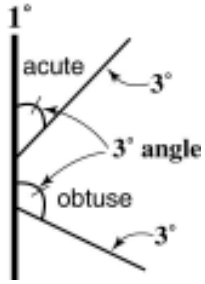
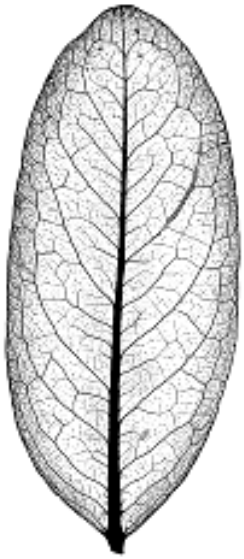


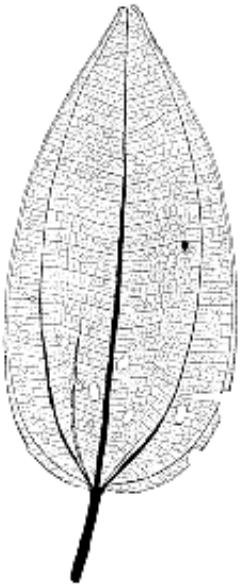
Fig. 38.1



Diospyros maritima **(Ebenaceae)**

Fig. 38.2

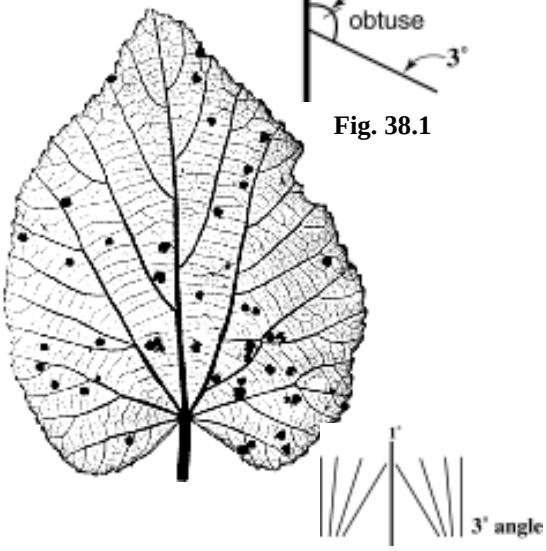
inconsistent - angle of the tertiaries varies randomly over the lamina.



Graffenrieda anomala **(Melastomataceae)**

Fig. 38.3

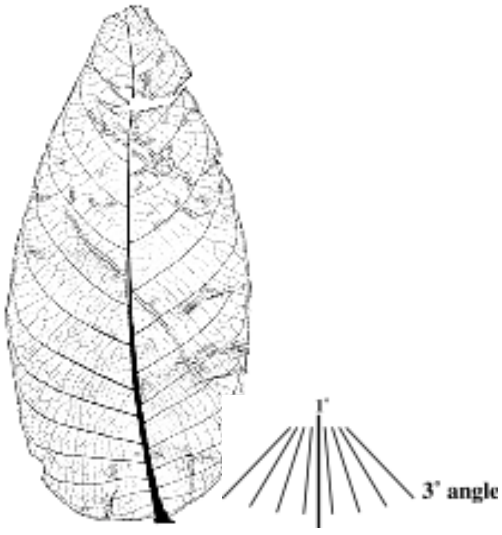
uniform - angles of the tertiaries do not vary over the surface of the lamina.



Eriolaena maliaceae **(Sterculiaceae)**

Fig. 38.4

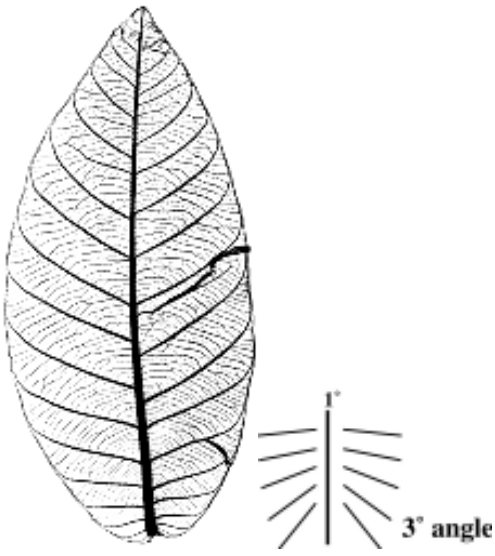
increasing exmedially - the angles of the tertiaries become more obtuse away from the axis of symmetry.



Juglans sinensis **(Juglandaceae)**

Fig. 38.5

decreasing exmedially - the angles of the tertiaries become more acute away from the axis of symmetry.



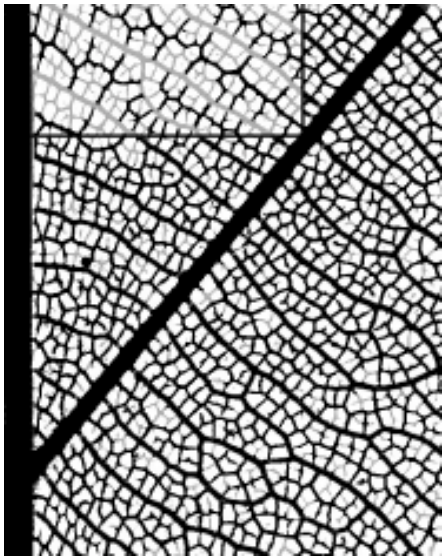
Odontadenia geminata **(Apocynaceae)**

Fig. 38.6

increasing basally - the tertiary angles become more obtuse toward the base of the lamina.

39. 4° VEIN CATEGORY

Fourth and higher order venational characters should be scored in the portion of the leaf that is roughly half way between the base and the apex unless the area is lacking.



Fagus engleriana **(Fagaceae)**

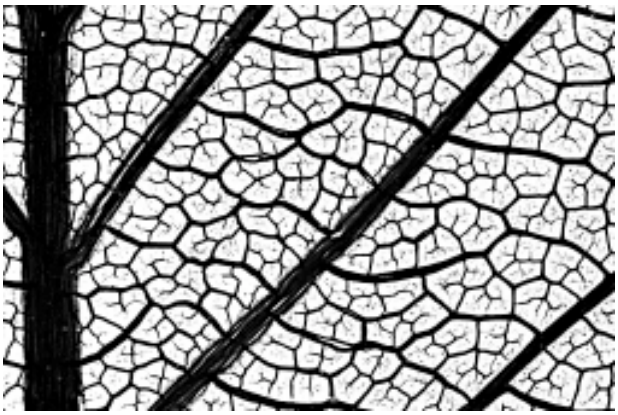
Fig. 39.1

alternate percurrent - 4°s cross between adjacent tertiaries with an offset (an abrupt angular discontinuity).

Actinidia latifolia **(Actinidiaceae)**

Fig. 39.2

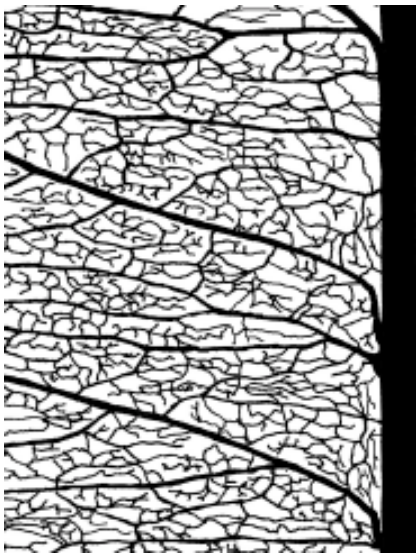
opposite percurrent - 4°s cross between adjacent 3°s in parallel paths without branching.



Aesculus parryi **(Hippocastanaceae)**

Fig. 39.3

regular polygonal reticulate - 4°s anastomose with other veins to form polygons of similar size and shape.

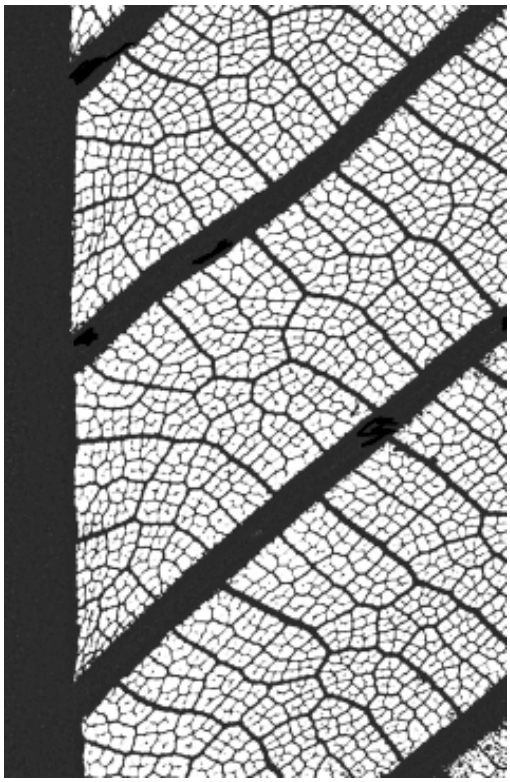


Sebastiana longicuspus **(Euphorbiaceae)**

Fig. 39.4

dichotomizing - 4°s branch freely and are the finest vein order the leaf exhibits.

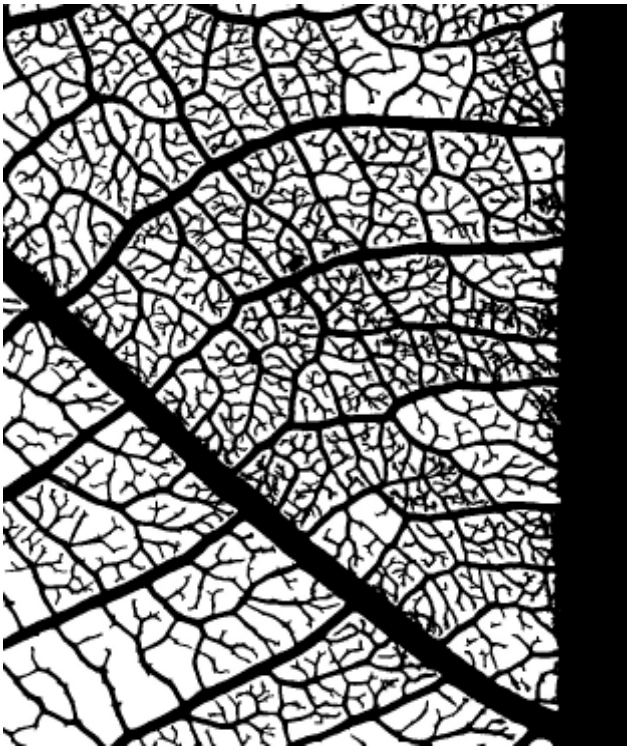
40. 5° VEIN CATEGORY



Pseudolmedia laevis **(Moraceae)**

Fig. 40.1

regular polygonal reticulate - veins anastomose with other veins to form polygons of similar size and shape.



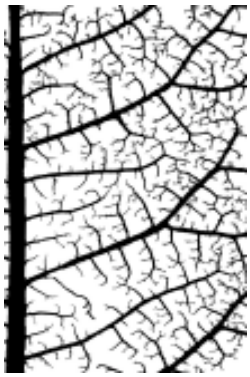
Ptychopyxis bacciformis **(Euphorbiaceae)**

Fig. 40.2

dichotomizing - 5os branch and are the finest vein class that the leaf exhibits.

41. AREOLATION

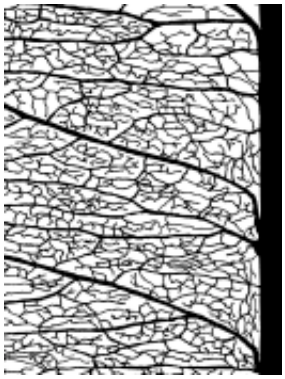
Areoles are the smallest areas of the leaf tissue surrounded by veins; taken together they form a contiguous field over most of the area of the lamina. Any order of venation can form one or more sides of an areole.



Rhus vernicifolia **(Anacardiaceae)**

Fig. 41.1

lacking - (rare) venation that ramifies into the intercostal area without producing closed meshes.



Sebastiana longicuspus **(Euphorbiaceae)**

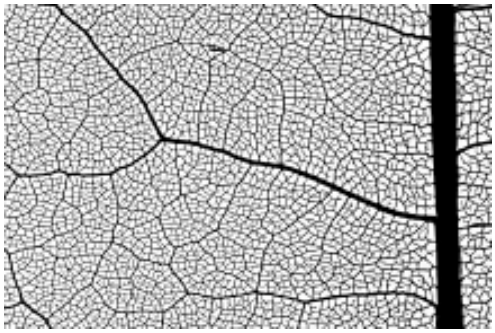
Fig. 41.2

poorly developed - areoles many sided (often >7) and of highly irregular size and shape.

Clusiella pendula **(Guttiferaceae)**

Fig. 41.3

moderately developed - areoles of irregular shape, more or less variable in size, usually fewer sided than in poorly developed areolation.



Piranhea trifoliolata **(Euphorbiaceae)**

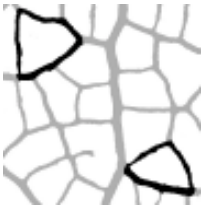
Fig. 41.4

well developed - areoles of relatively consistent size and shape.

Afrostyrax kamerunensis **(Huaceae)**

Fig. 41.5

paxillate - areoles occurring in oriented fields.



Piranhea trifoliolata **(Euphorbiaceae)**

Fig. 41.6

3 sided

Piranhea trifoliolata **(Euphorbiaceae)**

Fig. 41.7

4 sided

Piranhea trifoliolata **(Euphorbiaceae)**

Fig. 41.8

5 or more sided

42. F. E. V. S

"FEVs" are the freely ending ultimate veins of the leaf. The two database fields should contain the extreme states observed.

Fig. 42.1

absent

Fig. 42.2

unbranched - no branches, may be linear or curved.

Fig. 42.3

Fig. 42.4

1- branched - branches one time.

Fig. 42.5

Fig. 42.6

2 or more branched - branches more than once.

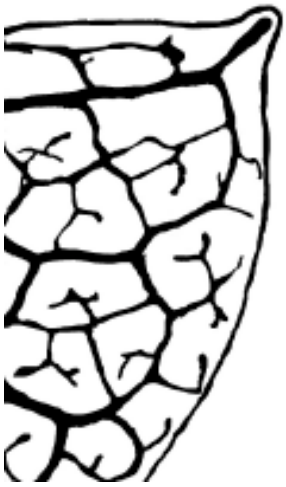
43. HIGHEST ORDER

Highest vein order of the leaf.

44. HIGHEST EXCURRENT

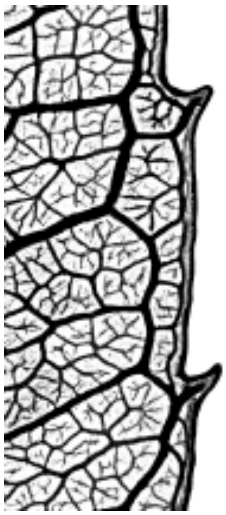
Highest vein order showing excurrent branching; that is, having true lateral branches rather than those produced by forking of the vein.

45. MARGINAL ULTIMATE (VENATION)

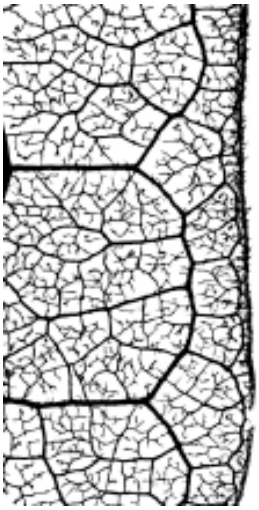


Eucryphia glandulosa **(Eucryphiaceae)**
Fig. 45.1
teeth

Carissa bispinosa **(Apocynaceae)**
Fig. 45.2
no teeth



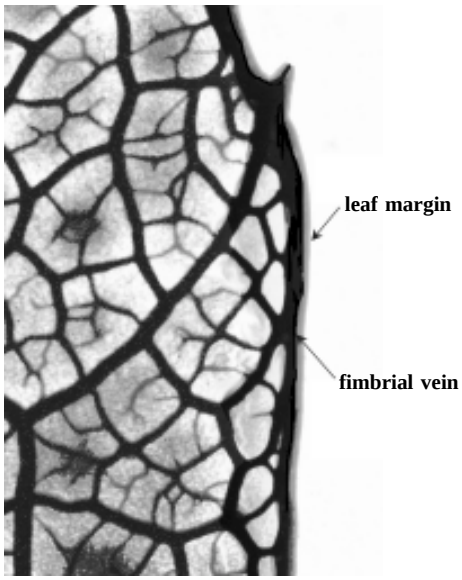
Mollinedia floribunda **(Monimiaceae)**
Fig. 45.3
teeth



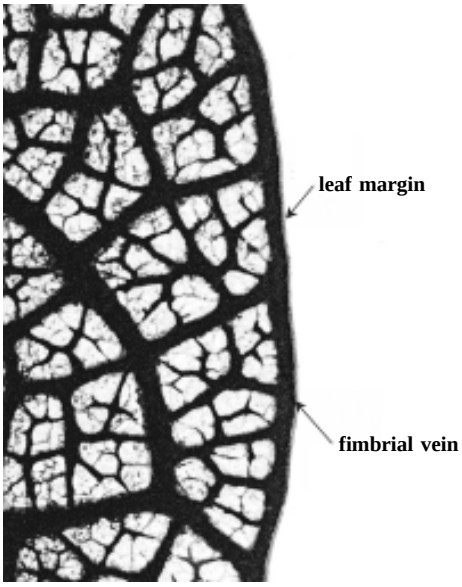
Picramnia krukovic **(Simaroubaceae)**
Fig. 45.4
no teeth

incomplete loops - freely ending veinlets adjacent to the margin.

looped - marginal ultimate vein recurved to form loops.



Pycnocoma littoralis **(Euphorbiaceae)**
Fig. 45.5
teeth

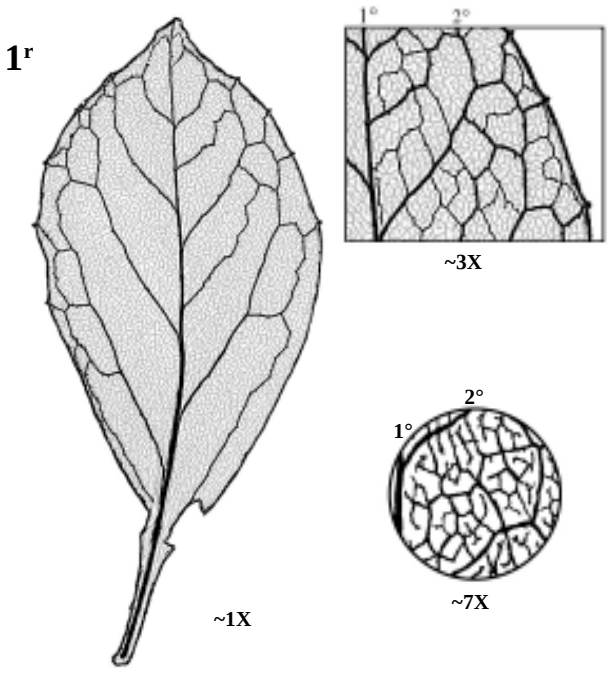


Cissampelos ciliafolia **(Menispermaceae)**
Fig. 45.6
no teeth

fimbrial vein - higher vein orders fused into a vein running just inside the margin.

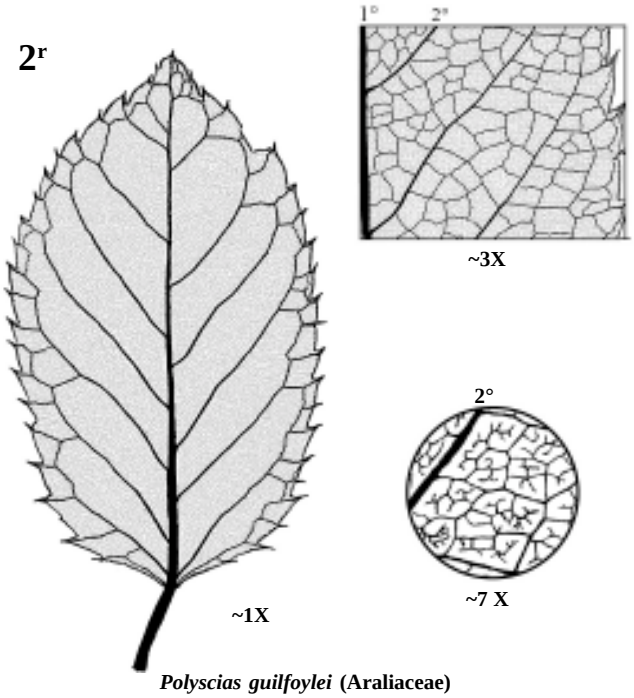
46. LEAF RANK

Leaf rank is a semiquantitative description of the regularity of the leaf's vein system, from an arbitrary level of 1r for the lowest rank or level of organization to 4r for the highest. The rank number corresponds to the highest order of veins that is well organized. The table on the next page gives the characters that define the ranks.



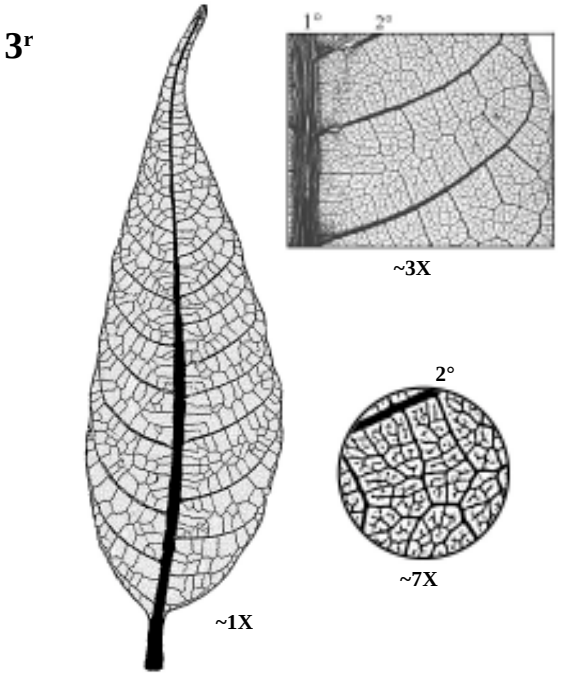
Schisandra glaucescens **(Schisandraceae)**

Fig. 46.1



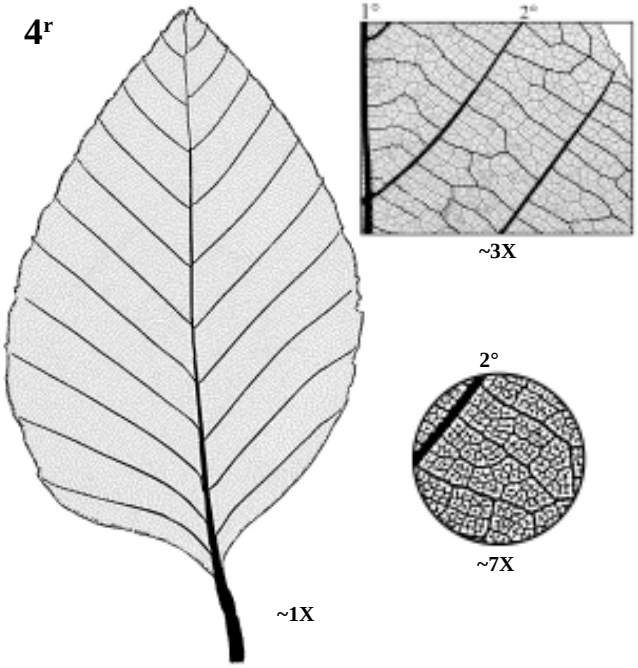
Polyscias guilfoylei **(Araliaceae)**

Fig. 46.2



Toona sureni **(Meliaceae)**

Fig. 46.3



Fagus tientaiensis **(Fagaceae)**

Fig. 46.4

Elements		**1r**	**2r**	**3r**	**4r**
1^{o} course		regular, rarely irregular	regular	regular	regular
2^{o} vein	course angle of origin spacing	irregular irreg. & decur. irregular	regular us. reg, not dec. irreg. to reg.	regular reg.- not dec. regular	regular reg. - not dec. regular
intercostal	area	shapes vary	shapes similar	shapes similar	shapes similar
3^{o} veins	course resolution resolution	irregular poor from 2^{o} poor from 4^{o}	irregular fair from 2^{o} poor from 4^{o}	regular good from 2^{o} good from 4^{o}	regular good from 2^{o} good from 4^{o}
areolation	shape size orientation	irregular irregular irregular	irregular irregular irregular	becoming reg. becoming reg. irregular	regular regular oriented
vein orders with excurrent branching		1^{o}-2^{o}	2-3^{o}	3-6^{o}	4-6^{o}
blade - petiole separation		poor	usually good	good	good

Fig. 46.5

Section 4: Teeth

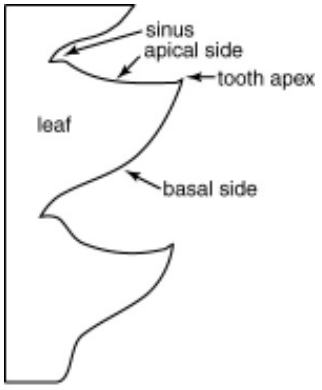
DEFINITIONS

Sinus - an incision between marginal projections of any sort (lobes, dentations, serrations, crenations). May be angular or rounded.

Tooth apex - the tip of a tooth.

Apical side - the side of the tooth that is toward the apex of the lamina.

Basal side - the side of the tooth that is toward the base of the lamina.

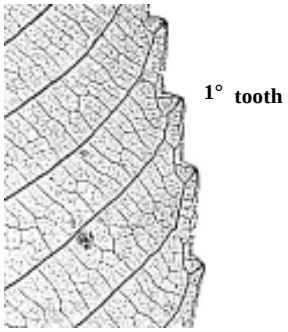


Parts of a tooth

Fig. 10

47. # OF ORDERS (OF TEETH)

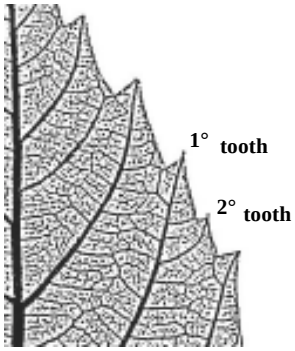
(**1°**, **2°** or **3°**) If the teeth can be separated into different size groups, they are called *compound*.



Leea macropus **(Vitaceae)**

Fig. 47.1

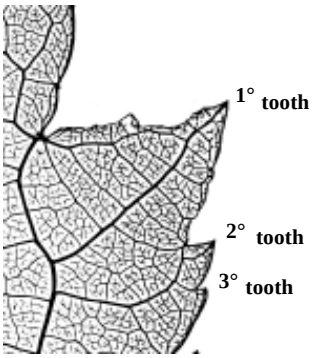
1 order



Celtis davidiana **(Ulmaceae)**

Fig. 47.2

2 orders



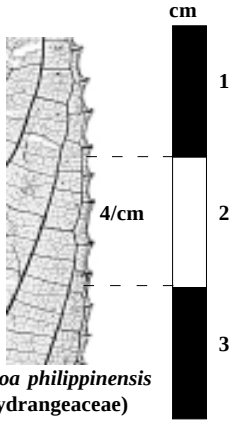
Physocarpus capitalus **(Rosaceae)**

Fig. 47.3

3 orders

48. TEETH/CM

The number of teeth/cm in the middle 50% of the leaf.



Dichroa philippinensis
(Hydrangeaceae)

Fig. 48.1

49. (TOOTH) SPACING

This refers to the interval between corresponding points on the teeth or crenations.

Fig. 49.1

Dichroa philippinensis **(Hydrangeaceae)**

regular - the interval varies less than 25%.

Fig. 49.2

Beauaertia mucronata **(Celastraceae)**

irregular - the interval varies more than 25%.

50. (TOOTH) SHAPE

Tooth shape is described in terms of the shape of the apical side and the basal side. The possible combinations are shown in the chart below. In the database, the following abbreviations are used:

cv (convex) **st** (straight) **cc** (concave) **fl** (flexuous) basally convex and apically concave **rt** (retroflexed) apically convex and basally concave

The apical shape is listed first. For example, cc/fl would be concave on the apical side and flexuous on the basal side of the tooth. Note that a given leaf can exhibit more than one tooth shape.

APICAL SIDE

BASAL SIDE

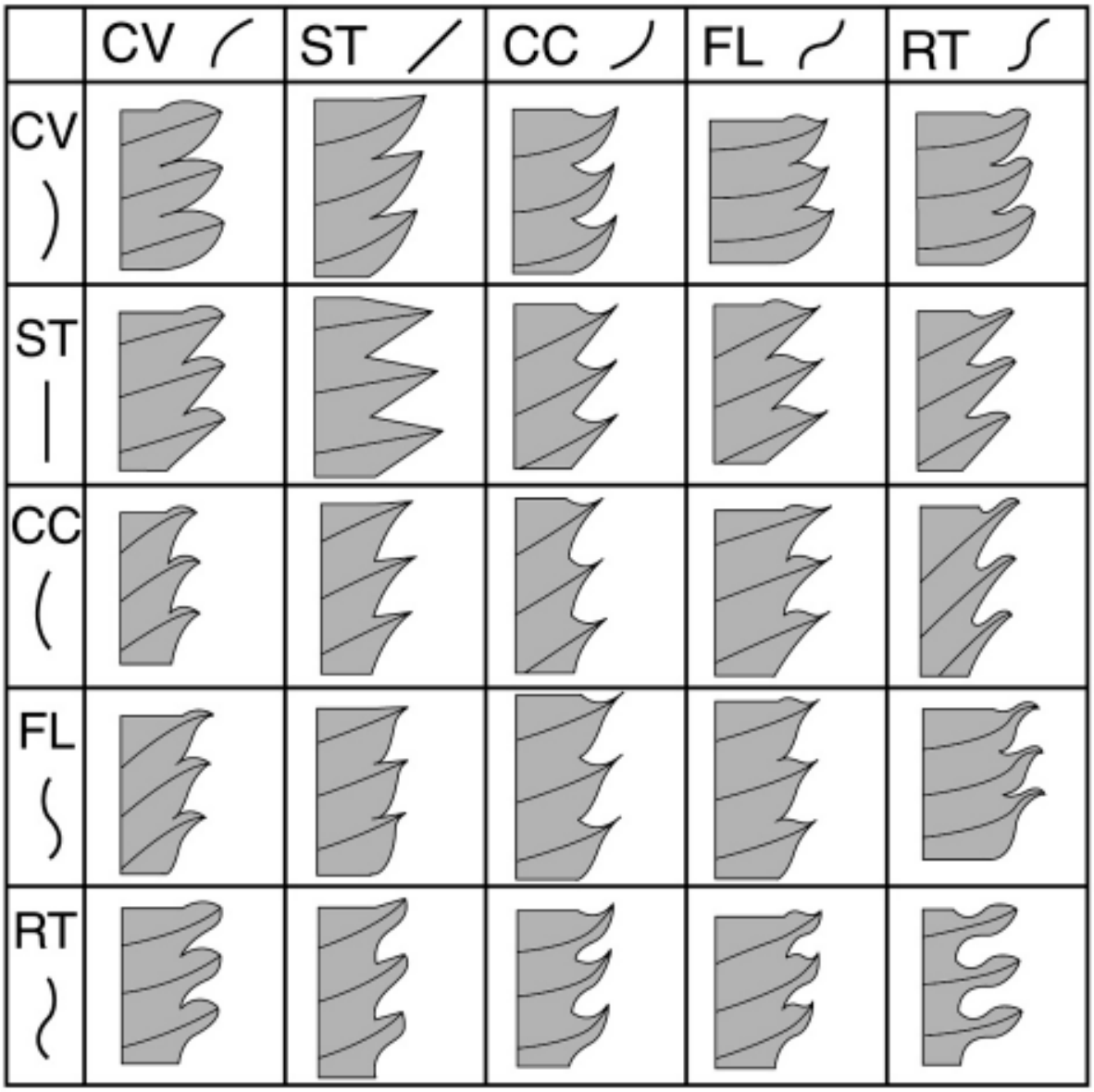


Fig. 50.1

51. SINUS (SHAPE)

The shape of the sinus of the tooth.

Celtis cerasifera **(Ulmaceae)**

Fig. 51.1

angular

Phylloclinium paradoxum **(Flacourtiaceae)**

Fig. 51.2

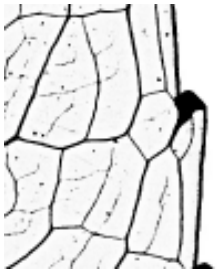
rounded

52. (TOOTH) APEX

There are three major types of tooth apex: simple, spinose, and glandular. In living leaves and some fossils, it may be possible to distinguish the following subsets of glandular: spherulate, papillate, foraminate, mucronate, and setaceous. For situations in which a more specific identification is not possible, use non-specific glandular.

Celtis cerasifera **(Ulmaceae)**
Fig. 52.1

simple - tooth apex formed by the change in direction of the leaf margin without additional elements.



Ascarina lanceolata **(Chloranthaceae)**
Fig. 52.2

non-specific glandular - in fossils, it may be impossible to distinguish between the different subtypes of glandular teeth. This character state is reserved for the description of fossil teeth with a visible concentration of material on the tooth apex.

Ilex dipryena **(Aquifoliaceae)**
Fig. 52.3

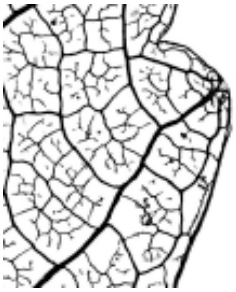
spinose - principal vein of tooth projecting beyond the apex.

Populus jackii **(Salicaceae)**
Fig. 52.4

spherulate - having a spherical callosity fused to the apex.

Haematostemon coriaceous **(Euphorbiaceae)**
Fig. 52.5

papillate - having a clear, nipple-shaped, glandular apical termination.



Leea macropus **(Vitaceae)**
Fig. 52.6

foraminate - with an apical cavity or foramen that broadens from the termination of the principal vein toward the exterior.

Daphandra crypta **(Monimiaceae)**
Fig. 52.7

mucronate - with an opaque or non-deciduous cap or mucro fused to the tooth.

Saurauia calyptrata **(Actinidiaceae)**
Fig. 52.8

setaceous - an opaque, deciduous bristle or cap thickened proximally and not fused firmly with the remaining tooth substance.

53. TOOTH VENATION

This describes the venation that is associated with the tooth. The *principal vein* is the thickest vein entering the tooth. Other veins in the tooth are *accessory veins*. Describe their characteristic arrangement.

Section 5: Cuticle

54. LEAF TEXTURE

Leaf texture is difficult to compare between localities. This is a relative scale for leaves preserved in a similar rock type.

not apparent - preservation does not allow the texture to be inferred.

membranaceous w/cuticle - compression appears to be very thin compared with other leaf types preserved in the same matrix; cuticle present.

membranaceous w/o cuticle - compression appears very thin compared with other leaf types preserved in the same matrix.

chartaceous w/cuticle - compression appears moderately thin compared with other leaf types preserved in the same matrix; cuticle present.

chartaceous w/o cuticle - compression appears moderately thin compared with other leaf types preserved in the same matrix.

coriaceous w/ cuticle - compression appears thick compared with other leaf types preserved in the same matrix; cuticle present.

coriaceous w/o cuticle - compression appears thick compared with other leaf types preserved in the same matrix.

55. STOMATA

Figures 55.1 - 56.3 are reprinted with permission from *Botanical Review*, vol. 40, no. 1, copyright 1974, The New York Botanical Garden, *Approaches to the identification of angiosperm leaf remains* by David Dilcher.

Anatomy of Stomata:

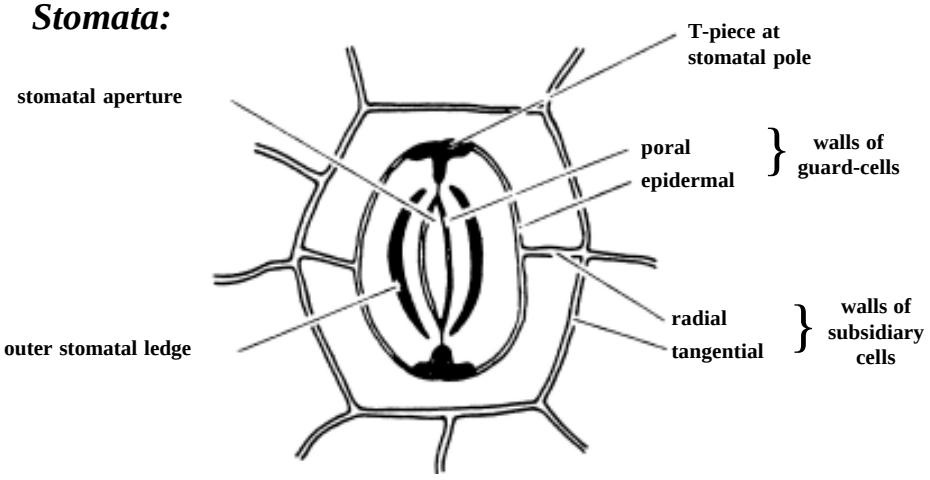
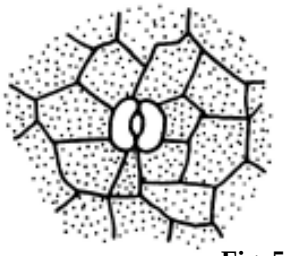


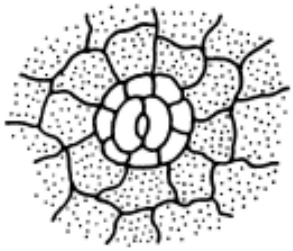
Fig. 55.1

polycytic - 5 or more cells enclosing the guard cells.



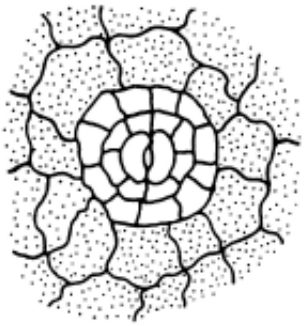
anomocytic - 5 or more cells enclosing the guard cells, cells adjacent to the guard cells not differentiated in any way from the normal epidermal cells.

Fig. 55.2



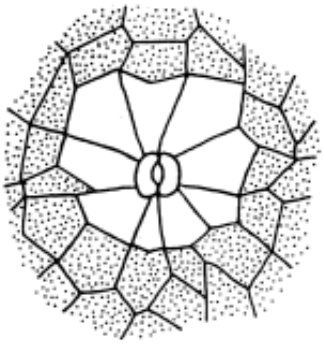
cyclocytic - single ring of 5 or more small cells enclosing the guard cells.

Fig. 55.3



amphicyclocytic - double ring of 5 or more cells each enclosing the guard cells.

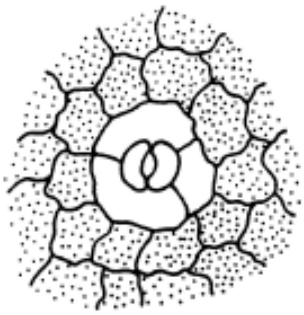
Fig. 55.4



actinocytic - single ring of 5 or more somewhat enlarged or elongated cells enclosing the guard cells.

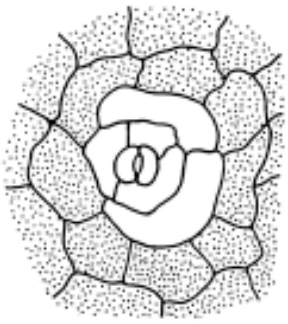
Fig. 55.5

anisocytic types - 3 cells, may be unequal in size, enclosing the guard cell.



anisocytic - single ring of 3 cells (2 larger, one smaller) enclosing the guard cells.

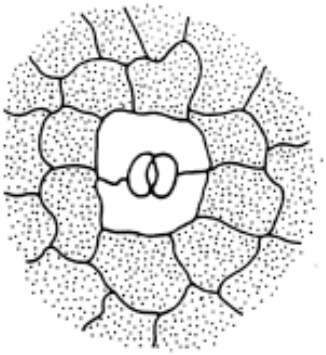
Fig. 55.6



amphianisocytic - double ring of cells enclosing the guard cells with the inner ring consisting of 3 cells (2 larger, one smaller); outer ring may be incomplete consisting of 2-3 or 4 cells.

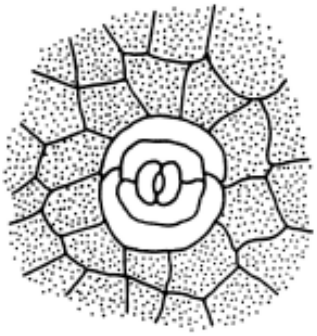
Fig. 55.7

diacytic types - 2 cells enclsing the guard cells at right angles to the long axis of guard cells.



diacytic - single ring of 2 cells enclosing the guard cells at right angles to the long axis of the guard cell.

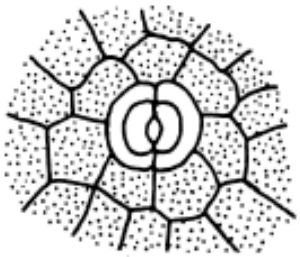
Fig. 55.8



amphidiacytic - double ring of 4 cells enclosing the guard cells at right angles to the long axis of the guard cells.

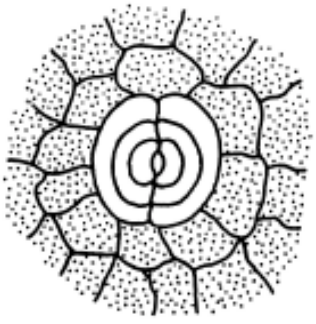
Fig. 55.9

paracytic types - 1 or 2 cells adjacent to the guard cells with their long axis parallel to the long axis of the guard cells.



paracytic - 2 cells completely enclosing the guard cells with their long axis parallel to the long axis of the guard cells.

Fig. 55.10



amphiparacytic - double ring of the 4 cells enclosing the guard cells with their long axis parallel to the long axis of the guard cells.

Fig. 55.11

paracytic types *continued*

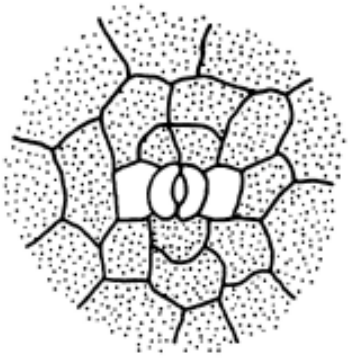


Fig. 55.12

brachyparacytic - 2 cells flanking the sides of the guard cells but not completely enclosing them, may or may not be elongate, parallel to the long axis of the guard cells.

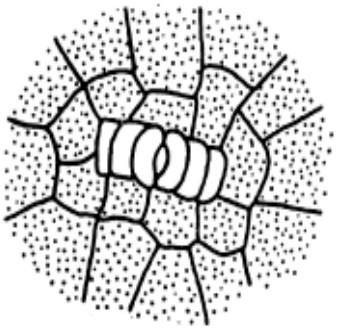


Fig. 55.13

amphibrachyparacitic - 4 cells flanking the sides of the guard cells but not completely enclosing them, may or may not be elongate, parallel to the long axis of the guard cells.

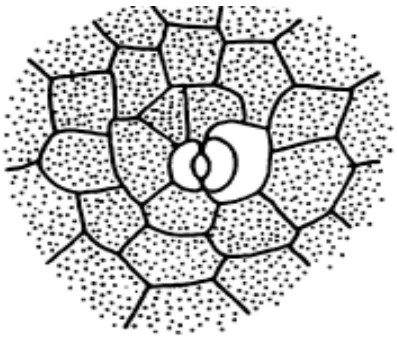
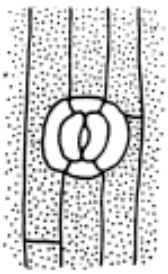


Fig. 55.14

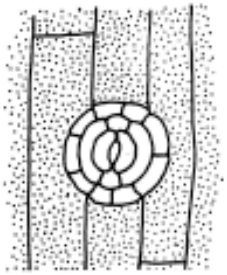
hemiparacytic - 1 of the cells adjacent to the guard cell enclosing it and parallel to its long axis, the other guard cell having three or more normal epidermal cells surrounding it.

tetracytic types - 4 cells adjacent to and enclosing the guard cell.



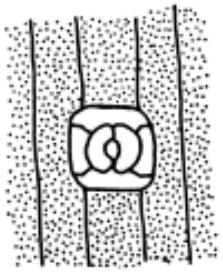
paratetracytic - 2 elongate cells lateral and parallel to the guard cells, 2 narrow polar cells.

Fig. 55.15



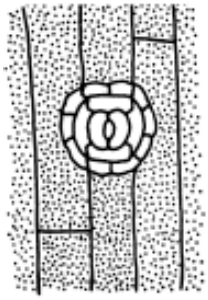
amphiparatetracytic - 2 elongate cells lateral and parallel to the guard cells, 2 narrow polar cells, all of which is surrounded by a ring of small cells.

Fig. 55.16



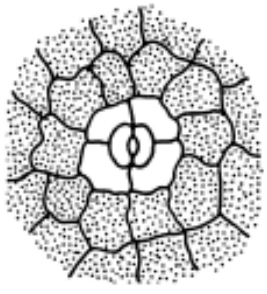
brachyparatetracytic - 2 short cells lateral and parallel to the guard cells, 2 wide polar cells.

Fig. 55.17



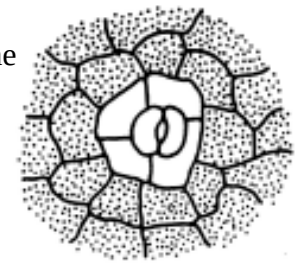
amphibrachyparatetracytic - 2 short cells lateral and parallel to the guard cells, 2 wide polar cells, all of which is surrounded by a ring of small cells.

Fig. 55.18



staurocytic - 4 cells, more or less equal in size, with the anticlinal walls of the subsidiary cells extending at right angles from the poles and middle of the guard cells.

Fig. 55.19



anomotetracytic - 4 cells enclosing the guard cells in an irregular and variable pattern.

Fig. 55.20

hexacytic types - 4 cells adjacent to the guard cells with 2 additional (lateral or polar)cells which can be distinguished from the epidermal cells.

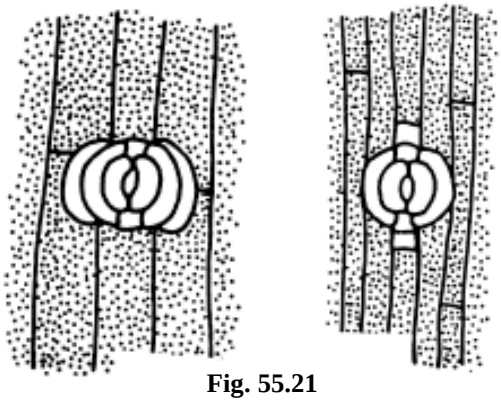


Fig. 55.21

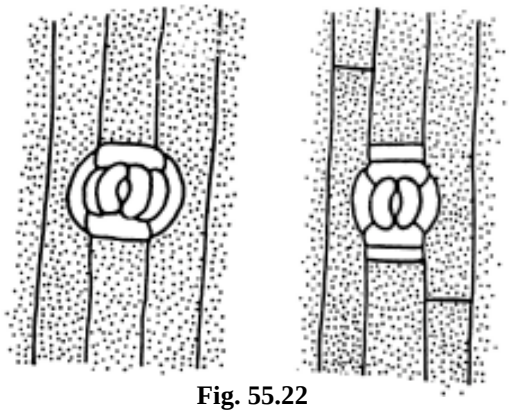


Fig. 55.22

parahexacytic - either 4 elongate cells alteral and parallel to the guard cells with 2 narrow polar cells OR 2 elongate cells lateral and parallel to the guard cells with 4 narrow polar cells.

brachyparahexacytic - either 4 short cells lateral to the guard cells with 2 wide polar cells OR 2 short cells lateral to the guard cells with 4 wide polar cells.

pericytic - one cell encloses both guard cells.

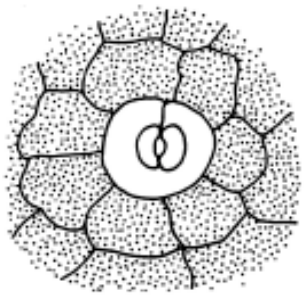


Fig. 55.23

desmocytic - 1 cell enclosing both guard cells with one anticlinal wall extending from one of the poles cutting the cell once.

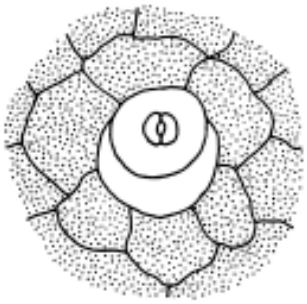


Fig. 55.24

copericytic - 1 cell (subtended by a crescent-shaped cell) enclosing both guard cells.

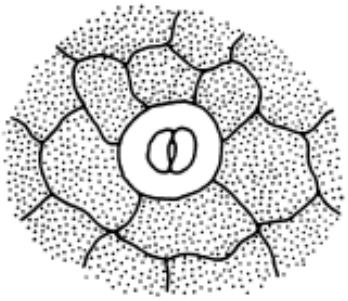


Fig. 55.25

amphipericytic - one cell enclosing both guard cells enclosed by a second single cell.

polocytic types - one cell nearly but not completely enclosing the two guard cells.

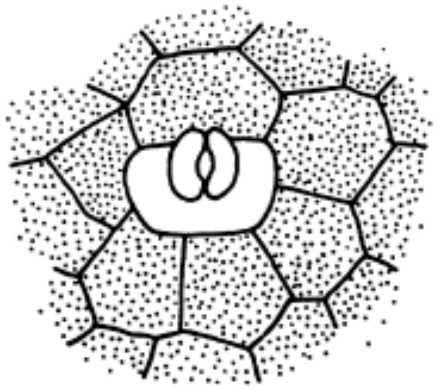


Fig. 55.26

polocytic - 1 cell nearly enclosing both guard cells except for one pole which is covered by a single epidermal cell.

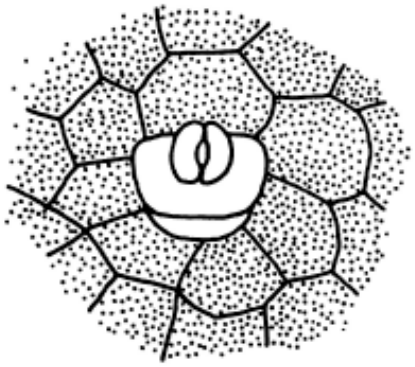


Fig. 55.27

copolocytic - 1 cell (subtended by a crescent shaped cell) nearly enclosing both guard cells except for one pole which is covered by a single epidermal cell.

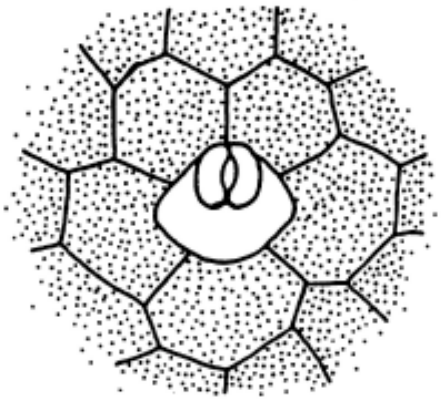


Fig. 55.28

axillocytic - 1 cell nearly enclosing both guard cells except for one free pole which is covered by two cells with a common anticlinal wall extending from the pole parallel to the long axis of the guard cell.

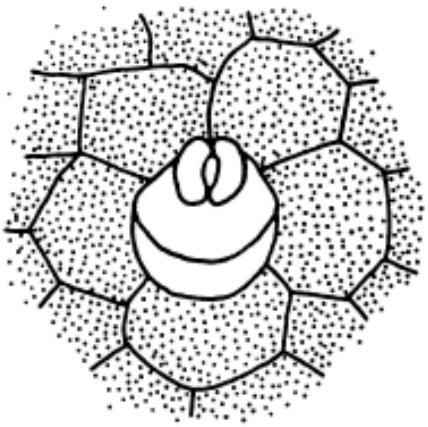


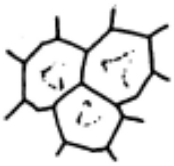
Fig. 55.29

coaxillocytic - 1 cell (subtended by a crescent-shaped cell) nearly enclosing both guard cells except for one free pole which is covered by 2 cells with a common anticlinal wall extending from the pole parallel to the long axis of the guard cells.

56. (CUTICULAR) FEATURES

striations

Fig. 56.1



papillae

Fig. 56.2

thickened areas

Fig. 56.3

hair bases
trichomes
unicellular hair
multicellular hairs
peltate hairs
simple hairs
stellate hairs

APPENDIX A

COMPENDIUM INDEX OF NORTH AMERICAN FOSSIL PLANTS
First Field

1— ANGIOSPERMS

Leaves with several orders of venation, cross-veins and vein anastamoses at several orders.

Leaves Preserving Compound Attachment

100 Leaf pinnately compound or (bi-) trifoliate, toothed
101 Leaf pinnately compound or (bi-) trifoliate, toothless
102 Leaf palmately compound

Leaves Preserved As Isolated Lamina
Petiole Attached at Base of Lamina

103 Lamina pinnately veined, deeply emarginate, or bilobed or in multiples of 2
104 Lamina pinnately veined, 3 or more lobes
105 Lamina pinnately veined, linear
106 Lamina pinnately veined, unlobed, oblong, toothed
107 Lamina pinnately veined, unlobed, oblong, toothless
108 Lamina pinnately veined, unlobed, elliptic, symmetrical, dentate
109 Lamina pinnately veined, unlobed, elliptic, symmetrical, serrate
110 Lamina pinnately veined, unlobed, elliptic, symmetrical, crenate

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111 Lamina pinnately veined, unlobed, elliptic, symmetrical, toothless
112 Lamina pinnately veined, unlobed, elliptic, asymmetrical
113 Lamina pinnately veined, unlobed, ovate, symmetrical, dentate
114 Lamina pinnately veined, unlobed, ovate, symmetrical, serrate
115 Lamina pinnately veined, unlobed, ovate, symmetrical, crenate
116 Lamina pinnately veined, unlobed, ovate, symmetrical, toothless, secondaries with uniform spacing and angle of origin
117 Lamina pinnately veined, unlobed, ovate, symmetrical, toothless, secondaries crowded toward the base
118 Lamina pinnately veined unlobed, ovate, symmetrical, toothless, one or more pairs of lower secondaries emerging at a lower angle than those above
119 Lamina pinnately veined, unlobed, ovate, symmetrical, toothless, with (an) intramarginal vein(s)
120 Lamina pinnately veined, unlobed, ovate, asymmetrical

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121 Lamina pinnately veined, unlobed, obovate, symmetrical, toothed
122 Lamina pinnately veined, unlobed, obovate, symmetrical, toothless
123 Lamina pinnately veined, unlobed, obovate, asymmetrical
124 Lamina pinnately veined, w/pectinal vein, unlobed, elliptic or oblong, toothed

125 Lamina pinnately veined, with pectinal vein, unlobed, elliptic or oblong, toothless
126 Lamina pinnately veined, with pectinal vein, unlobed, ovate, toothed
127 Lamina pinnately veined, with pectinal vein, unlobed, ovate, toothless
128 Lamina pinnately veined, with pectinal vein, unlobed, obovate
129 Lamina acrodromously veined, elliptic or oblong, toothless
130 Lamina acrodromously veined, elliptic or oblong, toothless
131 Lamina acrodromously veined, ovate, toothed
132 Lamina acrodromously veined, ovate, toothless
133 Lamina acrodromously veined, obovate
134 Lamina actino- or palinactinodromously veined, unlobed, elliptic, or oblong, toothed
135 Lamina actino- or palinactinodromously veined, unlobed, elliptic or oblong, toothless
136 Lamina actino- or palinactinodromously veined, unlobed, ovate, toothed
137 Lamina actino- or palinactinodromously veined, unlobed, ovate, toothless
138 Lamina actino- or palinactinodromously veined, unlobed, obovate
139 Lamina actino- or palinactinodromously veined, 2-lobed or lobes in multiples of 2
140 Lamina actino- or palinactinodromously veined, 3-lobed
141 Lamina actino- or palinactinodromously veined, 5 or more lobes
142 Lamina definitely palinactinodromously veined, 3 lobed
143 Lamina definitely palinactinodromously veined, 5 or more lobes
144 Lamina campylodromously veined
145 Lamina flabellately veined, very weakly pinnately or palmately veined or multistranded midvein
146 Lamina flat and unlobed, veins parallelodromous, pinnately attached to a costa
147 Lamina flat and unlobed, veins parallelodromous from a zone at the blade base
148 Lamina plicate or breaking into narrow-segments, venation parallelodromous, leaf shape and vein origin unknown
149 Lamina plicate and lobed, fan-shaped, venation palmate
150 Lamina plicate and lobed, feather-shaped, venation pinnate

Petiole Attached Inside Leaf Margin

151 Lamina pinnately veined, with or without pectinal veins
152 Lamina palmately veined, unlobed, orbicular
153 Lamina palmately veined, unlobed, ovate, toothed
154 Lamina palmately veined, unlobed, ovate, toothless
155 Lamina palmately veined, lobed

Petiole Attachment Various or Indeterminate
160 Lamina of special or unusual- shape (including needle, awl, and scale)
161 Lamina insufficiently characterized, pinnate (or unknown), toothed
162 Lamina insufficiently characterized, pinnate (or unknown), toothless (or unknown)
161 Lamina insufficiently characterized, palmate, toothed
164 Lamina insufficiently characterized, palmate, toothless (or unknown)

Other Organs

170 Flowers occurring as single units
171 Flowers aggregated into catkins or aments
172 Flowers aggregated into heads or capitulas
180 Fruits, dry,indehiscent, seed-containing portion relatively small (generally <5mm) or, if winged, the winged portion exceeding the size of the seed (achenes, caroyapsis, utricles, cypselas, samaras, etc.)
181 Fruits, dry, indehiscent, large (>5mm) or, if winged, the winged portion smaller than the seed bearing portion (acorns, balaustas, calybiums, nuts)
182 Fruits, dry, dehiscent capsules, follicules, or siliques
183 Fruits, dry dehiscent legumes or loments
184 Fruits, fleshy (berries, drupes, pomes, etc.)
185 Fruits, aggregate or multiple
186 Fruits, other - or of indeterminate characters
190 Wood or stems

2— GYMNOSPERMS
200 Pteridosperms (including Caytoniales)
210 Cycadophytes,leaves dissected, toothless, veins parallel except convergent at pinna apex and base, mainly forked
211 Cycadophytes,leaves dissected, toothless, veins parallel except convergent at pinnule apex and base, mainly unforked, pinnules <3cm long
212 Cycadophytes, leaves dissected, toothless veins parallel except convergent at pinnule apex and base, mainly unforked, pinnules >3cm long
213 Cycadophytes, leaves dissected, toothless, veins pinnate or radiating throughout length of pinnule
214 Cycadophytes, leaves dissected, pinnules toothed
215 Cycadophytes, leaves undissected, veins parallel, unforked
216 Cycadophytes, leaves undissected, veins parallel, forked
217 Cycadophyte leaves, habit indeterminable
218 Cycadophyte seeds, cones, and “flowers”
219 Cycadophyte stems and wood
220 Ginkgophytes, leaves fan-shaped, veins flabellate, includes the Neoggerathiales, Czekanowskiales
230 Conifers, scaley foliage, leaves appressed to stem for more than 1/2 of their length
231 Conifers, short needles: average <3cm
232 Conifers, long needles: average >3cm
233 Conifers, leafy blades 1<3cm, 1/w ratio >10:1 or 1>3cm l/w ratio 1.5 or less
234 Conifers, cones
235 Conifers, cone scales
236 Conifers, seeds
237 Coniferophytes, wood
238 Conifers, characters uncertain
240 Gnetophytes

300 ALGAE

350 FUNGI

400 BRYOPHYTES

5— *FERNS*
500 Blades dissected, veins open, ultimate laminar division w/o midribs
501 Blades dissected, w/ midribs, veins unforked
502 Blades dissected, veins closed, ultimate laminar divisions w/ midribs, veins forked
503 Blades dissected, veins closed, ultimate laminar divisions w/o midribs
504 Blades dissected, veins closed, ultimate laminar divisions with midribs
505 Blades undissected
506 Venation obscure or uncertain
507 Specialized fertile pinnae, fertile part much exceeding sterile tissue in at least a part of the leaf
508 Fern stems and rhizomes
509 Fragments too small to determine

600 SPHENOPSIDS

7— LYCOPSIDS
700 Lycopodium and Selaginella
710 Isoetales

800 GALLS AND LESIONS

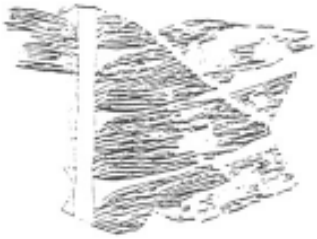
9— PLANTS OF INDETERMINATE RELATIONSHIPS
900 Stems with attached leaves or other structures
910 Rhizomes, roots and stems
920 Leaves
930 Seeds
940 Miscellaneous plant organs and parts
950 Indeterminate plant parts
990 NON PLANTS

BASIC ANGIOSPERM LEAF MORPHOTYPES

GYMNOSPERMS

200

210



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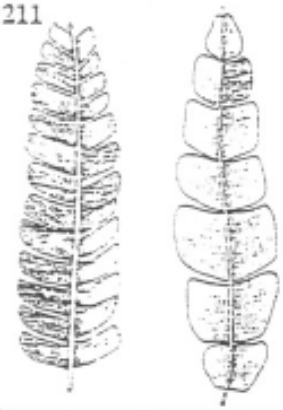

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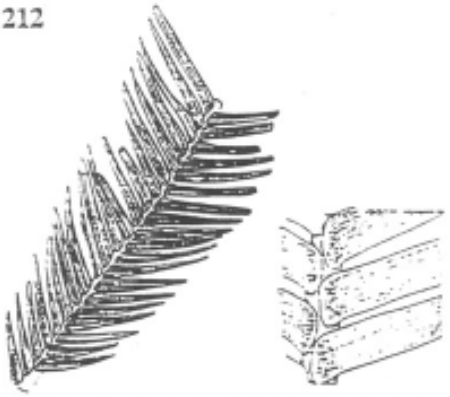

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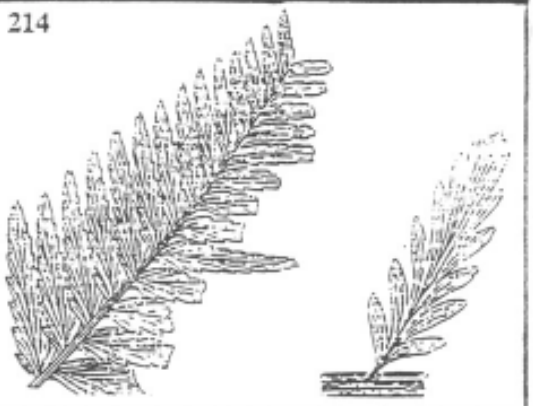

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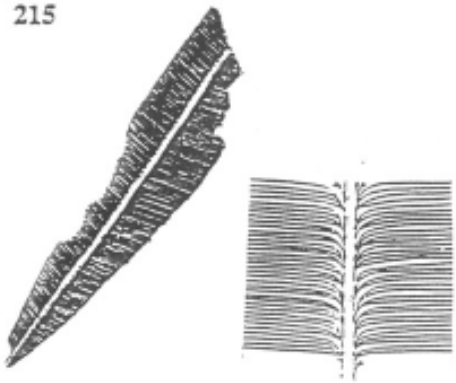

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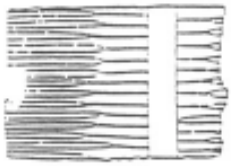

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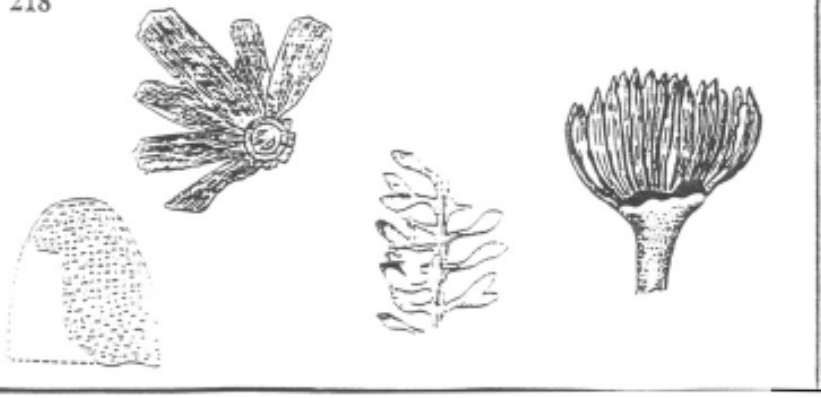

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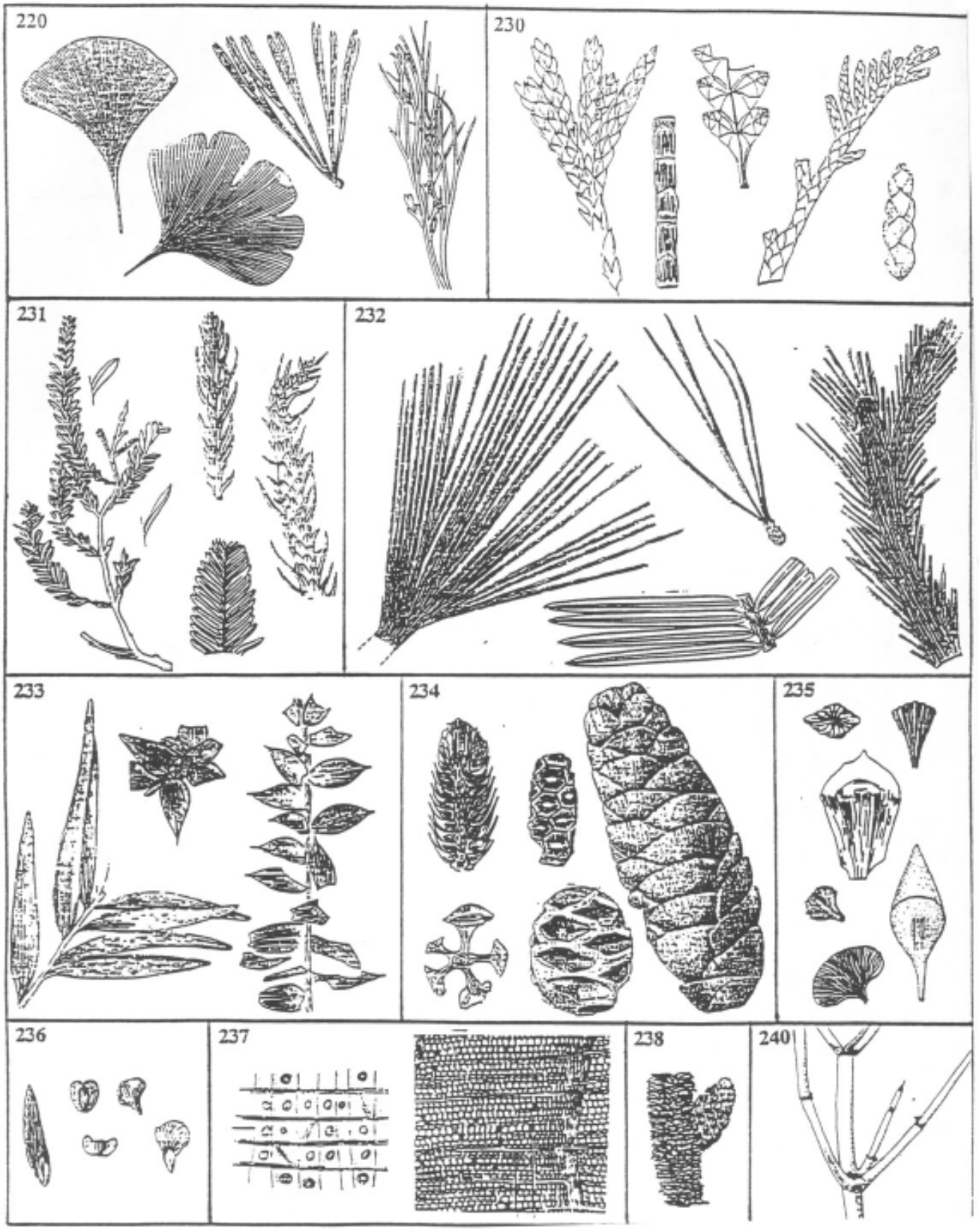


ALGAE

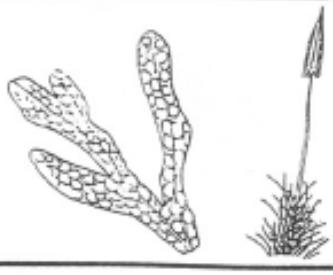
300

FUNGI

350

BRYOPHYTES

400



FERNS

500

501

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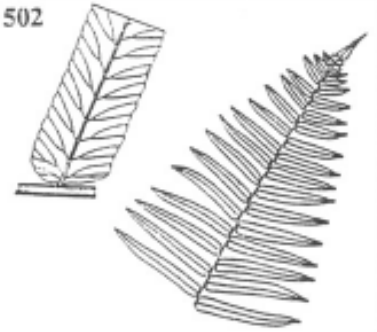

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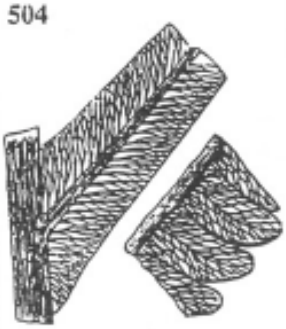

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SPHENOPSIDS

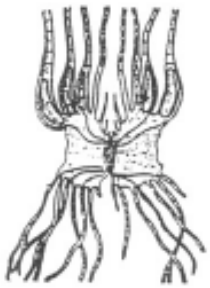
600

LYCOPSIDS

700

GALLS

710



800

900's

?