A STUDY OF LEAF VENATION IN THE BETULACEAE,
WITH ITS APPLICATION TO PALEOBOTANY

A DISSERTATION
SUBMITTED TO THE SCHOOL OF MINERAL SCIENCES
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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN GEOLOGY

By

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May, 1952
I certify that I have read this thesis and that in my opinion it is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

[I signed]

I certify that I have read this thesis and that in my opinion it is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

[I signed]

Approved for the University Committee on Graduate Study:

[Signature]
Merchants occasionally go through a wholesome, though troublesome and not always satisfactory, process which they term 'taking stock'. After all the excitement of speculation, the pleasure of gain, and the pain of loss, the trader makes up his mind to face facts and to learn the exact quantity and quality of his solid and reliable possessions.

The man of science does well sometimes to imitate this procedure; and, forgetting for the moment the importance of his own small winnings, to re-examine the common stock in trade, so that he may make sure how far the store of bullion in the cellar — on the faith of whose existence so much paper has been circulating — is really the solid gold of truth.

T.H. Huxley
# Table of Contents

**INTRODUCTION** .................................................. 1
  - Purpose .................................................. 1
  - Difficulties in Paleobotany ............................ 1
  - Acknowledgments ........................................... 11

**CHAPTER I. HISTORY OF VENATION STUDIES** .............. 13

**CHAPTER II. TECHNIQUE AND SAMPLING METHODS** ....... 19

**CHAPTER III. INTRODUCTION TO THE BETULACEAE** ....... 26
  - General .................................................. 26
  - Terminology and Definitions .......................... 29
    - Veins ................................................ 29
    - Segments ............................................ 35
    - Angles .............................................. 37
    - Cross Venation Patterns ............................ 38
    - Other Terms ......................................... 40
  - Criteria Studied in the Leaves ....................... 43
    - Criteria Examined in this Study .................. 43
    - Criteria of Others not Studied .................... 47
    - Discussion .......................................... 48

**CHAPTER IV. SYSTEMATIC DESCRIPTIONS** .................. 50
  - Betulaceae ............................................... 52
    - I. Alnus ............................................. 53
      - Extant Species of Alnus ......................... 54
      - Fossil Species of Alnus ......................... 59
    - II. Betula ........................................... 94
      - Extant Species of Betula ......................... 96
      - Fossil Species of Betula ......................... 127
    - III. Carpinus ........................................ 130
      - Extant Species of Carpinus ....................... 131
      - Fossil Species of Carpinus (?) ................... 152
    - IV. Corylus ........................................... 156
      - Species of Corylus ................................ 156
      - Discussion .......................................... 169
    - V. Ostrya ............................................. 171
      - Extant Species of Ostrya ......................... 171
      - Fossil Species of Ostrya ......................... 180
    - VI. Ostryopsis ........................................ 181
      - Species of Ostryopsis ............................ 182

**CHAPTER V. SPECIAL PROBLEMS WITHIN THE BETULACEAE** ... 185
Relationships within the Family .......................... 185
Morphological Considerations as a Result of this Study ................. 188

CHAPTER VI. SPECIES STUDIED FROM OTHER FAMILIES ............ 190

1. Aceraceae ............................................. 190
2. Fagaceae .............................................. 192
3. Hamamelidaceae ...................................... 195
4. Juglandaceae ........................................ 196
5. Salicaceae ........................................... 197
6. Tiliaceae ............................................... 197
7. Ulmaceae .............................................. 198

CHAPTER VII. CONCLUSIONS: A CRITIQUE OF THE METHOD AS APPLIED TO BOTANY AND PALYBOTANY .......... 200

BIBLIOGRAPHY ............................................. 206

APPENDIX A. Translation of Bianconi's venation classification, taken from his work titled Sul Sistema vascolare delle Foglie, considerato come Carattere distintivo per la Determinazione delle Piantine. .............. 216

APPENDIX B. Translation of Leopold von Buch's classification of veins taken from his article titled Über Blattvenen und die Gesetze ihrer Verteilung. ...................... 221

APPENDIX C. Translation of part of von Ettingshausen's Bericht über das Werk "Phylyotypia Plantarum Austriacarum". ......................... 223

APPENDIX D. Partial translation of a significant part of von Ettingshausen's work titled Die Blatt-Strukturen der Arten, eine Vorarbeit für Interpretation der Pflanzenreste. .................. 225

APPENDIX E. Translation of Konstantin F. Ritter von Ettingshausen's Die Blatt-Skelete der Dikotylen mit besonderer Rücksicht auf die Untersuchung und Feststellung der fossilen Pflanzenreste. .............. 228

APPENDIX F. List of Abbreviations used in Charts 1a, 1b, 2, 3, 4, 5, and 6 .................................. 248
LIST OF ILLUSTRATIONS

I. PLATES

<table>
<thead>
<tr>
<th>Plate</th>
<th>Following page</th>
</tr>
</thead>
<tbody>
<tr>
<td>I.</td>
<td><em>Alnus cordata</em> ................... 55</td>
</tr>
<tr>
<td>II.</td>
<td><em>Alnus crematostogyne</em> ............. 56</td>
</tr>
<tr>
<td>III.</td>
<td><em>Alnus crispa</em> .................... 57</td>
</tr>
<tr>
<td>IV.</td>
<td><em>Alnus crispa subsp. simuata</em> ...... 59</td>
</tr>
<tr>
<td>V.</td>
<td><em>Alnus fruticosa</em> ................. 61</td>
</tr>
<tr>
<td>VI.</td>
<td><em>Alnus firma</em> ..................... 62</td>
</tr>
<tr>
<td>VII.</td>
<td><em>Alnus firma</em> ..................... 62</td>
</tr>
<tr>
<td>VIII.</td>
<td><em>Alnus firmifolia</em> ............... 63</td>
</tr>
<tr>
<td>IX.</td>
<td><em>Alnus formosana</em> ................. 64</td>
</tr>
<tr>
<td>X.</td>
<td><em>Alnus glutinosa</em> ................ 65</td>
</tr>
<tr>
<td>XI.</td>
<td><em>Alnus glutinosa</em> ................. 65</td>
</tr>
<tr>
<td>XII.</td>
<td><em>Alnus incana</em> ................... 67</td>
</tr>
<tr>
<td>XIII.</td>
<td><em>Alnus incana</em> ................... 67</td>
</tr>
<tr>
<td>XIV.</td>
<td><em>Alnus japonica</em> ................ 70</td>
</tr>
<tr>
<td>XV.</td>
<td><em>Alnus jorullensis</em> .............. 72</td>
</tr>
<tr>
<td>XVI.</td>
<td><em>Alnus sp.</em> ....................... 74</td>
</tr>
<tr>
<td>XVII.</td>
<td><em>Alnus nepalensis</em> .............. 77</td>
</tr>
<tr>
<td>XVIII.</td>
<td><em>Alnus orientalis</em> ............. 78</td>
</tr>
<tr>
<td>XIX.</td>
<td><em>Alnus rhombifolia</em> .............. 79</td>
</tr>
<tr>
<td>XX.</td>
<td><em>Alnus rubra</em> .................... 81</td>
</tr>
<tr>
<td>XXI.</td>
<td><em>Alnus rubra</em> .................... 81</td>
</tr>
<tr>
<td>XXII.</td>
<td><em>Alnus rubra var. pinnatisecta</em> ... 82</td>
</tr>
<tr>
<td>Plate</td>
<td>Scientific Name</td>
</tr>
<tr>
<td>-------</td>
<td>---------------------------------</td>
</tr>
<tr>
<td>XXIII</td>
<td>Alnus rubra var. pinnatisecta</td>
</tr>
<tr>
<td>XXIV</td>
<td>Alnus rugosa</td>
</tr>
<tr>
<td>XXV</td>
<td>Alnus rugosa</td>
</tr>
<tr>
<td>XXVI</td>
<td>Alnus temuifolia</td>
</tr>
<tr>
<td>XXVII</td>
<td>Alnus trabeculosa</td>
</tr>
<tr>
<td>XXVIII</td>
<td>Alnus trabeculosa</td>
</tr>
<tr>
<td>XXIX</td>
<td>Alnus trabeculosa (?)</td>
</tr>
<tr>
<td>XXX</td>
<td>Betula alnoides</td>
</tr>
<tr>
<td>XXXI</td>
<td>Betula chinensis</td>
</tr>
<tr>
<td>XXXII</td>
<td>Betula corylifolia</td>
</tr>
<tr>
<td>XXXIII</td>
<td>Betula ermanii</td>
</tr>
<tr>
<td>XXXIV</td>
<td>Betula insignis</td>
</tr>
<tr>
<td>XXXV</td>
<td>Betula japonica var. szechuanica</td>
</tr>
<tr>
<td>XXXVI</td>
<td>Betula lenta</td>
</tr>
<tr>
<td>XXXVII</td>
<td>Betula luminifera</td>
</tr>
<tr>
<td>XXXVIII</td>
<td>Betula lutea</td>
</tr>
<tr>
<td>XXXIX</td>
<td>Betula sp.</td>
</tr>
<tr>
<td>XL</td>
<td>Betula maximowiczii</td>
</tr>
<tr>
<td>XLI</td>
<td>Betula nana</td>
</tr>
<tr>
<td>XLII</td>
<td>Betula nigra</td>
</tr>
<tr>
<td>XLIII</td>
<td>Betula papyrifera</td>
</tr>
<tr>
<td>XLIV</td>
<td>Betula papyrifera</td>
</tr>
<tr>
<td>XLV</td>
<td>Betula papyrifera var. occidentalis</td>
</tr>
<tr>
<td>XLVI</td>
<td>Betula papyrifera var. subcordata</td>
</tr>
<tr>
<td>XLVII</td>
<td>Betula populifolia</td>
</tr>
</tbody>
</table>
Plate Following page
XLVIII. Betula pubescens ................. 118
XLIX. Betula pumila .................... 120
L. Betula utilis ....................... 121
LI. Betula utilis var. sinensis ............ 123
LII. Betula verrucosa ................... 124
LIII. Carpinus betula ................ 131
LIV. Carpinus caroliniana ............. 133
LV. Carpinus erosae .................... 136
LVI. Carpinus fargesiana ............... 139
LVII. Carpinus henryana ............... 140
LVIII. Carpinus japonica ............. 141
LIX. Carpinus kweichowensis ........... 142
LX. Carpinus laxiflora ................. 143
LXI. Carpinus londoniana .............. 146
LXII. Carpinus monbeigiana .......... 147
LXIII. Carpinus orientalis ........... 148
LXIV. Carpinus turczaninowii ......... 149
LXV. Carpinus turczaninowii .......... 149
LXVI. Carpinus viminea ............... 151
LXVII. Corylus americana .............. 156
LXVIII. Corylus avellana ............... 157
LXIX. Corylus columna ................ 159
LXX. Corylus cornuta ................. 160
LXXI. Corylus cornuta var. californica 161
LXXII. Corylus cornuta var. tracyi .... 162
<table>
<thead>
<tr>
<th>Plate</th>
<th>Following page</th>
</tr>
</thead>
<tbody>
<tr>
<td>LXXIII</td>
<td>Corylus heterophylla</td>
</tr>
<tr>
<td>LXXIV</td>
<td>Corylus heterophylla var. sutchuensis</td>
</tr>
<tr>
<td>LXXV</td>
<td>Corylus rostrata var. mandshurica</td>
</tr>
<tr>
<td>LXXVI</td>
<td>Corylus tibetica</td>
</tr>
<tr>
<td>LXXVII</td>
<td>Ostrya baileyi</td>
</tr>
<tr>
<td>LXXVIII</td>
<td>Ostrya carpinifolia</td>
</tr>
<tr>
<td>LXXIX</td>
<td>Ostrya guatemalensis</td>
</tr>
<tr>
<td>LXXX</td>
<td>Ostrya knowltonii</td>
</tr>
<tr>
<td>LXXXI</td>
<td>Ostrya knowltonii</td>
</tr>
<tr>
<td>LXXXII</td>
<td>Ostrya rehderiana</td>
</tr>
<tr>
<td>LXXXIII</td>
<td>Ostrya virginiana</td>
</tr>
<tr>
<td>LXXXIV</td>
<td>Ostryopsis davidiana</td>
</tr>
<tr>
<td>LXXXV</td>
<td>Ostryopsis davidiana</td>
</tr>
<tr>
<td>LXXXVI</td>
<td>Acer carpinifolia</td>
</tr>
<tr>
<td>LXXXVII</td>
<td>Hamamelis virginiana</td>
</tr>
<tr>
<td>LXXXVIII</td>
<td>Tims alata</td>
</tr>
</tbody>
</table>
## II. FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Following page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Idealized diagram to illustrate the Principal Features found in Leaves of the Betulaceae</td>
</tr>
<tr>
<td>2.</td>
<td>Reproductions of Lesquereux's Original Figures (1883) of <em>A. corrallina</em> Lesq. and <em>A. carpinoides</em> Lesq.</td>
</tr>
<tr>
<td>3.</td>
<td>Drawings arranged to illustrate Changes in the Configuration of Loops and External Veins</td>
</tr>
<tr>
<td>Chart</td>
<td>Description</td>
</tr>
<tr>
<td>-------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>1a.</td>
<td>A Chart for the Determination of the Species of <em>Alnus</em></td>
</tr>
<tr>
<td>1b.</td>
<td>A Chart for the Determination of the Species of <em>Alnus</em> (cont)</td>
</tr>
<tr>
<td>2.</td>
<td>A Chart for the Determination of the Species of <em>Betula</em></td>
</tr>
<tr>
<td>3.</td>
<td>A Chart for the Determination of the Species of <em>Carpinus</em></td>
</tr>
<tr>
<td>4.</td>
<td>A Chart for the Determination of the Species of <em>Corylus</em> and <em>Ostryopsis</em></td>
</tr>
<tr>
<td>5.</td>
<td>A Chart for the Determination of the Species of <em>Ostrya</em></td>
</tr>
<tr>
<td>6.</td>
<td>A Chart for the Determination of the Species of the Betulaceae</td>
</tr>
</tbody>
</table>
INTRODUCTION

Purpose. - The primary purpose of this study is to present a description of the venation characteristics of the living Betulaceae (birch family), with the hope that it will be found useful to the paleobotanist in his investigations of late Mesozoic and Cenozoic floras. It is not a study of all members of this family, and the results set forth are only provisional, and should serve to emphasize the need for further studies of this kind.

Difficulties in paleobotany. - Paleobotany is beset with problems of many kinds. Several of these problems, including those with which this study is concerned, should be pointed out.

Ward (1885) referred to these difficulties when he wrote:

Paleobotany is a science of the nineteenth century. Never the less its dawn at the beginning of this century was preceded by a long fading twilight extending entirely through the eighteenth....It has as yet scarcely entered into the full light of day. (p. 368).

Chaney (1938) exposed the root of these problems when he wrote:

A paleobotanist must depend upon knowledge of existing vegetation for many of his fundamental conclusions. His procedure must be in the best accord with the practices of the botanist, whether it involves the taxonomic, the ecosystemic, or the distributional aspects of his study. He must combine at all times the point of view of the botanist with that of the geologist. (p. 371).
The most obvious of the paleobotanist's troubles was discussed early by Lindley and Hutton (1831-33):

Unfortunately, Fossil Botany is beset with difficulties of a peculiar character. The materials that the enquirer has to work upon, are not only disfigured by those accidents to which all fossil remains are exposed in common, but they are also those which would, in recent vegetation, be considered of the smallest degree of importance. There is, in most cases, an almost total want of that evidence by which the botanist is aided in the examination of recent plants; and not only the total destruction of the parts of fructification, and of the internal organization of the stem, but what contributes still more to the complexity of the subject, a frequent separation of one part from another, of leaves from branches, of branches from trunks, and if fructifications be present, of even it from the parts of the plant on which it grew, so that no man can tell how to collect the fragments that remain into a perfect whole. For it must be remembered, that it is not in Botany, as in Zoology, where a skilful anatomist has no difficulty combining the scattered bones of a broken skeleton. In Botany on the contrary, the component parts of both foliage and fructification are often so much alike in outline, which is all that the Fossil Botanist can judge from, as to indicate almost nothing when separated from each other, and from the axis to which they appertain. It is only by the various combinations of these parts that the genera and species of plants are to be recognized, and it is precisely these combinations that in fossils are destroyed. (pp. vii-viii).

Or, in the view of Gardner (1879), another English paleobotanist:

Botanists, when consulted have very often, unintentionally no doubt, deterred collectors from taking any further interest in fossil leaf forms by the emphatic stress they have laid upon the variation to which leaves belonging to the same species of plant are subject, and upon plants widely separated in a natural classification having the same form of leaf. Intending students have been led to think that leaves may not be separated into species when they are dissimilar in form, nor united in one when similar. Surely, however, it does not follow that, because the task is difficult, nothing should be attempted. (pp. 4-5).

Scott, (1926), reflects the pessimistic viewpoint of some botanists:

From a leaf alone accurate specific determination appears to be impossible. (p. 408).
Two problems, then, have already been mentioned: that of the separation of the parts of a plant, and that of similarity of leaf form in unrelated species along with variation in the leaf form of a single species. The former problem cannot be resolved; but the latter, in some measure, can. Gardner, in a continuation of his discussion, offers his suggestions:

However great the difficulties may be in determining these fossil plants from the isolated organs which alone for the most part we possess, the task is certainly not altogether hopeless. Fortunately we are not altogether dependent upon leaves, but have large series of seeds and fruits as well, and even occasional flowers to assist us.... But even where we have nothing but detached leaves to deal with, much may be done. Many plants can be recognized by the form of the leaves, still more by the venation, and their determination is more certain when the texture is preserved. The latter is of great importance; for instance, the leaves of a species of Nettle and of a Cinnamon have the same venation and form, yet owing to the difference in their texture, they could, even if fossil, hardly be mistaken.... Even the leaves of those plants which vary much can generally be recognized, if a large series be examined, by their venation, though in outline they may be quite dissimilar. The question is not, however, whether some plants so vary that it is impossible to determine them from their leaves, but it would be important to determine whether the species of the living genera to which these fossils have been referred are so variable. The habit of collecting and attentively examining fossils from deposits of one age, if extended over many years, induces so great a familiarity with their peculiarities of texture and aspect that they become easily recognizable by minor differences, which would escape even a botanical specialist who passed them under examination for the first time. (p. 5).

This problem of variability among the leaves of a species is one of the most vital problems facing the paleobotanist in his work. However, the problem is not confined to the paleobotanist alone.

The related problem of similar venation form in unrelated species has been at the roof of many misidentifications of fossil leaves. One well-known case is that of the confusion between *Cinnamomum*, a tropical
species, and Philadelphus, a temperate species. Many of Heer's misidentifications (1856, 1871) are due to such confusion. This problem has caused botanists to believe that paleobotany is an unreliable science, an attitude which has discouraged more workers from entering the field.

A third problem is closely related to that of the confusion of identical appearing forms in different species. The third problem is this: it is almost impossible for one man to know all of the leaf variations found within the plant kingdom. Paleobotanists have tried to learn the variations within so many plant families that no single family is sufficiently well known for all of its genera to be identified with absolute certainty. A remedy for this problem is for paleobotanists to become specialists in groups of families. The problem is well illustrated by the following example. Opposite impressions of the same fossil leaf (the cast and the mould) have been described as different species and even different genera. This points up clearly the lack of knowledge of the fundamental details of leaf venation.

Another problem is that modern species are usually compared with and related to fossil species. Thus the ecology of the modern plant is projected backwards to the fossil plant. Conclusions concerning the ecology of a fossil plant reconstructed by comparison with the ecology of a modern related plant, are sometimes tenuous because the assumption is made that the present is the key to the past, and often insufficient allowance is made for the possibility of a changed physiology or habitat through time. It is certain that the present is not always the key to
the past. It is dangerous to assume, as do some Cenozoic paleobotanists, that the communities of plants living today represent communities which lived together in the past, and that to reach their present habitat, they migrated en masse from their former habitat to their present one. Today, one can scarcely read a paper on Tertiary paleobotany without imagining myriads of plants engaged in a relentless march, either to the north or south, or up and down mountain slopes.

Related to this is a discussion by Cain (1947):

"...An interest in evolution has given paleontological taxonomy a meaning and dynamism....The introduction of the ecological point of view and method...has added further interest and possibilities to the attempt to interpret the story of the past. Topographic, climatic, vegetational, and animal history can be better reconstructed by addition of the paleoecological method than from a wholly geological approach. Much of the method hinges on the very important ability to recognize in modern floras the species that are equivalent to or nearly like those represented by the fossils....The paleoecologist reads from the fossil backward in the causal sequence suggestions as to the community which it represented, the climate which controlled the community, and the topography which controlled the climate. He reads forward from the plant fossil to its probable animal associations in the biome, because of their close food and shelter relations.

A false reference to subtropical species in a fossil flora, which is otherwise temperate...results in conclusions which are entirely false. The false assignment of certain fossils to subtropical genera in far-northern floras (Greenland, Spitsbergen) has caused the supposition that a subtropical climate existed at very high latitudes. This in turn has played a role in theories concerning the migration of the North Pole, in theories of continental drift, of oceanic continuities and of land bridges. The paleoecological method requires not only a wide familiarity with fossils and geology, but familiarity with modern plants, especially with modern vegetational types.

...Sometimes ecologically diverse plants have leaves which resemble one another. The paleoecologist must search
for those plants which not only resemble the fossil morphologically but match in the minute details of shape, texture, venation, etc., and which, above all, present no great ecological disharmony with the major composition of the fossil flora. The paleoecological method, it must be emphasized, opens up tremendous possibilities for the correct interpretation of history, but it also requires extreme care in the identification of fossils and their reference to modern types. This is the greatest single source of error and limitation of the method.

...The method is essentially inapplicable beyond the Tertiary (or Upper Cretaceous, at the most) because modern vegetations are so different taxonomically and in community structure. Down through the Cenozoic the method becomes increasingly accurate until in the Pliocene and the Pleistocene its conclusions may be drawn both finely and with great accuracy....

The possibility of a changed physiology (ecology) without a detectable morphological change should be kept in mind when conclusions are being made with respect to the significance of an element in a fossil flora. (pp. 35-37).

It is difficult to determine the exact meaning of the term element as used in the literature today. Cain seems to mean by element a constituent of a fossil flora. This varies somewhat from von Ettingshausen's original definition (1873):

Therefore, one may interpret the Tertiary flora, consistent with the living flora, as a mixed stock-flora, and split it into its component parts. These are called floral elements. Thus, by floral elements, I mean the sum total of all fossil plant forms whose present-day analogies belong to a naturally exclusive floral province. (p. 221).

Chancy (1924) presented a similar definition:

...definitions and a classification have been devised. A fossil flora may be broken down into elements whose living equivalent species are found in association at the present time. An element may be defined as a group of fossil plants whose modern related species occupy a major geographic and climatic province. It is essentially the equivalent of a plant formation as defined by Weaver and Clements..., or of the climax community. (pp. 6-7).

Thus, it is common parlance among paleobotanists to speak of the Western American Element, et cetera, in their discussions of fossil
floras. This points up the problem mentioned before, that it is
dangerous to assume that such elements or communities have remained
intact without appreciable change over long periods of time, and that
they have migrated in toto from place to place. Conversely, the pres-
ence of mixed fossil floras (with two or more elements) does not mean
that these two actually mingled together in life.

Another major problem confronting the paleobotanist is that of
age correlations of strata by means of plants. Plants are first of all
indicators of habitat conditions. A trip across the ranges on the Santa
Cruz Peninsula (San Francisco Peninsula) will emphasize this. Chaparral
and live oak associations live side by side, along with the isolated
remnants of the Redwood forest; yet none of these communities mingle to
any great degree. If leaves of all of these plants were found in a
single sedimentary deposit today, what kind of a plant community would
be constructed on the basis of the plants present? Gardner (1879) dis-
cusses this problem, too, when he writes:

In arriving at our decisions respecting the comparative ages
of isolated floras, besides taking into consideration those dif-
fferences which are most likely to be present when they are widely
separated, either by latitude or longitude, we must make allow-
ance for local causes which influence and even change the charac-
ter of neighboring floras at the present day....Plant-remains
from argillaceous, and arenaceous soils would more or less differ.
Limestones, serpentine, and basalts have distinctive plants. Peat
and soil impregnated with saline matters nourish plants that are
markedly dissimilar. Local differences in climate, such as are
caused by the prevalence of certain winds, excess of moisture,
proximity to mountain ranges, or to sea-currents of different
temperatures, exert a powerful influence on vegetation. Diff-
ferences of altitudes, it is well known, make almost as much change
in each foot vertically as in miles horizontally. Some of these
conditions have no doubt modified the floras to be described.
(p. 6).

Axelrod (1945) has described totally different fossil floras
found within two miles of each other in the same stratigraphic horizon. Von Ettingshausen (1869, 1861) has noted mixtures of temperate and tropical floras in various deposits of southern Europe. He explained these on the basis of vertical plant zonation in adjacent mountain ranges, but later (1874) abandoned this more probable hypothesis in favor of that of a cosmopolitan and undifferentiated flora. The fossil evidence for a former more widely distributed flora was the subject of a paper by Gray (1875), wherein he explains present day disjunctions and limitations of plant families which were once widespread groups by the onset of continental glaciation during the Pleistocene. Paleobotanical literature is replete with examples of mixed floras and explanations for them.

Connected with these problems is the future problem of distinguishing lowland from upland floras in the fossil record. As Gardner noted in a passage quoted earlier, a vertical change of 5000 feet is almost the same as a horizontal north-south change of 5000 miles. The Sutro flora, preserved in volcanic rocks near Virginia City, Nevada, is a good example. This flora exhibits certain temperate characteristics which one may attribute to (1) the possibility that the temperate zone, or a portion of it, included the area in the time during which the deposits were formed, or (2) the possibility that we are dealing here with an upland or montane flora above a sub-tropical flora. The latter possibility, in this case, seems fairly sound when one considers the many hundreds and even thousands of feet of continental volcanic beds lying below the deposit containing the Sutro flora.
Unfortunately, in many large areas of the western United States, age correlations can be made only by the use of plants, though vertebrate fossils may sometimes be present to help. But when one deals with plants alone, he is faced with an extremely intricate and complex problem. Chaney (1936) and Axelrod (1949) discuss this question at some length. By means of correlation of marine with continental deposits, the times in which various climatic zones occupied different parts of the Northern Hemisphere may be established. In this way, depending upon latitude, longitude, and estimated elevation, plant localities in areas isolated from marine deposits may be dated.

To consider an example, if tropical plant forms were found in continental beds in central California, the age would be designated as Eocene, because beds containing tropical plants intertongue with Eocene marine strata elsewhere. If there were more subtropical components, the flora might be called Oligocene, and if the flora in the same region were wholly moist-temperate, the age, based on these assumptions, might be considered Miocene or even Lower Pliocene. The dangers inherent in such a method are apparent, for one must assume a uniform migration rate over a long period of time without allowing for any major regression in climate. Axelrod (1950) attempts to establish a dating scale for Great Basin floras by this means. It is significant that where vertebrate or invertebrate fossil evidence is present, it is this evidence which is followed.

Still another difficulty is that of heterophyly in leaves of the same species. This problem may be illustrated by the following
examples.

In the case of the Quinaceae, studied by Foster (1950a, 1950b, 1951), the seedling leaves of Quina acutangula Ducke are pinnately lobed leaves, while the adult leaf is simple and entire. A second example is that of Populus dimorpha T.S. Frantsjey. This species inhabits Sonora and Sinaloa. Stump sprouts and seedlings have linear-lanceolate leaves similar to those of Salix (willow). The slowly growing branches of the adult tree have the ovate-deltoid form of the cottonwood. Seen as separate trees, they would never be considered the same species. Still a third example is that of Corylus heterophylla Fisch., a hazel from China. On the same branch of the same tree, both obdeltoid and ovate leaves may be observed (Plate LXXIII). Found as fossils, they would doubtless be described as different species.

One final problem is this: the assumption is often made that a fossil flora represents proportionately the woody plants which actually lived in that area. For example, Corylus cornuta californica (Corylus rostrata californica), a common species of the present Redwood forest, is seldom found as a fossil. This is due to the fact that the leaf is easily destroyed. Chaney (1936) points this out:

Among shrubs and vines there are likewise many, with leaves close to the ground, or structurally unsuited to preservation. Among these may be mentioned Corylus rostrata Aiton and Rhododendron occidentale Gray, both of which are abundant undershrubs in the modern redwood forest, but which are rarely preserved in the fossil record. (p. 379).

In conclusion, eight major problems have been discussed. These are only a few of the many which confront the paleobotanist. Many of
these very problems are encountered in the Betulaceae. The genus Alnus is confused with Betula, and some species of Betula with Carpinus. Carpinus is easily mistaken for Ostrya, and Ostrya, Ostryopsis and Corylus may all be mistaken for each other. This study will attempt to straighten out these confusions, and to place paleobotanical identifications upon a more sound basis.

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CHAPTER I

HISTORY OF VENATION STUDIES

Paleobotanists, because they have had almost no choice, have for many decades used the leaf as a taxonomic tool. Botanists, on the other hand, with a few recent exceptions, have regarded the leaf as of little value in taxonomic work.

Two reasons are chiefly responsible for the apathy on the part of botanists to use venation in taxonomic studies. First, the mistakes of paleobotanists in leaf identifications discouraged many botanists from attempting similar studies of living leaves. Second, the invention of the microtome as a biological "weapon" centered interest on sections of plant and animal parts, rather than on external features.

Interest in leaf venation dates back to the time of Theophrastus (ca. 287 B.C.). But it was not until Ulisse Aldrovandi published his book Museum Metallicum in 1610 that leaves began to be studied for their taxonomic value. In this volume, Aldrovandi identifies at least one fossil leaf by means of venation.

Sixty-nine years later, Johann Jacob Scheuchzer, author of the Noachian deluge concept to explain the existence of fossils, published his famous Herbarium Diluvianum in Zurich. In this work he bases the identification of several fossil leaves, including a specimen of Populus nigra, upon characters of leaf shape and leaf margin. He refers
another plant to the genus *Plantago* on the basis of leaf venation.

Ernst F., Baron von Schlotheim, and Kaspar Maria, Graf von Sternberg made numerous fossil plant identifications based upon leaf venation. It was Adolphe Brongniart, the so-called "Father of Paleobotany", who first explicitly emphasized the importance of venation in leaf identification. He wrote (1828):

> Among leaves, the disposition of the nerves, which indicates to us the proper framework of the organ, furnishes us the most essential criteria for distinguishing between them, and for determining the families to which they belong. (p.13).

Augustin de Candolle (1827) first initiated a classification and terminology of venation. Bianconi (1838) established another system of classifying leaves according to venation (Appendix A). His ideas are so advanced for their day that they will be discussed at length.

Bianconi posed five questions concerning leaf venation. Had his answers to these questions been given the attention they deserved, paleobotany today might be one century ahead. His five questions are:

1. Of what value is the character of the leaf margin?
2. Are the attitudes of the veins always uniform in every leaf of the same species?
3. Are these differences valuable in distinguishing one species from another?
4. In a genus or a family, is there a type which all of the species of the genus or family follow after?
5. Is it possible to establish a distribution within the genus or family based upon the relationships of the veins, which will have as its object the recognition of genera? Is the species as conceived in botany stable? (p. 376).

These five queries question the very roots of scientific dogma in Bianconi's day. His answers are even more startling when the
scientific thought of his time is taken into account.

Regarding the first question which concerns the value of the leaf margin as a taxonomic character, Bianconi replies that the value of the margin is difficult to estimate because margins are so variable in their configuration.

In the second question, Bianconi concludes that the midrib is the most constant vein within a species, but that other major veins are hopelessly variable. In this respect, he is more nearly correct than either his predecessor Brongniart or his successor von Ettingshausen.

In answer to the third question, as to whether or not venation differences are valuable for distinguishing one species from another, Bianconi concludes that in the tertiary and lesser veins, i.e., the minor venation, there are probably sufficient characters for species determination. This statement seems to be prophetic in the light of recent work by Foster.

The fourth question is whether or not all species in a genus possess a recognizable type. Bianconi answers, in effect, yes or no, depending upon the family. The truth of this statement, too, has only recently emerged in the literature.

The final question is whether or not a key can be established for the recognition of species based upon leaf characters. He answers that in his day, no, but that ultimately, it is probable. He states further that the paleobotanist must become acquainted with all variations of leaves in the plant kingdom if his identifications are to be correct.

After Bianconi, two other botanists, Mirbel and Link, around
1840, established classifications of venation, but none had the facility of Bianconi's. In 1846, Achille Richard published a large and cumbersome scheme for classifying veins. Again, in 1848, Lindley came forth with another complex classification.

Leopold von Buch (1852), for the first time, offered a new and streamlined classification (Appendix B). It was soon followed by the classification of von Ettingshausen (1861, Appendix E). Von Ettingshausen divided leaves into 7 major types, based upon von Buch's original 14 types. In this study, von Ettingshausen's terminology is used almost in its entirety.

Though von Ettingshausen is infrequently cited in modern paleobotanical literature, I would venture to state that above all others, he stands as the greatest pioneer in the field. He conceived comprehensive studies of fossil and living floras (1856a and others); he early utilized a crude but effective means of printing and studying leaves in their minutest details; and he originated much of the paleobotanical thought which, only today, is becoming standard paleobotanical theory. It is strange that few paleobotanists appear to realize their indebtedness to von Ettingshausen.

Thus ended the "classical" era of leaf venation studies. After von Ettingshausen's time, studies of external leaf form were all but forgotten.

Studies of leaf phylogeny became the next principal object of study. Charles Darwin unconsciously did his share in causing men to forget the fact that systematic descriptions come before scientific theorizing. Casimir de Candolle speculated upon leaf origins in 1868,
Frantl in 1883, Kern in 1896, Schuster in 1906 and 1910, Agnes Arber in 1918 and Bitter in 1929. This emphasis on leaf phylogeny may still be noted in the theories of H. J. Lam (1938) and in Arber's recent book (1955).

Despite the interest in leaf origin, some systematic venation studies have been made, e.g., the studies of stipule venation, bract and bracteole venation by Müller (1911), comparative studies of flower and leaf venation by Glick (1919) and Unruh (1941). Interest in evolution inspired studies by Schuster (1910) and Priestley and Scott (1937). A systematic description of venation in the monocotyledonous family Arecaceae was written by.eth (1932). Special phases of venation and leaves have been studied by Schüpp (1919), Kirchheimer (1926), Schröter (1935), and Troll (1938, 1939). Relationships between veins and reviews of methods of studies of venation may be found in the writings of Schmidt (1869), Garner (1877), de Cary (1894), Kern (1895), Zeiller (1900), Father (1907, 1908), Walton (1923, 1935, 1940) and Goebel (1922). There are other treatises as well. Work on the scale of that by von Kittingenhausen has not been done since his death.

Foster (1946, 1947) published two papers on the structure of terminal sclereids in Fournire. This marked the beginning of a modest, but definite renewal of interest in leaf venation studies. Though terminal sclereids had been studied before (Pirwitz, 1931), their possible use in taxonomy had not been realized.

Again, in 1950 and 1951, Foster published three papers on leaf venation in the Quinaceae. The peculiarities of venation found in this tropical family were so distinctive that studies were launched into
several families. Kasapligil (1950) and Pires (1950) noted distinctive types of venation in their studies. Thomas Pray at the University of California is studying the Rubiaceae and other families. The present study is a continuation of the type of work which von Ettingshausen started, using the techniques developed by Foster.
CHAPTER II

TECHNIQUE AND SAMPLING METHODS

The technique used is one developed by Foster (1950c). For the benefit of those persons wishing to use this method, and because it is one which has scarcely been utilized, it will be discussed in detail.

Foster's paper wherein he describes this method is worth quoting:

The difficulties of correctly determining and classifying the fossil leaves of angiosperms present serious problems to the paleobotanist. Comparisons with extant species based solely on leaf form are often misleading because of the polymorphism of the foliar organs in many plants. On the contrary, a precise and scientific approach to the problem requires a search for more critical diagnostic structural features which are likely to be evident in fossil material. One of such morphological characters is the foliar venation. But the proper use of this character for diagnostic purposes in turn depends upon a comprehensive knowledge of the types and degree of variation in the venation patterns of living angiosperms. Since unfortunately this subject has never been broadly explored by the morphologist, there is a great need for assembling extensive collections of permanent slides of venation patterns of a wide range of angiospermous genera. Such "slide herbaria" would prove invaluable to the paleobotanist in his difficult task of interpreting and classifying fossil leaf specimens. The successive steps in the technique used by the writer for studying venation patterns may be briefly summarized:

1. Clearing in 5% NaOH. Small leaves may be cleared in toto; large leaves should be subdivided to include representative portions of the venation. Removal of the pigments with heat provided by an electric oven (250°C) requires but a few days for many objects. Preliminary bleaching with "Eau de Javelle", followed by NaOH, may be necessary in some cases.
(2) Dehydration. After thorough washing in distilled water, the material is dehydrated in successive grades of alcohol (50%, 95%, 100%).

(3) Staining. A 1% solution of safranin, composed of equal volumes of alcohol and xylene, yields consistently good results. Sufficient staining is rapidly accomplished (10-20 minutes) and destaining is secured by either a mixture of absolute alcohol-xylene, or acidified alcohol. (For other stains valuable for cleared leaves cf. MORLEY in Stain Technology, 24, pp. 231-235, 1949). When satisfactory differentiation of the vascular system is attained, place the specimens for 15-30 minutes in pure xylene.

(4) Mounting. "Clarite", because it dries rapidly, is recommended in preference to Canada Balsam. The use of large slides and cover glasses (7.5 x 5 cm.) permits mounting of entire small leaves or generous portions of larger organs. Place slides on an electric slide warmer until they are thoroughly dry.

In the leaves of the Betulaceae, clearing was facilitated by the use of a 6% solution of NaOH. Only one leaf should be cleared in each solution of NaOH. The average clearing time of 310 betulaceous leaves was 5.7 days (Range: 1.1 - 13.3 days) at 32°C. There was a tendency for leaves of Carpinus and Ostrya to clear more rapidly. Leaves of Alnus and Corylus cleared less perfectly than the leaves of Carpinus and Ostrya. Leaves of Ostryopsis and Betula were intermediate. Because the leaves generally cleared from the margin to the center of the leaf, the margins became very delicate, and in Corylus often disintegrated totally. This latter fact is probably connected with the scarcity of Corylus in the fossil record. Imperfections and white areas in the leaves in the photographic plates represent uncleared portions.

The leaves were placed in distilled water for 10 minutes. If the leaf has not been completely cleared, it may be found advantageous to place it for 10 minutes each in two or more baths of distilled water.
so that the 50% alcohol solution will not be discolored too rapidly. It was found that if the leaves were well cleared, the 50% alcohol solution could be used from 10 to 12 times. Leaves should be kept in this solution for a minimum of 15 minutes.

The 95% solution also was used 10 to 12 times, for periods of no less than 15 minutes. The 100% alcohol solution was never used more than 6 times. The leaves remained in this solution for 20 minutes. If left longer than 45 minutes, they became hard and difficult to manipulate.

Satisfactory staining was accomplished in from 15 to 45 seconds, depending upon the leaf. However, a period of 10 minutes in the staining solution will not harm the leaf. Depending upon the length of time the leaf is kept in the safranin solution, the destaining process in xylene-alcohol will last from 20 to 40 minutes until the desired degree of coloration is produced. One safranin staining solution was used for 130 specimens without noticeable effect upon the solution.

The xylene-alcohol destaining solution was discolored rapidly by transfer of specimens from the staining solution to it. This solution was changed every 8 to 12 specimens. The 100% solution of xylene was used 15 times. Both solutions were used for periods of no less than 20 minutes. One should never leave a specimen in either solution for over an hour because in the destaining solution, the leaf will lose all color, and in the xylene solution, the leaf will become so brittle that it will be impossible to mount beneath a cover glass. This is especially true with more xerophytic types of leaves.
It may be found desirable to add a second 100% xylene step, because the first becomes too discolored by excessive use. This final 100% xylene step will insure that all of the alcohol is removed; otherwise upon contact with the moist air, the alcohol, xylene, and water from the air will react to form a precipitate which clouds the leaf.

In all cases, the more expensive toluene may be substituted for xylene.

Clarite was the best mounting medium used in this study, though it is now unobtainable. Canada Balsam should not be used because in time it will yellow and crack. Instead, piccolyte was the plastic most commonly used. It has a faint yellowish-orange color. Harleco synthetic resin may also be used. The latter required the longest time to dry, so, after Canada Balsam, is the least desirable.

Slides were placed upon an electric slide-warming plate set at 47°C for a period ranging from 5 to 10 days, depending upon the thickness of the plastic on the slide. In no case was a slide removed before 5 days. All slides must be kept flat for many months, because the plastics take that long to dry completely.

The ease of this method compares very favorably with the cruder methods used by von Ettingshausen and his contemporaries. Von Ettingshausen (1861, 1863) in the so-called "Naturselbstdruck" method, placed a dried leaf upon a very thin lead plate. A hard metal roller was then rolled over the leaf on the thin lead plate. The impressions of the veins were stamped into the lead plate, and this plate was used to make
positive-relief plates for printing purposes. Despite its drawbacks, the results of this method are remarkably good. Pokorny (1856) used a book-press to stamp out the leaf impressions into the thin lead plate. This avoided the use of a roller which would tend to deform the leaf. Pohl (1857) developed a crude self-photographic method wherein leaves were placed on sensitive paper in a heliotype, thus producing a self-photograph.

Three hundred and thirty-two individuals of the Betulaceae, selected from herbarium sheets of the Dudley Herbarium of Stanford University and from the University of California Herbarium, were studied.

Specimens were taken of each taxon in each herbarium. Loose leaves were found on almost every sheet. Because all sheets could not be sampled for lack of time, specimens were selected so that a wide geographic distribution might be obtained. The size of the leaves chosen varied, but the majority were found to fit easily into 2 in. by 3 in. slides without cutting into halves or quarters.

The photographs show as many leaves as possible to illustrate the text. They were made by projecting the slides onto photographic paper in a standard enlarger.

Winkler's monograph (1904) on the Betulaceae and his revision of *Carpinus* (1914) were used as standard references. Other references were supplementary.

Of the 16 species of *Alnus* recognised by Winkler, 13 were examined. In addition, more recently described species, and several varieties, making a total of 26 taxa, were studied.
Of the 37 species of *Betula* listed by Winkler, only 20 were studied. However, the major variations within the genus were examined, and in some cases, other species were examined briefly in order to test the identification methods established. Including varieties, 25 taxa were studied.

Of the 18 species of *Carpinus* listed by Winkler, 12 were studied. In all, 19 taxa were examined.

Five of the 8 species of *Corylus* recognized by Winkler were studied. Twelve taxa in all were examined.

Winkler lists only 2 species of *Ostrya*, but this is not believed to be correct by the majority of taxonomists. In all, 6 taxa were examined in the present work.

Winkler lists 1 species of *Ostryopsis*. Two species and 1 variety are now recognized, of which only the 1 listed by Winkler was available for study.

In summary, of the perhaps 140 taxa in the Betulaceae, many of which are varieties, 90 were studied. The majority of the forms omitted are in the genus *Betula* where I believe the major ranges in variation were covered in this study.

Regarding the value of herbarium specimens as population samples, Woodson (1947) says the following:

A false impression widely current among non-taxonomists is to the effect that herbarium specimens usually are collected because of some abnormality which attracts the fancy of the collector. The accusation reveals such prejudice that one is baffled for an effective retort. Perhaps a denial that falls far short of revealing the sincerity of a plant collector but may impress the critical outsider is the fact that plant collections habitually are made in multiplicate sets bearing identical serial numbers for purposes of sale or exchange amongst the numerous botanical institutions of the world. It would be difficult indeed for even an unusually perverse individual to pursue
his passion under such adverse circumstances. The chief
danger in plant collecting actually is that of choosing
too many "normal" specimens. The statistical errors
from such likelihood, however, should be ineffective.
(p. 36).  

Woodson continues:

The most reliable statistics concerning plant popula-
tions over a wide area must be made, not during a single
season but over a span of years, and the samples must be
randomly selected and as widely distributed as only genera-
tions of differently tempered naturalists can accumulate
them. It is possible to meet these requirements only by
the use of herbarium collections. It is not a new con-
venience: plant taxonomists have been enjoying it since
long before the birth of Linnaeus. (p. 365).  

But Stebbins (1950) has a somewhat different viewpoint:

As Woodson (1947) has pointed out, herbarium specimens
are never a random sample of the species population, since
they have been collected in great numbers near the centers
where universities and botanical gardens are located, as
well as in national parks and other points of interest,
while many intervening areas have been sampled little or
not at all. Furthermore, most herbarium specimens consist
of only a few individuals from any locality and therefore
cannot give a picture of the range of variation in a popula-
tion, a type of information which is of the utmost importance
in interpreting some of the genetic processes which may be
taking place. (pp/ 11-15).

What both men have to say is essentially true. However, I would
be more inclined to agree with Woodson.

Finally, of the 332 individuals studied, 35% were from Asia, 50%
from North America excluding Mexico, 10% from Europe, and 5% from Latin
America. An ideal distribution, based upon the number of species liv-
ing in these parts of the world would have been 45% from Asia, 25% each
from North America and Europe, and 5% from Latin America.
CHAPTER III

INTRODUCTION TO THE BETULACEAE

General

The family is composed of six genera: *Alnus* (alder), *Betula* (birch), *Carpinus* (ironwood or hornbeam), *Corylus* (hazel), *Ostrya* (hop-hornbeam and ironwood), and *Ostryopsis*. The family is confined to the Northern Hemisphere with the exception of the genus *Alnus*. This genus extends through Central America into the Andes and the deserts of northwestern Argentina, and in the Eastern Hemisphere, into southern Indonesia and Borneo.

*Alnus* and *Betula* sweep the Northern Hemisphere. *Corylus* has a disjunct distribution with a portion of the genus spread in a belt from China to Europe, and another portion confined to North America. The distribution of *Carpinus* shows three disjunct areas, one in eastern North America, one in southeastern Asia, and one in southern Europe. *Ostrya* is also disjunct, with an area in southern Europe, a more restricted area than that of *Carpinus* in southeastern Asia, and a larger area than that of *Carpinus* in North America. *Ostryopsis*, the most restricted form, is confined to interior China.

Of all the genera, *Alnus* extends the farthest south, and *Betula* extends the farthest north, into Greenland, Spitsbergen, and Novaya Zemlya.
The leaves of the Betulaceae are sufficiently distinctive so that the family is fairly easy to recognize. But the recognition of genera within the family is the most difficult problem. The distinguishing of species, especially in *Corylus*, may be quite difficult, not just for the leaf taxonomist, but also for the floral taxonomist. On the contrary, in *Carpinus*, species are relatively easy to distinguish.

A few quotations from recent paleobotanical literature will illustrate the current divergence of opinion regarding the usefulness of leaves in classification:

*Chaney (1925)*:

> Few botanists would attempt to distinguish certain species of *Alnus* from its close relative *Betula* (birch) on the basis of leaves, which are much alike in these two genera. If the fossil remains consisted only of leaves, it would probably be impossible to determine which of the two genera was represented. (pp. 7-8).

*Chaney (1927)*:

> The differentiation of *Carpinus* and the closely related genus *Ostrya*, on the basis of leaves, is a difficult matter in the case of the living trees, and an equal similarity between the leaves of these two genera may be supposed to have obtained in the Tertiary .... (p. 105).

Contrast this with *Chaney (1938)*:

> The modern botanist, with the more significant internal structures of flowers or fruit commonly available, does not often find it necessary to look for distinguishing leaf characters. As a result, he may never have observed significant differences between the leaves of *Carpinus* and *Ostrya* or between *Castanea* and *Quercus*, which the paleobotanist has been trained to recognize in the absence of other material. The student of fossil plants... recognizes distinguishing details of nervation and margin of which the average botanist is unaware. (p. 376).

When the question arises whether *Alnus* or *Betula* is represented by the leaves of a fossil flora, or whether the leaf is *Carpinus* or *Ostrya*, the presence of well preserved catkins of fruits, even though not in actual attachment, throws the weight
of the evidence on the side of the genus represented by the fruiting structure. Likewise the occurrence of generically determinable stems gives collateral evidence which will become increasingly more important when the fossil wood now available is sectioned and studied. (pp. 376-377).

Dorf (1933):

It is by no means a simple matter to separate the three modern alders of the West, *Alnus rubra* Pong., *A. tenuifolia* Nutt., and *A. rhombifolia* Nutt., on leaf characters alone. (p. 91).

I believe that this study should aid materially in showing that each of these three species is distinct in its leaf characters.

LaMotte (1936):

A scrutiny of the criteria employed by systematists to separate living material of these three species *A. rubra*, *A. sinuate*, and *A. tenuifolia* brings out the fact that the relationships are so close that leaf characters alone are valueless. (p. 118).

MacGinitie (1933):

There is no well-marked character which will serve to differentiate the leaves of *Alnus* from those of *Betula*. The result has been a great deal of confusion in the assignment of fossil forms among these genera.... (p. 50).

Condit (1938):

The reasons for calling the fossils *Betula* rather than one of these [other] genera were primarily the close match to leaves from Missoula that are associated with *Betula* fruiting material. (p. 259. Brackets mine).

In the paper just quoted, Condit was attempting to identify fossil leaves in Central California, and rests his identification on similar leaves in Missoula, Montana, 750 miles away! I examined the specimens of Condit and am able to state that they are *Betula*, but for reasons which are clearly visible in the venation.
Oliver (1936):

It is almost impossible to distinguish the leaves of Alnus and Betula. The entire lack of fruits adds to the difficulty of referring these leaves to another genus. However, the fact that Alnus is typically found in the present-day redwood forest would lead one to conclude that it is logical to refer this wealth of betulaceous leaves to the genus Alnus. (p. 19).

With these quotations, it is clear why Dr. Chaney first pointed out to me the necessity for studying this family. A new approach must be attempted if the problems in the family are to be resolved.

Terminology and definitions

In this dissertation, I propose to follow the terminology of von Ettingshausen except where otherwise indicated. For illustration of the major features which are defined, refer to Figure 1.

Veins

Primary veins. - In a pinnate leaf, the midrib is the only primary vein; in a palmate leaf, all of the major veins radiating from the leaf base are primary veins. In a sub-palmate leaf (for example, Populus), the basal radiating veins, including the midrib, may be considered as primary veins, as in the palmate leaf, or the lateral radiating veins may be considered as basal or No. 1 secondary veins as in the pinnate leaf. All leaves of the Betulaceae, even though some are almost sub-palmate, shall be considered as pinnate.

There is no genetic connotation to the terms primary, secondary, tertiary, et cetera, when referring to the veins. This classification is based upon size and mutual relationships only.

Bianconi (1838) terms the primary vein of a pinnate leaf the dorsal nerve. Kerner (1895) calls it the main strand.
Figure 1 Idealized diagram to illustrate the principal features found in leaves of the Betulaceae
Also the term costa is sometimes used.

Connecting vein. - This term is synonymous with the term midrib, and with primary vein if that vein runs from the base of the leaf to the apex. The term may also apply to secondary veins which run from the midrib to the leaf margin without looping or stopping.

Ertl's term length-nerves (1932) is a synonym for connecting vein.

Secondary veins. - In a pinnate leaf, the secondary veins are those which depart from the base of the midrib or laterally from points along the midrib. They are usually smaller in size than the basal portion of the midrib.

In this study, secondary veins are enumerated from the base to the apex of the leaf. This is justified by the fact that the uppermost secondary veins of a leaf are poorly developed and varying in position, while the lower ones are strongest, and, for the most part, constant in position, within limits. The lowest pair of secondary veins is termed basal secondary pair, basal secondaries, or the No. 1 secondaries; the next pair above these is the No. 2 secondary pair, or the No. 2 secondaries and so forth.

A reason for designating each secondary specifically is that the No. 1 secondaries have a characteristic relationship within a species to both the midrib and the leaf base. Furthermore, it is often convenient to refer to certain portions of the leaf bounded by precisely defined secondaries. Miss Jentys-Szaforowa (1950) enumerates secondary veins in the same manner, and for the same reasons.

The basal or No. 1 secondary veins may be difficult to specify on a leaf. Sometimes they are only weakly developed and may resemble
tertiary veins. However, several distinctive characters are usually present. They are roughly parallel to the No. 2 secondary veins, and are not parallel to any other order of veins. They usually extend into a marginal tooth, or else loop to join the No. 2 secondary vein above. Even if the No. 1 secondaries are not well developed in a few specimens of a species, they will be clearly evident in other specimens of that species. For the most part, there will be no difficulty in identifying them.

When the basal secondary pair is the largest pair of secondary veins other than the midrib, and when it dominates most of the area of the leaf, the leaf is then palmate. Troll (1939) says: "The size of the ...lateral nerves is different in individual leaf segments and is in general proportional to the width of the leaf segment dominated by it." (p.1081).

Troll believes that palmate venation is the result of a more rapid development of the basal one or two pairs of secondary veins.

Lindley (1848) calls the secondary veins primary veins. This usage is preferred by Jackson (1928). Lateral veins is another common term, and Oliver translates Kerner’s term (1895) for secondary veins by the words lateral strand.

Along the midrib, secondary pairs of veins are termed alternate, subopposite, or opposite.

Subsecondary veins. - Those veins, which, if present, are smaller than the secondary veins yet larger than the tertiary veins. This term, as defined here, is my own. Several types of subsecondary veins will be discussed in the following paragraphs.

External veins. - Those veins of lesser importance than the secondaries, and which depart from the secondaries distal to the midrib as branches from the hesiscopic side of the secondary veins. They are thicker than the tertiary veins, but are seldom parallel to them.
Different degrees of development of these veins may be seen in Figure 3.

External veins normally depart from the secondary veins as branches, rarely as forks. They either curve toward the margin and terminate in an intersecondary marginal tooth, or loop back to the secondary vein whence they originated. This latter case is particularly evident in Alnus nepalensis, illustrated in Drawing 7 of Figure 3, and shown on Plate XVII. External veins are one of the "trade marks" of the family.

Von Buch (1852) called these veins tertiary veins. Many modern paleobotanists call them abaxial tertiary veins because of their position on the abaxial or basiscopic side of the secondary veins. To call them tertiary veins is incorrect, because external veins (1) are not found on every leaf, and (2) are larger than true tertiary veins. If they were called tertiary veins, and, if in some leaf they were not present, the vein order would jump from secondary to quaternary without any intermediate order. Lindley (1818) used the term external vein, but more particularly for looped external veins in the sense used in this study. A non-looped or craspedodromous external vein (Drawing 2, Figure 3) would not have been called an external vein by Lindley while the looped external veins (Drawing 7, Figure 3) of Alnus nepalensis would have been so termed. Bianconi (1838) considered external veins as forks of secondary veins.

Counter-external veins. - My own term for those rare veins similar in appearance to external veins, but departing from the adaxial side of the secondary vein. These usually end in an intersecondary tooth (Drawing 3, Figure 3).

Interordinal veins. - This is a term proposed by myself for those veins which, while smaller than secondary veins, depart from the midrib parallel to the secondary veins and (a) either vanish into the tertiary and lesser network, or (b) turn sharply downward about halfway toward the
leaf margin to the next lower secondary vein. They are veins which join two other orders of veins, and are not of tertiary size at their points of origin.

The term is roughly synonymous with sub-secondary vein, as used by Axelrod, Chaney, and others. It is also approximately equal to the term intermediate vein as used by Foster (1950a), but, unlike his intermediate veins, cannot form a graded series between two secondaries. Lindley (1848) terms these veins costal veins.

Intersecondary vein. - The origin of this term is unknown. It refers to those secondary veins which reach the margin (thus is restricted in use to veins exhibiting a craspedodromous gross venation pattern), but which terminate not in the apices of marginal teeth but in recesses and sinuses along the margin. This type of vein was not observed in the Betulaceae, but is common in the Fagaceae.

Basimarginal vein. - A term proposed by myself for those veins which originate at the base of the leaf on the midrib below the No. 1 secondary veins, and which follow the leaf margin. If this vein should continue along the entire margin of the leaf, it is termed by Troll (1939) and others a marginal vein.

Loop vein. - This term refers to the ends of those secondary veins which loop upward to the next upper secondary vein. Such veins are rare in this family, but may be seen in Alnus nepalensis (Plate XVII, and Drawings 6, 7, Figure 3). When fully developed, the loop vein is a direct and unbroken extension of the secondary vein. For the various degrees of development of loops, refer to the drawings in Figure 3, and to the plates.

External veins may also be looped (Drawing 7, Figure 3). In this case, the loops are termed external loop veins.
As already stated, Lindley's term **loop veins** (1843) refers to external loop veins, and for the loops at the ends of secondaries, he uses the term **curved veins**. The common term for secondary loop veins is **loops**. Bianconi (1838) calls them **interanastomosing veins**. Kerner (1895) follows von Ettingshausen, and calls them **loop veins**.

**Tertiary veins.** - Those veins smaller than the secondary and subsecondary veins. They form the basic framework of the fine vein network or mesh extending between secondary veins, between the midrib and the secondary veins, and between the subsecondary veins and other veins of higher order.

There are two divisions of tertiary veins. The first of these comprises **joining tertiary veins** or **percurrent tertiary veins**, which are those tertiary veins joining two adjacent secondary or subsecondary veins. They form the bulk of the tertiary veins. More or less parallel to them, but nearer to the midrib so that they join secondary veins with the midrib are the **intra-angular tertiary veins**. I have proposed this term to indicate that these veins lie within the acroscopic angles between the midrib and the secondary veins. The only distinction between these and the joining tertiaries is that the former connect the midrib with a secondary vein, the latter connect two secondary or subsecondary veins.

The term **percurrent tertiaries** or **percurrent crossies**, used in recent paleobotanical literature, includes both joining tertiary veins and intra-angular tertiary veins. Von Ettingshausen used the term **joining tertiary veins** to include both types, except that he modified the intra-angular tertiary veins as used by myself with the adjective **axeständig** to indicate that they were attached to the midrib. For joining and intra-angular tertiary veins which are simple and undivided, Lindley (1843) uses the term **proper veinlets**; for those which are commonly forked and branched, he uses the term **common veinlets**. Bianconi (1838) included these veins in his term **nervules**.
Von Buch (1852) calls all tertiary and finer veins parenchyma veins.

Another relationship that tertiary veins may show is that of joining one another together. When joining tertiary veins or intrangular tertiary veins are joined to each other by small, short veins of tertiary size, located approximately midway between adjacent secondary veins, they are said to be connected by medials or medial tertiary veins, terms proposed by myself. Where there is a belt of medials extending from the midrib to the margin, this belt is termed a medial zone.

Quaternary veins. — Those veins in the finer reticulum which are next in size smaller than the tertiary veins.

Quinternary, sexternary, and septernary veins are self-evident terms. The terms net veins or vein mesh as used by von Ettingshausen (1861) refers to all veins of quaternary size or less. The term veinlets, nervules, and areolation may also be used.

Vein endings is a term used by Foster (1949) for the endings of unattached veinlets of quinternary or lesser size. I would suggest that the more specific term net vein endings be used instead.

Segments

Secondary segment. — That area of a leaf surface which is bounded above and below by a secondary vein, on a third side by the midrib, and on the fourth side by either the margin or a loop vein (Figure 1).

An equivalent term used by Troll (1939) and Foster (1950a) is intercostal field. This term is useful, especially in the Quinaceae, but may be objected to on the grounds that the term
Costa is generally reserved for the midrib, and is not applicable to the secondary veins.

Other terms which may be useful are external segments for areas bounded by two external veins, interordinal segment, intersecondary segment, and so forth.

The lowest secondary segment on a leaf is the segment bounded by the leaf base on two or three sides, in some cases by the midrib on one side, and by the No. 1 secondary vein above. This segment is termed the No. 1 secondary segment, or, preferably, the basal segment.

Thus, I employ the same numbering system used for secondary veins or segments. In each case, the number of the segment corresponds to the number of the upper of the two secondary veins bounding the segment.

In order to simplify the study of leaves, a segment is chosen arbitrarily for study and for reference. This segment is termed the principal segment. It is chosen from a representative or typical portion of the leaf, i.e., the lower part, which is more fully developed. In leaves having five or more secondary segments, the principal segment is the third segment from the leaf base, or is equivalent to the No. 3 secondary segment. The No. 3 secondary vein overlies it, and, as indicated earlier, is termed the supra-principal secondary vein, while the secondary vein bounding the principal segment below is termed the principal secondary vein. In the case of five or more secondary segments, either to the right or the left of the midrib, the principal secondary vein corresponds to the No. 2 secondary vein.

However, in the leaves of some plants, particularly in the genus *Stula*, there are only four secondary segments on either side of the
midrib. In this case, the No. 2 secondary segment, i.e., the segment directly above the basal secondary segment, is chosen as the principal segment.

Tertiary segment. - A portion of the leaf bounded on at least two sides by tertiary veins. Two possible terms are joining tertiary segment and intra-angular tertiary segment.

One type of tertiary segment which seems to have some taxonomic value is what I propose to call the circumtertiary segment. This is a segment bounded on all sides by tertiary veins, most commonly by only two tertiary veins which curve around and demarcate an oval-shaped space. Illustrations of this type of segment may be seen in Figure 1, in Drawings 3, 4, 5, and 6 of Figure 3, and in many of the plates.

A term synonymous with circumtertiary segment and in part with the general term tertiary segment is tertiary areole.

Quaternary segment, quinternary segment, sexternary segment, and septernary segment are self-explanatory terms. Synonymous are the terms quaternary areole, quinternary areole, etc.

A term used by Lindley (1846) for any type of segment is the word intervenium.

Angles

Secondary angle. - This is the angle between any secondary vein and the midrib on the adroscopic side of the secondary vein concerned. It is the angle most commonly referred to in the paleobotanical literature. One may refer specifically to the No. 1 secondary angle, the No. 2 secondary angle, and so forth. The angle is measured at the junction of the secondary vein and the midrib, regardless of the course of the secondary vein after leaving the midrib. In this study, the angle was measured
only on the lowest 5 secondary veins, not above.

**Intra-angular tertiary angle.** - This is the angle toward the apex of the leaf between an intra-angular tertiary vein where it attaches to the midrib, and the midrib. It may be referred to simply as the *intra-angular angle.*

**Upper joining tertiary angle.** - This is the angle, taken toward the leaf margin, between any joining tertiary vein and the basiscopic side of a secondary vein. It may be called the *upper tertiary angle.*

**Lower joining tertiary angle.** - This is the angle, taken toward the leaf margin, between any joining tertiary vein and the acroscopic side of a secondary vein. It may be called the *lower tertiary angle.*

Though he does not designate these last three angles by specific names, von Ettingshausen refers to them and measures them.

**Gross venation patterns**

The following terms are taken from von Ettingshausen, and his original definitions may be found in Appendix E. In this section, I shall discuss only those which apply to the Betulaceae.

**Craspedodromous venation.** - This type exists when all or most secondary veins proceed from the midrib to terminate at the margin, usually in a lobe or tooth. Von Ettingshausen (1856a, 1858c, 1861) separates craspedodromous venation into two parts: *simple,* if all secondaries and their branches or forks strike the margin, and *combined* or *complex* where interordinal veins are common, so that not all of the major veins proceeding from the midrib actually terminate at the margin.
Simple craspedodromous veins are equivalent to connecting veins as used by von Ettingshausen (1861), length-nerves as used by Fritzl (1932), and veins with peripheral endings as conceived by de Bary (1864). They are both von Buch's and von Ettingshausen's randläufig veins. They are Bianconi's (1838) separated secondary nerves. Bianconi divides these into two types: simple separated secondary nerves for those craspedodromous veins without external veins, which he considered as forks of the secondary veins; branched separated secondary veins for those which either bifurcate or have prominent external veins. Kerner (1895) calls craspedodromous venation undivided venation.

Camptodromous venation. - This is a type reserved for those pinnate leaves whose secondary veins do not reach the leaf margin. There are essentially three types, all of them involving the looping of veins.

Dictyodromous is the least prominent of them all. In this kind of venation, the secondary veins either thin down to the size of the tertiary veins before forming loops, so that loops are barely traceable in the net, or else the secondaries thin so much that they vanish, and loops are not traceable. I shall use the former definition; von Ettingshausen prefers the latter.

Brochidodromous or brachydodromous is a simple and prominent looping. The secondary veins and the loop veins are of approximately the same size, so that loops are obvious to the eye. As a rule, only the secondary vein loops (i.e. There are almost no external loop veins), and does so close to the margin.

True camptodromous is illustrated best by the lower secondary veins of Alnus jorullensis (Plate XV). It is also illustrated to a lesser extent by Alnus nepalensis (Plate XVII, and Drawing 7 of Figure 3). Here, in addition to the prominent secondary loops, are subsidiary
loops formed by branches emerging from the crests of the secondary loop veins and themselves looping; subsequent branches emerge from the crests of these loops, and so on, so that a series of progressively shrinking loops is formed. When true camptodromous venation is developed to its ideal extreme, it appears as if the secondary vein itself, rather than swinging to join the next secondary vein above, formed a series of little arcs along the leaf margin, prolonging its junction with the next upper secondary for as long a distance as possible.

This type of venation is termed a system of interanastomosing secondary nerves by Bianconi (1838). Both von Buch and von Ettingshausen use the adjective bogenläufig for this type of venation. Kerner (1895), as translated by Oliver, terms dictyodromous venation reticulate when the secondaries vanish into the net; arched or kamptodromous for true camptidromous; and looped for brochidodromous. Lindley’s names (1848) vary for these venation types, but his terms borrowed from Link (indirecte venosus, evanescenti venosus, and combine venosus) more or less cover the different types of camptodromy. de Bary (1884) would include both von Ettingshausen’s craspedodromous and camptodromous types of venation in the term craspedodromous, which de Bary believes to mean “marginally directed”. For veins with looped endings (von Ettingshausen’s camptodromous types), he uses the expression “veins with internal endings”.

Other terms of von Ettingshausen, not applicable to the Betulaceae are hyphodromous, paralleldromous, campylo-dromous, acrodromous, and actinodromous. These are explained in Appendix E. For dichotomous venation, Kerner (1895) uses the term diadromous.

Other terms

Length-width ratio of the leaf. - The ratio of the length of the leaf to the width of the leaf. This will be referred to as the L/W ratio.
**Midrib spacing.** - The spacing (distance apart) of the secondary veins along the midrib. This may be termed secondary spacing.

**Mean distance.** - The length of the leaf along the midrib divided by the number of secondary segments, or, the average spacing of the secondaries along the midrib. This figure is obtained by considering only one half of the leaf, i.e., one of the halves either to the right or to the left of the midrib. It makes no difference because the number of secondary veins on either side is usually the same.

**Principal distance.** - The absolute length of the principal segment along the midrib (it makes no difference which side of the midrib is considered) divided by the length of the leaf taken along the midrib.

**Principal distance - Mean distance ratio.** - The absolute value of the principal distance is divided by the figure for the mean distance. This will be referred to as the **P-M ratio**.

**Primary-Principal secondary ratio.** - The absolute length of the midrib of the leaf divided by the absolute length of the principal secondary vein. This will be referred to as the **PPS ratio**.

**Measure of Leaf Taper.** - The total length of the midrib divided by the distance from the apex of the leaf to that point where a line through the widest point of the leaf crosses the midrib. It will be referred to as the **MLT**.

**Forking (bifurcating) vs. branching.** - Forking (bifurcating) is the splitting of a vein into two or more veins, each of which goes in a direction different from the original direction. Branching is found when one vein leaves another vein, without any significant change
in the direction of the latter vein.

**Tertiary fold.** - Many joining tertiary and intra-angular tertiary veins are straight, but others are arched in varying degrees. This arch I call the tertiary fold. The hypothetical line passing through the crests of all of the tertiary arches or folds is the **crest line** or **fold line** as termed by von Buch (1852). The sum of all tertiary folds produces an **arcuate pattern** (Foster, 1950a).

**External area.** - A concept introduced by von Buch (1852): that area on any secondary vein in which external veins are present, and in which they depart from the secondary vein. Depending upon how close to the midrib along the secondary vein the external veins originate, and upon the angles of the secondary veins, external areas from secondary vein to secondary vein may or may not overlap.

**Terminal secondary teeth.** - These are also called **terminal teeth.** If the secondary veins end in a marginal tooth, I term those teeth in which they end **terminal secondary teeth.**

**Intersecondary teeth.** - My term for all teeth lying along the margin between the terminal secondary teeth, in which external veins often terminate. In the different types of camptodromy, minor veins-lasts terminate in them.

Terms useful for other families, but not needed for the Betulaceae, have been omitted.

Other forms of classification of veins, including a genetic classification by Frantl (1883), have been invented. Based as they are on vague hypotheses, they have been omitted. I trust that the terms given here will be found useful, though they by no means define absolute
and unvarying characteristics.

Criteria studied in the leaves

Criteria examined in this study

Leaf shape. - Is the leaf oval, elliptical, round, broadly ovate, obovate, linear, rhombic, or obdeltoid?

Leaf apex characteristics. - Is the apex acute, subacute, abruptly acute, apiculate, acuminate, round, or emarginate? (By the term subacute is meant an apex which is pointed, yet highly convex, i.e., a stage intermediate between rounded and acute).

Leaf base characteristics. - (a) Is the base flat and parallel to the No. 1 secondaries? (b) Is it flat but not parallel to the No. 1 secondaries? (c) Is it round, subcordate, cordate, or auriculate? (By subcordate is meant a stage intermediate between round and cordate). (d) Does the base have teeth? (e) Is the base symmetrical or asymmetrical? (f) What is the angle of the leaf base (the angle between the base on opposite sides of the midrib)?

Leaf margin characteristics. - (a) Is the margin incised, lobed, sinuous, entire, sparsely toothed, crenate, serrate, biserrate, dentate, or doubly dentate? (b) Has the terminal tooth any tendency to be bifid, or trifid, particularly in the upper half of the leaf? (c) Does the leaf have terminal secondary teeth only, without intersecondary teeth? (d) Variation in the number of intersecondary teeth from apex to base. There are almost always 0 intersecondary teeth between the two highest terminal teeth, but there are usually 1 or more intersecondary teeth between the No. 1 and No. 2 secondaries. The number of teeth on the basal segment
is not counted. The range in variation of the number of intersecondary teeth from apex to base is expressed, e.g., as 0-1, or 0-16, as the case may be; the first figure represents the number of teeth between the top two terminal teeth, the second figure the maximum number of intersecondary teeth on the leaf, regardless of which segment they are on (other than the basal segment). (e) Number of intersecondary teeth on the principal segment. In all cases of a biserrate or doubly dentate margin, the number of intersecondary teeth given refers to the smaller teeth. (f) Are the teeth large or small?

Length-width ratio and Measure of Leaf Taper were both examined.

Gross venation pattern. - (a) Craspedodromous, (b) dictyodromous, (c) brochidodromous, or (d) true camptodromous.

Primary vein (midrib). - Is it straight or is it crooked? Is it thick or is it thin? Is it thicker than the secondaries at the base or at the top? Is it straight to just below the apex?

Primary-Principal secondary ratio and the ratio between the width and the length of the principal secondary segment were both examined.

Secondary elements. - (a) Are the secondary veins parallel? (b) What are the secondary angles of the Nos. 1, 2, 3, 4, and 5 secondary veins (considered on one side of the midrib only)? (c) What is the angle of variation of the course of each of these secondaries? (d) Do the secondaries bend abruptly at the margin of the leaf, if they are craspedodromous? (e) Do the secondary veins bifurcate, and, if so, does this take place closest to the midrib or to the margin? (f) If camptodromous, does a prominent branch leave the crest of the secondary loop vein? (g) Do adjoining secondary veins diverge toward the midrib
or toward the margin? (h) Are all veins convex upward, concave upward, a mixture of both, or straight? (i) Are the secondaries concave, convex, or straight at the point of their junctions with the midrib? (j) Are many secondaries opposite, or subopposite, and, if so, which ones in particular? (k) How many secondary segments on one side of the midrib? (l) Number of complete secondary segments below the widest point of the leaf on one side of the midrib. This is stated simply as the number of complete secondary segments below the widest point. (m) Does the basal secondary segment expand as it approaches the midrib, remain even in width, contract, or contract all the way to 0 so that its width is not even represented on the midrib? In the latter case, one states simply that the basal segment contracts to 0. (n) Are the secondaries closer spaced toward the apex, the base, towards both the apex and the base, or is the spacing along the midrib even? (o) What is the absolute range in spacing along the midrib? This is expressed as follows: midrib spacing 0-12. This means that the basal segment has contracted to 0, and that the widest spacing on the midrib is 12 millimeters. (p) What is the mean distance? (q) What is the principal distance? (r) What is the principal distance-mean distance ratio?

Subsecondary elements. — (a) Number of intersecondary veins on the whole leaf. (b) The total number of interordinal veins. (c) Is a marginal vein developed? (d) Is a basimarginal vein present? (e) Are external veins present? (f) If so, are they slight or strong? (g) Are counter-external veins present? (h) The total number of external veins on one side of the midrib. (i) How many external veins on the Nos. 1,
2, 3, 4, and 5 secondaries on one side of the midrib? (j) The number of external veins on one side of the midrib above the No. 5 secondary. (k) Do the external veins extend over half the distance to the midrib from the margin on either the No. 1, 2, 3, or 4 secondaries? (l) Angle of the external veins with the secondaries to which they are attached; also their angle with the midrib if projected. (m) Size of external veins on the No. 1 secondary compared with the size on the No. 2 secondary. (n) Are the external veins looped or not looped? (o) Do external areas overlap or not? (p) Do the externals depart from the secondaries as branches or as forks?

Tertiary elements. - (a) Are the tertiary veins prominent or not? (b) Are medials developed? (c) Are tertiary veins commonly opposite one another along the secondary veins? (d) Are most secondaries simple or are most of them branching and complex? (e) The number of joining secondaries on the basiscopic side of the supraprincipal secondary vein. (f) The number of intra-angular secondaries in a principal segment. (g) The lower joining tertiary angle (approximate), the upper joining tertiary angle (approximate), and intra-angular tertiary angle (approximate). (h) Angle of the tertiary fold; is it sharp or is it gentle? (i) Number of circumtertiary segments in the principal segment. Are circumtertiary segments common in the leaf as a whole? (j) Are the simple and undivided tertiary veins more common in the leaf than the complex and branched ones? (k) Are the simple tertiary veins ragged and uneven or smooth in course?

Net elements. - (a) Is the quaternary net well or poorly developed? The quin ternary net? The sexternary net? (b) Is a sexternary
net present or not? A septernary net? (c) Are the smallest areoles square, round, or polygonal? (d) Absolute dimensions of the smallest areoles. (e) Are the net veins of a leaf of approximately the same diameter? (f) Are net vein endings common or rare? Complex or simple?

Miscellaneous. - Absolute leaf dimensions.

Criteria of others not studied

Leaf texture. - This is often important in leaf identification. Aside from the fact that texture was not preserved in the preparation of my slides, it seemed unimportant to consider this, because texture is a relatively constant feature within the family.

Features of the leaf cuticle. - Aside from the fact that this would have been an extremely time-consuming job, there were other reasons for not studying the cuticle. First, those differences noted would probably have been general ones at best. This, of course, cannot be stated with confidence. But the most important reason is that the cuticle is found only in very exceptionally preserved fossils. Such studies of living and fossil leaves have been conducted by Thomas and Bancroft (1913), and methods for the study of fossil cuticles may be found in Walton (1923, 1940) and Bather (1907, 1908).

Length of petiole. - This, again, is one of those inconclusive criteria which are generally helpful where present. In fossils, the petiole is usually partially preserved. Often it is found in its entirety. But in the collecting of herbarium specimens, it was found to be no simple matter to acquire an entire petiole on many herbarium sheets without damaging other leaves.
Angle of the leaf apex. - The precise measurement was found to have little value, though Jentys-Szaferowa (1949, 1950) used it with success in her studies of *Betula alba* L. In a general way, however, the terms acute, subacute, acuminate, or round substitute very well for a precise apical angle measurement, because the apex of each species varies only within limits.

Absolute size of net areoles. - Though occasionally used in taxonomic work, this criterion was not found helpful in this study.

Vein endings. - These were studied in a general way, but not in detail, because of their rarity on fossil impressions. But that they will be helpful in taxonomic work in the living plants cannot be over-emphasized. Many interesting and varying patterns were noted from species to species.

Discussion

In her study of the Linnean species *Betula alba* L., Miss Jentys-Szaferowa studied the following criteria examined by myself: length-width ratio, midrib spacing, length of leaf, measure of leaf taper, basal angles, number of secondary veins, number of teeth between the No. 2 and No. 3 secondary terminal teeth, and the absolute distance between the No. 1 and No. 2 secondary veins. All were found useful by her.

The criteria which she examined but which I did not are these: petiolar length, ratio of the length of the leaf to the distance along the leaf base to the first tooth, apex angle, ratio of leaf length to petiolar length, and the absolute distance from the midrib to the first
tooth on the base. These were also found helpful in her studies.

Jentys-Szaferowa presented her statistical data in the form of graphs. An examination of these graphs will show the differences between the various species formerly included in the single Linnean species *Betula alba*. In particular, she studied *B. pubescens* and *B. verrucosa*.

The very great amount of time which would have been involved prevented such statistical studies on my part. I feel certain that positive results would emerge from my statistical data, and from other data which can still be collected. Such studies should certainly be attempted.

Statistical indices have been computed by Anderson and Whitaker (1934), Anderson and Abbe (1934), and Fisher (1936). However, the necessary type of information for their type of index seemed to be lacking in my own studies. Other types of indices were tried without success.
CHAPTER IV

SYSTEMATIC DESCRIPTIONS

Because this study is neither a monograph nor a study of the floral parts of the plants, but a study of leaves of specimens already identified and catalogued, I adopted a standard reference which would list the principal known species of the Betulaceae and their synonyms. As indicated earlier, the work chosen was that of Hubert Winkler (1904) in Das Pflanzenreich, and, in addition, Winkler's revision of the genus Carpinus (1914).

New species described after Winkler's work usually find their way into herbaria, so that many species not known at the time of Winkler came into my hands. In these cases, synonyms and original citations were investigated. Thus, in addition to Winkler, other authors were referred to constantly: Marshall (1788), Sargent (1916), Standley (1920), Abrams (1923), Lee (1935), Hulten (1944), Fernald (1950), and Sharp (1951). In addition, the Gray Index, Index Kewensis, Index Londonensis, and many original sources were checked. In the main, however, I follow Winkler.

In all descriptions, the number of secondary segments and the number of external veins refer to the number on one side (it does not matter which) of the midrib. Concerning the number of joining and intra-angular tertiary veins, these numbers always refer to the number on the principal segment, which, too, may be located on either side of the midrib.
The abbreviations used are: L–W ratio for length-width ratio of the leaf; MLT for measure of leaf taper; PPS ratio for Primary–principal secondary ratio; and P–M ratio for principal distance–mean distance ratio.
Three hundred and thirty-two specimens of extant Betulaceae studied; 7 fossil specimens. Chart 6.

Description. - Leaves pinnate, oval, ovate, or broadly ovate, less often rhombic or round, very rarely lanceolate, linear, obdeltoid, or obovate, never oblong, oblanseolate, spatulate, sagittate, or cuneate. Apex usually acute, subacute, or acuminate, less often rounded, spiculate, or abruptly acuminate, very rarely emarginate, never truncate. Base round, flat, subcordate, cordate, rarely auriculate, never reniform, sagittate, or hastate. Margin serrate, biserrate, dentate, or doubly dentate (sinuous or entire in a few species of Alnus), almost never crenate, incised, or lobed; teeth usually extending from apex to base, and on base itself. Gross venation pattern, craspedodromous, occasionally dictyodromous, brochidodromy and true camptodromy almost entirely confined to isolated species of Alnus. Secondary vein angles usually between 70° and 80°, smaller angles in the center and upper middle portions of leaf, larger angles at very base and very top. Secondary veins often subparallel, No. 1 secondary pair (except Alnus) originating at or near the leaf base, contracting basal segment to 0 at the midrib. External veins on all but a few species, branching from secondaries, rarely forking. Interordinal veins rare. Intersecondaries almost non-existent. Tertiary and sub-tertiary vein network orderly and well arranged, areoles well-developed, usually polygonal, mesh relatively loose, size differences between orders of veins pronounced.
I. ALNUS Gartn. Fruct. et sem. II: 5b. 1791.

One hundred and five specimens of extant Alnus studied; 2 fossil specimens. Charts 1a and 1b.

Description. - Leaf usually ovate, oval, or rhombic. Apex usually acute or subacute, most commonly convex, less commonly concave; occasionally rounded, rarely emarginate (A. glutinosa). Base usually symmetrical, most commonly flat and parallel to No. 1 secondaries, less commonly not parallel, very rarely cordate. Angle of leaf base between 90°-150°, rarely as low as 60°. Margin dentate, doubly dentate, serrate; never biserrate; teeth small to average sized; intersecondary teeth rarely exceeding 9, sometimes reaching 16 (A. cordata, A. crispa and its varieties, A. maximowiczii). Craspedodromous, sometimes dictyodromous, rarely brochidodromous to true camptodromous. Midrib characteristically straight, usually very thick at base (crooked only in A. crispa and its varieties, A. incana hirsuta). Secondaries thick, straight, concave in camptodromous forms, tending to change direction at junction with externals in some species. 7-16 secondary segments, most commonly 9-13, with 2-4, rarely 5 below widest point of leaf; basal segment never closed to 0 at midrib, except in A. crispa and varieties, A. maximowiczii, and A. orientalis, often expanding toward midrib (a peculiarity of Alnus alone).
Number of external veins approximately the same on secondaries No. 1, 2, 3, 4, generally less on the No. 1 than on the Nos. 2, 3, and 4, thus distinguishing this genus from Betula (number of externals on No. 1 same as on No. 2 in A. maximowiczii and A. tenuifolia); number of externals above the No. 5 secondary varying from 0 to 15, usually greater than 3;
externals extending over half the distance to the midrib usually on the
No. 1, or the No. 2, or the No. 3, or any combination of the 3. Tertiary
veins usually exhibiting a gentle fold, from 40% to 80% branch-
ing. Upper tertiary angle always acute, the lower usually so, the intra-
angular angle variable. Set vein endings usually common and complex,
some very bizarre.

Extant species of *Alnus*

   
   Betula arguta Schlecht. Linnaea 7: 139. 1832.
   
   Acad. lxxi: 610. 1909.
   
   *Alnus arguta* (Schlecht.) Spach. var. *subsericea* Bart. Proc.
   Amer. Acad. lxxi: 610. 1909.

Two leaves studied.

**IL SALVADOR:** Departamento Santa Ana; Volcan de Santa Ana,
Feb. 19, 1946, Margery C. Carlson 710 (UC).

**MEXICO:** Guerrero; Distrito Mina; Sierra Madre del Sur,
Petlacala, Dec. 17, 1937, Ynes Maria 8979 (UC).

**Description.** - Leaf oval-ovate. L-W ratio 1.8-1.9. MLT 1.8-2.3
Apex acute to subacute. Base round or flat, parallel to No. 1 secondar-
ies. Margin doubly dentate, the lesser teeth average sized or very small;
0-4 to 0-5 intersecondary teeth on principal segment; base without teeth.
Craspedodromous. Midrib straight. PIS ratio 3.1-4.0. Secondary angles
50° at base to 70° above; secondaries concave, not commonly opposite.
12-13 secondary segments, 3 below widest point; 1.5-2 mm. spacing at
base to 7-8 mm. spacing above; basal segment expanding. P-L ratio 1.1-1.4. 12-14 external veins, moderately strong, never extending over half distance to midrib, except possibly on the No. 1 secondary. 9-13 joining tertiaries, 3-6 intra-angular tertiaries, predominantly simple; tertiaries straight to gently folded, seldom or commonly opposite. Not not prominent, fairly well developed to quaternary level.

Leaf 45-66 mm. long, 24-36 mm. wide.


21 2ll. 1815. (Plate I).

Betula cordata Lois. Not. s.l. pl. a ajouter a la Fl. de Fr.: 139. 1810.


Alnus cordifolia Ten. Fl. napol. prodr. 54. 1820.


Three leaves studied.

ITALY: Calabria: Fiore, near San Giovanni, June 6, 1933, J. Bornm. 213 (UC); St. Vesuvius, June 14, 1933, J. Bornm. 255 (UC)(2 specimens).

Descriptions. - Leaf broadly ovate. L-W ratio 1.1-1.5. MLT 1.5-1.6. Apex apiculate to abruptly acute. Base cordate to subcordate.

Margin very evenly serrate, serrations small to average; intersecondary teeth varying in number from 6-7 to 2-11, with 5-11 on principal segment; base with few teeth. Dicydromous to brachydromous. Midrib straight. PPS ratio 1.3-2.0. Secondary angles from 60° at base to 35°
Plate I. Alnus cordata (Lois.) Desf.
ITALY: Calabria; Fiore, near San Giovanni, June 6, 1933, J. Bornmüller 213 (UC). (x 2.7)
26: 499. 1899. (Plate II).

Three leaves studied.

CHINA: Kiangsu; Pukow, Lor Shan, Oct., 1922, S.N. Lei
2995 (UC); Szechuan; Lu-hsien, Dec. 25, 1930, W.P. Fang
9907 (DS); Szechuan; Lo-shan-hsien, Aug. 4, 1930, W.P. Fang
2810 (DS).

Description. - Leaf roughly oval. L-W ratio extremely variable:
1.4-2.4 (Fang 9907 and Lei 2995 1.5-1.5). M-LT 1.8. Apex acute or apiculate.
Base rounded to almost flat, not parallel to No. 1. Margin evenly
serrate, serrations suppressed, far apart, strongly asymmetrical toward
apex; 0-2 to 0-3 intersecondary teeth, 0 to 3 on principal segment; teeth
on base rare, suppressed. Dictyodromous to true camptodromous. Midrib
straight. PFS ratio 3.1-5.4 (Fang 9907 and Lei 2995 3.1-3.2). Secondary
angles 60°-65° throw itself; secondaries concave upward, rarely opposite
(except Lei 2995). 11-13 secondary segments, 3-5 below widest
point; 1-4.5 mm. spacing on Fang 9907, 1.5-11.5 on Lei 2995, 1-9.5 on
Plate II. Alnus crematostegyna Burk.

CHINA: Kiangsu; Fukow, Lorr Shan, Oct., 1922, S.H. Lei 2995 (UC). (x 2.2)
Fang 3840; basal segment expanding. P-W ratio C.8 on Fang 3840, 1.4 on others. 13-15 externals, weak except on Lei 2995; never over half distance to midrib except on Lei 2995. 5-9 joining secondaries, 2-3 intra-angulaires; tertiary fold gentle; all tertiary angles acute; seldom opposite. Act developed to sexternary level. Leaf 32-71 mm. long, 23-30 mm. wide.

Remarks. - Fang 3840 has many characters strikingly different from the other two, but it is actually Lei 2995 which is basically the most different. The latter only is dictyodromous, has strong external veins, varies from 60°-45° in secondary angles, has lower secondary veins convex at midrib junction, exhibits high degree of opposite-ness, has strongly overlapping external areas. None the less, it may be only a variety.

I. ALNUS CRISPA (Ait.) Pursh. Fl. amer. sept.

II: 623. 1814. (Plate III).

Betula alnus crispa Michx. Fl. bor.-am. II: 161. 1803.
Alnus alnobetula (hrh.) Hartig var. crispa (Ait.) H. &inkl.
Plate III. *Alnus crispa* (Ait.) Pursh.

Canada: Quebec; Rimouski County; Bic, June 23, 1905,

F.F. Forbes s.n. (NS). (x 3.3)
One leaf studied.

CANADA: Quebec; Rimouski County; Bic, June 23, 1905,
F. F. Forbes s.n. (DS).

Description. - Leaf oval or ovate. L-W ratio 1.4. MLT 2.1.
Apex rounded to subacute and acute. Base flat to roundish, tending
to be parallel to No. 1 secondary vein until close to midrib. Margin
evenly and finely dentate, to unevenly so and even doubly dentate;
teeth small, sharp, delicate, often pointed; 0-13 intersecondary teeth
with 13 on principal segment, base with teeth. Craspedodromous. Mid-
rib crooked. PPS ratio 2.6. Secondary angles 65° at base, 32° above;
secondaries straight, random secondaries opposite, particularly the No.1.
9 secondary segments, 2 below widest point; spacing 0-8.5 mm. basal seg-
ment often 0, sometimes reaching 1.5. P-W ratio 0.7. 27 external veins;
6 on No. 2 alone, strong; over half the distance to midrib on No. 1 and
No. 2. 7-9 joining, 1 intra-angular tertiary, predominantly branching;
tertiary fold gentle; all tertiary angles acute; tertiaries seldom oppo-
site; circumtertiary segments common. Net veins well developed to quin-
ternary level. Leaf 52 mm. long, 36 mm. wide.

Remarks. - Compare with *A. crispa sinuata* and *A. fruticosa*, to
follow. This species and its relatives are extremely wide-spread and,
in the fossils, are often confused with *A. rhombifolia*. There are many
similarities between these two species, but marginal characteristics, as
well as several other details, are quite different.

Lunds. Univ. Årsk. N.F. Aud. 2. hO. 1: 587.

1944. (Plate IV).

Alnus viridis Cham. Linnaea 6: 538. 1831.


2: 53. 1845.

Alnaster fruticosus Ledeb. Fl. Ross. 3: 655. 1846-51
(pro parte).


Alnus viridis q simulata Regel. In A.DC. Prodr. XVI.

2: 183. 1864 (pro parte).

Alnus viridis var. sibirica Rothr. Sketch Fl. Alaska:

1854. 1867 (pro parte).


(pro parte).


Alnus alnobetula var. fruticosa (Rupr.) H. Winkl.


Alnus fruticosa var. sinuata (Regel) Hult. Fl. Aleut.

Is.: 153. 1937.

Six leaves studied.
Plate IV. *Alnus crispa* subsp. *simuata* (Regel) Hulten.

UNITED STATES: Oregon; Crater Lake National Park, Aug. 30, 1916, A.A. Heller 12,622 (US). (x 2.7)

CANADA: British Columbia; across Fraser River from Hope, June 18, 1911, C.L. Hitchcock and J.S. Martin 7369 (DS).

UNITED STATES: California; Del Norte County; Casquet, May 30, 1931, H.L. Parks and J.P. Tracy 9209 (DS); Montana; Missoula County; Mission Range, near Glacier Peaks, Aug. 12, 1930, C.R. and R.P. Rosbach 230 (DS); Oregon; Crater Lake National Park, Aug. 30, 1916, A.A. Heller 12,622 (DS); Washington; Mt. Rainier National Park; Narada Falls, July 17-23, 1922, L.R. Abrams 9166 (DS).

Description. - Oval or ovate, rarely broadly ovate. L-W ratio 1.2-1.5; L-T 1.6-2.0. Apex acute to subacute. Base round in overall outline, small flat area close to midrib, not parallel; occasionally subcordate. Margin doubly dentate; teeth small to average; 0-10 to 0-15 intersecondary teeth, with 10-14 on principal segment; base with many teeth. Craspedodromous. Midrib straight to crooked. PFS ratio 2.3-3.7. Secondary angle varying from 60°-90° at base to 25°-45° above; secondaries generally straight, with appreciable angular divergence between No. 1 and 2, or between No. 2 and 3 secondaries; random secondaries opposite, most commonly the No. 2, 9-12 secondary segments, 3 below widest point; spacing from 0.1-1.5 mm. at base to 8.5-12.5 above. P-W ratio 0.5-0.9 (in one case 1.2). 22-30 (usually 22-26) externals, strong; over half distance to midrib on Nos. 1 and 2, or Nos. 2 and 3, the latter most common. 3-7 joining, 1-3 intra-angular secondaries, branching; tertiary fold usually sharp, usually 100°-130°; as in Betula, secondaries fading toward middle of secondary segments; all tertiary angles 90° to acute; secondaries rarely
opposite; circumtertiary segments common. Net veins developed to sexternary level. Leaf 47-74 mm. long, 33-52 mm. wide.

Remarks. - This species cannot be confused with Betula because of the large number of teeth on the principal segment. The greatest number of intersecondary teeth on a principal segment in Betula is in B. maximowiczii, and this is 7. Large numbers of external veins above the No. 5 secondary and the large number of segments below widest point (3) are also diagnostic.


(Plate V).


**Alnus viridis** Cham. *Linn. 6: 538. 1831.*


**Betula viridis** Turcz. *Cat. baikal.: 1059. 1856 (?).*

**Alnaster viridis** Turcz. *Fl. baikal. dah. II: 131. 1856.*


**Alnus alnobetula** var. **fruticosa** H. Winkl. *Pflanzenr. IV. 61.*

**Betul.**: 106. 1904.

One leaf studied.
Plate V. *Alnus fruticosa* Rupr.
U.S.R.: Krasnojarsk; *Kas River*, June 14, 1927,
N. Schipczinsky s.n. (08). (x 2.5)
UNION OF SOVIET SOCIALIST REPUBLICS: Siberia; Krasnojarsk District; near the headwaters of the Yenisei River, Kas River, June 11, 1927, N. Schipszinsky s.n. (DS).

Description. — Leaf ovate. L-W ratio 1.3. NLT 2.1. Apex acute. Base cordate. Margin dentate to doubly dentate, with small, pointed, delicate, long teeth; 0-16 intersecondary teeth, with 16 on principal segment; base covered with teeth. Crassodromous. Midrib crooked. PPS ratio 2.0. Secondary angles 70° near base to 60° above; secondaries straight, alternate; strong divergence in angle between course of Nos. 1 and 2 secondaries. 11 secondary segments, 2 below widest point; spacing 0-8mm., basal segment contracting at 0 at midrib. P-M ratio 1.2. 31 external veins with 7 on No. 1 secondary alone, strong; over half distance to midrib on No. 1 secondary. 12 joining, 2 intra-angular tertiary veins, mostly branching; tertiary fold gentle; all tertiary angles pronouncedly acute; tertiaries seldom opposite; circumtertiary segments fairly common. Net well developed to sexternary level. Leaf 57 mm. long, 43 mm. wide.

Remarks. — The identity of this form with Alnus crispa sinuata is apparent; its relationship to Alnus crispa is very close. All of these forms seem to be related to Alnus maximowiczii Callier, a Japanese alder not examined here. This latter species is very similar to Betula, especially B. maximowiczii, in having a crooked midrib, broadly ovate shape, long thin teeth, and a basal segment contracting to 0. However, it may be told from Betula by the presence of 11 or more intersecondary teeth, on its principal segment.

Plate VI. *Alnus firma* Sieb. & Zucc.
JAPAN: Nagasaki; Minami-takah County; Abama, Mount Nodake, June 8, 1924, *Tyosaburo Tanaka 199* (UC). (x 3.0)
Plate VII. *Alnus firma* Sieb. & Zucc.

JAPAN: Nagasaki; Kinami-Takah County; Abana, Mount Nodake, June 6, 1924, **Tyozaburo Tanaka** 199 (UC). (x 2.3)
Betula alnus Thunb. Fl. japon.: 76. 1784.

Two leaves studied.

JAPAN: Nagasaki; Minami-takahi Prefecture; Abama, Mt. Nodake, June 8, 1924, Tyozaburo Tanaka 199 (UC).

Description. — Oval to lanceolate. L-W ratio 1.5-2.4 (on a single twig). MLT 1.5-1.6. Apex acute. Base flat, parallel to No.1, asymmetrical. Margin evenly serrate, teeth average sized; 0-3 to 0-4 intersecondary teeth, with 3-4 on principal segment; base without teeth. Graspedodromous. Midrib straight. PPS ratio 2.4-3.7. Secondary angles 55°-70° at base, 45° above; secondary veins somewhat concave, bending abruptly toward apex at leaf margin, alternate. 10-14 secondary segments, 2 below widest point (number of secondary segments a function of leaf length); spacing 2-7 mm.; basal segment even. P-M ratio 1.2-1.3. 17-19 external veins, weakly developed, extending over half distance to midrib on No. 1 secondary. 9 joining, 2-3 intra-angular teraryes, generally branching; teraryes straight, little or no fold developed; joining tertiary angles acute to 90°, intra-angular angles 90° to obtuse; teraryes seldom opposite; circumterary segments common. Net well developed to quinary level, size differences not pronounced. Leaf 71-53 mm. long, 29-35 mm. wide.

Remarks. — Very similar to Carpinus except for the lack of medials, and the nature of the base.

Plate VIII. Alnus firmifolia Fern.
MEXICO: Mexico D.F.; Mt. Popocatepetl,
Provincial Paraje, Huayavalol, Apr. 11, 1938,
E.K. Balls Bl.168 (UC) (x 3.2)
One leaf studied.

MEXICO: Mexico D.F.; Paraje Provincial; Mt. Popocatepetl, Huayavalol, Apr. 11, 1933, E.K. Bals B4168 (UC).

Description. - Oval. L-W ratio 1.9. MLT 2.3. Apex subacute. Base flat, parallel to No. 1. Margin evenly serrate, teeth average sized; 0-5 intersecondary teeth, 5 on principal segment, base without teeth. Craspedodromous. Midrib straight. FFS ratio 2.8. Secondary angle 45° at base to 30° above; secondary veins straight, opposite or subopposite. 9 secondary segments, 2-3 below widest point; spacing 1.5-9 mm. (Large for such a small leaf); basal segment even. P-W ratio 0.5. 15 externals, strong, over half distance to midrib on No. 2. 8-12 joining, 2 intra-angular terciaries; terciaries straight; joining tertiary angles approximately 90°, intra-angular angles generally obtuse; terciaries commonly opposite. Not developed to sexternary level. Leaf 48 mm. long, 25 mm. wide.


Two leaves studied.

PHILIPPINE ISLANDS: Luzon; Benguet Province; cultivated at Nagdio, Aug. 1-18, 1928, W.S. Clemens 18,327 (UC).

RYUKYU ISLANDS: Okinawa; Nago, Nov. 13, 1945, W.D. Field and O.G. Loew 1341g (UC).
Plate IX. *Alnus formosana* Mak.

PHILIPPINE ISLANDS: Luzon; Benguet Province; Baguio (cultivated), Aug. 1-18, 1928,
M.S. Clemens 18,327 (UC). (x 3.0)
Description. - Oval to linear. L-W ratio 1.7-5.0. M/L 1.5-1.7. Apex acuminate, abruptly acute, less often acute. Base flat or slightly rounded, parallel or subparallel to No. 1. Margin evenly serrate, teeth very small, strongly asymmetrical toward apex, pressed close into margin; 0-1 to 0-4 intersecondary teeth, 1-4 on principal segment; base with few teeth. Dictyodromous to true camptodromous, with prominent branches at crest of secondary loop veins. Midrib straight. PFS ratio 2.4-10.0. Secondary angles 40°-65° at base, 40°-50° above; secondary veins strikingly concave, almost parallel, all to most secondaries opposite. 11 secondary segments, 2-3 below widest point; spacing 1 mm. at base, 8-9 mm. above; basal segment even. P-M ratio 1.0-1.1. 9 external veins, slight, over half distance to midrib on Nos. 1 and 2 secondaries. 3-15 joining, 3 intra-angular tertiary veins; tertiary fold gentle; joining tertiary angles 90° to acute, intra-angular angles obtuse; tertiaries seldom opposite; simple tertiaries often irregular in course. Net developed to sexternary level. Leaf 53-70 mm. long, 11-32 mm. wide.

Remarks. - Compare this species with A. japonica and A. maritima; A. formosana has been considered synonymous with both. Though they appear to be related, there are several fundamental differences, particularly in the external veins.


Betula alnus glutinosa L. Spec. pl.: 983. 1753.

Plate I. Alnus glutinosa (L.) Gärtn.
BERKSHIRE: Sonning, Oct. 29, 1864.
Lemon Herbarium s.n. (UC). (x 3.0)
Plate XI. Alnus glutinosa (L.) oswt.
FRANCE: Across from Tadu, Tetara River, July 7, 1927, Dr. Font Quer 129 (UC). (x 3.0)


Two leaves studied.

ENGLAND: Berkshire; Sonning, Oct. 29, 1844, ex Lemmon Herb. s.n. (UC).

FRENCH MOROCCO: Ketana River, across from Radu, July 7, 1927, Dr. Font Quer 129 (UC).

Description. - Oval, ovate, or round, occasionally appearing slightly rhombic. L-W ratio 1.2-1.5. M-LT 2.3-3.2. Apex usually round or emarginate, rarely acute or subacute. Base flat, parallel to No. 1 secondaries; basal angle 80°-100°. Margin dentate to sharply doubly dentate; smaller teeth small, blunt, tipped by sclereids; 0-3 intersecondary teeth, 3 on principal segment; base with few or no teeth. Craspedodromous, the No. 1 showing true camptodromy. Midrib straight. PPS ratio 2.1-2.3. Secondary angles 50°-60° at base; 40°-50° above; secondaries opposite, straight, expanded at ends. 8-9 secondary segments, 2-3 below widest point; spacing 4-8.5 mm.; basal segment expanding. P-W ratio
0.9-1.1. 14-16 externals, weakly developed, over half distance to midrib on No. 1 or No. 2 secondary; externals expanding at tips, terminating in teeth blunted by sclereids. 9-11; joining, 2 intra-angular ter- tiaries, branching; tertiary fold pronounced, almost sharp; all tertiary angles acute; tertaries seldom opposite. Net veins well-developed to sexternary level. Leaf 55 mm. long, 37-45 mm. wide.


1794.  (Plates XIII and XIII).

Betula alnus \( ^\beta \) incana L. Spec. pl.: 983. 1753.

Alnus febrarua var. incana O. Ktze. Taschenfl. Leips.: 239. 1867.

Twelve leaves studied.

CANADA (introduced): Ontario; Thunder Bay district; Sibley Township, Camp Lake, July 11, 1936, T.W.C.Taylor, S.T.Loses, and M.W.Pannan 382 (DS); Quebec; Natale County; Gaspe, Aug. 8, 1901, F.F.Forbes s.n. (DS); Quebec; Rimouski County; Bic, June 21, 1905, F.F.Forbes s.n. (DS).

FRANCE: Savoy, June 5, 1910, M.Bouchard s.n. (DS); Strasbourg, date unknown, collector unknown (DS 336,066).

SWEDEN: Swedish Lapland; 68°20' N. Latitude, near Abisko, Aug. 21-29, 1936, Jens Clausen 1179 (DS).

UNITED STATES (introduced): Indiana; Elkhart County; near Bristol, Aug. 21, 1916, C.C.Deam 20,298 (DS); Michigan; Port Huron, July 25, 1901, C.K.Dodge s.n. (DS); New Hampshire;
Plate XII. Alnus incana (L.) Koehne.
FRANC: Savoy; June 5, 1910, M. Bouchard s.n. (NS), (x 2.3)
Plate XIII. *Alnus incana* (L.) Moench.

UNITED STATES: Indiana; Elkhart County; near Bristol (introduced), Aug. 21, 1916, C.C. Dean 20,998 (US). (x 2.5)
White Mountains, Pinkham Notch, Aug. 11, 1902, F.F. Forbes (DS); New York; Sullivan County; Lake Shangies, Aug. 11, 1918, R. Wilson s.n. (DS); Vermont; Peacham, July 12, 1885, F. Blanchard s.n. (DS); Wisconsin; Shawano County; Keshena, June 8, 1925, E.J. Palmer 27742 (DS).

Description. - Broadly oval to rounded. L-W ratio 1.2-1.5. M/LT 1.8-2.7 (usually 1.8-2.3). Apex subacute, apiculate, or rounded. Base flattish or rounded, commonly parallel to No. 1. Margin doubly dentate, the larger dentations not prominent, giving appearance of wavy outline to leaf; teeth small to average, dentations broad and low; 0-4 to 0-16 intersecondary teeth, 4-14 on principal segment, 0-6 to 0-9 most common variation in number of intersecondary teeth, 6-9 most commonly on principal segment; base with prominent teeth, often close to midrib. Craspedoderous. Midrib straight or wavy. PPS ratio 1.9-4.0, all but 3 being 1.9-2.0, these 3 being 3.9-4.0, possibly indicating a mistake in the identification of the No. 1 secondary. Secondary angles 60°-85° near base, 35°-55° above; secondaries straight, random secondaries opposite, or all alternate; Nos. 1 and 2 secondaries characteristic convex at junction with midrib. 9-16 secondary segments, usually 10-14; 2-3, rarely 4, below widest point; spacing 1-2.5 mm. at base to 6-9 mm. above; basal segment usually even, rarely contracting or expanding slightly. P-M ratio 0.6-1.6 (all but 2 being 0.8-1.3). 15-32 (usually 22-30) external veins, strong, over half distance to midrib on Nos. 1 and 2, rarely on Nos. 1, 2, and 3. Counter-external veins may be prominent. 7-17 joining tertiaries (usually 9-12), 1-3 intra-angulars; tertiary fold pronounced, the fold being evenly rounded; joining tertiary angles acute, intra-angular angles about 90°; tertiaries commonly opposite; circumtertiary segments fairly common. Not developed to sexternary level.
Leaf 38-72 mm. long, 32-53 mm. wide.

Remarks. - Hultén (1944) in referring to A. incana says: "The western American alder of this type is usually taken as a separate species A. tenuifolia." (p. 591). That the two are very closely related is certain. However, A. tenuifolia differs in having a less rounded base, a more acute apex, and larger L-W ratios, as well as more prominent dentations. In the fossils, the two may easily be confused.

12. ALNUS INCANA (L.) Moench. var. HIRSUTA (Turcz.) Spach. 
Ann. sc. nat. 2. ser. XV: 207. 1841.


One leaf studied.

Description. - Roundish or oval. L-W ratio 1:1. M-LT 2:1. Apex rounded. Base flat, parallel to No. 1. Margin doubly dentate, the larger dentations large and rounded in outline, prominent, the lesser
teeth small and pointed. 0–9 intersecondary teeth, 9 on principal segment; base with teeth at outer edge. Craspedodromous. Midrib sinuous. PPS ratio 1.7. Secondary angles 60° at base, 35° above. Secondaries sinuous along an essentially straight course, alternate. 7 secondary segments, 2 below widest point; 1.5–3.0 variation in spacing; basal segment even. P–M ratio 1.0. 15 strong external veins, over half distance to midrib on No. 1 and No. 2 secondaries. 8–10 joining, 4–7 intra-angular tertiaries, branching; tertiary fold varying from sharp to gentle; joining tertiary angles acute, intra-angulares 90° to obtuse; tertiaries commonly opposite. Net developed to sexternary level. Leaf 4.9 mm. long, 4.4 mm. wide.

Remarks. — This entity is often given specific rank as A. hirsuta Turcz. It certainly exhibits greater differences with A. incana than does A. temuifolia, but it is closely related in many details. The leaf form of A. incana suggests that it is a combination of the characters of A. temuifolia and A. incana hirsuta.


1846. (Plate XIV).

Betula alnus Thunb. Fl. japon. 376. 1784.


Alnus japonica var. minor Miq. Prolus. fl. jap. 69. 1865.

Alnus maritima var. minor Miq. Prolus. fl. jap. 358. 1865.

Plate XIV. **Alnus japonica** Sieb. & Zucc.

CHINA: Shantung; Taingtao, June 6, 1930,
C.Y. Chiao 2378 (UC). (x 3.4)


Two leaves studied.


JAPAN: Yamato Province; Mt. Kagusayama, Nov. 6, 1949, M. Hiroe 5095 (UC).

Description. - Oval. L-W ratio 2.0-2.1. WLT 2.0-2.1. Apex acuminate. Base round. Margin evenly serrate, teeth small, apically directed; 0-4 intersecondary teeth, 1-4 on principal segment, base without teeth. Craspedodromous. Midrib straight. PPS ratio 3.2-4.6. Secondary angles uniformly about 60°; secondary veins concave, changing direction at points of departure of external veins, alternate. 9-10 secondary segments, 3-4 below widest point; spacing 1 mm. at base, 7-8 mm. above; basal segment even to slightly contracted. P-M ratio 0.8-0.9. 10-14 externals, strong, leaving mostly as forks, extending over half distance to midrib on alternate secondaries, Nos. 1-4. 6-8 joining, 3-4 intra-angular tertaries; tertiary fold gentle to almost straight; upper joining tertiary angles acute, the lower both acute and obtuse, the intra-angular angle obtuse; tertaries rarely opposite. Net veins developed to sexternary level. Leaf 46-51 mm. long, 23-28 mm. wide.

Remarks. - The forked, prominent externals are distinctive features of this species. These two criteria were sufficient to distinguish
A. japonica from A. formosana in all specimens examined. Hence the two appear to be distinct species, although they have been described in the literature as synonymous.


1817. (Plate XV).

Two leaves studied.

**MEXICO:** Nidalgo; San Vicente, July 16, 1937, Mary T. Edwards 856 (US); Jalisco; Sierra Madre Occidental, Real Alto, Feb. 20, 1927, Ynes Mexia 1717 (US).

**Description.** - Cval. L-W ratio 1.7-2.1. KLT 2.2-2.7. Apex rounded. Base rounded, slightly asymmetrical. Margin sparsely serrate with small teeth; intersecondary teeth, 2 on principal segment, base without teeth. Dicryptodromous to true carpodromous, prominent branch leaving crest of loop vein and proceeding to margin. Midrib extremely thick in lower two-thirds, very thin at top. PPS ratio 3.5-7.1. Secondary angles 70° at base, 50° above; secondary veins somewhat concave, randomly opposite. 10 secondary segments, 3 below widest point; spacing 2.5 mm. at base, 16 mm. above; basal segment even. P-W ratio 0.9-1.1. No external veins. 21 joining, 1 intra-angular tertiaries, either simple or branching; tertiaries straight; joining tertiary angles 90° to acute, intra-angular angles 90° to obtuse; tertiaries commonly opposite. Set developed to quaternary level. Leaf 30-100 mm. long, 48-52 mm. wide.

**Remarks.** - This species is quite distinct from A. jorullensis ferruginea and Alnus sp. (from Argentina) which follow. The Argentine
Plate IV. Alnus jorullensis H.B.K.
MEXICO: Hidalgo, San Vicente, July 16, 1937,
Mary T. Edwards 856 (US). (x 2.8)
specimen was described as A. jorullensis. That there is a relationship seems certain from a comparison of data, but their identity as separate taxa is not to be doubted from the material presented here.

15. **Alnus jorullensis H.S.K. var. petroselina (H.S.K.) 0. Ktze.**


**Alnus ferruginea H.S.K.** Nov. gen. et spec. III: 17, 1817.

**Alnus acuminata H.S.K. var ferruginea Regel.** Monog. Betul.

Two leaves studied.

**QUADOR: Province Carchi; Canton Espejo; near Angel, Rio Tasquasa, July 20, 1935, Ynes Mecia 7536 (UC).**

**PERU: Province Santiago de Chico; Departamento La Libertad; Cachicaian, Nov. 25, 1936, H.E. Stork and 0. B. Horton 9978 (UC).**

**Description.** - Oval to ovate. L-W ratio 1.5-2.1. MLT 1.7-1.9. Apex acute. Base flat, parallel to No. 1. Margin evenly serrate, teeth few, small; 0-3 intersecondary teeth, 2-3 on principal segment, base with few or no teeth. Craspedodromous above, dictyodromous below, true camptodromous on No. 1 secondaries. Midrib extremely thick in lower two-thirds, very thin above. PPS ratio 2.3-3.5. Secondary angles 60°-80° at base, 45°-50° above; secondaries generally straight, or slightly concave, randomly opposite, especially Nos. 1 and 2 secondaries. 7-9 secondary segments, 2-3 below widest point; spacing 1-3 mm. below, 7.5-8 above; basal segment even. P-M ratio 0.4-0.8. 11-17 external veins, thick, short, never over half distance to midrib. 13-16 joining, 2-3 intra-angular tertiaries; tertiaries straight; upper joining tertiary
angles acute, lower obtuse, the intra-angular angles 90° to obtuse; tertiaris commonly opposite. Not well developed to sexternary level. Leaf 50-60 mm. long, 33-41 mm. wide.

Remarks. - Hexia 7526 was labeled A. ferruginea; Stork and Norton 9576 was labeled A. jorullensis. Both differ from A. jorullensis in the following respects; they have a lesser degree of camptodromy, external veins, lower PPS ratio, lower P-M ratio, and only half the maximum spacing of A. jorullensis. Other characters, such as the midrib, show their relationship with A. jorullensis.

16. ALNUS SP. (Plate XVI).

One leaf studied.

ARGENTINA: Tucuman; Departamento Graucas, Sept. 28, 1920; S.Venturi 1047 (UC).

Description. - Ovate. L-W ratio 1.5. M/L 1.8. Apex subacute. Base round to subcordate. Margin evenly serrate, teeth small, tipped with sclereids; 0-4 intersecondary teeth, 4 on principal segment, base with teeth. Craspedodromous. Midrib thick, straight. PPS ratio 2.2. Secondary angle 95° at base, 50° above; secondaries straight, all convex at junction with midrib except upper 2 or 3; random secondaries opposite. 11 secondary segments, 2 below widest point; spacing 1 mm. at base to 8.5 mm. above; basal segment contracting at midrib. P-M ratio 1.1. 22 short, thick external veins, never over half distance to midrib. 19 joining, 3 intra-angular tertiaris, simple, closely spaced; tertiary veins straight to folded gently; upper joining tertiary angles acute, lower 90° to obtuse, intra-angular tertiaris obtuse; tertiary veins
Plate XVI. *Alnus* sp.
ARGENTINA: Tucuman; Departamento Causcas,
Sept. 28, 1920, S. Venturi 1017 (UC). (x 2.5)
commonly opposite. Net developed to quinternary level. Leaf 60 mm. long, 40 mm. wide.

Remarks. - That this is a distinct entity is shown by the following features: many externals, larger number of teeth, greater number of tertiary veins, and craspedodromy. Midrib and shortness of external veins suggest relationship with A. jorullensis and A. jorullensis fer- runina.


One leaf studied.


Description. - Slightly obovate to broadly oval. L-W ratio 1.4. MLA 2.1. Apex rounded. Base round, more or less parallel to the No. 1 secondaries. Margin sparsely serrate, large, highly asymmetrical serrations; 0-2 intersecondary teeth, 0 on principal segment, base without teeth. Dictyodromous to brochidodromous, prominent branch from crest of secondary loop veins to margin. Midrib straight, lower two-thirds very thick. PPS ratio 3.3. Secondary angles 60° below to 85° above, almost uniform; all secondaries strongly concave, opposite. 12 secondary segments, 4 below widest point; spacing from 2.5 at base to 9.5 mm. above; basal segment even. P-M ratio 0.9. More than 11 externals, weak, almost none above No. 5 secondary, never extending over half the distance to the midrib. 9 joining, 2 intra-angular tertiaries; tertiary fold gentle; upper joining tertiary angles acute, the lower 90° to obtuse, intra-angular angles obtuse; tertiaries commonly opposite;
circumtertiary segments common. Not developed to sexternary level.

Leaf 80 mm. long, 57 mm. wide.

Remarks. - This form seems to be related to A. nepalensis and A. trabeolosa.


A. oblongata Mill. Gard. ed. 7: n.2. 1757.


Two leaves studied.

UNITED STATES: Maryland; Wicomico County, June, 1935, A.V. Smith s.n. (US); Oklahoma; Johnston County; Devil's Den, Apr. 30, 1939, C.T. Robbins 3265 (UC).

Description. - Oval to slightly obovate. L-W ratio 2.0. Midrib straight. PPS ratio 2.0-2.2. Apex acute to subacute. Base flat, not parallel to No. 1. Margin evenly serrate, teeth small, closely pressed to margin, strongly asymmetrical toward apex; 0-3 intersecondary teeth, 2-3 on principal segment; teeth rare on base. True carpodromous. Midrib straight. PPS ratio 2.5-3.1. Secondary angles 75° below to 60° above; secondary veins strongly concave, randomly opposite to none opposite. 9-11 secondary segments, 2-3 below widest point; 1.5-3 mm. spacing at base, 8-9 mm. above, basal segment expanding. P-N ratio 0.6-1.2. 8-13 moderately strong external veins, over half the distance to midrib on No. 1 secondary, the No. 2 secondary, or both. 7-10 joining, 2-4 intra-angular tertiary veins, simple; tertiary fold gentle; joining tertiary angles
90° to acute, the intra-angulars acute to obtuse, varying; tertiaries commonly opposite. Net veins developed to sexternary level. Leaf l/7 mm. long, 23 mm. wide.

Remarks. - The two areas from which each specimen came are dis-junct. The specimens appear to be almost identical. In its marginal characters, this taxon is most closely related to *A. formosana*; its external veins are intermediate between those of *A. formosana* and *A. japonica*.


**Betula boshia** Buch.-Ham. ex D.Don. Prodr. fl. nepal.: 58. 1825.

**Betula leptostachya** Wall. Herb. ex cat.: n.2799. 1828.


Five leaves studied.

**CHINA**: Kweichow; Tating, Schwanghan, Sept. 16, 1930, Y.Tsiang 8959 (UC); Szechuan; Yen-yuan-hsien, Sept. 29, 1930, W.P.Fang 5251 (DS); Yunnan; 25 miles northwest of Kunming, Apr. 30, 1949, R.S.Ferris 12,030 (DS).

**INDIA**: Punjab; Simla and Siwaliks, 1885, J.R.Drummond 22,570 (UC).

**INDO-CHINA**: Chapa, July, 1927, ex herb. de l'ecole superieure d'agriculture et de sylviculture d'Hanoi n.s.n. (UC).

**Description.** - Broadly to narrowly oval, or obovate. *L-W* ratio 1.4-2.4 (Fang 5251 and Tsiang 8959 2.3-2.4; the others 1.4-1.7.). *MLT* 2.1-2.3, Fang 5251 3.2. Apex rounded, apiculate, subacute, or acute.
Plate XVII. *Alnus nepalensis* D.Don.

CHINA: Szechuan; Yen-yuan-hsien, Sept. 29, 1930, W.P. Fang 5251 (OS). (x 2.5)
Base rounded or cuneate. Margin sparsely serrate or entire; teeth low, suppressed, strongly asymmetrical toward apex; 0-2 to 0 intermediate teeth, usually the latter, 0-2 on principal segment, base without teeth. True camptodromous or brochidodromous. Midrib thick, straight. PFS ratio 2.1-10.0. Secondary angles 65°-80° at base, 60°-70° above; secondary veins concave, randomly opposite to alternate. 10-11 secondary segments, 3-5 below widest point; spacing 2-7 mm. at base, 7-11 mm. above; basal segment expanding at midrib, sometimes greatly. P-M ratio 0.6-0.9, one specimen 1.3. 0-9 externals, 0-3 the rule, looped, difficult to distinguish loops and externals, slight; rarely extending half the distance to the midrib. 1-10 interordinal veins. 3-16 joining, 2-4 intra-angular tertiaries, predominantly simple; upper joining tertiary angles 90° to acute, the lower 90° to obtuse, intra-angulars varying; simple tertiaries usually irregular in course, rarely opposite. Net veins developed to sexternary level. Leaf 65-97 mm. long, 26-58 mm. wide.

20. ALNUS ORIENTALIS Decne. Ann. sc. nat. 2. ser. IV:
348. 1835. (Plate XVIII).

Two leaves studied.


Description. - Ovate. L-W ratio 1.3-1.9. MTL 2.0. Apex acute or subacute. Base round to subcordate, slightly asymmetrical. Margin doubly dentate, larger dentations broad and angular, smaller teeth minute, widely separated, sharp, tipped with sclereids; 0-3 to 0-7 intermediate secondary teeth, 3-7 on principal segment, base with few minute teeth.
Plate XVII. Alnus orientalis secne.
SYRIA: near Beirut, Aug. 5, 1855, Th. Kotschy 372 (DS). (x 2.5)
Craspedodromous with hint of dictyodromy. Midrib straight. PPS ratio 2.8–3.0. Secondary angles 75° near base, 50° above; secondaries slightly concave, randomly opposite, including Nos. 1 and 2, to all alternate. 8 secondary segments, 2–3 below widest point; spacing 0–0.5 at base, 13–14 mm. above, basal segment contracting at midrib, sometimes to 0. P-M ratio 1.1–1.2. 9–10 externals, 0–1 above No. 5 secondary, strong, over half distance to midrib on No. 3 secondary, often looped, sometimes leaving secondaries as forks. 3–7 joining, 3–6 intra-angular tertiaris, simple; tertiary fold gentle; joining tertiary angles acute, intra-angular 90° to obtuse; tertiaris commonly opposite. Net veins developed to sexternary level. Leaf 62–65 mm. long, 32–50 mm. wide.

Remarks. — One character of Betula is present; the basal segment may contract to 0. But the fact that the greatest number of externals is on the No. 3 secondary indicates that this is an alder leaf. *Alnus harneyana* Chancy & Axelrod, a fossil alder from the Blue Mountains Flora of Oregon, is similar in some respects to *A. ovientalis*, except that it possesses a crooked midrib, and its margin is different.


*Alnus californica* Hort.

Ten leaves studied.

UNITED STATES: California; Lake County; on the Sel River below Hullville, Aug. 11, 1902, A.A. Heller 60k5 (DS); Monterey County; Sur River, Aug., 1903, W.R. Dudley s.n. (DS); Plumas
Plate XIX. Alnus rhombifolia Nutt.

UNITED STATES: California; Shasta County; Round Fountain, June 23, 1929, E. I. Applegate 5346 (US). (x 2.7)
County; 8 miles north of Greenville, Sept. 27, 1921, E.L. Applegate 3346 (DS); San Diego County; 2 miles above Bonita on road to Pala, June 13, 1928, E.L. Wiggins 3072 (DS); Santa Clara County; Stanford University, Sept., 1902, L.F. Abrams 2227 (DS); Shasta County; Round Mountain, June 23, 1929, E.L. Applegate 5846 (DS); Tuolumne County; Stanislaus River near Rawhide, Aug. 7, 1915, Roxana Stinchfield 55 (DS); Idaho; Washington County; Snake River Valley, Sept. 1, 1899, H.F. Jones 6533 (DS); Oregon; near Moro, Rock Creek Canyon, June, 1921, W.C. Lawrence 2916 (DS); Josephine County; Dew Creek, near its crossing of Grant’s Pass-Crescent City Highway, Aug. 11, 1928, Doris K. Kildale 6272 (DS).

Description. - Ovate to slightly rhombic. \( W \) ratio 1.3-1.9 (all but one 1.3-1.7). \( W \) ratio 1.5-2.6 (usually 1.9-2.2). Apex rounded to subacute. Base flat, parallel to No. 1. Margin unevenly dentate to doubly dentate; if unevenly dentate, terminal teeth larger than intersecondary teeth, teeth average to very small, terminal teeth the same size, intersecondary teeth the same size; 0-4 to 0-6 (all but one 0-4 to 0-6) intersecondary teeth, 3-8 (usually 4-6) on principal segment; base with few or no teeth. Craspedodromous. Midrib usually straight, rarely wavy. \( PFS \) ratio 2.2-3.1. Secondary angles 40°-50° at base (in one case 70°), 30°-50° above; secondaries straight, relatively parallel, exhibiting high degree of oppositeness, sometimes all opposite, lower two-thirds of secondaries convex at junction with midrib, 10-15 secondary segments, 2-4 below widest point; spacing 1-2 mm. at base, 6-10 mm. above; basal segment even, sometimes expanding or contracting very slightly. \( PM \) ratio 1.1-1.4, 17-27 (usually 19-24) externals, weak to strong; generally subdued, over half distance to midrib on No. 1 or not at all. Counter-external veins occasionally prominent. 7-14 (usually 10-14) joining, 2-5 intra-angular secondaries, branching; tertiary fold gentle, with pronounced direction changes.
at crest; upper tertiary angles acute to $90^\circ$, the lower obtuse to $90^\circ$; intra-angular angles obtuse to $90^\circ$; terrieries commonly or rarely opposite; circumteriary segments common. Not veins developed to sex-teriary level. Leaf 42-72 mm. long, 32-41 mm. wide.

**Remarks.** - See the discussion under the fossil species *A. corrallina* Lesq., and compare with drawings, Figure 2.


Ser. II: 162, 1833. (Plates XX and XXI).


_Fasc. 13: 157, t. 17, f. 3-4. 1861._

Eleven leaves studied.

UNITED STATES: California; Del Norte County; Crescent City, Aug. 23, 1927, E.I. Applegate 5294 (DS); Humboldt County; Fig Lagoon, June 28, 1906, Doris K. Kildale 2161 (DS); Marin County; near Inverness, along Tomales Bay, Aug. 22, 1931, C. S. Wolf 2343 (1215) (DS) (seedling); Mendocino County; Albion River, June, 1903, James Mackmurphy 13 (DS); Monterey County; Sur Post Office, Aug. 3, 1903, W. R. Dudley s.n. (DS); San Mateo County; Año Nuevo Point, Apr. 18, 1925, J. W. Millespie s.n. (DS); Oregon; Curry County; Rogue River, Agness, May 13, 1932, E. I. Applegate 7192 (DS); Lincoln County; between Elk City and Chitwood on the Yaquina River, Aug. 25, 1929, R. S. Ferris 7766 (DS); Washington County; T2N, R2W, Sec. 6; Dixie Mountain, Davis Farm, Oct. 12, 1940, C. V. Matthews Sheet No. 10 (DS) (Type specimen); Washington; Long Beach, Shoalwater Bay, Aug. 17, 1907, E. A. MacGregor s.n. (DS); Lake Chelan, Stehekin, July 6, 1911, M. E. Jones s.n. (DS).

**Description.** - Oval, ovate, or somewhat rhombic, rarely obovate.

$L/W$ ratio 1.3-1.8. MLT 1.8-2.8 (all but two 1.8-2.1). Apex acute to subacute, rarely rounded. Base always flat, possibly, but not usually parallel to No. 1; basal angle 60°-150° degrees. Margin doubly dentate,
Plate IX. *Alnus rubra* Bong.

UNITED STATES: Oregon; Washington County;
Dixie Mountain, Davis farm, T2N, R2W, Section 6,
Oct. 12, 1940, type specimen, C.V. Mathews
Sheet No. 10 (38). (x 370)
Plate XXI. *Alnus rubra* Bong.

UNITED STATES: California; Humboldt County;
Big Lagoon, June 28, 1906, Doris K. Kildale 2181
(ds). (x 2.5)
the larger dentations prominent and sharp, the minor teeth as minute serrations grouped usually on basiscopic side of larger dentations, apically pointed, margin very distinctive; 0-3 to 0-6 intersecondary teeth, base with few or no teeth. Craspedodromous. Midrib straight. PPS ratio 1.8-3.7 (all but three 2.4-3.2). Secondary angles quite variable, 25°-90° at base (60° the rule), 30°-50° above, the lower angle depending upon basal angle; secondaries straight, randomly opposite, rarely all alternate or opposite. 9-14 secondary segments, 2-4 below widest point; spacing 2-3 mm. at base to 7-9.5 above; basal segment usually expanding, rarely even. P-M ratio 0.3-1.5 (all but one 0.8-1.1). 15-25 (usually 15-19) externals, rather weak, over half distance to midrib on No. 1 or No. 2 secondary, never on both, sometimes not on any; lower externals usually looped. Counter-externals may be prominent. 9-16 joining, 2-4 intra-angular secondaries, branching; tertiary fold gentle; upper joining tertiary angles acute, the lower 90° to acute, the intra-angular angles 90° to acute; secondaries commonly opposite; circumtertiary segments common. Net veins developed to sexternary level. Leaf 45-70 mm. long, 30-50 mm. wide.

Remarks. - Base and margin distinguish it from A. tenuifolia which it superficially resembles. Of these 11 specimens, C.B. Wolf 23b3 (1215) is not A. rubra, but A. tenuifolia. It possesses the A. tenuifolia margin, and base, and has one other feature of A. tenuifolia, a small number (5) of joining secondaries.

Plate XXII. Alnus rubra var. pinnatisecta Starker.

CANADA: British Columbia; Vancouver Island,
Lake Cowichan, June 26, 1940,
C.Y. Mathews s.n. (DS).

(x2.2)
Plate XXXII. **Alnus rubra** var. **pinnatisecta** Starker.
UNITED STATES: Washington; Skamania County;
Clearwater Creek, July 20, 1910,
C.V. Mathews s.n. (US).
(x 2.5)
Two leaves studied.

CANADA: British Columbia; Vancouver Island; Lake Cowichan, June 26, 1940, C.V. Mathews s.n. (DS).

UNITED STATES: Washington; Skamania County; Clearwater Creek, July 20, 1940, C.V. Mathews s.n. (DS).

Description. - Ovate. L/W ratio 1.6-2.2. M/L 1.5-1.6. Apex acute. Base flat, parallel to No. 1. Margin incised or lobed; if incised: small serrations present, 0-3 intersecondary teeth, 3 on principal segment; if lobed: no minor teeth; in both cases, base without teeth. Craspedodromous. Midrib straight. Secondary angles 30° and 50° at base to 25° and 50° above; secondaries straight or curved, randomly opposite, sometimes including Nos. 1 and 2 secondaries. 10-11 secondaries; 3 below widest point; spacing 1-2.5 mm. at base, 7-13 mm. above; base contracting slightly. P-W ratio 0.6-1.0. If lobed, no externals; if incised: 33 externals, weakly developed, extending over half distance to midrib on No. 1. 10-19 joining (depending upon presence of externals), 2-5 intra-angular secondaries; tertiary fold gentle to sharp; joining tertiary angles generally acute, intra-angulars acute or obtuse; secondaries commonly opposite; circumtertiary segments common. Net developed to sextertiary level. Leaf 68-107 mm. long, 31-53 mm. wide.

Remarks. - C.V. Mathews from British Columbia is a form intermediate between A. rubra and C.V. Mathews from Washington. Lobes in the Washington specimen exhibit feather-veined secondaries, the veins always at acute angles. One of the lobes of the Washington specimen has 2
secondary veins.


1826. (Plates XXIV and XXV).


Nine leaves studied.

UNITED STATES: Arkansas; Pike County; New Hope, Oct. 15, 1932, Delcie Demaree 2719 (DS); Massachusetts; Cape Cod; Brewster Township, Blueberry Pond, Oct. 13, 1929, R. Padicaluri 2121 (DS); New York; head of Cayuga Lake, Sept. 12, 1883, T. H. Dudley s.n. (DS); Oklahoma; LeFlore County; Page, Sept. 6, 1913; C. W. Stevens 2619 (DS); Kentucky County; Broken Bow, July 11, 1926, E. A. Palmer 10492 (DS); Pennsylvania; Luzerne County; Lily Lake, July 31, 1926, S. H. Heider, 14, 179 (DS); South Carolina; Anderson County; Simpson's Mill, Aug. 29, 1914, John Davis s.n. (DS); Texas; Wood County; Lake Ellis, June 14, 1940, C. L. Lindell and Amelia L. Lindell 9489 (DS); West Virginia; Raleigh County; Beckley, July 17, 1931, S. L. Core 3137 (DS).

Description. - Obovate to oval, faintly rhombic. L/W ratio 1.6-2.0. NLI 2.3-3.6 (usually 2.3-3.0). Apex apiculate, rounded, or subacute. Base flat, usually not parallel to No. 1; basal angle characteristically 60°-85°. Margin very finely serrate, occasionally very finely dentate, terminal teeth slightly larger than intersecondary teeth; 0-4 to 0-7 intersecondary teeth, 3-5 on principal segment; base almost without teeth, or with very minute teeth at outer edge. Craspedodromous, tending toward dictyodromy. Midrib straight. PFS ratio 2.6-3.9 (all but one 2.6-3.4). Secondary angles 40°-70° below, 40°-60° above,
Plate XXIV. Alnus rugosa (Du Roi) Sprang.
UNITED STATES: Oklahoma; McCurtain County; Broken Bow,
July 1st, 1926, E. J. Palmer 10.4.22 (Os). (x 3.1)
Plate XIX. Alnus rugosa (Du Roi) Spreng.
UNITED STATES: [ARKANSAS] Pike County; New Hope, Oct. 15, 1932, Delius 3749 (US). (x 2.3)
generally 55°-60° below, 45°-50° above; secondaries slightly concave, randomly opposite, including Nos. 1 and 2 secondaries, or all alternate. 10-13 secondary segments, 3-5 (usually 3-4) below widest point; spacing 1-3.5 at base to 6.5-9.5 mm. above; basal segment occasionally even, usually expanding. P-W ratio 1.0-1.5. 18-28 externals (all but one 18-23), rather weak, sometimes over half distance to midrib on No. 2, rarely on No. 1, sometimes on none. 6-12 joining, 3-5 intra-angular tertiaries; tertiaries straight to slightly folded, often wavy or sinuous en route; upper tertiary angle acute, lower either acute or obtuse, intra-angular angles acute or obtuse; tertiaries rarely opposite; few or no circumtertiary segments. Net veins developed to sexternary level. Leaf 43-73 mm. long, 23-44 mm. wide.

Remarks. - This species is similar in many respects to A. rhom- 
bifolia, to which it is closely related. But A. rugosa shows a finer, more evenly toothed (usually serrate) margin, a frequent suggestion of dictyodromy, a slightly obovate-oval shape, a high ILT, and several other characters.

1842. (Plate XVI).

Alnus incana var. glauca Regel. non. Betul. in Mem. Soc. 

Alnus incana var. virescens "ats. Brewer & Watson Bot. 
Calif. II: 81. 1880.

t.78. 1892.
Plate XXVI. *Alnus tenuifolia* Nutt.

UNITED STATES: Arizona; Rincon Mountains, Manning Camp, Sept. 27, 1909, J.C. Blumer 3420 (US). (x 2.3)
Twelve leaves studied in detail; 5 in general.

ALASKA: Fairbanks, July 30, 1934, F.W. Went 326 (UC).

CANADA: British Columbia; 6 miles north of Kingsgate on Boyle River, July 2, 1914, J.A. Weber 2238 (UC); Mackenzie District; Yellowknife, July 9, 1919, H. J. Cody and J. B. McCanse 2531 (IC); Yukon Territory; 3 miles east of Dawson, Bear Creek, June 20, 1919, J. A. Calder and L. G. Millard 3220 (UC).

UNITED STATES: Arizona; Rincon Mountains, Manning Camp, Sept. 27, 1909, J. C. Blumer 3120 (DS); California; Sierra County; Packer Lake Creek, July 2, 1926, H. A. Parker 53 (DS); Siskiyou County; North Fork of Salmon River, July 7, 1928, Doris K. Kildal 55th (DS); Colorado; Montrose County; south of Cerro Summit, Sept. 2, 1937, R. C. Rollins 192 (DS); Idaho; Latah County; Viola Mountains, Flanagan Creek, Viola-Pottach Road, July 19, 1919, K. S. Ferris and Dana Duthie 1330 (DS); Montana; Flathead Lake, Big Fork, July 15, 1908, Mrs. Joseph Cleere s.n. (DS); Park County; southeast of Livingston, Little Mission Creek, Aug., 1950, A. A. Meyerhoff s.n.; Nevada; Elko County; East Fork of Prineau River, July 31, 1937, Percy Brain 577 (DS); New Mexico; San Miguel County; upper part of Capelle River, July 15, 1917, R. S. Ferris 11,543 (DS); Oregon; upper Rogue River region, July 12, 1929, A. E. Applegate 2967 (DS); Utah; San Juan County; 4 miles west of Utah-Colorado line, LaSal Creek, July 9, 1929, H. C. Cutler 2612 (DS); Washington; Night Hawk, Sept. 23, 1911, E. E. Jones s.n. (DS); Wyoming; Carbon County; Pass Creek, Aug. 20, 1901, E. W. Gooding 316 (DS).

Description. - Broadly to moderately oval. L/M ratio 1.1-1.8. M/L 1.6-2.1. Apex acute to subacute. Base small, flat, parallel to subparallel to No. 1, 150^0 to 180^0. Margin doubly dentate, small to average sized; 0-5 to 0-9 intersecondary teeth, 5-9 on principal segment; base with teeth. Craspedodromous. Midrib straight, occasionally bending within 8 mm. of apex. PPS ratio 1.6-3.6 (all but two being 2.1-3.0). Secondary angles 50^0-90^0 at base, 10^0-50^0 above (generally 50^0-65^0 at base, 10^0-50^0 above); secondaries straight, randomly opposite, Nos. 1 and 2...
most commonly so, rarely all alternate. 10-13 secondary segments, 2-6 (usually 3-4) below widest point; spacing 0.5-2.5 at base, 7-10 mm. above; basal segment even or contracts. P-M ratio 0.8-1.5 (all but one 1.1-1.5). 17-33 (usually 17-23) externals, moderately strong to weak, those on Nos. 1 and 2 often looped, over half distance to midrib on No. 1, occasionally on No. 2 or both. 6-11 joining, 2-3 intrangular tertiaries, rarely 4, branching; tertiary fold gentle, usually with sharp change in direction at crest; upper joining tertiary angles acute, the lower and the intra-angulars about 90°; tertiaries commonly opposite; circumtertiary segments common. Net veins developed to sexternary level. Leaf 44-105 mm. long, 31-75 mm. wide.

Remarks. - Though perhaps only a variety of *A. incana* (vice versa), this form generally is distinct. On the whole the relationship is close. Weber 2238 is indistinguishable from *A. incana*. *A. tenuifolia* is often compared with the fossil *A. carpipinoides* Lesq., but it will be shown later that this is probably a bad comparison.


Light leaves studied.

CHINA: Anhwei; Kwantung, Po Shan, Oct. 26, 1926, F.A. McClure 4030 (UC); Chekiang; Tien-tai-hsien, July 1, 1932, S. Chen 4927 (US); Chekiang; Tihtainan, May 5-13, 1924, R.C. Ching 1524 (UC); Fukien; northern part near Chekiang border, Aug., 1926, R.C. Ching 2295 (UC); Kwantung; northwestern part near Hunan border, Kau-Kung, Aug., 1928, Fenzel 50 (UC); Kwantung; Loh Ch'ang District; Chong Uen
Plate XXVII. *Alnus trabeculosa* Hand.-Mazz.
CHINA: Chekiang; Tien-tai-hsien, July 1, 1932,
S. Chen 468 (C3). (x 3.0)
Plate XXVIII. *Alnus trabeculosa* Hand.-Mazz.
CHINA: northwestern Kwantung near Hunnan border;
Saufung, August, 1928, Fenzel 50 (UC). (x 3.6)
Plate XXIX. Alnus trabeculosa (?) Hand.-Mazz.
CHINA: Kweichow; Kweiting, June 30, 1930,
y. Tsien: 5499 (UC). (x 3.3)
Shan near Kau-Fung, Nov. 2-20, 1932, W.T. Tsang 20650 (UC); Kwantung; Lokchong, near Jui-feng, Hwan-kun, Oct., 1928, Y. Tsang 123h (UC); Kweichow; Kweiting, June 30, 1930, Y. Tsang 5499 (UC).

Description.—Oval, broadly oval, roundish. L/W ratio 1.4-2.2 (usually 1.4-1.7). WLT 1.5-2.2 (usually 1.9-2.2). Apex abruptly acuminate, acute, subacute, or rounded. Base round, rarely parallel to no. 1. Margin serrate, varying from unevenly and sparsely so to evenly and thickly serrate; one specimen with sinusous margin, teeth variable in size; 0-3 to 0-6 intersecondary teeth, 3-5 on principal segment, base with teeth. Prochidodromous to dictyodromous; where dictyodromous, also slightly craspedodromous. Midrib straight. PPS ratio 2.4-5.1. Secondary angles 50-100° at base, 90-120° above; secondaries concave, randomly opposite or none opposite. 7-15 secondary segments (usually 11-15), 2-5 below widest point; spacing 1-2 mm. at base, 6.5-12 mm. above; basal segment usually contracting, rarely expanding. P-W ratio 0.6-1.1 (usually 0.7-1.1; only Y. Tsang 5499 0.4). 10-15 externals, slight; external areas not overlapping; few externals above no. 5, often departing from secondaries as forks, over half distance to midrib on no. 1, less often on no. 2. 6-10 (usually 6-7)Joining, 2-4 (usually 2-3) intra-angular secondaries, simple except in Tsang 5499; secondaries straight except in Tsang 5499; upper joining tertiary angles acute, the lower and intra-angular angles obtuse; secondaries commonly opposite (except in Tsang 5499). Net veins developed to sexternary level. Leaf 38-76 mm. long, 22-46 mm. wide.

Remarks.—Tsang 5499 is not A. trabeculosa but is related to it. It is shown on Plate XXIX.
Fossil species of Alnus

An insufficient number of fossils was studied to make any final conclusions. However, despite the lack of time, which prohibited further fossil studies, one fact emerges: the method used in this study is quite successful in its application to fossils, as well as to living plants.


Pl. LI. f.1-3. 1883. (Figure 2).


Immediately we encounter the difficulties of paleobotany. Knowlton assigned a series of leaves to *Prunus*. The leaves of *Prunus* do not resemble those of *Alnus* at all. In my opinion, there is also some doubt about relegating *A. hollandica* to synonymy.

Two leaves studied in detail; several other studied by means of plates, which, unfortunately, do not show all the detail frequently found on the specimens themselves.


Description. - Ovate or slightly rhombic. L=W ratio 1.4-1.8. MLP 1.3-2.0. Apex subacute. Base flat, parallel to No. 1. Margin
Figure 2. Reproductions of Lesquereux's original figures (1883) of Alnus corrallina LesqX. and Alnus carpinoides LesqX.
unevenly dentate, terminal teeth larger and more pronounced than inter-
secondary teeth, terminal teeth same size, intersecondary teeth same
size; teeth small; 0-2 to 0-3 intersecondary teeth, 2-3 on principal
segment, base without teeth. Craspedodromous. Midrib straight. FFS
ratio 2.8-2.9. Secondary angles 55° at base to 45°-55° above; secondaries
almost parallel, straight, all opposite or nearly opposite. 10 sec-
dary segments, 3 below widest point; spacing 1-2 mm. at base, 7.5-9 mm.
above; basal segment even. P-W ratio 0.9-1.1. 12-14 externals, weak
to moderately strong, over half distance to midrib on No. 1. 3-13
joining, 3 intra-angular terciaries; tertiary fold gentle; all tertiary
angles acute; terciaries commonly opposite; circumtertiary segments not
common. Mes well developed to sexternary level. Leaf 55-70 mm. long,
31-46 mm. wide.

Remarks. - This leaf is almost identical with that of A. rhom-
bifolia. Except for the circumtertiary segments, almost every other
major detail is matched.

LacCunitie (1933) figures Univ. Calif. Coll. Paleob. 567 as a
paratype of Betula lacustris MacG. This error is apparent upon compari-
son of this specimen with his other figured specimens of B. lacustris
(Univ. Calif. Coll. Paleobot. 566 and 568). When I examined these speci-
mens, the words Almus were written upon No. 567 so that doubtless a
mistake was made in the preparation of the illustrations. Chaney
(personal communication) believes that No. 567 is typical of the fossil
leaves which he has been calling A. carpinoides Leaix. Thus, in addi-
tion to the error of LacCunitie, there is apparently some confusion
between the two fossil species, \( A. \) carpinoides and \( A. \) corrallina.

Univ. Cal. Coll. Paleont. No. 567 corresponds closely in its details to \( A. \) rhombifolia Nutt., one of the Pacific coast alders. The relationship between \( A. \) corrallina Lesq. and \( A. \) rhombifolia Nutt. is well established by the work of Scott (1926), and is supported by the findings of others (Brown, 1937; Condit, 1938).

Reference to the work of Lesquereux (1863) shows that \( A. \) corrallina is distinct from \( A. \) carpinoides. Lesquereux's drawings are reproduced in Figure 2. The upper two drawings are of \( A. \) corrallina. Compare these two drawings with \( A. \) rhombifolia shown in Plate XIX.

Lesquereux's drawings of \( A. \) carpinoides are either too poor, or insufficient diagnostic detail was lacking in the fossil specimens themselves to make drawings good enough for determining the modern equivalent, if any, of \( A. \) carpinoides. I believe that the modern equivalent of Figure 11, Plate L and Figure 5, Plate LI as drawn by Lesquereux (See Figure 2) is \( A. \) crispa sinuata, also referred to commonly as \( A. \) sinuata, \( A. \) sitchensis, \( A. \) viridis, or \( A. \) alnobetula. But without more detail, Figure 4, Plate LI of Lesquereux may not even be a species of Alnus, but of Carpinus. None the less, Figure 11, Plate L and Figure 5, Plate LI are of Alnus. Reference to Figure 2 will show that these latter two figures of Lesquereux are quite different from his drawings of \( A. \) corrallina.

\( A. \) carpinoides is compared frequently with the living alder \( A. \) tenuifolia Nutt. to which it bears a slight resemblance (Chaney, 1925; LaMotte, 1936; Brown, 1937; Condit, 1938). However, its margin and base are totally different from those of \( A. \) tenuifolia (compare the
drawings of *A. carpinoides* reproduced in Figure 2 with Plate XXVI of
*A. tenuifolia*. The doubly dentate margin of *A. tenuifolia* is one of
that species’ identifying characters, a character which does not ap-
pear at all in Lesquereux’s specimens. The drawings by Lesquereux of
*A. carpinoides* compare very favorably with specimens of *A. crispa sinuata*,
unfortunately not chosen for illustration in my own plates of *A. crispa
sinuata*.

Brown’s plate (1937; Pl. 48, f.1,5.) purporting to illustrate
specimens of *A. carpinoides* may not be this species at all, for it is
not similar to Lesquereux’s drawings. The leaf illustrated in Brown’s
Figure 5, Plate 48, while superficially resembling some of my own speci-
mens of *A. crispa sinuata*, shows an even more striking resemblance to
*Betula chinensis* Maxim. or to *Betula alnoides* Buch.-Ham., both of which
live today in China. The large marginal teeth in Brown’s figure indi-
cate that this specimen is *Betula*. It is certainly not similar to *A.
tenuifolia* in any respect, nor is it very similar to Lesquereux’s plates.
However, this leaf of Brown’s must be examined in detail, for the figure
does not show sufficient diagnostic detail.

LaMotte (1936) identified Univ. Cal. Coll. Paleob. No. 790 (Plate
7, Figure 1) as *A. carpinoides* Lesq. He allies it with the living *A.
tenuifolia*. This specimen, too, while only examined generally by myself,
shows almost all the characters of *A. rhombifolia* Nutt.

Chaney (personal communication) regards the fossil *A. hollandia*
Jennings as a synonym of *A. carpinoides* Lesq. Brown (1937) lists it as
a synonym of *A. corallina* Lesq., which illustrates the confusion exist-
ing in the literature. Jenning’s plates are too inconclusive for a final
decision, but they together with his description of the species suggest that this fossil species is closely related to the living eastern alder, *A. rugosa* (Du Roi) Spreng. Brown (1937) recognized this possible equivalence, but also suggests that *A. rugosa* is close enough to *A. rhombifolia* to be placed in synonymy with *A. corrallina*, the fossil equivalent of *A. rhombifolia*.

Nevertheless, if it can be demonstrated that *A. hollandia* is more closely related to *A. rugosa* (and this should not be difficult if the fossil species has not changed appreciably), then *A. hollandia* is a valid species, and should not be placed in the synonymy of *A. corrallina*. It should definitely not be placed in synonymy with *A. carpinoides* as Chaney (personal communication) has considered doing. Were this done, *A. corrallina* would equal *A. carpinoides*!

In conclusion, *A. corrallina*, illustrated in Figure 2, is related to *A. rhombifolia*; *A. carpinoides* may be related to *A. crispa sinuata*. More study should be made of *A. carpinoides* which is confused with *A. corrallina* in current paleobotanical literature. New and old specimens alike must be compared carefully with the original or type specimens, and with *A. hollandia*, before any further confusion is caused.
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<th>A chart for the determination of species of Alnus</th>
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<td>Craspedodromous</td>
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<td>Brachyodromous</td>
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<td>Dictyo-dromous</td>
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<td>True camptodromous</td>
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<td>Apex acuminata</td>
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<td>Apex apiculate</td>
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<td>Apex round</td>
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<td>Base round</td>
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<td>Base subcordate</td>
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<td>Margin serrate</td>
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<td>Margin doubly dentate</td>
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<td>Intersec. teeth 0-1 to 0-9</td>
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<td>Intersec. teeth 0-10 to 0-15</td>
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<td>Leaf base 60° - 90°</td>
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<td>Leaf base 150° - 180°</td>
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<td>Lower sec. convex at midrib</td>
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<td>All sec. concave-str. at midrib</td>
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<tr>
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<td>Basal segment 0</td>
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<td>Basal segment contracts, not 0</td>
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<td>Basal segment even</td>
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<td>Basal segment expands</td>
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<td>No. tertiary veins 0-9</td>
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<td>Margin serrate</td>
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<tr>
<td>Margin dentate</td>
<td>x</td>
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<tr>
<td>Margin doubly dentate</td>
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<td>Margin lobed</td>
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<td>Margin sinuous</td>
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<td>Intersec. teeth 0-1 to 0.5</td>
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<tr>
<td>Intersec. teeth 0.5 to 0.9</td>
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<td>x</td>
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<tr>
<td>Intersec. teeth 0-10 to 0-15</td>
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<tr>
<td>Leaf base $60^\circ - 90^\circ$</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>x</td>
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<tr>
<td>Leaf base $90^\circ - 120^\circ$</td>
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<tr>
<td>Leaf base $120^\circ - 150^\circ$</td>
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<tr>
<td>Leaf base $150^\circ - 180^\circ$</td>
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<tr>
<td>Lower sec. convex at midrib</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>All sec. concave - str. at midrib</td>
<td>x</td>
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<tr>
<td>No. externals 0</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>No. externals 1-15</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>No. externals 16</td>
<td>x</td>
<td>x</td>
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<td>x</td>
<td>x</td>
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<tr>
<td>Basal segment 0</td>
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<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>x</td>
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<tr>
<td>Basal seg. contracts, not 0</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>Basal segment even</td>
<td>x</td>
<td>x</td>
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<td>x</td>
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<tr>
<td>Basal segment expands</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>No. tert. veins 0-9</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>No. tert. veins 10-21</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>No. tert. veins 22</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Most tertiaries simple</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>x</td>
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<tr>
<td>Most tertiaries branch</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Tert. commonly opposite</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Tert. rarely opposite</td>
<td>x</td>
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<tr>
<td>Tertiaries straight</td>
<td>x</td>
<td>x</td>
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<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Tertiary fold gentle</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Tertiary fold sharp</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Lower tert. angle $90^\circ$ - acute</td>
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<td>x</td>
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<tr>
<td>Lower tert. angle $90^\circ$ - obtuse</td>
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<td>x</td>
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<tr>
<td>Intra-angulares acute</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Intra-angulares obtuse</td>
<td>x</td>
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<tr>
<td>Circumtertiary seg. common</td>
<td>x</td>
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89 specimens of extant Betula studied; two fossil specimens. Chart 2.

Description.—Base usually flat or round, rarely cordate or subcordate, most commonly symmetrical, may be asymmetrical. 0-1 to 0-7 intersecondary teeth, except for B. maximowiczii with 0-9; teeth, on the average, larger for leaf size than in any of the other genera. Craspedodromous, very rarely dictyodromous. 75% of midribs crooked, characteristically, but not always, thick. Basal segment most commonly contracting to 0 at midrib on at least one side of the leaf base.

Externals large and prominent, particularly on No. 1 secondary; largest number of externals on No. 1 secondary vein, occasionally the same number on the No. 2 as on the No. 1; externals extending over half distance to midrib on the No. 1, on very rare occasions on the No. 2. Tertiary mostly branching; tertiary folds sharper than in Alnus; tertiary angle almost always acute, including the intra-angular angle. Met vein endings common and complex.

Because there is so much variation within Betula, Winkler's (19 subdivisions of the genus will be considered individually:


Subsection COSTATAE (incl. subsection Lentae) Regel. in A.D.C. Prodr. IVI. 2: 162. 1868.

This subsection includes all those types likely to be confused with Alnus on one hand (B. corylifolia and B. nigra) and with Carpinus on the other hand (Subsection Lentae: B. chinensis, B. ermanii, B. insignis, B. lenta, B. lutea, and B. utiliss and its varieties).
Description of the *B. corylifolia-nigra* group: Base flat, without teeth. Margin with large dentations, or doubly dentate. Basal segment even. Few or no externals in *B. corylifolia*, almost none above No. 5 secondaries in *B. nigra*.

The second group in the subsection *Costatae* (subsection *Lentae*) has almost all of the characteristics of *Carpinus*, with two exceptions: (1) The net vein endings in the *Lentae* are very complex and numerous; (2) the intra-angular tertiary angles of the lower one-half of the leaves of the *Lentae* are always acute or else the majority of the intra-angular tertaries exhibit acute angles. The intra-angular angle in *Carpinus*, from apex to base of the leaf, is generally obtuse. *Betula delavayi* Franch. and *Betula ulmifolia* Sieb. & Zucc. var. *costata* (Traut Regal, also of the *Lentae*, were obtained late in this study. It was found that both characters hold true for them as well.

Subsection *NANAE* Regel. in A.D.C. Prodr. XVI. 2: 162. 1868.

This subsection includes *B. nana* and *B. pumila*. These have the following characters: the only blunt and rounded apices in the genus, rounded bases, large teeth for such small leaves, no teeth on base, concave-straight secondary veins with a concave attachment at midrib, very few secondary segments, no externals above the No. 4 secondaries.


This subsection includes *B. japonica szechuanica*, *B. papyrifera* and its varieties, *B. populifolia*, *B. pubescens*, *B. verrucosa*, and the fossil species *B. lacustris*. This group is characterized by broadly
ovate leaves, acuminate apices, a flat base not parallel to the
No. 1 secondaries, few secondary segments, 1, or at the most 2 below
the widest point, a fair angular divergence between the Nos. 1 and
2 secondaries, external veins rare above the Nos. 4 or 5 secondaries,
large external overlaps, wide spacing of secondary and tertiary veins,
and relatively sharp tertiary folds.
Mosc. 13: 73. 1861.


This group includes B. alnoides, B. luminifera, and B. maximowiczii. The distinguishing characters are: a serrate or dentate
margin consisting of fairly large, long, acuminate teeth, and intra-
angular tertiary angles which are commonly obtuse. In B. alnoides
and B. luminifera, there are 0-1 to 0-3 intersecondary teeth; in B.
maximowiczii, there are 0-9 intersecondary teeth.

Extant species of Betula

1. BETULA ALNOIDES Buch.-Ham. in D. Don. Prodr. fl. nepal.: 58. 1825.


Two leaves studied.

CHINA: Yunnan, southern part; between Keng Hung and

INDIA: Siwalik or Jaunsar Division; Chakrata, Apr. 17,
1922, Babu Ram 113 (UC).
Plate XIX. *Betula alnoides* Buch.-Ham.
INDIA: in Siwalik or Sunkar Division; Chakra, Apr. 17, 1922, Babu Ram 113 (UC). (x 2.4)
Description. - Ovate. L-M ratio 1.7-2.2. MLT 1.5-1.7. Apex acute. Base round, smooth to within 1 cm. of midrib, or flat, parallel to No. 1. Margin unevenly serrate; terminal teeth large and long (3 mm.) with short, average sized intersecondary teeth (1 mm.); 0-3 intersecondary teeth, with 3 on principal segment; base with teeth on outer edge. Graspodialomous with tendencies toward dictyodromy, or dictyodromous. Midrib crooked, sometimes only in upper one-third. PPS ratio 3.0. Secondary angles 60° below, 45° above; lowest secondaries strongly convex at junction with midrib, making a 30° angle; secondaries straight, bending at margin, randomly opposite including Nos. 1 and 2 secondaries. 10-11 secondary segments, 2-3 below widest point; spacing 0-1 at base, 3-9 mm. above; basal segment 0 at midrib or even, without contracting. P-M ratio 1.2-1.3. 11 externals, 5 on No. 1 secondary, strong, over half distance to midrib on No. 1, rarely on No. 2. 11 joining, 4 intra-angular terciaries; tertiary fold gentle; upper and lower tertiary angles acute, intra-angulars tending to be obtuse; terciaries commonly opposite; circumtertiary segments fairly common. Net veins developed to sexternary level. Leaf 59-70 mm. long, 32-41 mm. wide.

Remarks. - Except for the distribution of external veins and the crooked midrib, this leaf resembles Alnus. Compare this leaf with Brown's illustration of Alnus carpinoides Lesq. (Brown, 1937, Pl. 48, fig. 5).

Plate XXXI. *Betula chinensis* Maxim.

CHINA: Hopei; Po Hau Shan, June, 1926,
T.F. King 73 (US). (x 3.0)
Two leaves studied.

CHINA: Chihli; Pei T'ai road, Hsiao Wu T'ai Shan, Aug. 6, 1928, J.C. Liu 1903 (US); Hopei; Po Hua Shan, June, 1926, T.F. King 73 (US).

Description. - Ovate. L-W ratio 1.0-1.4. KL 1.5-1.6. Apex acute. Base round, smooth and flat to 8 mm. away from midrib. Margin coarsely and unevenly dentate to doubly dentate, teeth average to large, terminal teeth larger than intersecondary teeth, most on intersecondary teeth clustered below terminal teeth; 0-4 to 0-5 intersecondary teeth, 0-5 on principal segment, base with teeth. Craspedodromous. Indications of dictyodromy. Midrib crooked, offset at junctions with secondaries. PPS ratio 2.2-2.6. Secondary angles 70° below, 40° above; secondaries straight, lower half to three-quarters strongly convex at junction with midrib, all opposite or subopposite. 10-11 secondary segments, 2 below widest point; spacing 0-1.5 below, 5-8 mm. above; basal segment 0 on at least one side of midrib. P-W ratio 1.0-1.1. 19-23 externals, moderately strong, 6 on No. 1, 5 above the No. 5, over half distance to midrib on the No. 1, sometimes on the No. 2. 7 joining, 2 intra-angular secondaries, mostly branching; tertiary fold rather sharp; all tertiary angles acute; secondaries commonly opposite; circumtertiary segments common; course of individual secondaries irregular, sometimes forming a sag toward midrib midway in their courses. Net veins developed to sexternary level. Leaf 38-57 mm. long, 38-40 mm. wide.
Plate XXXII. *Betula corylifolia* Regel & Maxim.
JAPAN: Honshu; Nagano Prefecture; Mount Shirouma, July 28, 1917, Shipetaka Suzuki UC-51 (UC). (x 3.9)
Remarks. - Somewhat similar to *A. crispa sinuata* except for number of intersecondary teeth.


One leaf studied.


**Description.** - Oval-rhombic. **L-W** ratio 1.8. **MLT** 2.2. Apex acute. Base flat, parallel to No. 1. Margin coarsely serrate, only large terminal teeth, intersecondary teeth rare, teeth 3 mm. by 3 mm. in size, base without teeth. Graspedodromous. Midrib straight. **PPS** ratio 2.2. Secondary angles 50° below, 40° above; secondaries straight, close together, parallel, bending at margin, randomly opposite. 12 secondary segments, 3 below widest point; spacing 1 mm. at base, 6 above; basal segment uniform. **P-M** ratio 0.8. No external veins, without intersecondary teeth present. 3 joining, 2 intra-angural tertiaries, branching; tertiary fold gentle to sharp; upper and lower joining tertiary angles acute; intra-angural angles acute above, obtuse below; tertiaries rarely opposite; circumtertiary segments common. Met veins developed to sexternary level. Leaf 41 mm. long, 23 mm. wide.

Remarks. - This species is similar to *Alnus* in many respects. Winkler (1904, p.60, fig.17) shows occasional intersecondary teeth, and associated externals.

Plate XXXIII. Betula ermanii Cham.
JAPAN: H. Manabe s.n. (US 1542015). (x 3.0)
One leaf studied.

**JAPAN**: locality unknown, date unknown, H. Manabe s.n. (DS 164, 315).

**Description.** - Broadly ovate. L/W ratio 1.5. MLT 1.5. Apex acuminate. Base round, symmetrical. Margin coarsely dentate, somewhat unevenly so; teeth average to large, terminal teeth largest; 0-3 intersecondary teeth, 3 on principal segment, base with teeth. Craspedodromous. Midrib crooked. PFS ratio 2.2. Secondary angles 70° at base, 45° above; secondaries straight, bend at margin, only No. 1 secondaries opposite. 12 secondary segments, 2 below widest point; spacing 0-0.5 mm. at base, varying on either side of midrib, 6 mm. above. P-W ratio 1.3. 19 externals, 5 on No. 1, 4 above No. 5, moderately strong; over half distance to midrib on No. 1. 9 joining, 2 intra-angular tertiaries; tertiary fold gentle; all tertiary angles acute; circumtertiary segments common; tertiaries irregular in course. Net veins developed to sexternary level. Leaf 50 mm. long, 33 mm. wide.

**Remarks.** - This leaf appears at first glance to be more closely related to subsection *Albae*, but actually has most of the characters of subsection *Costatae* to which it belongs.


One leaf studied.

**CHINA**: Szechuan; southeastern Tachienlu, Aug. 19, 1930, W.C. Cheng 1745 (DS).

**Description.** - Narrowly oval to lanceolate. L-W ratio 2.6. MLT
Plate XXXIV. Betula insignis Franch.
CHINA: Szechuan; southeastern Tachienlu,
Aug. 19, 1930, W.C. Cheng 1745 (DS). (x 2.7)
1.8. Apex narrowly acute. Base round, symmetrical. Margin unevenly dentate; 1 intersecondary tooth between each pair of terminal teeth on lower three-quarters of leaf, none in upper one-quarter, 1 on principal segment; base with 1 tooth on each side of midrib. Dictyodromous. Midrib straight. PPS ratio 5.2. Secondary angles uniformly 55°; secondaries straight, bending into loops at margin, randomly opposite. 15 secondaries; 5 below widest point; spacing 0 mm. at base, 5.5 mm. above, basal segment contracting to 0. P-V ratio 0.7. No externals. 9 joining, 2 intra-angular terciaries, branching; upper and lower tertiary angles 90° to slightly acute, intra-angular acute; tertiary veins commonly opposite; circumtertiary segments scattered, not too common; terciaries irregular in course. Net veins developed to quinquenary level; net orders not well differentiated, of equal dimensions. Leaf 57 mm. long, 22 mm. wide.

Remarks. - The species is similar in many respects to *Almus firma*, except for the teeth and the type of base.


One leaf studied.

CHINA: Szechuan; western Tachienlu, June 20, 1930, W.C. Cheng 1251 (DS).

Description. - Broadly ovate. L-W ratio 1.4. WLT 1.7. Apex acuminate. Base flat, not parallel to No. 1, asymmetrical. Margin unevenly dentate, terminal teeth largest, teeth as a whole small; 0-4 intersecondary teeth, 4 on principal segment, base with teeth at outer
Plate XXXV. Betula japonica Sieb. var. szechuanica Schneid.
CHINA: Szechuan, western Tachienlu, June 20, 1930,
W.C. Cheng 1251 (US). (x 2.3)
Secondary angles 40°-50° at base, 30° above; secondaries
straight, all alternate. 9 secondary segments, 1 below
widest point; spacing 0 mm. (rarely 0.5 mm.) at base, 12 mm.
above. P-M ratio 1.9. 11 externals, strong, none above No.
5, over half distance to midrib on No. 1. 7 joining, 6 intra-
angular tertiaries, branching; tertiary fold sharp; all tertiary
angles acute; tertiaries rarely opposite; circumtertiary seg-
ments common; medials developed. Net veins developed to sex-
ternary level. Leaf 58 mm. long, 41 mm. wide.

Remarks. — This species resembles B. verrucosa in
several respects. Studies should be made to determine the
various ways in which it differs from B. verrucosa.

7. BETULA LENTA L. Spec. pl.: 983.
1753. (Plate XXXVI).

Betula nigra Du Roi. Obs.: 30. 1771.
Betula carpinifolia Ehrh. Beitr. z. Naturk. VI:
99. 1791.


Betula lenta ♀ typica Regel. in A.DC. Prodr. XVI.
2: 179. 1868.
Plate XXVI. *Betula lenta* L.

UNITED STATES: Pennsylvania; Elk County; Whippoorwill Camp of J. W. Boise Lumber Company, June 20, 1911, A. H. Heller, 10,311 (35).

(x 2.2)
One leaf studied.

UNITED STATES: Pennsylvania; Elk County; Whippoorwill Camp of Du Bois Lumber Company, June 20, 1911, L.A. Heller 10,311 (DS).

Description. - Oval-ovate. L/\(W\) ratio 1.9. M/L 1.7. Apex acute. Base round, asymmetrical. Margin fairly evenly serrate, terminal teeth only slightly larger than intersecondary teeth, small; 0-6 intersecondary teeth, 3-6 on principal segment, base with teeth. Craspedodromous, partially dictyodromous. No. 1 secondaries with true camptodromy. Midrib straight, exceedingly thin at top. PPS ratio 2.7.
Secondaries ho-50\(^{\circ}\), relatively parallel, straight, bending at margin, mostly opposite. 15 secondary segments, 3 below widest point; spacing 0 mm. at base, 7.5 above, basal segment contracting to 0. P-M ratio 1.4. 2\(^{\circ}\) externals, 11 above No. 5 secondary, weakly developed, over half distance to midrib on the No. 1. 11 joining tertiaries, 2 intrangulars; tertiary fold gentle; all tertiary angles slightly acute; tertiaries rarely opposite; circumtertiary segments common; tertiary veins irregular in course. Net developed to sexternary level. Leaf 68 mm. long, 35 mm. wide.

Remarks. - The leaves of this species, if not identical with those of \(B.\) lutea, are probably indistinguishable from them.

Three leaves studied.
Plate XXXVII. *Betula luminifera* H. Winkl.

CHINA: Chekiang; Tien-tai-shan, Aug. 3, 1932, S. Chen 481 (US). (x 2.2)
CHINA: Anhwei; southern part; Wu-yuan, Chang Gon Shan, Aug. 17, 1925, Ren-Char Ching 3238 (UC); Chekiang; Tien-tai-shan, Aug. 3, 1932, S. Chen 181 (OS); Kwansi, June 10, 1928, R. C. Ching 5924 (UC).

Description. - Oval. L/W ratio 1.8-2.2. M/L 1.9-2.0. Apex acute to abruptly acute. Base flat, not parallel to No. 1. Margin coarsely serrate, teeth rare to common, scattered, long, pointed, tips of teeth hooking toward apex; terminal teeth largest; intersecondaries smaller; 0-2 to 0-6 intersecondary teeth, 2 on principal segment, base with few or no teeth. Craspedodromous to dictyodromous. Midrib straight to crooked, very thick. PFS ratio 2.7-3.1. Secondaries 35° to 40° straight, relatively parallel, randomly opposite; sometimes only No. 1 secondaries opposite. 10-14 secondary segments, 3 below widest point; spacing 0 at base, 8-11.5 mm. above, basal segment usually contracting to 0 but sometimes 0.5 on one side of midrib. P-W ratio 1.0-1.2. 5-17 externals, none above No. 5 in two specimens, branching; tertiaries straight to gently folded; upper joining tertiaries acute, lower 90° to slightly acute, intra-angular angles 90° to slightly acute; tertiaries rarely opposite; circumtertiary segments rare to fairly common. Net developed to sexternary level. Leaf 68-80 mm. long, 33-38 mm. wide.

Remarks. - The margin resembles that of Betula maximowiczii.

9. BETULA LUTEA Michx. f. Hist. arb. forest d. 1'Am. II: 152. t. 5. 1812. (Plate XXXVII).


Betula lenta var. lutea Regel. in A.D.C. Prodr. XVI. 2: 179. 1868.
Plate XXXVIII. *Betula lutea* Michx.

UNITED STATES: Vermont; Rutland County; Rutland, Oct. 3, 1898, W.W. Eggleston 344 (US). (x 2.4)
Nine leaves studied.

CANADA: Nova Scotia; Digby County; Bear River, Oct. 5, 1924, J.J. Jack 3715 (UC).

UNITED STATES: Maine; Troy, Aug. 9, 1909, S.S. Berry s.n. (DS); Massachusetts; Hampshire County; south of Northampton; summit of Mt. Tom, Aug. 11, 1901, Edgar A. Means 85 (DS); Michigan; Cheboygan County; near Michigan Biological Station, July 15, 1920, Frank C. Gates 11,793 (DS); Kasey County; Ludington, Hamlin Lake, Sept. 20, 1910, R.W. Chaney 239 (DS); Minnesota; headwaters of the Mississippi River, Itaska Park, June 16, 1932, W.F. Paell 215 (UC); Pennsylvania; Cameron County; Hick's Run, June 25, 1911, A.A. Heller 10,318 (DS); Rhode Island; Warwick, May 25, 1877, J.W. Gillespie s.n. (DS); Vermont; Rutland County; Rutland, Oct. 3, 1898, W.W. Eggleston 314 (DS).

Description. - Oval-ovate. L-W ratio 1.6-2.4 (usually 1.6-2.0). MLT 1.7-1.9. Apex acute to acuminate. Base rounded to subcordate, asymmetrical. Margin biserrate, serrations small to average; 0-3 to 0-7 intersecondary teeth, 2-7 on principal segment; base with teeth. Craspedodromous with dictyodromous tendencies. Lower one-half to two-thirds of midrib straight, upper part crooked. PPS ratio 2.2-4.0. Secondary angles 40-60° at base, 40-50° above; secondaries straight, parallel, bending sharply at margin, randomly opposite. 11-18 secondary segments, 3-4 below widest point; spacing 0 mm. at base (one case 1 mm. at base), 7-8 mm. above (only one being 7 mm., the rest 8 mm.); basal segment contracting to 0 (except for one specimen). P-M ratio 0.7-1.2. 8-35 externals, generally weak, over half distance to midrib on the No. 1. 8-17 joining, 2-4 intra-angular secondaries, branching moderately common; secondaries straight to gently folded; all tertiary angles acute, with a few scattered intra-angular angles obtuse near bases of leaves, but majority acute; secondaries commonly opposite;
circumtertiary segments not common with a few exceptions; tertiaries slightly irregular in their courses. Net veins developed to sexternary level. Leaf 53-90 mm. long, 27-53 mm. wide.

Remarks. - Essentially similar to B. lenta.


(Plate XXXIX).

One leaf studied.

UNITED STATES: Vermont; Peacham, Sept. 27, 1886,
F. Blanchard s.n. (DS).

Description. - Broadly ovate. L/W ratio 1.4. W/L 1.7. Apex acute. Base flat, not parallel to No. 1. Margin unevenly or doubly dentate, teeth average to large; 0-4; intersecondary teeth, 3 on principal segment, base with teeth at outer edge. Craspedodromous. Midrib straight. PPS ratio 1.7. Secondary angles 40°; secondaries straight, parallel, slightly bent at margin, opposite to subopposite. 8 secondary segments, 1 below widest point; spacing 0-10 mm., basal segment contracting to 0. P-M ratio 1.8. 11 externals, 5 on No. 1, none above No. 4, strong, over half distance to midrib on No. 1 secondary, almost so on No. 2. 7 joining, 7 intra-angular tertiaries, branching; tertiaries straight to gently folded, sometimes almost sharply folded; all tertiary angles acute; tertiaries rarely opposite; tertiary veins slightly irregular in course. Net veins developed to sexternary level. Leaf 43 mm. long, 32 mm. wide.

Remarks. - This is a form of *P. papyrifera* Marsh., incorrectly labeled *P. lutea*. 
Plate XXXIX. Betula sp.
UNITED STATES: Vermont; Peacham, Sept. 27, 1836,
F. Blanchard s.n. (US). (x 3.8)


One leaf studied.

JAPAN: Hokkaido; Iwanai forest, Sept., 1904,
K.Faurie 5781 (DS).

**Description.** - Broadly ovate-cordate. L-W ratio 1.1. MLT 1.3.

Apex acute. Base strongly cordate, asymmetrical. Margin evenly dentate, all teeth slender, pointed; terminal teeth longer (1.5-2 mm.) than inter-secondary teeth (0.5-1 mm.); teeth thus small to average; 0-9 intersecondary teeth, 7 on principal segment; base densely covered with teeth.

Craspedodromous. Midrib slightly crooked, very thick at base, very thin at top. PPS ratio 2.0. Secondary angles 85° at base, 55° above; secondaries straight, randomly opposite, including Nos. 1 and 2 secondaries. 12 secondary segments, 2 below widest point; spacing 0-9 mm., basal segment contracting to 0 at midrib. P-W ratio 1.1. 25 externals, 9 on No. 1 alone, only 2 above the No. 5, strong, over half the distance to midrib on the No. 1. 17 joining, 2 intra-angular secondaries, branching; tertiary fold gentle, symmetrical above, more prominent below; joining tertiary angles acute, intra-angular angles obtuse; secondaries rarely opposite; circumtertiary segments common. Net veins developed to sexternary level.

Leaf 66 mm. long, 60 mm. wide.

Plate XL. *Betula maximowiczii* Regel

JAPAN: Hokkaido; Iwanai Forest, Sept., 1904,

H. Faurie 5761 (US). (x 2.1)
Plate XLI. *Betula nana* L.

**Sweden:** Småland, 1866, *N. J. W. Schentz s.n.* (DS). (x 4.6)
Alnus nana Clairville. Man.: 280. 1811 (ex Gaud. fl. helvet.).

1846-51.


Chamaebetula nana Opiz. Lotos V: 259. 1855.

Five leaves studied.

GREENLAND: western part; Diskofiord near Tarajar-
titsog, Aug. 7, 1932, Johs.Crontved 293 (DS) (3 leaves);

SWEDEN: Smaland, 1866, N.J.W.Schents s.n. (DS).
(2 leaves).

Description. - Round to obovate. L-W ratio 1.0. KIT 3.0. Ape
rounded in outline. Base round to subcordate, symmetrical. Margin
coarsely crenate, large for leaf size; 0-3 intersecondary teeth, 0-1
on principal segment, base with or without teeth. Craspedodromous,
among palpate. Midrib crooked. FFS ratio 1.3-1.5. Secondary angle
40°-50° below, 30°-40° above; secondary veins straight, rarely opposite.
4-5 principal segments, 1-2 below widest point; spacing 0-5 mm., base
segment contracting to 0. P-W ratio 1.1-2.0. 5-7 externals, none ab
No. 6, irregular in course but strong, over half distance to midrib o
Nos. 1 and 2 secondaries. 3-4 j. branching, 2-4 intra-angular tertiaries,
branching; tertiary fold not obvious; all tertiary angles acute, fre-
quently as low as 50°; tertiaries rarely opposite, irregular, poorly
developed, almost same size as rest of net; medials developed. Net
veins developed to sexternary level. Leaf 6-12 mm. long, 6-12 mm. wide.

13. BETULA NIGRA L. Spec. pl. 982

1753. (Plate XLII).


Betula rubra Michx. f. Hist. arb. am. II: 142. t.3. 1812.

Eleven leaves studied.

UNITED STATES: Arkansas; Eureka Springs, Apr. 24, 1928, Aven Nelson 10,884 (DS) (2 leaves); District of Columbia; Washington, May, 1887, Frank Tweedy s.n. (DS); Georgia; Clark County; Oconee River, Apr. 30, 1923, J.W. Gillespie s.n. (DS); Illinois; Washington County; April, 1872, E.French s.n. (DS); Iowa; bank of the Mississippi River, July, 1880, E.R. Dudley s.n. (DS); Massachusetts; cultivated at Amherst, May 23, 1910, S.C. Brooks s.n. (UC); Oklahoma; LeFlore County; Rich Mountain, May 21, 1913, Milton Hopkins, Aven and Ruth Nelson 593 (DS); Pennsylvania; Montgomery County; Zieglerville, Aug. 19, 1931, J.W. Adams and Myrtle Adams 1598 (US); Texas; Brazos County; near College Station, Navisota River, Apr. 1, 1916, E.J. Palmer 2350 (DS); Wisconsin; Sauk County; Devil's Lake, June 6, 1925, E.J. Palmer 27,676 (DS).

Description. - Ovate-rhombic. L-W ratio 1.3-1.5. MLT 1.2-1.7.

Apex acute, rarely subacute. Base large, flat, parallel to No. 1, symmetrical; basal angle 115-135°. Margin sharply and prominently doubly dentate to somewhat biserrate; teeth small to average; 0-3 to 0-5 inter-secondary teeth, 2-5 on principal segment, base without teeth. Craspediaodromous. Midrib straight, bending just below apex. PPS ratio 2.0-2.4. Secondary angles 50-60° below, 35-50° above; secondaries straight, possibly bending at margin, little oppositeness except for No. 1 secondary. 10-11 secondary segments, rarely 7, 1-2 below widest point; spacing 1-3 mm. at base, h-9 mm. above; basal segment even. P-W ratio
Plate XLII. *Betula nigra* L.

UNITED STATES: Oklahoma; Le Flore County; Rich Mountain, May 21, 1943, Milton Hopkins, Aven and Ruth Nelson 593 (OS). (x 2.0)
1.0-1.3. 11-26 (usually 16-21) externals, moderately strong to weak; 0-6 externals above No. 5, over half the distance to midrib on No. 1. 7-14 joining, 2-4 intra-angular tertiaries, branching; branching often distinctive, with many tertiaries arching midway across secondary segment to terminate against next adjacent tertiary vein; tertiary fold gentle; upper and lower tertiary angles acute, the intra-angular angle varying from acute to obtuse in different specimens; tertiaries rarely opposite; circumtertiary segments common. Net developed to sexternary level. Leaf 29-70 mm. long, 19-47 mm. wide.

Remarks. - Superficially resembles Alnus.

1h. BETULA PAPYRIFERA Marsh. Arb. amer.: 19.

1785. (Plates XLIII and XLIV).

Betula grandis Schrad. Ind. hort. bot. geett.: 2. 1833.


Betula ermanii Rothr. Smithsonian Rep.: 454. 1867.

Plate XLIII. Aesculus papyrifera Marsh.
CANADA: Quebec; Algonquin County; Ilc, June 25, 1905,
P. H. Forb. n.v. (05). (x 2.4x)
Plate XLIV. *Betula papyrifera* Marsh.

UNITED STATES: New York, Shelburne Falls, July, 1890,
Mrs. D.B. Fitch s.n. (DS). (x 3.2)

Betula pumilolia and Betula macrostachya Hort.

Eight leaves studied.


CANADA: Quebec; Rimouski County; Bic, June 25, 1905, F.F.Forbes s.n. (DS).

UNITED STATES: Colorado; Boulder County; Boulder, Boulder Canyon, June 18, 1933, E.I.Applegate 8572 (DS); Michigan; Gogebic County; Imp Lake, July 24, 1937, R.R. Wilson 172 (DS); Vermont: Willoughby Mountain, May 27-28, 1903, W.W.Eggleston 3188 (DS); Wisconsin; Madison, May 25, 1913, James Mackmurphy s.n. (DS).

Description. - Broadly ovate to somewhat roundish. L-W ratio 1.1-1.8 (usually 1.1-1.5). W-LT 1.3-1.8. Apex acute to acuminate. Base usually flat, parallel to No. 1, less commonly subcordate or rounded with a flat portion extending 8 mm. out from midrib. Margin unevenly dentate, often coarsely so, occasionally doubly dentate to biserrate; teeth usually large, sometimes small; 0-2 to 0-6 intersecondary teeth, 1-4 on principal segment, teeth rare on base. Craspedodromous. Midrib crooked, occasionally straight to just below apex. PFS ratio 1.6-2.1. Secondary angles 35-70° at base, 45-100° above; secondary veins straight, randomly opposite, always including No. 1. 7-10 secondary segments, 1 below widest point; spacing 0-3 mm. at base, 6.5-12 mm. above, always contracting at base, often to 0. P-W ratio 0.7-1.9 (all but one 1.3-1.9). 6-11 externals, none above No. 4, over half distance to midrib on No. 1, rarely on No. 2. 4-11 joining, 3-6 intra-angular
tertiaries, branching; tertiary fold gentle to quite sharp; all tertiary angles acute; tertiaries rarely to commonly opposite; circum-tertiary segments sometimes common; tertiaries often irregular in courses; medials sometimes developed. Net veins developed to sexternary level. Leaf 30-70 mm. long, 24-50 mm. wide.

Remarks. - This species is not in any way basically different from Betula sp. (described earlier) and is very similar to both B. papyrifera occidentalis, and one fossil B. lacustris.

15. BETULA PAPYRIFERA Marsh. var. MINOR (Tuckerm.) Wats. & Coult.

Gray Man. ed. 6: 472. 1890.

Betula papyracea var. minor Tuckerm. Am. Jour. Sci. 45:
31. 1843.

Betula dahurica $\beta$ americana Regel. in A.DC. Prodr. XVI.
2: 175. 1868.

Betula alba subsp. papyrifera $\gamma$ humilis Regel. in A.DC.
Prodr. XVI. 2: 166. 1868.

Betula alba var. minor (Tuckerm.) Fern. Am. Jour. Sci. 16:
178. 1902.


One leaf studied.

UNITED STATES: New Hampshire: Mt. Washington, July 29,
1886, C.E. Faxon s.n. (DS).

Description. - Broadly ovate. L-W ratio 1:4, WLT 1:4. Apex
acute-acuminate. Base flat, not parallel to No. 1. Margin unevenly
dentate, large teeth for leaf size; 0-2 intersecondary teeth, 2 on prin-
PPS ratio 2.3. Secondary angles 35°-40°; secondary veins more or less parallel, straight, Nos. 1 and 2 secondaries opposite. 7 secondary segments, 1 below widest point; spacing 0-7.5 mm., basal segment contracting to 0. P-W ratio 1.4. 8 externals, strong, none above No. 5, extending half distance to midrib on No. 1. 8 joining, 5 intra-angular tertiaries, branching; tertiary fold sharp; all tertiary angles acute; tertiaries commonly opposite, irregular in their courses. Net veins developed to sexternary level. Leaf 29 mm. long, 22 mm. wide.

Remarks. - There is nothing to distinguish this from *B. papyrifera* unless it is the small size and high PPS ratio.


Ten leaves studied.

ALASKA: Skagway, June, 1899, *Wm. Trelease* 3507 (DS).
Plate XLV. *Betula papyrifera var. occidentalis* (Hook.) Sarg.
UNITED STATES: Montana; Mission Creek, Aug. 17, 1909, E.E. Jones s.n. (US). (x 2.6)
Description. - Broadly ovate, rarely round. L-W ratio 1.1-1.8 (usually 1.1-1.4); MLT 1.3-1.9. Apex acute, subacute, acuminate, even apiculate. Base flat, not parallel to No. 1, sometimes round, smooth for 8-10 mm. from midrib. Margin rather coarsely and unevenly dentate or doubly dentate, teeth large to average, rarely small; 0-2 to 0-7 intersecondary teeth, 1-7 (usually 1-3) on principal segment, base with teeth. Craspedodromous. Midrib crooked, but usually straight to just below apex, rarely completely straight. PPS ratio 1.6-2.6 (all but two 1.6-2.1). Secondary angles 35°-60° at base, 35°-50° above (usually 45° below, 35° above); secondaries straight, randomly opposite, only occasionally with the No. 1 opposite, rarely all opposite. 5-10 secondary segments (usually 7-10), 0-2 below widest point; spacing 0-2 mm. at base, 4.5-10.5 above, basal segment always contracting, usually to 0. P-W ratio 1.0-1.5. 6-22 (usually 6-13) externals, strong, rare above No. 5, over half distance to midrib on No. 1. 4-11 joining, 2-6 intra-angular terciaries, usually branching; tertiary fold varies from sharp to gentle; most tertiary angles acute; terciaries commonly opposi
circumtertiary segments quite common; medials developed. Net veins developed to sexternary level. Leaf 32-61 mm. long, 27-53 mm. wide.

**Remarks.** - Very close to *B. papyrifera*; the differences are general and gradational. In fossils they would be almost impossible to distinguish.

17. **BETULA PAPYRIFERA** Karsh. var. **SUBCORDATA** (Rydb.) Sarg.


Two leaves studied.

**UNITED STATES:** Washington; Okanogan County; near Loomis, June 28, 1931, *J.W. Thompson 7071* (03).

**Description.** - Oval to ovate. L-W ratio 1.9. ULT 1.9-2.1.

Apex acute to acuminate. Base flat, subparallel to No. 1. Margin rather coarsely and unevenly dentate, teeth large to average sized; 0-3 intersecondary teeth, 3 on principal segment, base with 1-2 teeth. Craspedodromous. Midrib straight to just below apex. FFS ratio 1.8-1.9. Secondary angles 35° at base, 40° above; secondaries straight, alternate. 8-9 secondary segments, 2 below widest point; spacing 0 mm. at base, 7.5-8 mm. above, basal segment contracting to 0. P-W ratio 2.0. 11 externals, fairly strong, extending over half distance to midrib on the No. 1. 5-6 joining, 3-4 intra-angular tertiaries, branching; tertiary fold sharp; all tertiary angles acute; tertiaries commonly opposite; circumtertiary segments common. Net veins developed to sexternary level. Leaf 37-40 mm. long, 21-22 mm. wide.

**Remarks.** - This form is similar in several fundamental respects
Plate XLVI. *Betula papyrifera* var. *subcordata* (Rydb.) Sarg.

UNITED STATES: Washington; Okanogan County; near Loomis, June 28, 1931, *J.W. Thompson 7071* (WS). (x 3.8)
to *B. papyrifera*, specifically, the nature of the midrib, the margin, and net. The P-W ratio, L-W ratio, NW, and base give it a distinction of its own. It is noteworthy that several features carry through all varieties of *B. papyrifera*. The most unusual of these features is the midrib. In almost every form of *B. papyrifera*, the midrib is straight to just below the apex. Midrib characteristics, such as this one, seldom carry through a single species, even less so through the varieties of the species.


(Plato XLVII).


*Betula cuspidata* Schrad. ex Regel in A. DC. Prodr. XIV; 161, 1868.

Five leaves studied.

**Canada:** Quebec; Deux-Montagnes, May, 1929, P. Louis Marie s.n. (DS).

**United States:** Maine; Alford Lake, Sept. 10, 1933, L.R. Abrams 13, s.h2 (DS); Vermont; North Duxbury, July 4, 1913, W.H. Blanchard s.n. (DS); Lincoln, Aug. 19-21, 1903, W.W. Engleston 3043 (DS); Rutland County; Rutland, Sept. 27, 1899, W.W. Engleston 177 (DS).
Plate XLVII. Betula populifolia Marsh.
UNITED STATES: Vermont; North Duxbury, July 4, 1918,
W.H. Blanchard s.n. (DS). (x 2.7)
Description. - Broadly ovate. L-W ratio 1.2-1.5. MLT 1.3-1.5. Apex very narrowly acuminate. Base large, broad, and flat, not parallel to No. 1, symmetrical. Margin doubly dentate, teeth average to small; 0-4 to 0-7 intersecondary teeth, 3-5 intersecondary teeth on principal segment; base with small teeth 8-11 mm. from midrib. Craspedodromous. Midrib crooked, rarely straight. Secondary angles 35°-50° near base, 35°-60° above; secondary veins straight, randomly opposite, always including No. 1. 9-13 secondary segments, 1 below widest point; spacing 0-1 mm. at base, 9.5-10.5 mm. above, basal segment always contracting at midrib, often to 0. 6-12 externals, none above the No. 5, strong, over half distance to midrib on the No. 1 secondary. Tiny, short interordinal veins common in apex. 8-9 joining tertiary veins, 3-6 intra-angular tertiaries, branching; tertiary fold gentle to sharp; all tertiary angles acute; tertiaries commonly opposite; circumtertiary segments rare. Net veins developed to sexternary level. Leaf 34-68 mm. long, 23-41 mm. wide.


*Betula populifolia laciniata* Hort.

*Betula pendula* Hort.

*Betula laciniata* Hort.

Two leaves studied.

UNITED STATES: California (cultivated), Nov. 10, 1928, H.L. Dale s.n. (US).

Description. - Broadly ovate. L-W ratio 1.0-1.1. MLT 1.7.

Apex acute to acuminate. Base flat, almost or not at all parallel to
No. 1 secondaries; basal angle 90°-150°, symmetrical. Margin incised or laciniate, smaller teeth on the lobes, teeth large to average; 0-2 intersecondary teeth, 2 on principal segment, base without teeth. Craspedodiromous. Midrib straight. PPS ratio 2.8. Secondary angles 50°-55° below, 60° above; secondaries straight, randomly opposite, including the No. 1, sometimes the No. 2 secondaries. 6 secondary segments, 1 below widest point; spacing 2 mm. at base, 9.5 mm. above, basal segment either contracting gradually or uniform in width. P-M ratio 1.4. 6-7 externals, none above the No. 3, strong, over half the distance to the midrib on the No. 1. 5 joining, 5 intra-angular tertiaries; joining tertiaries not properly joining because of marginal incisions; branching; tertiary fold sharp if present; all tertiaries at acute angles, rarely opposite. Net veins developed to sexternary level. Leaf 33 mm. long, 32 mm. wide.

Remarks. — On the basis of leaves, this form is probably not too closely related to B. populifolia. The nature of the base, the L-W ratio, the MLT, the midrib, the PPS ratio, the distribution of the externals, the oppositeness of the tertiaries, and other features show many fundamental differences.


1793. (Plate XLVIII).

Betula alba L. Spec. pl.: 782. 1752.
Plate XLIII. *Betula pubescens* Pbrh.
U.S.S.R.: Krasnojarsk, Yenisei River, July 10, 1927,
N. Schipczinsky 228 (DS). (x 3.6)
**Betula odorata** Rechst. *Dane I: 78. 1797.*

**Betula alba** var. *pubescens* Spach. *Ann. sci. nat. 2 ser.*

XVI: 187. 1861.

**Betula pendula** Reichb. *Icon. fl. germ. XII: t.625. f.1287.*

1850.


**Betula alba** subsp. *pubescens* Regel. *in A.D.C. Prodr. XVI.*

2: 166. 1868.

One leaf studied.

**UNION OF SOVIET SOCIALIST REPUBLICS: Siberia; Krasnojarsk Jistrit; Kas River at Krasnojarsk, July 10, 1927, N. Schipczinsky 228 (NS).**

Description. — Somewhat broadly ovate. L=W ratio 1.3. WLT 1.6. Apex acute. Base flat, not parallel to No. 1, asymmetrical. Margin evenly dentate, teeth average to large; 0-4 intersecondary teeth, 2 on principal segment, base without teeth. Craspedodromous. Midrib crooked. PPS ratio 1.8. Secondary angles 50° at base, 30° above; secondary veins straight, randomly opposite. 6 secondary segments, 1 below widest point; spacing 1-9 mm., basal segment contracting at midrib, sometimes to 0. P-W ratio 1.5. 10 externals, strong, none above the No. 1, over half distance to midrib on the No. 1 secondary. 6 joining, 4 intra-angular tertiaries; tertiary fold gentle; all tertiary angles acute; tertiaries commonly opposite; medials developed. Net veins developed to sexternary level. Leaf 39 mm. long, 30 mm. wide.
Remarks. - Not enough specimens were studied to make any decisions regarding this species.


(Plate XLIX).


Chamaebetula pumila Opiz. Lotos V: 259, 1855.

Two leaves studied.

UNITED STATES: Connecticut; Litchfield County; near Chapinville, July 23, 1881, R.R. Dudley s.n. (US); Illinois; Champaign County; Urbana, Sept. 15, 1935, Deliae Denaree 11692 (US).

Description. - Round. L/W ratio 1.0-1.3. W/T 2.0. Apex rounded. Base rounded, smooth to almost 8 mm. from midrib. Margin coarsely serrate, teeth large for leaf size, biconvex; 0-2 to 0-4 intersecondary teeth, 1-2 on principal segment, base without teeth. Craspedodromous. Midrib crooked. PPS ratio 1.6-1.8. Secondary angles 10°-15° at base, 10°-70° above; secondaries concave, Nos. 1 and 2 sometimes opposite. 5-6 secondary segments, 1-2 below widest point; spacing 0-1 mm. at base, 7.5-11.5 above; basal segment always contracting, sometimes to 0. F-W ratio 0.6-0.9. 6 externals, strong, none above the No. 3, over half distance to midrib on Nos. 1 and 2 secondaries. Intersecondary veins sometimes prominent. 8 joining, 3 intra-angular ter-
tiaries; tertiary fold sharp to gentle; all tertiary angles acute; ter-
tiaries commonly opposite; medials developed. Net veins developed to sexternary level. Leaf 24-32 mm. long, 19-34 mm. wide.

Remarks. - Note the many similarities with **B. nana**.
Plate LXI. Betula pumila L.
UNITED STATES: Illinois; Champaign County; Urbana, Sept. 15, 1935, Delzie D emanc 11,692 (OS). (x 1.0)
22. BETULA UTILIS D.Don. Prodr. Fl. nepal.: 58.
1825. (Plate L).

Betula bhijpattra Wall. Pl. as. rar. II: 7, 1832.

Three leaves studied.

CHINA: Szechuan; Ma-pien-hsien, June 19, 1930, W.P. Fang 524 (OS).

India: Punjab; Kangra; Spiti, Hane, Sept. 22-23, 1933, Walter Koelz 7222 (UC).

Tibet: southeastern part; Salwin-Kiu Chang divide, Tsarong, Oct., 1921, George Forrest 20,927 (UC).

Description. - Ovate to broadly ovate. L-W ratio 1.3-2.1.
(Koels 7222 2.1, the others 1.3-1.7). W-LT 1.6-1.9. Apex acute-acuminate. Base round to subcordate. Margin slightly biserrate or unevenly serrate (Koels 7222 doubly dentate), teeth average sized (Koels 7222 large); 0-4 to 0-5 intersecondary teeth, 3-5 on principal segment, base with teeth at outer edge. Craspedodromous, with dictyodromous tendencies. Midrib straight throughout to crooked throughout (Koels 7222 crooked). PFS ratio 2.0-3.0 (Koels 7222 2.0, the others 2.3-3.0).
Secondary angles 50°-65° at base (sometimes 35° with highly convex junctions of secondaries with midrib), 45° above; secondaries straight to slightly concave, randomly opposite, most commonly the No. 1. 10-14 secondary segments (Koels 7222 with 10); spacing 0 at base, 7-10 mm. above, basal segment contracting to 0 on one side of midrib at least. P-E ratio 1.0-1.7. 15-24 externals (Koels 7222 with 15, the others 24),
Plate L. Betula utilis D. Don.

TIBET: southeastern part; Tsarong, Salwin-Kiu Chang divide, Oct., 1921, George Forrest 29,967 (UC). (x 2.5)
slight to strong, extending over half the distance to the midrib on
No. 1. 9-li joining, 4-5 intra-angular terciaries; terciaries straight
to gently folded; upper joining tertiary angles acute, the lower and
intra-angular angles mixed acute and obtuse, mostly acute; terciaries
commonly opposite; circumtertiary segments common. Net veins developed
to sexternary level. Leaf 60-73 mm. long, 35-46 mm. wide.

Remarks. - Fang 452h and Koels 7222 are the extreme end members
of a series, of which all other members of this species and its varie-
ties which were studied are intermediate cases. Plates L and LI show
these two extremes.

23. BETULA UTILIS D. Don. var. PRATTII Park. Jour. Linn. Soc. XXVI:
499. 1899.

Three leaves studied.

CHINA: Szechuan; western Tachienlu, June 10, 1930,
W.C. Cheng 1139 (DS); Hung-yu-hsien, Aug. 13, 1930,
W.P. Fang 2094 (PC); Ta-pien-hsien, June 16, 1930, W.P.
Fang 1902 (DS).

Description. - Ovate. L-W ratio 1.8-2.2. E2T 1.8-1.9. Apex
acute-acuminate. Base varying from round, to flat, not parallel to No.
1 secondary veins. Margin unevenly serrate to slightly biserrate, teeth
average to fairly large; 0-3 to 0-5 intersecondary teeth, 3-5 on prin-
cipal segment, base without teeth except at outer edge. Craspedodromous
to dictyodromous. Midrib straight to crooked in upper half. PPS ratio
2.8-3.4. Secondary angles 40-55° below 35-40° above; secondaries straight,
randomly opposite, including the Nos. 1 and 2 secondaries and many others
12-13 secondary segments, 2-4 below widest point; spacing 0-1.5 mm. at
base, 7-9.5 mm. above, basal segment always contracting at base, sometime
to 0. P-W ratio 0.8-1.4. 17-20 external veins, slight, extending over half distance to midrib on No. 1 secondary. 10-11 joining, 2-4 intra-angular tertiaries, branching; tertiaries straight to gently folded; joining tertiary angles acute, intra-angular angles mostly acute; tertiaries commonly opposite; medials slightly developed. Net veins developed to sexternary level. Leaf 53-71 mm. long, 23-32 mm. wide.


Four leaves studied.

CHINA: Kansu; near Lichen, Touling, July 7-9, 1923, F.C.Ching fl. 8 (UC); Szechuan; southwestern part; Muli territory; west slope of Mount Wutsuga, Oct., 1932, J.F. Rock 24.516 (UC); Yunnan; northwestern part; Mekong-Salween watershed; mountains above Tsaku and Tsechung, 1923, J.F. Rock 9289 (UC).

TIAM: Salween-Irrawadi watershed; near Chumpu-ton, Mount Kenyichunpo, 1923, J.F. Rock 10,231 (UC).

**Description.** - Oval to ovate. L-W ratio 1.4-1.9. KLT 1.5-1.9. Apex acute to highly acuminate. Base usually round, to slightly subcordate, or even somewhat auriculate. Margin unevenly serrate to slightly biserrate, teeth average to large; 0-3 to 0-7 intersecondary teeth, 3-6 on principal segment, base with a few scattered teeth. Craspedodromous to dictyodromous. Midrib perfectly straight to crooked throughout, (Ching fl.8 crooked throughout). PFS ratio 1.2-3.7 (Ching fl.8 1.9, the others 2.5-3.7). Secondary angles h0°-70° below, h0°-50° above; secondaries straight or slightly convex, randomly opposite,
Plate LI. *Betula utilis* var. *sinensis* Franch.
CHINA: Kansu; near Lichen, Toul-ping, July 7-9, 1923,
R.C. Ching the (UC). (x 2.4)
usually the No. 1. 10-18 secondary segments (Ching 14:8 with 10),
2-5 below widest point; spacing 0-2 mm. below, 4.5-13 mm. above
(Ching 14:8 with 13), basal segment contracting, often to 0. P-V
ratio 1.0-1.4. 2i-i35 externals, slight (except in Ching 14:8), ex-
tending over half distance to midrib on the No. 1 secondaries. 12-16
joining, 2-6 intra-angular tertiaries, branching; tertiaries straight
to gently folded; joining tertiary angles acute, the intra-angul-
ars mixed acute and obtuse, mostly acute or 90°; tertiaries commonly op-
posite; circumtertiary segments common; radials slightly developed.
Net developed to sexternary level. Leaf 48-92 mm. long, 31-48 mm.
wide.

Remarks. - Considering B. utilis and its varieties as a whole,
Ching 14:8 and Koels 7222 represent one extreme, Fang 1524 and Rock
21,516 another. All other specimens are gradations between. Koels
7222 and Ching 14:8 are separated by 1000 miles. The ten specimens
studied do not break down into 3 types as presented here. What does
seem to be present is a series with two end-members, each of which is
a species. The intermediate forms may be the results of hybridization.

1791. (Plate LII).

Betula pendula Roth. Tent. pl. germ. I: 405. 1788.
Betula alba var. macrocarpa et verrucosa Wallr. Sched. crit.:
495. 1822.
Plate LIII. Betula verrucosa
U.S.S.R.: Kansk District, June 8, 1909,
A.P. Ermolaev s.n. (UC), (x 2.3)
Betula rhombifolia Tausch. Flora: 751. 1838.
Betula odorata Reichb. Icon. fl. germ. XVI: 2. t. 626.

Betula alba var. typica Trautv. in Maxim. Prim. fl. amur.: 219. 1859.
Betula alba subsp. verrucosa × vulgaris Regel. in A. DC. Prodr. XVI. 2: 163. 1868.

Nine leaves studied.

GERMANY: Freudenberg, Aug. 6, 1876, Utsch s.n. (DS); Alterswil, June 9, 1923, M. Jaquet s.n. (DS).
ICELAND: Reykjavik, July 19, 1895, E. Taylor s.n. (DS); northern part; Hals, July 1, 1895, E. Taylor s.n. (DS).
UNION OF SOVIET SOCIALIST REPUBLICS: Siberia; Tomsk, Ob River, Aug. 12, 1927, N. Schipezinsky 496 (DS); Semipalatinsk, Irtish River, 1921, C. Kossinsky 500 (DS); Jeniseisk District, July 20, 1914, J. W. Kusnezow 1712 (DS); Kansk District, June 8, 1909, A. P. Emel'yanov s.n. (UC).

Description. — Broadly ovate to rhombic. L−W ratio 1.1−1.8
(usually 1.1−1.3). MLT 1.5−2.3 (usually 1.4−1.9). Apex acute or acuminate. Base most commonly flat, not parallel to No. 1, sometimes flat and
parallel to No. 1 secondaries, other times roundish. Margin unevenly dentate to doubly dentate, teeth large; 0-4 to 0-8 (usually 0-6 to 0-8) intersecondary teeth, 4-6 on principal segment, teeth usually confined to outer edge of base; when roundish, teeth almost to midrib. Craspedodromous. Midrib crooked. PPS ratio 1.6-2.3. Secondary angles 30°-40° at base, 45°-55° above; secondary veins straight, randomly opposite, the No. 1 secondaries most commonly, to all or none opposite. 6-11 secondary segments (usually 6-8), 1 below widest point; spacing 0-2 mm. at base, 7-12 mm. above, basal segment always contracting at midrib, sometimes to 0. P-M ratio 1.1-1.8. 6-11 externals, 3-6 on No. 1 secondary, none above No. 4 secondary, strong, extending over half distance to midrib on No. 1 secondary. 2-3 joining, 1-6 intra-angular secondaries, branching; tertiary fold usually sharp, rarely gentle; all tertiary angles acute; secondaries rarely opposite; circumtertiary segments sometimes common; secondaries irregular in courses; medials partially developed. Net veins developed to sexternary level. Leaf 30-68 mm. long, 24-38 mm. wide.

Remarks. - Miss Jentys-Szaferowa (1919) says:

Betula verrucosa displays characteristic local variability of leaf shape, owing to which in some birch aggregations we encounter trees having leaves with an acute base, and in others leaves with a wide base and all other characteristics correlated with this property. (pp. 212-213).

The species shows many characters of B. papyrifera and its varieties. Whether or not it can be distinguished from that species is uncertain; presumably it can. There seem to be several differences; the mode of attachment of the lower secondaries to the midrib, number of teeth on the leaf base, distribution of external veins, and nature of
Two leaves studied.


Description. - Ovate. L/W ratio 1.4-1.9. MLT 1.7-1.9. Apex acute to acuminate. Base flat, not parallel to No. 1. Margin doubly dentate, teeth average sized; 0 to 0-5 intersecondary teeth, 4 on principal segment, base with teeth. Craspedodromous. Midrib crooked. PPS ratio 2.0-3.0. Secondary angles 50°-60° at base, 35°-50° above; secondary veins straight, alternate or randomly opposite, including Nos. 1 and 2 secondaries. 7-13 secondary segments, 2-3 below widest point; spacing 0 mm. at base, 14-15 mm. above, basal segment contracting to 0 at midrib. P-M ratio 1.3-1.8. 16-20 externals, strong, few, if any above the No. 5, extending over half distance to midrib on secondaries No. 1 and 2. 4-8 joining, 4 intra-angular tertiaries; tertiary fold sharp; all tertiary angles acute; tertiary veins commonly opposite; circumtertiary segments fairly common. Not developed to externary level. Leaf 60-100 mm. long, 12-53 mm. wide.

Remarks. - This species is unquestionably related to B. papyrifera or B. papyrifera occidentalis. MacGinitie believes that it resembles the latter most closely.
It was pointed out in the discussion of *A. corrallina* Lesq. that Univ. Cal. Coll. Paleobot. No. 567, illustrated by MacGinitie as a paratype of *P. lacustris*, is not *P. lacustris*, but *A. corrallina*. The specific reasons for stating this may now be pointed out in detail:

1. The basal segment contracts to 0 at the midrib on Nos. 566 and 568; the basal segment is of uniform width in No. 567.

2. The midribs of Nos. 566 and 568 are crooked; that of No. 567 is straight.

3. The externals on Nos. 566 and 568 are large, prominent veins extending almost to the midrib on the No. 1 secondary, slightly over half the distance to the midrib on the No. 2 secondary, rapidly diminishing in number upwards. The largest number of externals (5-6) is on the No. 1 secondary. In No. 567, the externals are slight to moderately prominent, just over half the distance to the midrib on the No. 1 and very poorly developed on this secondary. The number of externals on the No. 1 secondary in No. 567 is 2, on the No. 2 secondary 3, and from the No. 2 upwards, the number decreases. In other words, the greatest number of externals lies on the No. 2 secondary. This character alone will distinguish *Alnus* from *Betula*.

4. The secondaries of Nos. 566 and 568 show a low degree of oppositeness and are widely spaced; those of No. 567 show a high degree of oppositeness, and are closely spaced.

5. The teeth of Nos. 566 and 568 are large and coarse compared with those of No. 567, whose teeth are small, short, and pointed.

6. The joining tertiaries of Nos. 566 and 568 are sharply folded and widely spaced; those of No. 567 are smaller, gently folded.
by comparison, and closely spaced.

In summary, the best criterion for distinguishing the two genera is the distribution of the external veins. If this criterion, combined with others, fails, intimate knowledge of all the living species of the two genera should still result in a positive answer regarding the identity of the genus. Though it is not an easy task, I am convinced that in leaves with sufficient venation detail, the two genera can be told apart.

Fifty-six specimens of extant Carpinus studied; 1 fossil specimen (?). Chart 3.

Description. — Ovate, oval, or elliptical. Apex usually acute or acuminate, rarely subacute, always one of the three. Base subcordate to cordate, sometimes round, rarely auriculate; basal angle always 150° or greater; most commonly asymmetrical, sometimes symmetrical. Intersecondary teeth 0-3 to 0-7, with more than 0-7 noted in only 2 species; terminal teeth larger than intersecondary teeth, often bifid or trifid in upper half of leaf, base usually with teeth. Craspedodromous, very rarely with traces of dictyodromy. Midrib variable, crooked or straight within a single species, never as crooked as in Betula. Secondaries usually bending at margin just before entering terminal teeth, rarely bifurcating. 3-5 secondary segments below widest part of leaf, occasionally 2, rarely 6-8; basal segment always contracting toward midrib, if only on 1 side of leaf, usually to 0. Externals small, not prominent, short, originating on secondaries fairly close to margin, characteristically shorter than in Ostrya; external areas overlapping slightly or not at all, unlike Ostrya; externals extending over half distance to midrib on the No. 1, commonly on the No. 2, rarely on the No. 2 alone. Tertiaries characteristically irregular in course; circumtertiary segments common in all species; tertiary veins straight or only slightly folded; upper and lower joining tertiary angles acute to 90°, intra-angulares obtuse to 90°, acutely attached intra-angulares rare and always in minority; medials and medial zones common. Net vein endings common to rare, always simple; size differentiation of net veins not pronounced.
Extant species of Carpinus

1. CARPINUS BETULUS L. Spec. pl.: 998. 1753.

(Plate LIII).

Carpinus sepium Lam. Fl. franc. II: 212. 1779.
Carpinus compressa Gilib. Exerc. II: 399. 1792.
Carpinus carpinifolia Kit. in Pest. Fl. austr. II: 626. 1831.
Carpinus intermedia Wierzb. in Reichb. Icon. Fl. germ. XII:

l. f. 1297. 1850.

Carpinus nervata Cullac. Fl. haut. pyr.: 111. 1867.

Nine leaves studied.

AUSTRIA: upper part; Schwertberg, 1874, H. Leek s.n. (UC).
ENGLAND: Middlesex; Twickenham, 1845, T. Twining s.n. (UC).
FRANCE: between Cauterets and Pont Audemer, July 8, 1933, L.R. Abrams 13,472 (DS); Beauvais, in forest, Oct., 1817, collector unknown, s.n. (DS 10,412).
ITALY: Lake Como, between Bellagio and Como, June 3, 1933, L.R. Abrams 13,440 (DS).
SWEEDEN: near Upsala, Sept., 1876, G. Lofgren s.n. (UC).
UNION OF SOVIET SOCIALIST REPUBLICS: Kuban Province; Batalpashinsk region, June 25, 1916, A. Kryshchofovich s.n. (UC).
YUGOSLAVIA: Serbia; Tara Plain, near Saovina, Sept. 16, 1907, C.K. Schneider 11,685 (UC).
Plate LiII. Carpinus betulus L.
FRANCE: Beauvais, Oct., 1817, collector unknown s.n.
(CS 10,442). (x 2.3)
Description. - Oval, ovate, or elliptical. L-W ratio 1.5-2.3 (all but one 1.5-1.9). WLH 1.6-2.1. Apex acute to subacute. Base cor- date to round, slightly asymmetrical. Margin biserrate, upper terminal teeth commonly trifid, teeth small to very small; 0-4 to 0-8 intersecondary teeth, 4-6 on principal segment, base with teeth beginning 8 mm. from midrib. Craspedodromous. Midrib straight to slightly sinuous. FPS ratio 2.5-3.8 (all but one 2.5-2.0). Secondary angles 40°-60° at base, 35°-50° above; secondaries straight, sometimes bending abruptly at margin, random to all secondaries opposite, usually including Nos. 1 and 2 secondaries. 12-13 secondary segments, 2-4 below widest point; spacing 0-1.5 mm., 5-8 mm. above, basal segment always contracting at midrib, usually to 0 on at least one side of midrib. P-M ratio 0.5-1.3 (all but one 0.3-1.1). 20-35 (usually 27-35) externals, weak to moderately strong, over half distance to midrib on No. 1, sometimes on No. 2. 11-19 joining (average 15.6), 1-4 (usually 1-2) intra-angular terciaries; terciaries straight to gently folded; joining tertiary angles about 90°, intra-angular angles obtuse; terciaries commonly oppo- site; circumtertiary segments common; terciaries very irregular in course, often with slight sag toward midrib midway in course; medials developed. Net veins developed in quinnternary level, vein endings com- mon, simple. Leaf 38-77 mm. long, 22-40 mm. wide.

Remarks. - Very similar to C. caroliniana at first glance though actually quite distinct.

2. CARPINUS BETULUS L. f. SUBACUTA Jomin. No citation found.

One leaf studied.

Description. - Oval. L-W ratio 1.8. MLT 1.9. Apex acute. Base slightly cordate. Margin doubly dentate, terminal teeth commonly trifid, teeth very small; 0-6 intersecondary teeth, 4 on principal segment, a few subdued teeth on base. Craspedodromous. Midrib straight. PPS ratio 3.0. Secondary angles 60°-80° at base, 45°-50° above; secondaries straight, opposite. 13 secondary segments, 4 below widest point; spacing 1.5-4.5 mm., basal segment contracting slightly possibly to 0 in some specimens. P-M ratio 1.0. 18 externals, weak, over half distance to midrib on the No. 1 secondaries. 16 joining, 3 intra-angular ter- tiaries; tertiaries straight; joining tertiary angles acute, intra- angular angles obtuse; tertiaries commonly opposite; circumtertiary segments common; tertiaries irregular in course; medials developed. Net veins developed to quinternary level, vein endings simple, rare. Leaf 48 mm. long, 29 mm. wide.

Remarks. - There are two significant differences between C. betulus and this form; in the latter, the net vein endings are rare, and the margin is doubly dentate. There are other minor differences.

3. CARPINUS CAROLINIANA Walt. Fl. carol.: 236. 1788, (Plate LIV).

Carpinus betulus L. Spec. pl.: 998. 1753. (pro parte).
Carpinus americana Michx. Fl. bor.-amer. II: 201. 1803.
Plate LIV. *Carpinus caroliniana* Walt.

UNITED STATES: Pennsylvania; McK County; Whipspoorwill Camp of Du Boise Lumber Company, June 20, 1911, A. L. Weller 10,313 (M&G). (x 2.6)
Ten leaves studied.

CANADA: Ontario; Ottawa, Aug. 6, 1916, Brother Holland (DS).

MEXICO: Jalisco; San Sebastian; Sierra Madre, trail to Monte Oscura, Feb. 8, 1927, Dnes Bexla 1416 (DS).

UNITED STATES: Arkansas; Miller County; along creek bank, Texarkana, Aug. 20, 1936, Delifie Dezarae 13479 (DS); District of Columbia; Washington, Rock Creek, June 17, 1899, T. A. Williams s.n. (DS); Georgia; Dougherty County; Dr. Gillespie's Pocoson place, May 16, 1928, J. W. Gillespie 5037 (DS); Maine; Lincoln County; 1/2 miles from Dresden Mills, Sept. 5, 1932, Margaret C. Ries 1170 (DS); Pennsylvania; Elk County; Whippoorwill Camp of Dubois Lumber Company, June 20, 1911, A. A. Heller 10,313 (DS); Texas; Matagorda County; near Bay City, Peyton Creek in woods, May 2, 1916, E. J. Palmer 9637 (DS); Virginia; Princess Anne County; near Virginia Beach, Great Neck, in woods, June 24, 1936, L. N. Smith and A. B. Hodsdon 6IB (DS); West Virginia; Tyler County; Davenport, June 23, 1930, E. E. Berkeley s.n. (DS).

Description. - Oval to slightly ovate. L-W ratio 1.7-2.1. 

MLT 1.5-1.9. Apex acuminate, sometimes acute. Base round to subcordate, asymmetrical or symmetrical. Margin biserrate, teeth small, terminal teeth larger, upper terminal teeth sometimes trifid; 0-4 to 0-8 intersecondary teeth, 3-8 on principal segment, base with teeth. Craspedodromous. PPS ratio 3.0-4.2. Secondary angles 35°-70° at base, rarely 85° to 35°-50° above; secondaries straight, often bending at margin, randomly opposite, usually including the No. 1, sometimes No. 2, rarely all. 12-18 secondary segments, 3-5 below widest point; spacing 0 mm. at base, 4.5-9 mm. above, basal segment contracting to 0 at midrib. P-W ratio 0.9-1.6 (all but one 0.9-1.3). 18-34 (usually 18-26) externals, weakly developed, over half the distance to the midrib on the No. 1, sometimes on the No. 2. 5-15 (usually 7-12) joining tertiary
veins (average 9.8), 2-3 intra-angulares, branching or simple; ter-
tiaries straight to gently folded; joining tertiary angles acute, 
intra-angulares obtuse; tertiaries commonly opposite, irregular in 
course; medials developed. Net veins developed to quinternary and 
sexternary level, varying from leaf to leaf, net veins common, simple. 
Leaf 38-98 mm. long, 19-47 mm. wide.

Remarks. - Differences with C. betulus are marked, particularly 
in the number of tertiary veins.

4. CARPINUS CAROLINIANA Walt. var. VIRGINIANA (Marsh.) Fern. 


20: 43. 1893.

Two leaves studied.

UNITED STATES: Michigan; Ann Arbor, Nichols Arboretum, 
Aug. 18, 1937, F.J. Hermann 9137 (DS); New Hampshire; 
Strafford County; Durham, along Great Bay near Newmarket 
town line, June 16, 1938, A.R. Hodgdon and E.R. Mills 9141 (DS).

Description. - Oval to elliptical. L-W ratio 2.2-2.3. WLT 
1.7-1.9. Apex acuminate. Base subcordate, symmetrical. Margin un-
evenly serrate to biserrate, upper terminal teeth simple to bifid, 
teeth small; 0-4 to 0-5 intersecondary, 4 on principal segment, base 
with teeth. Craspedodromous. Midrib straight to slightly sinuous. 
PFS ratio 4.1-5.2. Secondary angles 50°-80° at base, 45°-50° above; 
secondary veins straight, randomly opposite, including Nos. 1 and 2 
secondaries. 15-16 secondary segments, 4-5 below widest point; spac-
ing 0 mm. at base, 5-6 mm. above, basal segment contracting to 0.
P-W ratio 0.7-1.3. 18-26 externals, weak, over half distance to mid-rib on No. 1 secondary. 7-10 joining tertiaries, 2-3 intra-angulars; tertiaries straight; joining tertiary angles acute, intra-angulars obtuse; tertiaries commonly opposite; circumtertiary segments common; tertiaries irregular in course; medials developed. Net developed to quin-tertary level. Leaf 53-62 mm. long, 24-53 mm. wide.

Remarks. - Though very similar to C. caroliniana, possible critical differences are the L-W ratio, the PPS ratio, and the marginal characteristics.

1850. (Plate LV).


One leaf studied in detail, two in general.


HANCHURIA: Litankhetsky, along railway, Aug., 1926, P.H. Dorsett 6466 (UC).

Description. - Broadly ovate. L-W ratio 1.7. M/L 1:4. Apex acuminate. Base very highly cordate, symmetrical or asymmetrical. Margin unevenly dentate, teeth relatively small, terminal teeth often longer (2 mm.); margin characteristic, bases of teeth broad, low, 2 mm. wide, thinning in 1 mm. vertically to 0.5 mm. width, terminated by 1-2 mm. long needle-like teeth; 0-7 intersecondary teeth, 3 on principal segment, base with many teeth. Craspedodromous. Midrib straight in
Plate LV. 

Carpinus erosu 31.

JAPAN: Honshu; Hakone, Stone Pass, May 15, 1927,
T. Sawada x 2 (UC). (x 2.5)
lower one to two-thirds, crooked upper one to two-thirds. PPS ratio 3.1. Secondary angles 135° at base, 50° above; secondary veins straight, randomly opposite, including Nos. 1 and 2 secondaries. 17-21 secondary segments, 2-4 below widest point; spacing 0 mm. at base, 6 mm. above, basal segment contracting to 0. P-W ratio 0.7. 25-28 externals, lower strong, upper weak, over half distance to midrib on No. 1 secondaries, sometimes on No. 2. 17 joining, 1 intra-angular secondaries; tertiaries straight to gently and symmetrically folded; joining tertiary angles acute, intra-angular angles obtuse; tertiaries commonly opposite; circum-tertiary segments very common in a prominent medial zone; medials common; tertiaries irregular in course. Net veins developed to quinternary level, vein endings rare, simple. Leaf 62-110 mm. long, 37-62 mm. wide.

Remarks. - Carpinus erosæ, often called C. cordata, was given a separate species status by Blume on the basis of fragmentary remains. Sargent (1916) and Winkler (1914) have synonymised the two.

Carpinus erosæ has been reported from the Miocene of Shantung Province (Hu and Chaney, 1940, C. miocordata Hu and Chaney). In this study, the following statement is made:

The possibility must be mentioned that certain of the leaves here included under C. miocordata may actually be referable to C. micropseudaninowii, but in any case there have been no criteria recognized by which they may be differentiated. (p. 32).

This study should provide ample criteria for distinguishing the two living equivalents, C. erosæ and C. turcsaninowii.

6. CARPINUS FACINEA Lindl. in Wall. Pl. as. rar. II: 5. 1831.

One leaf studied.
Description. - Narrowly ovate. L-W ratio 2.2. MGT 1.5. Apex acuminate. Base rounded, asymmetrical, tending to parallel No. 1 secondaries. Margin serrate, teeth narrow, tapering, 1 mm. long, hooked strongly toward apex, small; 0-3 intersecondary teeth, 2 on principal segment, base without teeth. Craspedodromous. Midrib straight. PPS ratio 2.7. Secondary angles 70° at base, 40° above; secondary veins slightly concave, bending sharply just before entering terminal teeth, randomly opposite. 21 secondary segments, 2-3 below widest point; spacing 1.5 at base, 7.5 mm. above, basal segment contracting slightly at midrib. 20 externals, strong, very few in number considering large leaf size, over half distance to midrib on the No. 1 secondary. 20 joining; 2 intra-angular terciaries, branching, straight; joining terciaries at 90°, intra-angulars obtuse; terciaries commonly opposite; circumtertiary segments common, characteristically angular and polygonal; terciaries irregular in course; Net veins developed to sexternary level, vein endings rare, simple. Leaf 88 mm. long, 40 mm. wide.

Remarks. - The number of tertiary veins and the shape of the tertiary segments are quite distinctive characters if they are found in other specimens of the species.


One leaf studied.

Base cordate, symmetrical. Margin unevenly serrate, teeth large to average, terminal teeth longer and more tapering than intersecondary teeth; 0-7 intersecondary teeth, 6 on principal segment, base with teeth. Craspedodromous. Midrib straight. PFS ratio 5.1. Secondary angles 90° at base, 45° above; secondaries straight, bending at margin, occasionally bifurcating both near margin and midrib, randomly opposite. 33 secondary segments, 7-8 below widest point; spacing 0 mm. at base, 8 mm. above, the basal segment contracting to 0. P-M ratio 0.6. 10 externals, strong, 3½ above the No. 5, over half the distance to the midrib on Nos. 1 and 2 secondaries. 21 joining, 2 intra-angular tertiaries, predominantly simple; tertiary fold gentle; joining tertiaries acute, intra-angulars obtuse; tertiaries rarely opposite; circumtertiary segments common. Net veins developed to sexternary level. Leaf 162 mm. long, 70 mm. wide.

Remarks. - The bifurcations of the secondaries are not externals leaving as forks; externals leaving as forks terminate in smaller intersecondary teeth. Forks of the secondaries terminate in large terminal teeth.


One leaf studied.


Description. - Ovate. L-W ratio 1.8. MLT 1.5. Apex acute.
Plate LVI. *Carpinus fargesiana* H. Winkl.
CHINA: Szechuan; northeastern Tachienlu, Sept. 25, 1930, W.C. Cheng 1930 (DS) (x 4.0)
Base cordate, asymmetrical. Margin biserrate to doubly dentate, teeth average to small, teeth characteristically blocky in outline, angular, with a broad base, bifid in upper half of leaf; 0-3 inter-secondary teeth, 2 on principal segment, base with teeth. Craspedodromous. Midrib crooked. PFS ratio 3.2. Secondary angles 60° below, 50° above; secondaries straight, large and prominent bend in secondaries at margin, randomly opposite. ll secondary segments, 3 below widest point, spacing 0 at base, 5.5 mm. above, last segment contracted to 0 at midrib. P-W ratio 1.1. 20 externals, moderately strong, over half distance to midrib on Nos. 1 and 2 secondary veins. 12 joining, 2 intra-angular tertiaries, branching, straight to gently folded; joining tertiary angles acute, the intra-angular angles obtuse; tertiaries rarely opposite; circumtertiary segments fairly common; tertiaries irregular in course; medials developed. Net developed to quaternary level, vein endings common, simple. Leaf 61 mm. long, 23 mm. wide.

Remarks. — Similar in several respects to C. orientalis, particularly the leaf margin.


Three leaves studied.

CHINA: Chekiang; near Siachu; May 22-25, 1921; R.C.Ching 1619 (UC); southern part; King Yuan region, Aug.-Sept., 1921; R.C.Ching 2534 (UC); Yunnan; Lungshan
Plate LVII. Carpinus henryana H. Winkl.

CHINA: Chekiang; near Siachu, May 22-25, 1924,
R.C. Ching 1619 (UC). (x 4.3)
region; Yangtze drainage basin, east of Likiang, 1923, J.F.Rock 10,72 (UC).

Description. - Oval-ovate to slightly oblong. L-W ratio 2.1-2.6. MLT 1.4-1.7. Apex acute-acuminate. Base subcordate to cordate, symmetrical. Margin serrate, teeth small, but large for leaf size, simple, equal in size, almost no intersecondary teeth; 0 to 0-1 intersecondary teeth, 0 on principal segment, base without teeth. Craspedodromous with dictyodromous tendencies. Midrib straight to slightly crooked. PPS ratio 4.0-4.1. Secondary angle 45°-100° at base, 35°-50° above; secondaries straight to slightly concave, the No. 1 often concave, bending into cordate portion of leaf; secondaries bending at margins, commonly opposite, particularly in lower half of leaf. 17-18 secondary segments, 4-5 below widest point; spacing 0-1 mm. at base, 2.5-6 mm. above, basal segment contracting at midrib, sometimes to 0. P-M ratio 0.5-1.0. 4-5 externals occurring only with intersecondary teeth, weak, if present, extending over half distance to midrib on No.1 secondary. 16-18 joining, 1 intra-angular tertiary veins, branching, straight; joining tertiary angles acute, intra-angular angles obtuse; tertiaries commonly opposite; circumtertiary segments common; tertiaries irregular in course; medials developed. Net veins developed to quinary level, vein endings rare, simple. Leaf 36-62 mm. long, 15-44 mm. wide.


1850. (Plate LVIII).

Plate LVIII. *Carpinus japonica* Bl.
JAPAN: Honshu; Hakone, Sengoku, June 11, 1927,
*T. Sawada* s.n. (UC). (x 4.0)

**Carpinus carpinus** Sarg. *Card. & Forest. VI: 36h. f.56. 1893.*

One leaf studied.

**JAPAN: Kanone, Sengoku, June 14, 1927, T. Sawada s.n. (UC).**

**Description.** - Ovate. L-W ratio 1.9. MLT 1.6. Apex acut-acuminate. Base cordate, slightly asymmetrical. Margin unevenly serrate to unevenly dentate, teeth small, long, pointed, the terminal teeth longest; 0-3 intersecondary teeth, 3 on principal segment, base with teeth. Craspedodromous. Midrib straight. PPS ratio 5.3. Secondary angles 90° at base, 60° above; secondary veins straight, bending at margin, commonly opposite. 21 secondary segments, 7 below widest point; spacing 0-3 mm., basal segment contracting to 0. P-W ratio 0.6. 27 externals, weak, 15 above the No. 5, over half the distance to the midrib on the No. 1 secondary. 19 joining, 1 intra-angular tertiaries, branching; tertiary fold gentle; joining tertiary angles slightly acute, intra-angulors obtuse; tertiaries rarely opposite; circumtertiary segments common, forming prominent rows in medial zones; tertiaries irregular in course. Net developed to quinternary level. Net endings rare, simple. Leaf 14.2 mm. long, 22 mm. wide.

**Remarks.** - Medial rows of circumtertiary segments are a very distinctive feature of the leaf.


1931. (Plate LIX).
Plate LIX. Carpinus kweichowensis Hu
CHINA: Kweichow; Chengfeng, Oct. 17, 1930,
Y. Tsiang 4638 (UC). (x 3.0)
One leaf studied.

CHINA: Kwêichow; Chengfeng, Oct. 17, 1930, Y. Tsieang 1638 (UC).

Description. - Ovate. L-W ratio 1.9. WIL 1.6. Apex acute-acuminate. Base subcordate, asymmetrical. Margin unevenly serrate, serrations relatively widely spaced, broad, teeth coming to a point directly without tapering gradually, small to average, terminal teeth largest, simple; 0-1 intersecondary teeth, 1 on principal segment, base with teeth. Craspedodromous. Midrib crooked. FFS ratio 3.3. Secondary angles 90° at base to 50° above; secondaries straight, bending at margins, rarely opposite, the No. 1 secondaries subopposite. 1st secondary segments, 3 below widest point; spacing 0 mm. at base to 7.5 above, basal segment contracting to 0. P-W ratio 1.0. 16 externals, relatively strong, over half the distance to the midrib on the Nos. 1 and 2 secondaries. 7 joining, 2 intra-angular secondaries; tertiary fold gentle; joining tertiary angles acute, intra-angular angles acute above, obtuse below; secondaries commonly opposite; circumtertiary segments common; secondaries fairly regular in course; medials poorly developed. Net developed to sexternary level, vein endings rare, simple. Leaf 59 mm. long, 32 mm. wide.


Plate LI. *Carpinus laxiflora* (Sieb. & Zucc.) Bl.

CHINA: Chekiang; Th-tai-shan, May 5-18, 1924,
R.C. Ching 1663 (UC). (x 2.5)
Six leaves studied.

CHINA: Chekiang; Suichang-heien, May 1, 1933, S.Chen 1259 (DS); Tien-tai-hean, July-Aug., 1927, C.Y.Chiao 1049 (UC); Tih-tai-hean, May 15-18, 1924, R.C.Ching 1193 (UC); Kwangsi, June 8, 1928, R.C. Ching 5839 (UC); Kwantung, 1928, K.Fenzel 122 (UC).

JAPAN: Honshu; Tochigi Prefecture; Mt. Isuru, May 19, 1917, Shigetaka Suzuki 11053 (UC).

Description. - Ovate, rarely oval. L/W ratio 1.7-2.3. MLT 1.4-1.9. Apex acuminate to abruptly acute. Base subcordate, round, or cordate. Margin biserrate, teeth small, long, narrow, pointed, bifid or simple; 0-4 to 0-10 intersecondary teeth, 3-7 on principal segment, base with teeth. Craspedodromous. Midrib usually crooked, at least in upper portion, rarely straight. PPS ratio 3.2-4.2. Secondary angles 30°-65° at base (30° with highly convex junction of secondary with midrib), 45°-50° above; secondaries straight, bending at margin, randomly opposite, often including Nos. 1 and 2 secondaries. 1h-18 secondary segments, 2-4 below widest point; spacing 0 mm. at base, h-7.5 mm. above, base contracting to 0 at midrib. P-M ratio 0.8-1.8 (all but one 0.8-1.3). 19-33 externals (all but one 19-27), weak, over half the distance to the midrib on the No. 1, often the No. 2 secondary. 11-19 joining, 1-4 intra-angular tertiaries, branching; tertiary fold gentle; joining tertiary angles slightly acute, intra-angulare obtuse; tertiaries rather commonly opposite; tertiaries irregular in course; medials poorly developed. Net veins developed to sexternary level, net vein endings rare, simple. Leaf 38-78 mm. long, 22-58 mm. wide.

Remarks. - The abruptly acute apex is typical of this species.


Four leaves studied.

CHINA: Anhwei; southern part; Chu Hwa Shan, June 28, 1925, Ren-Chang Ching 2801 (UC); Hainan; Five Finger Mountains, May 15, 1920, Woon Young Chun 1516 (UC); Kwantung; Lung Tau Shan, near Yu, June 7, 1921, To Kang Peng, Ts'ang Wai Tak, and Ts'ang Un Xin 415 (UC); Szechuan; Owei-shan, July 17, 1930, W.F. Wang 6580 (DS).

**Description.** Narrowly oval to slightly ovate. L-W ratio 1.9-2.6. MLT 1.4-2.1. Apex highly acuminate. Base round, symmetrical. Margin biserrate to unevenly serrate, teeth small, slightly pointed, bifid or simple; 0-3 to 0-7 intersecondary teeth, 3-5 on principal segment, base with teeth. Craspedodromous, with faintest hints of dictyodromy. Midrib straight except for flexure near middle. FFS ratio 2.9-3.7. Secondary veins 50-70° at base, 30-45° above; secondaries straight, bending abruptly at margin, randomly opposite, including Nos. 1 and 2 secondaries. 11-18 secondary segments, 3-4 below widest point; spacing 0 mm. at base to 7 mm. above, basal segment contracting to 0. P-M ratio 1.0-1.6. 16-27 externals, weak, over half the distance to the midrib on the No. 1, sometimes on the No. 2 secondary. Interordinal veins developed in apex of leaf. 11-15 joining, 2-3 intra-angular
tertiaries, branching; tertiary fold gentle; joining tertiary angles slightly acute, intra-angular angles obtuse; terciaries fairly commonly opposite; circumtertiary segments common; tertiary veins irregular in course; medials poorly developed. Net developed to sexternary level, net vein endings rare, simple. Leaf 54-78 mm. long, 21-33 mm. wide.


Two leaves studied.

BURMA: Keng Tung territory; southeastern Shan States; Mah Len Valley, between Pang Sop Lao and Ban Yang Kha, Jan. 29, 1922, J.P. Rock 2167 (UC).

INDO-CHINA: Tonkin; Chapa, Sept., 1928, A. Petelot (UC).

Description. - Oval to ovate. L-W ratio 2.5. MLT 1.4-1.6. Apex acuminate. Base round, parallel to No. 1 secondary, asymmetrical. Margin unevenly serrate, teeth small to average, terminal teeth much larger than intersecondary teeth, pointed, intersecondary teeth blunted to slightly pointed; 0-4 to 0-6 intersecondary teeth, 3-6 on principal segment, base with few or no teeth. Craspedodromous. Midrib faintly sinuous to straight. PPS ratio 3.1-3.2. Secondary angles 55° at base, 90° above; secondaries straight to slightly concave, No. 1 secondary camptodromous, No. 2 secondary dictyodromous, secondaries bending slightly at margin, alternate except for the No. 1. 12-14 secondary segments, 2-3 below widest point; spacing 0 mm. at base, 8-9 mm. above, basal segment contracting to 0. P-W ratio 1.5-1.6. 14-19 externals,
Plate LXI. Carpinus londoniana H. Winkl.

BURMA: Keng Tung territory; southeastern Shan States; valley of the Leh Len, between Fang Sop Lao and Ban Yang Kha, Jan. 29, 1922, J.P. Rock 2167 (UC). (x 2.3)
weak, over half distance to midrib on Nos. 1 and 2 secondaries. 9-10 joining, 2-3 intra-angular tertiaries; tertiaries straight to gently rolled; joining tertiary angles acute, intra-angulars acute above, obtuse below; tertiaries rarely opposite; circumtertiary segments common; tertiaries irregular in course; medials developed. Net veins developed to sexternary level, net vein endings fairly common, simple. Leaf 50-79 mm long, 20-32 mm wide.


One leaf studied.

CHINA: Yunnan; east slopes of Si Shan above Kunming Lake, near third temple, May 9, 1929, E.S. Ferris and Yun-Chun Hsu 12,089 (NS).

Description. - Ovate. L/W ratio 2.0. M/L 1.8. Apex acute-acuminate. Base subcordate, asymmetrical. Margin biserrate, teeth small, upper terminal teeth bifid; 0-4 intersecondary teeth, 4 on principal segment, base with teeth almost to midrib. Craspedodromous. Midrib crooked. PPS ratio 3.4. Secondary angle 80° at base, 55° above; secondaries straight, bending very sharply at margin, randomly opposite. 11 secondary segments, 3 below widest point; spacing 0 mm. at base, 6 mm. above, basal segment contracting to 0. P-W ratio 1.0. 20 externals, strong, over half the distance to midrib on secondaries No. 1 and 2. 13 joining, 4 intra-angular tertiaries, branching; tertiaries straight; joining tertiary angles 90°, intra-angulars obtuse; tertiaries fairly commonly opposite; circumtertiary segments fairly common in the medial zone; tertiaries irregular in course. Net developed to sexternary
Plate LXII. *Carpinus mongolica* Hand.-Mazz.

CHINA: Yunnan; east slopes of *Shan* above Huang Lake, near 3rd Temple, May 9, 1949, R.S. Ferris and
Lur-Chun Han 12,082 (BM). (x 3.0)
level, net vein endings fairly common, simple. Leaf 69 mm. long,
28 mm. wide.


(Plate LXIII).

Carpinus duinensis Scop. Pl. carniol. II: 243. t. 60. 1772.

Carpinus edentula Waldst. & Kt. Pl. rar. hungar. II: 32. 1805.

Three leaves studied.

GREECE: Eurytania: Megalochorio; tributary of the Karpentis River between Kaliakuda and Chalidoni, Aug. 1, 1926, Joh. Mattfeld 2581 (DS); Thrace; near Putwiran and Hamidli, Sept. 30, 1926, Joh. Mattfeld 3122 (DS); near Guredzik, north of Drama, Sept. 19, 1926, Joh. Mattfeld 2921 (DS).

Description. - Oval to almost oblong. L-W ratio 2.0-2.1. L/W 1.6-1.8. Apex acute to subacute. Base round to subcordate, symmetrical or asymmetrical. Margin biserrate, teeth small to very small, terminal teeth largest, bifid, terminal teeth typically blocky and angular, giving the margin a step-like appearance; 0-3 to 0-4 intersecondary teeth, 2-3 on principal segment, base with teeth. Craspedodromous. Midrib straight to slightly sinuous. PPS ratio 3.6-4.0. Secondary angles 30°-90° at base (30° where strongly convex at junction with midrib), 40°-50° above; all secondaries convex upward, the No. 1 secondary often concave, bending slightly at the margins, all or mostly opposite, 13-16 externals, 4-5 below widest point; spacing 0 mm. at base, 3.5-6 mm. above,
Plate LXIII. Carpinus orientalis Mill.
GREEK: Eurytanis; Megalochorio; tributary of Karpenisi River between Kaliskuda and Chalidoni, Aug. 1, 1926,
Joh. Kattfeld 2551 (DS). (x 4.0)
basal segment contracting to 0. P-W ratio 0.7-1.3. 23-31 externals, weak, large number for such small leaves, over half the distance to the midrib on No. 1 secondaries, sometimes on No. 3. 9-10 joining, 1-4 intra-angular tertiaries, branching; tertiary fold gentle; joining tertiary angles acute, intra-angular angles 90° or slightly obtuse, occasional acute angles; tertiaries commonly opposite; circum-tertiary segments common; tertiaries very irregular in their courses, with a characteristic sag toward midrib midway in their courses; medials poorly developed. Net developed to quinquenary level, sometimes to sexternary, net vein endings common, usually simple. Leaf 36-50 mm. long, 17-25 mm. wide.


Six leaves studied.

CHINA: Chihli; Kwan Tso Ling, Aug. 15, 1927, J.C. Liu 1171 (UC); Hopei; Kiang Hsuei Ho, July 7, 1936, T.F. King 135 (UC); Kiangsu; Bau Hwa Shan, June 23, 1925, A.H. Steward 3477 (UC); Shantung; not far from Tsiananfu, Lung Tung, Sept. 7, 1930, C.Y. Chiao 3071 (UC); in mountains, Sept. 19, 1907, F.N. Meyer 226 (UC); Szechuan; Pin-wu, Aug. 19, 1931, W.C. Cheng 2965 (US).

Description. - Ovate, rarely oval. L-W ratio 1.6-2.1. M-LT 1.4-1.9. Apex acute to acuminate. Base very distinctive, symmetrical or asymmetrical, either slightly cordate or auriculate, paralleling No. 1 secondaries to within 2 mm. of midrib, then turning abruptly to junction of No. 1 secondary and midrib, a Hamamelis type base (Plate LXXXVII) in miniature. Margin biserrate to almost doubly dentate, teeth average to small, similar to those of C. orientalis, terminal teeth large, with
Plate LXIV. Carpinus turczaninowii Hance.

CHINA: Szechuan; Pin-wu, Aug. 19, 1931, W.C. Chang 2965 (08). (x 2.5)
Plate LIV. *Carpinus turczaninowii* Hance.

CHINA: Shantung; near Tsinanfu, Lung Tung, Sept. 7, 1930, C.Y. Chiao 2071 (UC). (x 2.5)
broad base, suggesting step pattern along margin, teeth sometimes very subdued; 0-2 to 0-5 intersecondary teeth, 1-4 on principal segment, base without teeth. Craspedodromous with dictyodromy faintly developed. Midrib characteristically straight in lower half, crooked in upper half. PPS ratio 2.2-3.3. Secondary angles 40°-100° at base, 35°-50° above; secondaries straight, slightly concave or convex, No. 1 secondary slight and short, all bending slightly at margin, randomly opposite, usually the Nos. 1 and 2. 11-16 secondary segments, 2-4 below widest point; spacing 0 at base, 1-6 mm. above, contracting to 0 at midrib. P-M ratio 0.9-1.1. 10-15 externals, rare on No. 1 secondary, moderately strong to weak, over half distance to midrib on No. 2 secondaries, sometimes on No. 1 secondaries, never on both. 7-18 joining, 2-4 intra-angular tertiaries, branching; tertiary fold gentle; joining tertiary angles acute, intra-angular angles obtuse; tertiaries rarely opposite; circumtertiary segments common; tertiaries often irregular in courses; medials developed. Net veins developed to quinquentinary level, net vein endings simple, fairly common to common. Leaf 35-61 mm. long, 17-38 mm. wide.


1899. (pro parte).


(pro parte).

Two leaves studied.
CHINA: Shansi; Lin-kon Shan, July 13, 1925, K. Ling 9333 (UC); Ja Siu, Aug. 26, 1923, C. T. Ren 6115 (UC).

Description. - Oval to ovate. L:W ratio 1.6-1.7. MLT 1.6-1.7. Apex acute. Base similar to C. turczaninowii, symmetrical. Margin unevenly dentate to doubly dentate, teeth average to small, broad, simple or bifid; 0-4 to 0-5 intersecondary teeth, 1-3 on principal segment, base without teeth. Craspedodromous. Midrib straight to slightly sinuous. PFS ratio 2.5-2.8. Secondary angles 80°-85° at base, 45°-50° above secondaries straight, bending at margin, No. 1 secondary slight, shorter than others, random secondaries opposite including Nos. 1 and 2 secondaries. 13-15 secondary segments, 3-5 below widest point; spacing 0 mm. at base, 3.5-6 mm. above, basal segment contracting to 0. P-M ratio 1.1. 12-19 externals, moderately strong, over half the distance to the midrib on the No. 2 secondary. 12-17 joining, 2 intra-angular secondaries, branching; tertiary fold gentle; joining tertiary angles acute, intra-angular angles obtuse; secondaries fairly commonly opposite; circumtertiary segments common; secondaries irregular in their courses; medials fairly well developed. Net veins developed to quinquinary level, net vein endings common, simple. Leaf 33-55 mm. long, 20-34 mm. wide.

Remarks. - This form does not seem to be significantly different from C. turczaninowii.

19. CARPINUS VIMINEA Lindl. in Wall. Pl. as. rar. II: t.106. 1831. (Plate LVII). One leaf studied.
Plate LXVI. _Carpinus viminea_ Lindl.

CHINA: Chekiang; Tien-tai-hsien, June 24, 1932,
S. Chen 395 (DS). (x 2.1)
Description. - Elliptical. L-W ratio 2.9. NLT 1.6. Apex abruptly acuminate, long, tapering. Base round to almost flat, parallel to No. 1 secondary veins almost to midrib, then cutting to junction of midrib and No. 1 secondary, symmetrical. Margin biserrate, teeth small, terminal teeth larger, bifid in upper half; 0-7 intersecondary teeth, 4 on principal segment, base without teeth except on outer edge. Craspedodromous. Midrib straight in lower two-thirds, sinuous in upper one-third. PPS ratio 1.0. Secondary angles 55° at base, 60° above; secondaries straight, bending at margin, randomly opposite, including Nos. 1 and 2 secondaries. 18 secondary segments, 4 below widest point; spacing 0 mm. at base, 7 mm. above, basal segment contracting to 0 at midrib. P-W ratio 1.3. 24 externals, moderately strong, over half the distance to the midrib on Nos. 1 and 2 secondaries. 12 joining, 5 intra-angular secondaries; secondaries straight; joining secondaries 90° to acute, intra-angular angles obtuse; tertiary veins rarely opposite; circumtertiary segments common; secondaries somewhat irregular in course; medials poorly developed. Net developed to sexternary level, net endings rare, simple. Leaf 79 mm. long, 28 mm. wide.

Remarks. - The shape of this leaf is different from any other so far considered.

Fossil species of Carpinus (?)

I have studied one specimen labeled C. grandis Unger, which, after a complete examination, does not appear to be a specimen of Carpinus, but of Ostrya. I present it here in order to emphasize its
differences with **Carpinus**.

**Carpinus grandis** Unger. *Synop. Fl. Foss.: 220. 1845.*

One leaf studied.


**Description.** - Oval-ovate. L-W ratio 2.7. MLT 1.8. Apex acuminate. Base round to auriculate, symmetrical. Margin unevenly serrate, teeth small, simple, terminal teeth largest; 0-5 intersecondary teeth, 4 on principal segment, base with teeth. Craspedodromous. Midrib straight. PFS ratio 1.9. Secondary angles 50° at base, 55° above secondaries slightly concave, randomly opposite, including Nos. 1 and 2 secondaries. 17 secondary segments, 4 below widest point, diverging slightly toward midrib; spacing 0 mm. at base, 8 mm. above, basal segment contracting to 0 at midrib. P-M ratio 1.0. 16 externals (probably more), moderately strong to weak, extending over half distance to midrib on Nos. 1, 2, and 3 secondaries, 9 joining, 3 intra-angular ter tiaries; tertiary fold gentle; all tertiary angles acute; ter tiaries commonly opposite, remaining details uncertain due to imperfection of preservation. Net veins developed at least to quaternary level. Les 83 mm. long, 31 mm. wide.

**Remarks.** - The delicate features of this leaf resemble those of **Carpinus** very closely and for this reason the leaves are not only unlike those of **Ostrya** in general, but superficially do not resemble those of **Ostrya** found with it. In the same deposit, however, are leaves of
A comparison of this leaf with other specimens of *Carpinus*
from the same deposit is interesting. *Univ. Cal. Coll. Paleobot.*
Nos. 28 and 32 (Chaney, 1927, Pl. 9, figs. 6 and 10 respectively)
show several differences with No. 33. The basal secondaries of Nos.
28 and 32 are strongly convex at their junctions with the midrib; the
secondary segments diverge toward the margin, never toward the midrib;
and the intra-angular tertiary angles are obtuse, not acute. These
are characters of generic importance. Specimens Nos. 28 and 32 are
correctly referred to *Carpinus*.

Despite superficial differences between No. 33 and Nos. 34,
35, and 36, all identified as *Ostrya oregoniana* Chaney, there are
several similarities. Two are diagnostic criteria for distinguishing
between the two genera. First, in *Carpinus*, secondary segments
do not diverge toward the midrib, but so in *Ostrya*. Second, external
veins in *Carpinus* do not extend over half the distance to the midrib
on the 3 lowest secondaries, but at the most on the lowest 2; it is
common for the externals to extend over half the distance to the mid-
rib on the lowest 3 secondaries in *Ostrya*.

Auxiliary evidence may be found in the intra-angular angles.
No. 33 has acute intra-angular angles from apex to base. This feature
is not common in *Ostrya* but is never present in *Carpinus*, at least in
all of the leaves studied. Another character found almost exclusively
in *Ostrya* is an auriculate base; No. 33 has a somewhat auriculate base.

In summary, *Univ. Cal. Coll. Paleobot.* No. 33 is *Ostrya*, not
Carpinus. I do not know to which living species of Carpinus it should be referred.
<table>
<thead>
<tr>
<th>Chart 3</th>
<th>A chart for the determination of species of CARPINUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>x = 50% - 100%</td>
<td>x = x = x</td>
</tr>
<tr>
<td>- = 15% - 50%</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>? = unknown</td>
<td>x = x = x</td>
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</table>

<table>
<thead>
<tr>
<th>Dictyodromous in part</th>
<th>x = x = x</th>
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<tbody>
<tr>
<td>Midrib straight</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Midrib not straight</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Apex acute</td>
<td>x x x x x x x x x x x</td>
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<tr>
<td>Apex acuminate</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Base symmetrical</td>
<td>x x x x x x x x x x x</td>
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<tr>
<td>Base asymmetrical</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Base flat, parallels #1's</td>
<td>x x x x</td>
</tr>
<tr>
<td>Base round</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Base subacute</td>
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<tr>
<td>Base ciliate</td>
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<tr>
<td>Base has teeth</td>
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</tr>
<tr>
<td>Base has no teeth</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Margin serrate</td>
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<td>Margin doubly dentate</td>
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<tr>
<td>Intersec, teeth 0-1 to 0-3</td>
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<tr>
<td>Intersec, teeth 0-4 to 0-7</td>
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<tr>
<td>Intersec, teeth 0-8 to 0-10</td>
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<td>Terminal teeth simple</td>
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<td>Terminal teeth bifid</td>
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<tr>
<td>Terminal teeth trifid</td>
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<tr>
<td>Leaf broadly ovate</td>
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<tr>
<td>Lower sec. convex at midrib</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Only #1 convex at midrib</td>
<td>x x x x x x x x x x x</td>
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<tr>
<td>All sec. concave-str. at midrib</td>
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<tr>
<td>No. externals 1-15</td>
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<tr>
<td>No. externals 15-30</td>
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<td>No. externals 31-40</td>
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<td>Externals over ½ on #1</td>
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<td>Externals over ½ on #2</td>
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<td>Secondary bifurcate</td>
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<td>Basal segment 0</td>
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<tr>
<td>Basal sec. contracts, not 0</td>
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<tr>
<td>No. tert. veins 0-9</td>
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<tr>
<td>No. tert. veins 10-21</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>No. tert. veins 22-24</td>
<td>x x x x x x x x x x x</td>
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<tr>
<td>Most tertaries simple</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Most tertaries branch</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Tert. commonly opposite</td>
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<tr>
<td>Tertiaries straight</td>
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</tr>
<tr>
<td>Tertiary fold gentle</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Intra-angulic acute</td>
<td>x x x x x x x x x x x</td>
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<tr>
<td>Intra-angulic obtuse</td>
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<tr>
<td>Medials developed</td>
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<tr>
<td>Sexternary net present</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Sexternary net not present</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Intert, vein endings common</td>
<td>x x x x x x x x x x x</td>
</tr>
<tr>
<td>Intert, vein endings rare</td>
<td>x x x x x x x x x x x</td>
</tr>
</tbody>
</table>
IV. CORYLUS L. Gen.: 730. 1737.

Forty-two specimens of extant Corylus studied; no fossils.

Chart I.

Description.- Oval, broadly oval, or round. L-W ratio 1.0-1.7. Apex usually abruptly acute, less often acute or acuminate. Base always cordate, symmetrical or very slightly asymmetrical. 0-7 to 0-19 intersecondary teeth, average in size, margin doubly dentate, rarely simply dentate, C. tibetica alone biserrate or serrate, base always with teeth. Craspedodromous, the only tendencies toward dictyodromy in C. tibetica. Midrib rarely straight, almost always crooked, thick. Secondary angles diverging mostly between Nos. 2 and 2 secondaries; secondaries usually slightly concave, widely spaced, rarely opposite except in C. tibetica. 2-3 secondary segments below widest point, usually 2, basal segment always contracting to 0. Externals rare above the No. 5 except in C. cornuta and C. tibetica, over half distance to midrib on No. 1, usually on the No. 2, occasionally so on No. 3. Tertiaries widely spaced, tending to be mostly simple; tertiaries straight or folded gently; upper joining tertiary angles acute, the lower varying but in lower half of leaf tending to be 90° or obtuse, the intra-angular angles 90° to obtuse. Sexternary net always present, septernary net not uncommon, net vein endings common except in C. tibetica, mostly complex.

Species of Corylus

1. CORYLUS AMERICANA Walt. F. carolin. 236.

1788. (Plate LVII).

Plate LXVII. Corylus americana Walt.
UNITED STATES: Michigan; Constantine, June 29, 1923,
G.L.Fisher s.n. (UC). (x 2.3)
Corylus serotina, Corylus humilis, Corylus pumila Hort.

Six leaves studied.

UNITED STATES: Indiana; near Lake Wazunkuk, 1900, J.T. Scovell and J.W. Clark 794 (H3); Massachusetts; Hampshire County; Amherst, June 23, 1909, S.C. Brooks s.n. (UC); Michigan; Constantine, June 29, 1923, G.L. Fisher s.n. (US); Oklahoma County; Ottawa County; Ottawa, Aug. 30, 1913, E.W. Stevens 9260 (DS); Rhode Island; Warwick, June 2, 1877, J.A. Ellisiep s.n. (DS); West Virginia; Summer County; Blue Stone River, July 16, 1930, E.E. Berkeley s.n. (DS).

Description. — Oval to round. L-W ratio 1.3-1.7. WLT 1.5-1.8. Apex acute to acuminate, sometimes abruptly acuminate. Base cordate to subcordate, symmetrical. Margin doubly dentate to unevenly dentate, teeth average to large; 0-7 to 0-11 intersecondary teeth, 6-10 on principal segment, base with teeth almost to midrib. Craspedodromous. Midrib crooked, very thick in lower two-thirds. PPS ratio 2.0-2.1. Secondary angles 50-70° at base, 65-60° above; secondaries concave, rarely opposite except for No. 1. 8-12 secondary segments, 2 below widest point; spacing 0 at base, 6-8 mm. above. P-M ratio 1.1-1.9. 11-20 externals, strong, 5-7 on No. 1 alone, rare or none above No. 5, over half the distance to midrib on Nos. 1 and 2 secondaries. 5-10 joining, 2-5 intra-angular terciaries; tertiary veins straight to gently folded; joining terciaries 90° to acute, intra-angulars 90° to obtuse; terciaries fairly commonly opposite. Net developed to sexternary level, vein endings common and complex. Leaf 39-101 mm. long, 23-77 mm. wide.

Plate LXVIII. Corylus avellana L.

GERMANY: Munich, June, 1501. Herb. Monacense s.n.
(UC). (x 2.5)

Corylus sylvestris Salisb. Prodr. 392. 1796.

Corylus serenyiana Pluskal. in Oestr. bot. Zeitschr. II: 393. 1852.

Four leaves studied.


GERMANY: Munich, June, 1901, ex herb. monacense, s.n. (UC).


UNION OF SOVIET SOCIALIST REPUBLICS: Kuban Province; Batalnaschinsk region, June 25, 1916, A. Kryshtofovich s.n. (UC).

Description. - Round to slightly obdeltoid. L-W ratio 1.1-1.4. MLT 1.5-2.5 (all but one 1.5-1.8). Apex abruptly acuminate. Base cordate to almost auriculate, symmetrical. Margin doubly dentate, teeth average to large; 0-11 to 0-18 intersecondary teeth, 5-12 on principal segment, base with teeth almost to midrib. Craspedodromous. Midrib crooked. PPS ratio 1.9-2.0. Secondary angles 55°-85° at base, 40°-60° above; secondaries slightly concave, rarely opposite except the No. 1. 11-12 secondary segments, 2-3 (usually 2) below widest point; spacing 0 mm. at base, 10-11.5 mm. above. P-W ratio 1.4-1.7. 16-18 externals, strong, none above No. 5 secondary, over half distance to midrib on Nos. 1 and 2 secondaries. 5-11 joining, 2-4 intra-angular ter- tiaries; tertiary fold gentle; joining tertaries 90° to acute, intra-
angulars tending to be obtuse at least in lower half of leaf; ter-
taries rarely opposite. Not developed to sexternary level, vein
endings common, complex. Leaf 52–91 mm. long, 46–72 mm. wide.

(Plate LXIX).

Corylus jacquemontii Decne. in Jacqem. Voy. Ind. IV:
160. 1832.
Corylus tiliacea Decne. in Jacqem. Voy. Ind. IV:
160. 1832.
Corylus bysantina Hort.

One leaf studied.

ITALY: Bologna, in woods, July, 1849, collector
unknown (DS 336,058).

Description. - Obovate to obdeltoid. L-W ratio 1.3. MLT 2.5.
Apex abruptly acute. Base cordate, symmetrical. Margin doubly dentate,
teeth small; 0–11 intersecondary teeth, 11 on principal segment, base
with teeth to midrib. Craspedodromous. Midrib straight in lower half,
slightly crooked in upper half. PPS ratio 2.0. Secondary angles 75°
below, 40° above; secondaries slightly concave, rarely opposite except
for No. 1 secondaries. 11 secondary segments, 3 below widest point;
spacing 0 mm. at base, 9 mm. above. P-W ratio 1.3. 24 externals,
strong, over half distance to midrib on Nos. 1 and 2 secondaries. 9
joining, 3 intra-angular tertiaries, simple; tertiaries straight to
gently folded; upper joining tertiary angles slightly acute, lower
Plate LXIX. Corylus colurna L.
ITALY: Bologna, July, 1849, collector unknown
s.n. (US 336058). (x 2.5)
and intra-angular angles 90° to slightly obtuse; tertiaries seldom opposite. Net veins developed to sexternary level, vein endings common, complex. Leaf 60 mm. long, 4.8 mm. wide.


**Corylus cornuta** Du Roi. ex Steud. Nom. ed. 1: 229. 1821.

**Corylus cornuta** Hort., ex Goeschke, Die Haselnuss: 89. t. 73. 1887.

Eight leaves studied.

**JAPAN**: Honshu; Koyasan, Aug. 26, 1907, U. Faurie 7 (DS).

**UNITED STATES**: Colorado; southwest of Colorado Springs, Bear Canyon, Aug. 21, 1921, R. Acipanum 321 (DS); Massachusetts; Chatham, July 20, 1918, E. L. Fernald 354 (DS); Michigan; Iron County; Gold Lake, June 27, 1937, E. L. Wilson 133 (DS); New York; Lisbon, July 9, 1914, Orre F. Phelps 364 (DS); North Carolina; Forsyth County; Winston-Salem, July 6, 1902, Biltmore Herbarium 322 (DS 79,007); Vermont; Brandon, July 12, 1922, E. L. Dutton s.n. (DS); Wyoming; Limestone Range, in woods, Jul. 1912, Aven Nelson 9537 (DS).

**Description.** - Oval to ovate. L-W ratio 1.3-1.7. (Faurie 7.2.0). MLT 1.6-2.2. Apex acute to acuminate. Base cordate, rarely auriculate. Margin doubly dentate, teeth small to average, rarely large; 0-7 to 0-17 intersecondary teeth, 7-14 on principal segment, basal teeth almost to midrib. Graspedodromous. Midrib slightly crooked. PPS ratio 1.7-2.6. Secondary angles 30°-80° (50°-80° except for Faurie 7); secondaries slightly concave (No. 1 secondary of Faurie 7 highly convex), rarely opposite except for either No. 1 or 2, never both. 8-12 secondary segments, 2-3 below widest point; spacing 0 mm. at base, 9-12 mm. above. P-M ratio 1.0-1.4 (1.0-1.3 except Faurie 7). 16-30 externals (20-22 most common), strong, over half
Plate LXX. Corylus cornuta Marsh.

UNITED STATES: Wyoming; Laramie Range, July 27, 1912, Aven Nelson 2537

(PS), (x 2.7)
distance to midrib on Nos. 1 and 2 secondaries. 6-11 joining, 2-5 intra-angular tertiary veins; tertiaries gently folded; upper joining tertiary angles slightly acute, the lower and intra-angulurs slightly obtuse; tertiaries fairly commonly opposite. Net veins developed to sexternary level, net vein endings common, usually complex. Leaf 52-72 mm. long, 36-43 mm. wide.

Remarks. - Faurie 7 is probably not C. cornuta.


Corylus rostrata var. californica A.D.C. in A.D.C. Prodr. XVI. 2: 133. 1861.

Corylus californica Rose. Card. & Forest. 8: 263. 1895.

Ten leaves studied.

CANADA: British Columbia; ½ mile north of Hope, June 20, 1911, C.I. Hitchcock and J.S. Morgan 7387 (DS);

UNITED STATES: California; Mendocino County; Fort Bragg region, July 15, 1921, C.D. Duncan 271 (DS); San Mateo County; Pescadero, July 3, 1901, W.S. Atkinson s.n. (DS); Santa Clara County; Creek Road, July 10, 1977, Josephine D. Randall s.n. (DS); Santa Cruz County; Glenwood, July 19, 1909, H.R. Dudley s.n. (DS); Siskiyou County; Shasta Springs, Sept. 15, 1902, C.B. Grant s.n. (DS); Tulare County; Sequoia National Forest; Boulder Creek, Nelson Camp, July 26-28, 1911, R. Macalun, I.L. Dickinson and R.S. Ferris 2815 (DS); Tuolumne County; Crane Creek 2 miles west of Yosemite National Park, June 20, 1939, L.I. Wiggins 2236 (DS); Oregon; Jefferson County; Battle Lake, July 19, 1925, W.F. Peck 14214 (DS); Washington; Seattle, June 11, 1902, W.E. Jones s.n. (DS).

Description. - Round to oval. L-W ratio 1.1-1.4. MLT 1.6-2.2. Apex subacute to abruptly acute or apiculate. Base cordate. Margin
Plate LXXI. Corylus cornuta var. californica (A. DC.) Sharp
UNITED STATES: California; San Mateo County;
Pescadero, July 3, 1901, W.S. Atkinson s.n.
(ES). (x 2.8)
doubly dentate, teeth small to average; 0-10 to 0-17 intersecondary teeth, 8-14 on principal segment, base with teeth almost to midrib. Craspedodromous. Midrib very crooked to sinuous, rarely straight. PPS ratio 1.7-2.0. Secondary angles 45°-70° at base, 140°-155° above; secondaries slightly concave, rarely opposite except for No. 1, rarely No. 2 secondary. 8-11 secondary segments, 2 below widest point; spacing 0 mm. at base, 7-12 mm. above. F-W ratio 1.2-1.7 (usually 1.3-1.7). 19-27 externals, strong, rare above No. 4 secondaries, over half distance to midrib on Nos. 1 and 2 secondaries, sometimes on No. 3. 4-11 joinings, 3-4 intra-angulars; tertiary fold gentle; joining tertiary angles mostly acute, lower tertiary angles rarely obtuse, intra-angulars 90° to acute; tertiary veins commonly opposite. Net veins developed to sexternary level, net vein endings common, complex. Leaf 38-68 mm. long, 3½-5½ mm. wide.

Remarks. - This variety is surprisingly different from C. cornuta, particularly in the statistical data. The differences are as large as those found between other species in the family, so that this form might deserve specific rank.

comb. nov. (Plate LXXIII).

Corylus rostrata var. tracyi Jeps. in Jeps. Man. fl. pl.
Calif.: 271. 1923.

One leaf studied.

UNITED STATES: California; Del Norte County; 3 miles east of Crescent City, July 31, 1931, J.P. Tracy 13,520 (DS).
Plate LXXII. Corylus cornuta var. tracyi (Jeps.) Meyerhoff.
UNITED STATES: California; Del Norte County; 3 miles east
of Crescent City, July 31, 1932; J.P. Tracy 13,520
(3S). (x 3.0)
Description.—Oval. L-W ratio 1.4. NZT 1.6. Apex subacute.
Base cordate. Margin doubly dentate, teeth small to average; 0-1 inter-
secondary teeth; 10 on principal segment, base with teeth to midrib.
Crasspedodromous. Midrib straight. PPS ratio 1.9. Secondary angles
60° at base, 30° above; secondaries almost straight, rarely opposite
except for No. 1. 10 secondary segments, 2-3 below widest point; spac-
ing 0 at base, 8.5 above. P-M ratio 0.9. 22 externals, strong, over
half distance to midrib on Nos. 1 and 2 secondaries. 11 joining, 2
intra-angular secondaries; secondaries straight to gently folded; upper
joining tertiary angles slightly acute, the lower and intra-angular
angles slightly obtuse; secondaries commonly opposite. Net developed
to sexternary level, net vein endings common, complex. Leaf 47 mm.
long, 34 mm. wide.

Remarks.—This leaf appears to be more closely related to C.
cornuta than to C. cornuta californica. I regret having to make a
nomenclatural change, but the form does appear to be slightly different.


Corylus tetrathylla (error typ.) Ledeb. in Denkschr. bayr.

Corylus hasibani Sieb. in Ann. Soc. pour l'encour. d. l'hortic.
Pays-Bas: 27. 1844.
Plate LXXIII. Corylus heterophylla Fisch.
MANCHURIA: Er Tsing Tier Tze, June 1, 1925,
P.H. Jorsett 3125 (UC). (x 2.0)

Two leaves studied.

MANCHURIA: Er Tsing Tien Tze, June 1, 1925, P.H. Dorsett 3125 (UC).

Description. - Oval to obdeltoid. L-W ratio 1.2-1.3. 1.9-5.2. Apex acute to abruptly acute. Base subcordate to cordate, symmetrical. Margin deeply doubly dentate, teeth small to average; 6-7 to 8-9 intersecondary teeth, 6 on principal segment, base with teeth to midrib. Craspedodromous, obdeltoid forms simulating supalmate condition. Midrib crooked. PPS ratio 3.6-5.1. Secondary angles 40° below, 50°-60° above; seconadiaries straight, rarely opposite except for No. 1 secondary. 6-8 secondary segments, 2-3 below widest point; spacing 0 mm. at base, 13-16.5 mm. above. P-M ratio 0.5-0.6. 16 externals, none above No. 5, strong, over half distance to midrib on No. 1, sometimes on No. 2. 6-8 joining, 3-4 intra-angular tertiaries, simple; tertiary fold gentle; all tertiary angles slightly acute, seldom obtuse; tertiaries commonly opposite. Net veins developed to sexternary level, vein endings common, complex. Leaf 52 mm. long, 40 mm. wide.

Remarks. - Both leaves used for this study were taken from the same branch. The obdeltoid form of the leaf has No. 1 secondaries extending halfway to the top of the leaf, No. 2 secondaries extending all of the way to the top of the leaf.


Plate LXXIV. Corylus heterophylla var. szechuensis Franch.

CHINA: Szechuan; Har-kuahshien, Sept. 12, 1930,
W. F. Fan 2040 (98). (x 2.9)

One leaf studied.

CHINA: Szechuan; Han-yuanihsien, Sept. 12, 1930, W.P. Fang 9010 (DS).

Description. — Broadly oval. L-W ratio 1.4. MLT 1.8. Apex abruptly acuminate. Base cordate to auriculate, symmetrical. Margin dentate, teeth average to small; 0-10 intersecondary teeth, 7 on principal segment, base with teeth. Craspedodromous. Midrib crooked. PPS ratio 1.8. Secondary angles 60° at base, 40° above; secondaries straight to slightly concave, rarely opposite except for No. 1 secondary. 11 secondary segments, 2 below widest point; spacing 0 mm. at base, 8.5 mm. above. P-M ratio 1.7. 21 externals, rare above No. 5, strong, over half distance to midrib on Nos. 1 and 2 secondaries. 9 joining, 3 intra-angular tertiaries, simple, straight; upper tertiary angle 90° to slightly acute, lower 90° to slightly obtuse, the intra-angular angles obtuse; tertiaries fairly commonly opposite. Net veins developed to sexternary level, net vein endings common, complex. Leaf 55 mm. long, 40 mm. wide.

Remarks. — This leaf is different from C. heterophylla, and appears to be more closely allied to C. rostrata mandschurica and C. rostrata sieboldiana.


One leaf studied.
CHINA: Yunnan; 25 miles west of Kunming, Apr. 29, 1949, R.S. Ferris 11,990 (DS).

Description. - Roundish. L-W ratio 1.2. MLT 2.0. Apex abruptly acute. Base cordate, asymmetrical. Margin unevenly dentate, terminal teeth largest, teeth small; 0-8 intersecondary teeth, 5 on principal segment, base with teeth almost to midrib. Craspedodromous. Midrib straight. PPS ratio 1.8. Secondary angles 80° at base, 40° above; secondaries slightly concave, rarely opposite, sometimes including Nos. 1 and 2. 9 secondary segments, 2-3 below widest point; spacing 0 mm. at base, 3.5 mm. above. F-W ratio 1.2. 15 externals, none above No. 5, strong, over half distance to midrib on Nos. 1 and 2 secondaries. 13 joining, 2 intra-angular secondaries, simple, straight; upper joining secondaries slightly acute, the lower slightly obtuse, lower half of intra-angulars slightly obtuse, upper half slightly acute; secondaries fairly commonly opposite. Ret veins developed to sexternary level, vein endings common, complex. Leaf 35 mm. long, 30 mm. wide, and much larger.


Corylus mandshurica Maxim. Fl. amur.; 2d1. 1859.

Corylus sieboldiana Hall. var. mandshurica Schn. Citation not known.

Two leaves studied.

CHINA: Hopei; Po Hua Shan, June, 1936, T.F. King iv7 (UC); Shansi; Ja Siu, Aug. 26, 1923, C.T. Ren 12 (UC).
Plate LXXV. Corylus rostrata Ait. var. mandschurica (Maxim.) Regel.

CHINA: Shansi; Jia Siu, Aug. 26, 1923,
C.T. Ren 12 (UC). (x 2.9)
Description. - Broadly oval to round. L-W ratio 1.2-1.4. MLT 1.7-2.0. Apex abruptly acute. Base cordate, asymmetrical. Margin doubly dentate, teeth small; 0-12 to 0-17 intersecondary teeth, 8-11 on principal segment, base with teeth almost to midrib. Craspedodromous. Midrib crooked. P:S ratio 1.7-1.8. Secondary angles 40°-50° below, 40° above; secondary veins very slightly concave, rarely opposite except for No. 1 secondary. 10 secondary segments, 2 below widest point; spacing 0 mm. at base, 11 mm. above. P-M ratio 1.5-1.7. 20-24 externals, strong, over half distance to midrib on Nos. 1 and 2 secondaries, sometimes the No. 3 secondaries. 7-19 joining, 3-4 intra-angular tertiaries; tertiaries straight to gently folded; upper joining tertiary angles slightly acute, the lower 90° to either slightly acute or obtuse, the intra-angular angles 90° tertiaries commonly opposite. Net veins developed to sexternary level, net vein endings common, fairly complex. Leaf 50-60 mm. long, 36-50 mm. wide.


One leaf studied.

Japan: Honshu; Yamagata Prefecture; Mt. Zowo, Aug. 11, 1950, Shigetaka Suzuki UC-299 (UC).

Description. - Broadly oval. L-W ratio 1.6, MLT 1.8. Apex abruptly acute. Base cordate, asymmetrical. Margin doubly dentate,
teeth small to average, 0–19 intersecondary teeth, 8 on principal segment, base with teeth to midrib. Craspedodromous. Midrib crooked. PPS ratio 1.9. Secondary angles 70° below, 45° above; secondaries faintly concave to straight, rarely opposite except for the No. 1 secondary. 1½ secondary segments, 2 below the widest point; spacing 0 mm. at base, 11 mm. above. P-W ratio 1.6. 28 externals, 15 on Nos. 1 and 2 secondaries together, strong, over half distance to midrib on Nos. 1 and 2 secondaries. ½ joining, 5 intra-angular secondaries, simple; tertiary fold gentle; upper joining tertiary angle slightly acute, the lower and intra-angulars slightly obtuse; secondaries commonly opposite. Net veins developed to sexternary level, vein endings common, complex. Leaf 91 mm. long, 58 mm. wide.

Remarks. — This and C. rostrata manschurica were not renamed C. cornuta manschurica and C. cornuta sieboldiana respectively because I do not believe there were sufficient grounds for doing so.


Corylus ferox Wall. var. tibetica (Hatal.) Franch. Jour. de Bot. XIII: 201. 1899.

Five leaves studied.


Description. — Oval to ovate. L-W ratio 1.6–2.3. MLT 1.6–1.9
Plate LXXVI. Corylus tibetica Batal.

CHINA: Szechuan; Opien-hsien, July 12, 1930,
W.P. Fang 7308 (DS). (x 3.0)
(one being 2.8). Apex acuminate. Base cordate, symmetrical to slightly asymmetrical. Margin evenly serrate to biserrate, teeth small to average; 0-8 to 0-11; intersecondary teeth, 4-13 on principal segment, base with teeth from 1-6 mm. from midrib. Craspedodromous, the No. 1 secondaries often exhibiting dictyodromy. Midrib perfectly straight to crooked throughout. PFS ratio 1.8-3.1. Secondary angles 30°-60° at base, 30°-45° above; secondaries slightly concave to straight, bending at margins, most to all opposite, including Nos. 1, 2, and 3 secondaries. 9-19 secondary segments, 2-3 below widest point; spacing 0 mm. at base, 5.5-14 mm. above. P-M ratio 1.2-1.8. 22-33 externals (all but one 22-24), strong, 1-7 above the No. 5, usually 1-3 above No. 5, over half distance to midrib on Nos. 1, 2, and sometimes 3 secondaries. 6-20 joining (usually 12-20), 3-5 intra-angulars, straight to gently folded; upper joining tertiary angles slightly acute, the lower and intra-angular angles slightly obtuse; tertiaries not commonly opposite; circumtertiary segments fairly common; medials developed. Net veins developed to quinquenary level, rarely to sextenary, net vein endings fairly common to rare, complex. Leaf 68-94 mm. long, 25-40 mm. wide.

Remarks. — Superficially, this species resembles Carpinus and Ostrya; but these characters readily distinguish it: slightly obtuse lower tertiary angles, large number of intersecondary teeth, strong externals, and 2-3 segments below widest point.

Discussion

All of the species of Corylus are apparently closely related except for C. tibetica. Corylus tibetica and its related species
C. ferox, (not studied here) form one distinct group; the remaining species form another group. Within this latter group several generalized subgroups may be distinguished. C. americana and C. cornuta (with its varieties) seem to be close to one another; this subgroup intergrades with and resembles closely the next subgroup formed of C. heterophylla (with its varieties), and the varieties of C. postrata. The chief difference between these two subgroups is that the Asiatic one displays a striking variety of form, while the American subgroup exhibits morphological stability. The third, or European, subgroup (C. avellana, C. columna, C. maxima (not studied here)) shows the same morphological stability as does the American subgroup, and, like the American species, possesses characters which overlap those of the Asiatic subgroup.

There are very few fossil species of Corylus in the record. They are not easily preserved for the reasons outlined earlier. Chaney (personal communication), in all of the fossil specimens of Corylus studied, has noted very little variety of form, and has concluded that there are probably no more than three or four species of Corylus, either living or fossil. This view concurs with the results presented here.
<table>
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<tr>
<th>CHART h</th>
<th>A chart for the determination of species of Corylus and Ostryopsis</th>
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<td>x = 1% - 50%</td>
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<td>Lower tert.angle 90° acute</td>
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<tr>
<td>Lower tert.angle 90° obt.</td>
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<tr>
<td>Intra-angulars 90° acute</td>
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<td>Intra-angulars 90° obtuse</td>
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<td>Circumtertiary seg.common</td>
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<td>Net vein endings common</td>
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<td>Net vein endings complex</td>
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<tr>
<td>Net vein endings simple</td>
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</table>

*Table continues with more species and characteristics.*
V. OSTRYA Scop. Fl. carniol. ill. 1760.

Thirty-two specimens of extant Ostrya; 2 fossils studied.

Chart 5.

Description. — Oval, rarely ovate to roundish. Apex acute, seldom acuminate, rarely rounded. Base round or subcordate, seldom cordate or auriculate, generally asymmetrical; basal angle 150° or greater. Margin usually serrate, often with bifid terminal teeth, terminal teeth largest; usually 0-3 to 0-10 terminal teeth, occasionally 0-16; base with teeth. Craspedodromous. Midrib straight, rarely sinuous, never strongly crooked. Secondaries less parallel than in Carpinus as a whole, wider spacing on midrib, secondaries sometimes deflected in course at points of departure of externals, secondaries sometimes bifurcating. 3-5 secondary segments below widest point, rarely 2, segment always contracting at midrib, contracting to 0 (except for O. virginiana), segments in upper half of leaf usually diverging toward midrib. Externals strong, much stronger than in Carpinus, always over half distance to midrib on No. 1, almost without exception on the No. 2, and in over half of the leaves on the No. 3, in all cases extending farther toward midrib than in Carpinus. Upper tertiary angles acute, lower and intra-angular angles usually obtuse with O. baileyi and O. knowltonii exceptions; medials rarely well developed. Net vein endings either common or rare, simple or complex, not coarser than that of Carpinus.

Extant species of Ostrya

Plate LXXVII. Ostrya baileyi Rose
UNITED STATES: Texas; Culberson County;
Guadalupe Mountains, McKittrick Canyon, July 17, 1931,
J.A. Moore and J.A. Steyermark 3h83 (DS) (x 4.0)
One leaf studied.

UNITED STATES: Texas; Culberson County; Guadalupe Mountains, Kittrick Canyon, July 17, 1931, J.A. Moore and J.A. Steyermark 3488 (DS).

Description. - Oval. L-W ratio 1.7. MLT 1.7. Apex acute to subacute. Base subcordate to cordate, slightly asymmetrical. Margin tiserrate, teeth small, terminal teeth bifid in upper portion of leaf; 0-6 intersecondary teeth, 1 on principal segment, teeth to within 1 mm. of midrib at base. Craspedoicromous. Midrib straight, very faintly curving. "P" ratio 3.0. Secondary angles 85° below, 55° above; secondaries slightly concave, randomly opposite, including Nos. 1 and 2 secondaries. 11 secondary segments, 3 below widest point, some diverging toward midrib; spacing 0 mm. at midrib, 5 mm. above, basal segment contracting to 0. P-M ratio 1.3. 21 externals, strong, over half distance to midrib on Nos. 1 and 2 secondaries. 5 joining, 3 intra-angular teriaries; teriaries straight to gently folded; upper joining tertiary angles slightly acute, the lower slightly obtuse, the intra-angulares varying from slightly obtuse to acute; teriaries rarely opposite; circunteriary segments common; teriaries irregular in course. Net developed to quinunternary level, net vein endings rare, simple to complex. Leaf 35 mm. long, 21 mm. wide.


1772. (Plate LXXXIII).


1801.
Plate LXXVIII. Ostrya carpinifolia Scop.
TURKEY: southern part; northwest of Mersina, Gomne, Aug. 16, 1931, A. Fig and I. Zohary s.n. (UC) (x 3.0)
Ostrya carpinifolia var. corsica Fliche. ibid. 1888.

Five leaves studied.

FRANCE: Maritime Alps; Loubet; along the Loup above the Villeneuve, June 1h, 1935, Ivar Tidestrom 13,669 (UC).


Turkey: southern part; northwest of Mersina, Gozne, Aug. 16, 1931, A. Big and K. Zohary 1,412 (UC).

Description. - Ovate to oval. L-W ratio 1.5-2.1 (all but one 1.7-2.1). WLT 1.5-1.8. Apex acute to acuminate. Base round to subcordate, slightly asymmetrical. Margin biserrate, upper terminal teeth often bifid, teeth small; 0–4 to 0–7 intersecondary teeth, 4–6 on principal segment, base with teeth. Craspedodromous. Midrib straight to very faintly crooked. PPS ratio 2.6–3.8. Secondary angles 35°–50° below, 40°–50° above; secondaries straight, sometimes forked midway to margin, randomly opposite, usually No. 1, occasionally No. 2. 13–19 secondary segments, 3–5 below widest point, some segments in upper half of leaf
diverging toward midrib; spacing 0 mm. at midrib, 5-7 mm. above, basal segment contracting to 0. P-M ratio 0.9-1.2. 20-38 externals, 3 specimens having 33-38, 2 having 20-22, strong, over half distance to midrib on No. 1, usually on No. 2, 6-13 joining, 2-4 intra-angular tertiaries, branching; tertiary fold slight to fairly pronounced; joining tertiaries all 90°; or upper ones slightly acute, lower tertiaries slightly obtuse, intra-angulares obtuse; tertiaries fairly commonly opposite, irregular in course; medials partly developed. Net veins developed to quinternary level, net vein endings rare, simple. Leaf blade 56 mm. long, 27-31 mm. wide.


Ostrya italica subsp. virginiana var. guatemalensis H.Winkl.


Six leaves studied.

MEXICO: Chihuahua; banks of the Rio Negro, Sept. 1, 1937, Horde Lesueur 1305 (UC); Guerrero; Distrito Hina; Sierra Madre del Sur, Cerro de los Amoles, Jan. 5, 1936, Ynes Mexia 2080 (UC); Jalisco; trail to Tajo de Santiago, Real Alto, Feb. 23, 1927, Ynes Mexia 1745 (US); Hina Tresso; Petlacala, Dec. 30, 1939, H.S.Hinton et al. 154400 (US); Nuevo Leon; trail from La Trinidad to Sierra de la Cebolla, Montemorelos, Aug. 20, 1939, C.H. Muller 2367 (UC); Vera Cruz; Jalapa, May 23, 1929, C.A. Pringle 8-n. (UC).

Description. - Oval-elliptical. L-W ratio 1.6-2.1. W-LT 1.6-1.9. Apex subacute, acute, or acuminate. Base subcordate to auriculate, slightly asymmetrical. Margin biserrate to unevenly serrate, terminal teeth in upper part may be bifid, teeth small; 0-5 to 0-10 intersecondary teeth, 0-6 on principal segment, base with teeth. Craspedodromous. Midrib
Plate LXXIX. *Ostrya guatemalensis* (H. K. K.) Rose.
MEXICO: Chihuahua; banks of Río Negro, Sept. 1, 1937,
Harie Le Sneur 1305 (IX). (× 3.2)
straight or slightly crooked. PPS ratio 2.2-3.9. Secondary angles 60-110° below, 35-60° above; secondaries concave, commonly opposite, always the No. 1, usually the No. 2. 10-35 secondary segments, 3-4 below widest point, diverging toward midrib in upper portion of leaf; spacing 0 mm. at base, 5.5-7 mm. above, basal segment contracting to 0. P-N ratio 0.6-1.1. 18-26 externals, strong, over half distance to midrib on the No. 1 and 2 secondaries, often on No. 3 secondaries. 6-11 joining, 1-5 intra-angular secondaries, mostly branching, straight; upper tertiary angles slightly acute, the lower and intra-angular angles 90° to obtuse; secondaries commonly opposite. Net developed to quaternary, sometimes to sexternary level, vein endings rare, simple. Leaf 39-57 mm. long, 24-28 mm. wide.

I. OSTRYA KNOWLTONII Cov. (Gard. & For. VII: 114. f.23.)

1894. (Plates LXX and LXXXI).

Six leaves studied.

UNITED STATES: Arizona; Grand Canyon Nat'l Park; Bright Angel Trail, May 26, 1903, O. S. Grant 5695 (OS); Grand Canyon Nat'l Park, July 12, 1892, J. W. Tourney 272 (OS); Grand Canyon Nat'l Park; Bright Angel Trail, June 4, 1901, W. R. Dudley s.n. (OS); Grand Canyon Nat'l Park, July 11, 1905, L. N. Abrams s.n. (OS); Utah; Moab, June 7, 1913; June 9, 1913, E. L. Jones s.n. (OS).

Description. - Oval-ovate to roundish. L-W ratio 1.3-1.8. MLT 1.6-2.2. Apex acute, subacute, or round. Base round, to faintly subcordate, asymmetrical or symmetrical. Margin biserrate to bidentate, teeth large to fairly small, convex or concave, terminals usually bifid in upper portion; 0-3 to 0-8 intersecondary teeth, 2-9 on principal segment, base with teeth. Craspedodromous. Midrib straight or straight
Plate LXXX. Ostrya knowltonii Cov.

UNITED STATES: Utah; Moab, June 9, 1913,
M.E. Jones s.n. (DS). (x 3.3)
Plate LXXXI. Ostrya knowltonii Cov.
UNITED STATES: Arizona; Grand Canyon National Park,
Bright Angel Trail, June 21, 1901, W.R. Dudley, s.n.
(38), (x 4, s)
only in lower half. PPS ratio 2.2-3.0. Secondary angles 30°-55° at base, 45°-50° above; secondaries generally straight in upper part, possibly bending at margins, No. 1 secondaries characteristically short, poorly developed, highly convex in course, No. 2 secondaries slightly to highly convex, prominent, No. 3 straight to concave, secondaries randomly opposite, including No. 1, sometimes No. 2, or all alternate. 8-12 secondary segments, 3 below widest point, segments diverging toward midrib in upper part of leaf; spacing 0 mm. at base, 6-9 mm. above, basal segment contracting to 0. P-M ratio 0.8-1.6 (most commonly 1.1-1.4). 11-24 externals, usually 15-20, strong, over half distance to midrib on Nos. 1 and 2 secondaries, often on No. 3. 1-6 joining, 2-4 intra-angular secondaries, branching; tertiary fold gentle to pronounced; all tertiary angles acute; secondaries fairly commonly opposite; circum-tertiary segments moderately common; secondaries irregular in course; medials developed. Net developed to sexternary level, net vein endings common, complex. Leaf 33-61 mm. long, 22-3½ mm. wide.

Remarks. - This species breaks many of the "rules" peculiar to Ostrya but in doing so emphasizes those which are important: the mode of development of the external veins, the lack of well-developed medials, the relatively small number of tertiary veins, the divergence of secondary segments toward the midrib, and the type of base. This species and O. baileyi are similar, while the remaining species are similar to one another, forming, thus, two general groups.

Plate LXXXII. Ostrya rehderiana Chun.
CHINA: Chekiang; Tien-Lu-Shan, Aug. 12, 1929,
S.S. Chien 783 (NS). (x 3.0)
One leaf studied.

CHINA: Chekiang; Tien-mu-shan, Aug. 12, 1929, S.S. Chien 783 (DS).

Description. - Oval. L-W ratio 2.2. M L T 1.8. Apex acuminate-acute. Base subcordate, slightly asymmetrical. Margin biserrate, terminal teeth bifid in upper portion, small; 0-1; intersecondary teeth, 6 on principal segment, base with teeth. Craspedodromous. Midrib straight. PFS ratio 3.7. Secondaries uniformly 10⁰, slightly concave, randomly opposite, including Nos. 1 and 2 secondaries. 15 secondary segments, 4 below widest point, commonly diverging toward midrib in upper portion; spacing 0 at base, 7 mm. above, basal segment contracting to 0. P-M ratio 1.4. 28 externals, strong, over half distance to midrib on Nos. 1, 2 and 3 secondaries. 7 joining, 3 intra-angular tertiaries, mostly simple; tertiaries straight; upper tertiary angles slightly acute, the lower 90⁰; the intra-angular angles slightly obtuse; tertiaries rarely opposite; circumtertiary segments fairly common. Net developed to quinquentary level, vein endings common, majority complex. Leaf 55 mm. long, 25 mm. wide.

Remarks. - This species is one of 2 oriental species, the other of which is O. japonica Sarg., which Winkler (1904) believes to be synonymous with O. virginiana. Thus most species of Ostrya, unlike the other genera, are in southern North America.


Plate LXXXIII. Ostrya virginiana (Will.) Koch.
UNITED STATES: West Virginia; Tucker County; Canaan Valley, June 29, 1931, E.L.Core 2860 (DS). (x 2.1)
Carpinus virginica Münch. Hausvat. V: 120. 1770.

1781.
Carpinus triflora Monch. Keth.: 694. 1794.

1803.
Zugilus virginica Raf. Fl. Ludov.: 159. 1817.
Ostrya mandschurica Rudischtschew. ex Trautv. in Acta Hort. petropol. IX: 166. 1884.
Ostrya italicca subsp. virginiana H. Winkl. Pflanzennr. IV. 61.
Betul.: 22. 1904.

Thirteen leaves studied.

MEXICO: Sinaloa; Sierra Surotato, Ocurahui, Sept. 1-10, 1941, H. S. Gentry 6325 (DS).
UNITED STATES: Georgia; Clark County, Ocone River, Oct., 1922, J. H. Miller s.n. (DS); Dougherty County; near Albany,
Oct. 10, 1925, J.W. Millespie s.n. (DS); Indiana: Lake Maxinkuckee, Long Point, Oct. 22, 1900, J.T. Scovell and H.W. Clark 850 (647) (DS); Maine: Troy, Aug. 9, 1909, S.S. Merry s.n. (DS); Michigan: Cheboygan County; Michigan Biological Station, Aug. 7, 1920, Frank C. Gates 12,302 (DS); Minnesota; Martin County, Aug. 1885, R.L. Cratty s.n. (DS); Missouri; Allenton, July 1, 1884, C.H. Letterman s.n. (DS); Nebraska; Cass County; Louisville, June 15, 1931, J.L. Morrison 1110 (DS); Oklahoma; Ottawa County; Ottawa, Aug. 27, 1915, G.W. Stevens 24077 (DS); Vermont; Brandon, July 30, 1922, T.L. Dutton s.n. (DS); West Virginia; Tucker County; Cama Valley, June 29, 1931, E.L. Core 2860 (US); Wisconsin; Chippewa County; Chippewa Falls, June 10, 1925, L.J. Palmer 27,814 (US).

**Description.** - Oval-elliptical. L-W ratio 1.5-2.2, M-L 1.7-2.1. Apex acuminate, rarely acute. Base auriculate or subcordate, symmetrical or asymmetrical. Margin biserrate, sometimes unevenly serrate, teeth average to small, terminal teeth usually bifid in upper portion, often long, narrow and pointed; 0-4 to 0-16 intersecondary teeth (usually 0-4 to 0-9), 3-11 (usually 4-8) on principal segment, base with teeth. Craspedodromous. Midrib straight. M-F ratio 2.7-5.7, (all but two 3.1-3.9). Secondary angles 35°-35°, depending upon convexity of midrib junction, 45°-60° above; secondaries somewhat concave, possibly bending slightly at margin, randomly opposite, always No. 1 secondary, less often the No. 2. 15-19 (all but two 15-16) secondary segments, 3-5 (all but one 3-4) below widest point, diverging slightly toward midrib in upper part; spacing 0-3 mm. at base, 6.5-10.5 mm. above, basal segment always contracting to 0 at midrib, sometimes to 0. P-V ratio 1.1-1.6 (all but two 1.2-1.3). 18-40 externals (usually 23-29), strong, over half distance to midrib on Nos. 1 and 2 secondaries, often on No. 3. 8-15 joining, 2-4 intrangular tertiaries, usually straight, sometimes folded gently; upper
joining tertiary angles slightly acute, the lower 90°, the intra-
angular tertiary angles obtuse; tertiaries rarely opposite; circum-
tertiary segments fairly common; tertiaries often irregular in course
medials common. Net developed to sextenary level, vein endings fair
common, about half simple, half complex on a single leaf. Leaf 52-10
mm. long, 33-60 mm. wide.

Fossil species of Ostrya

pl. 9. f.l2, pl.10. f.1-4. 1927.

Two specimens studied.

UNITED STATES: Bridge Creek (Crooked River) Flora, Oregon; 1927, R.W. Chaney, Univ. Cal. Coll. Paleobot. 34
(Carn. Inst. Wash. Publ. 346: 106-107, pl. 9, f.12),
holotype; Bridge Creek (Crooked River) Flora, Oregon;
10, f.14), paratype.

Description. - Ovate-ovate. L-W ratio 2.2-2.3. MLT 1.7-2.0.
Apex acute-acuminate. Base round, asymmetrical. Margin biserrate,
teeth large to small, upper terminal teeth often bifid; 0-4 to 0-5
intersecondary teeth, 4 on principal segment. Craspedodromous. Mid-
rib straight. FPR ratio 3.5-3.5. Secondary angles 45°-60° below, 40°
above; secondaries slightly concave, sometimes forking midway to
margin, randomly opposite to all opposite. 1h-16 secondary segments,
3-4 below widest point, diverging noticeably toward midrib in upper
portion of leaf; spacing 0 mm. at base, 7-10 mm. above, basal segment
contracting to 0. P-K ratio 1.1-1.5. 21-24 externals, strong, over
half distance to midrib on Nos, 1 and 2 secondaries, sometimes on
No. 3 secondaries. 6-8 joining, 2-3 intra-angular tertiaries, branching; tertiary fold gentle but more pronounced than in any specimen of Ostrya studied thus far; upper tertiary angles acute, lower acute and obtuse, the intra-angular angles acute; tertiaries commonly opposite; circumtertiary segments common. Net developed to sexternary level, vein endings indeterminate. Leaf 70-84 mm. long, 31-39 mm. wide.

Remarks. — In certain diagnostic details this species is unlike any living species studied. However, the details of the tertiary venation show that it is closely allied with the *O. baileyi* — *O. knowltonii* group. It bears closest resemblance to *O. baileyi* and may be identical with that species; not enough specimens of *O. baileyi* were studied to be certain of this.


Nine specimens of extant Ostryopsis studied; no fossils.

Chart 1.

Description. — Oval to somewhat broadly ovate or obovate. Apex acute to acuminate. Base cordate or subcordate. Margin doubly dentate; 0-5 to 0-9 intersecondary teeth, usually 0-7 to 0-9, base with many teeth. Craspedodromous. Midrib crooked, thick. Secondary veins widely spaced on midrib, usually concave, commonly opposite. 2 secondary segments below widest point, dentations at ends of No. 1 secondaries larger than other dentations, thus causing these dentations to coincide with widest point; segments diverging toward midrib, basal segment always contracted, usually to 0. Externals extending over half the distance to the midrib on Nos. 1 and 2 secondaries, commonly on the No. 3 secondary. Tertiaries usually wide-spaced on secondaries, straight; upper
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<th>Chart 5</th>
<th>A chart for the determination of species of Ostrya</th>
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<td>/ = possible</td>
<td><em>O. crenata</em></td>
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<th><em>O. virginiana</em></th>
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<td>Tertiary fold gentle</td>
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<td>Lower tert. angle 90°-acute</td>
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<td>Lower tert. angle 90°-obtuse</td>
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<td>Intra-angulars acute</td>
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<td>Intra-angulars obtuse</td>
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<td>Circumtertiary seg. common</td>
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<tr>
<td>Simple tert. irregular</td>
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<tr>
<td>Medials developed</td>
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<tr>
<td>Sexternary net present</td>
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<tr>
<td>Sexternary net not present</td>
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<tr>
<td>Net vein endings common</td>
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<td>Net vein endings rare</td>
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<td>Net vein endings complex</td>
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<td>Net vein endings simple</td>
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and lower joining tertiary angles about 90°, the intra-angulares obtuse. Net veins always developed to sexternary, sometimes septernary level, net vein endings common and complex.

Remarks. — Winkler (1904) knew only one species of Ostryopsis: O. davidiana. Now 2 species and 1 variety are recognized: O. davidiana, O. davidiana var. cinerascens, and O. nobilis. O. davidiana is confined to the Hwang-He drainage basin of northern China, O. davidiana cinerascens and O. nobilis to southern China in Szechuan and Yunnan.

The genus is very similar to Corylus, so much so, in fact, that the two might easily be confused. The acute apex of Ostryopsis is found only in Corylus americana, C. cornuta, C. cornuta californica and C. heterophylla. Of the 42 specimens of Corylus examined, only 10 had less than 0-10 intersecondary teeth, while Ostryopsis rarely has more than 0-9. While wide spacing of secondaries, divergence toward the midrib, and concave secondaries are all found in Corylus, the same features in Ostryopsis are more nearly like those of Ostrya than of Corylus. The degree of oppositeness of the secondaries is noticeably higher in Ostryopsis than in Corylus. The P-W ratio of Ostryopsis is generally less than that of Corylus. Finally, the lower joining tertiary angle of Corylus is usually obtuse, while that of Ostryopsis is usually 90°. While none of these criteria alone will distinguish Ostryopsis from Corylus, a combination of these characters will; perhaps, as a result, Ostryopsis may be recognized in the fossil record in many plant localities.

Species of Ostryopsis

Corylus davidiana Mill. Hist. pl. VI: 22h. 1877.

Nine leaves studied.

CHINA: Chihli; Hsiao Wu T'ai Shan, Aug. 8, 1913, F.N.Meyer 1125 (DS); Hsiao Wu T'ai Shan, Aug. 6, 1928, J.C.Liu 1784 (UC); Kansu; near Lichen, Hsia Ho K'ou, July 7-8, 1923, R.C.Ching 351 (UC); southwestern part; Choni district; Tiao River basin, Oct. 1925, J.F.Rock 13,513 (UC); Shansi; Mien Shan, June 1, 1933, R.W.Chaney 1081 (UC); Chung Tai Yu, Chin Yuan, July 6, 1925, X. Ling 1539 (UC); Tung Tsa, July 10, 1924, Lee and Loudermilk 6008 (UC); Yunnan; Niou-lan-kian, May, 1910, Naire 363h (UC).

Description. - Oval to ovate or slightly obovate. L-W ratio 1.1-1.9. MLT 1.6-2.2. Apex acute to slightly acuminate. Base cordate to subcordate, symmetrical or slightly asymmetrical. Margin doubly dentate, sometimes slightly biserrate, dentation at ends of No. 2 secondaries occasionally larger than rest giving appearance of small rudimentary lobes to these dentations, teeth average to small; 0-5 to 0-12 intersecondary teeth (0-7 to 0-9 most common), 3-7 on principal segment, base with teeth. Craspedodromous. Midrib crooked. PPS ratio 1.4-2.2. (Naire 363h being 1.4, probably a juvenile leaf, the rest 1.9-2.2). Secondary angle 60°-80° at base, 40°-60° above; secondaries slightly concave to straight, randomly opposite, often including the Nos. 1 and 2 secondaries. 8-12 secondary segments, 2 below widest point, diverging toward midrib; spacing 0-1 mm. at base, 5-10 mm. above, basal segment contracting at midrib, usually to 0. P-W ratio 1.3-2.0 (usually 1.3-1.6). 11-23 externals (usually 16-23), strong,
Plate LXXXIV. Ostryopsis davidiana Decne.
CHINA: Chihli; Hsiao Wu T'ai Shan, Aug. 6, 1928,
J.C.Liu 1781 (UC). (x 3.0)
Plate LXXXV. Ostryopsis davidiana Decne.
CHINA: Shansi; Tung Tsa, July 19, 1924,
Lee and Loudermilk 6005 (UC). (x 2.7)
0-3 above the No. 5 secondary, over half the distance to midrib on Nos. 1 and 2, sometimes No. 3 secondaries, secondaries sometimes changing direction where externals depart. 5-8 joining, 2-6 intra-angular (usually 4-6) secondaries, mostly simple, straight, rarely gently folded; joining tertiary angles about 90°, intra-angular tertiary angles 90° to obtuse; secondaries commonly opposite. Not developed to sexternary level, sometimes to septernary level, net vein endings common and complex.

Leaf 15-65 mm. long, 11-34 mm. wide.

Remarks. - Haire 3624 is probably O. davidiana var. cinerascens Franch., because it comes from Yunnan. No specimens of O. nobilis Balf. & Sm. were available. A more thorough study of this genus is necessary.
<table>
<thead>
<tr>
<th>CHART 6</th>
<th>A chart for the determination of genera of the Betulaceae</th>
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<tbody>
<tr>
<td></td>
<td>Almus</td>
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<td>Graspedodromous only</td>
<td>x</td>
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<tr>
<td>Dictyodromy exists</td>
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<td>Brachydromy exists</td>
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<td>True camptodromy exists</td>
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<td>Midrib usually thick, straight</td>
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<td>Midrib usually thin, straight</td>
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<td>Midrib usually crooked</td>
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<td>Apex always pointed</td>
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<td>Apex usually pointed</td>
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<td>Base often flat</td>
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<td>Base never flat throughout</td>
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<td>Base never parallel to #2's</td>
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<tr>
<td>Base always cored</td>
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<tr>
<td>Margin usually dentate or doubly dentate</td>
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<tr>
<td>Margin usually serrate or biserrate</td>
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<tr>
<td>Intersec. teeth usually 0-10 to 0-10</td>
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<td>Intersec. teeth usually 0-10 to 0-18</td>
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<td>Teeth usually small</td>
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<td>Teeth usually large</td>
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<tr>
<td>Terminal teeth largest</td>
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<td>Leaf base usually 90°-150°</td>
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<td>Leaf base usually 150°</td>
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<tr>
<td>Externals usually strong</td>
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<tr>
<td>Externals usually slight</td>
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<tr>
<td>Often no externals above #5</td>
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<td>No. ext. veins on #1 often less than #2</td>
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<tr>
<td>Externals usually over $\frac{1}{2}$ on #1</td>
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<td>Externals usually over $\frac{1}{2}$ on #2</td>
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<tr>
<td>Externals commonly over $\frac{1}{2}$ on #2</td>
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<tr>
<td>External areas often overlap greatly</td>
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<td>External areas seldom overlap greatly</td>
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<tr>
<td>Secondaries may bifurcate</td>
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<td>Secondaries often diverge to midrib</td>
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<td>Basal segment 0 to contracted</td>
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<td>Basal segment rarely 0</td>
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<td>Basal segment may be even</td>
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<td>Basal segment often expands</td>
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<td>Basal segment never expands</td>
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<td>Common no. of complete sec. seg. below widest point</td>
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<td>Midrib spacing usually wide</td>
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<td>Midrib spacing seldom wide</td>
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<td>Lower tert. angle usually acute</td>
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<td>Lower tert. angle usually obtuse</td>
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<td>Intra-angulals usually acute</td>
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<td>Intra-angulals usually obtuse</td>
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<tr>
<td>Circumtert. segments usually common</td>
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<td>Simple tertiaries often irregular</td>
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<td>Medials often prominent</td>
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<td>Net vein endings common</td>
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<td>Net vein endings rare</td>
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<td>Net vein endings complex</td>
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<td>Net vein endings simple</td>
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CHAPTER V

SPECIAL PROBLEMS WITHIN THE BETULACEAE

Relationships within the family

The results of this study of leaves support many of the taxonomic findings already published and may help to resolve the endless controversies within families, genera, and species. On the generic level, this study demonstrates the close relationship existing between *Alnus* and *Betula*. *Carpinus* and *Ostrya* are also related closely, but not as closely as are *Alnus* and *Betula*. In *Betula* the *B. corylifolia - B. nigra* group in subsection *Costatae* shows the closest relationship to *Alnus*; subsection *Acuminatae* shows almost as close a relationship. In subsection *Costatae*, the *Lentae* group is very similar to *Carpinus*. For this reason, I would divide subsection *Costatae* into two subsections, making a total of 5 in the genus *Betula*.

Concerning the family as a whole, some have divided it into two separate families: the Betulaceae, including *Alnus* and *Betula*; and the Corylaceae, including *Carpinus*, *Corylus*, *Ostrya*, and *Ostryopsis*. In von Ettingshausen's day, it was customary to place *Alnus* and *Betula* in the Betulaceae, but to place *Carpinus*, *Corylus*, and *Ostrya* (*Ostryopsis* was as yet undiscovered) in the Cupuliferae, a family including not only these three genera, but also the family now known as the Fagaceae. Some persons, such as Fernald (1950), place all six genera of the
186

Betulaceae in the Corylaceae, and abandon the name Betulaceae. Others, while retaining either the name Betulaceae or Corylaceae for all six genera, divide the family into two tribes, the Betuleae (Alnus and Betula) and the Coryleae (Carpinus, Corylus, Ostrya, and Ostryopsis).

I feel that my results support this latter two-fold division within the family.

Glancing for a moment at the tribe Coryleae, we may note several similarities between its genera. The similarities between Carpinus and Ostrya have been discussed. Ostrya, if the midrib is made more crooked, the cordate base exaggerated, and both the tertiary and secondary veins spaced farther apart along their respective axes, becomes Ostryopsis. This relationship between these three genera is pointed out by Anderson and Abbe (1934), who say, in effect, that Carpinus develops by a few modifications into Ostrya, and Ostrya, by a few further modifications, into Ostryopsis. They place Corylus separately.

Corylus may be derived in several ways. A few modifications of the leaf of Ostryopsis might produce a leaf of Corylus; likewise, modifications of the leaves of Carpinus could produce Corylus tibetica. Again, a few changes of the leaves of Betula lenta would also produce C. tibetica, just as minor changes in the leaves of the subsection Albae could produce the remaining species of Corylus. But leaf structure is quite different from floral structure and may be the result of other factors.

If any single genus in the family can be called the progenitor of all of the other forms in the family, it is Betula. This genus might have developed in one extreme into Alnus, in the other extreme into the
tribe Corylleae.

Another possible approach regarding relationships between the genera may be through the study of net vein endings. This subject requires much more investigation.

On the species level, there are several interesting problems which deserve more study. The relationships between Alnus crispa, A. crispa simuta, and A. fruticosa are well substantiated by this study. That there may be a relationship between these forms and A. maximowiczii, not studied here, has already been pointed out. The similarities between A. incana and A. tenuifolia have been verified by this work, and, though varietally distinct from one another, they are probably not specifically distinct. A possible link between Alnus and Betula may be sought in a study of A. crispa, and its relatives, in A. orientalis, or in A. maximowiczii. This latter species is remarkably like Betula maximowiczii, with the greatest difference between the two being in the nature of the leaf base. A. orientalis is similar to, but not identical with the fossil Alnus harneyana Chaney and Axelrod. I have not studied A. harneyana thoroughly, and it may be Betula.

In Betula, B. lenta and B. lutea are so nearly alike that, as fossils, at least, they would not deserve separate specific rank. In Corylus, the relationships have already been discussed. The similarity of Corylus to C. davidiana is emphasized by the synonymy of the latter species, where it was renamed, Corylus davidiana Baill.

This study, unfortunately, is too brief and limited in scope to deal with these problems more thoroughly. Yet, in the final analysis, leaves may prove more helpful than they are now generally thought to be.
Morphological considerations as a result of this study

A few morphological details clarified by this study are worth noting. First, the relationships of loops and external veins in a series of specimens suggest a development sequence shown in Figure 3.

Second, differences between the leaves of the seedling and of the adult were examined briefly in one species, *A. temulolia*. No significant differences were noted. Lack of time and the lack of sufficient specimens prevented further study of this important problem. But it is doubtful that such fundamental differences between the seedling and adult leaves exist as do in the leaves of the Quinaceae (Foster 1950a, 1950b, 1951) and of *Populus dimorpha* T.S.Brandeg., mentioned earlier.

There were no significant distinctions noted between the immature and mature leaves of the adult tree. It may be said that the young leaves of an adult tree are "caricatures" of the mature leaves. The shape is the main difference. Certain features, such as the size of the teeth and the size of the sinuses between the teeth are exaggerated in their importance relative to the size of the leaf in the youthful form, while in the adult form, these same features are more subdued. *Alnus rubra* offers a good example of this. Plate XX shows a young leaf on a mature tree of that species, while Plate XXI shows an adult leaf, though not on the same tree.

A third morphological problem concerns the varying degrees of development of the No. 1 secondaries in some species. It might seem an easy task to identify the No. 1 secondaries, but this is certainly
Figure 3. Drawings arranged to illustrate changes in the configuration of loops and external veins.
not true for Alnus incana, A. tenuifolia, and A. crispa simata. A. incana shows some very tiny No. 1 secondary veins in a few specimens. This is illustrated on Plate XIII. In some specimens, the No. 1 secondary is developed on only one side of the midrib. In other specimens, these tiny secondary veins are not so small that they do not have a few looped external veins developing. On still other leaves, such as that illustrated in Plate XII, the No. 1 secondaries will be large, prominent, and impossible to misidentify. There are all gradations between the two extremes illustrated in Plates XII and XIII.
CHAPTER VI

SPECIES OF OTHER FAMILIES

Several other families were investigated briefly in order that those leaves most likely to be confused with leaves of the Betulaceae might be examined for differences. The following pages present descriptions of those species similar to the Betulaceae found in other families.

1. Aceraceae (Maple family)

**Acer carpinifolia** Sieb. & Zucc. (Plate LXXXVI).

One leaf studied.

JAPAN: Honshu; southern part; Mount Asara, July 14, 1904, U. Faurie s.n. (OS).

Description. - Margin biserrate, large serrations pointed apically, 0-3 auxiliary (smaller) serrations on basiscopic side of the large serrations, also apically pointed; each larger serration completely separated by a cleft from its neighbor, thus differing from *Carpinus*. 27 secondary segments, secondary veins closely spaced, almost parallel. P-V ratio 1.0. 6-9 circumtertiary segments in principal segment; tertiary veins often curved, incomplete, developing sag toward midrib midway in their courses across secondary segments, similar in this respect to *Carpinus orientalis* and *Ulmus alata*. Net very irregular, many complicated net endings. Leaf 75 mm. long, 32 mm. wide.
Plate LXXXVI. *Acer carpinifolia* Sieb. & Zucc.
JAPAN: southern Honshu; Mount Asama, July 14, 1904,
U. Faurie s.n. (23). (x 2.2)
Remarks. - Thomas Pray (personal communication), after investigating this leaf, stated that it has a typical *Acer* net; the net is quite unlike those of the Betulaceae.

*Acer aureum* Fanch.

One leaf studied.

**CHINA**: Szechuan; Omei-shan, July 22, 1930, W.P. Fang 7866 (DS).

Description. - Marginal teeth subdued, rounded, apically pointed. Dictyodromous, subpalmate venation. Excessively thick, crooked midrib near base, thin at top. Lower 7 of the 17 secondary veins prominent, owing to palmate nature of leaf, upper eight barely developed. P-M ratio 2.1. Typical *Acer* net. Leaf 58 mm. long, 38 mm. wide.

*Acer Tartaricum* L.

One leaf studied.

**HUNGARY**: Suabhegy, May, 1875, Richter s.n. (DS).

Description. - Dictyodromous to brochidodromous, more distinctly palmate than other species of *Acer* considered. Many externals and interordinal veins, externals irregular in course, looped. P-M ratio 2.1. Joining tertiaries from opposite secondary veins not meeting, fading in middle of secondary segments, branching. Typical *Acer* net. Leaf 91 mm. long, 47 mm. wide.

*Acer Tetramerum* Pax var. *Elongatatum* Rehd.

One leaf studied.
CHINA: Szechuan; Ma-yien-hsian, June 17, 1930, W.F. Fang 3931 (DS).

Description. - Craspedodromous, subpalmate. Many interordinal veins; 1 intersecondary vein. F-W ratio 2.1. Large tertiary veins at very acute angles (50°-60°). Typical Acer net. Leaf 73 mm. long, 56 mm. wide.

2. Fagaceae (Beech family)

NOTHO FAGUS ANTARCTICA (Forst.) Orst.

Two leaves studied.

CHILE: Port Famine, 1838, D'Yrville s.n. (DS).

Description. - Base strongly asymmetrical. Margin irregularly and deeply crenate. Dictyodromous. Medials very well developed, almost parallel to secondary veins. Externals not clearly defined, same size as teraries. Net disordered and loose. Leaf 22 mm. long, 18 mm. wide.

FAGUS GRANDIFOLIA Ehrh. (Beech).

One leaf studied.

UNITED STATES: Pennsylvania; Elk County; Whippoorwill Camp of DuBoise Lumber Company, June 20, 1911, A.A. Holler 10299 (DS).

Description. - Small teeth only at terminations of secondaries, no intersecondary teeth. Craspedodromous. Secondaries straight, closely spaced, convex at junction with midrib. Externals rare. Many tertiary veins, closely spaced, straight; many circumtertiary segments. Leaf 79 mm. long, 40 mm. wide.
CASTANEA PUMILA (L.) Will. (Chestnut).

One leaf studied.

UNITED STATES: South Carolina; Anderson County; Anderson, July 18, 1921, John Davis s.n. (DS).

Description. - Marginal teeth long, pointed, at terminations of secondaries only. Craspedodromous above, lower two-thirds of secondaries true camptodromous. Secondaries sometimes bifurcating near margin. No external veins. Leaf 76 mm. long, 36 mm. wide.

LITHOCARPUS DENSIFLORA (Hook. and Arn.) Rehd. (Tan oak).

One leaf studied.

UNITED STATES: California; San Mateo County; King's Mountain Road, June 29, 1907, Josephine D. Randall 129 (DS).

L-W ratio 2.9. Margin crenate above, sinuate below, crenations and crests of lobes only at terminations of secondary teeth, teeth sharpening apically. Craspedodromous. Secondaries uniformly 75°, short compared with leaf length. Net extremely dense, well developed. Leaf 92 mm. long, 33 mm. wide.

QUEUCUS ALIENA Bl. (Oak).

One leaf studied.

CHINA: Fukien; Baek-liang, Aug. 25, 1929, Chen Hsi Cheng 3262 (DS).

externals. Leaf 75 mm. long, 31 mm. wide.

**Quercus atrиJAJS** F. Март. (Oak).

One leaf studied.

*MEXICO: Temascaltepec District; Ypericones, Nov. 19, 1931, F. M. Hinton 6992 (DS).

*Description.* - Base cordate. Margin sinuate with crests at ends of secondaries. Lower two-thirds of leaf brochidodromous, upper one-third camptodromous to dictyodromous. Many interordinal and intersecondary veins. Leaf 50 mm. long, 26 mm. wide.

**Quercus bicolor** Willd. (Swamp white oak).

One leaf studied.

**UNITED STATES:** Georgia; Clark County; Athens, June 9, 1923, J. H. Miller s.n. (DS).

*Description.* - Margin sinuate to sublobate, one lobe per secondary vein. Craspedodromous. Externals present, looped, grading into tertiary veins. Leaf 63 mm. long, 39 mm. wide.

**Quercus wislizeni** A. DC. (Interior live oak).

One leaf studied.

**UNITED STATES:** California; Marin County; Mt. Tamalpais, date unknown, H. E. McKinn 271 (DS).

*Description.* - Teeth long, spiny, located at terminations of secondary veins only. Brochidodromous to dictyodromous. Secondaries irregular in course, at divergent angles, convex, concave, or straight in random arrangement. Interordinal veins common. Net disorganized,
no orderly pattern. Leaf 50 mm. long, 26 mm. wide.

3. *Hamamelidaceae* (Witch-hazel family)

*Hamamelis japonica* Sieb. & Zucc.

One leaf studied.

**JAPAN**: southern Hokkaido, 1884, W.P. Brooks s.n. (UC).

**Description**. - Resembling *Corylus*. Base asymmetrical, cordate appearance; base fairly flat, parallel to No. 1 secondaries until within 3 mm. of midrib, then cutting abruptly and sharply to midrib, the basal segment thus contracting to 0, a larger-scale base of the *Carpinus turzainowii* type. Externals in large number on No. 1 secondary, mostly looped, upper externals not looped. Not poorly developed below quinquenary level, loose, vein endings common, feather like and bizarre. Leaf 77 mm. long, 67 mm. wide.

*Hamamelis virginiana* L. (Plate LXXXVII).

One leaf studied.

**CANADA**: Nova Scotia; Shelburne County; Shelburne, Sept. 15, 1924, J.G. Jack 2462 (UC).

**Description**. - Base similar to that of *H. japonica*, but flatter with straighter basal secondaries. Margin broadly dentate, almost sinuate. Craspedodromous. Externals numerous on No. 1 secondary, looped, similar in size to secondaries, most prominent externals on the No. 2 secondary. Not much looser than in *Corylus*, poorly developed below quinquenary level, many common and complex net vein endings. Leaf 59 mm. long, 38 mm. wide.
Plate LXXXVII. Hamamelis virginiana L.
CANADA: Nova Scotia; Shelburne County; Shelburne,
Sept. 15, 1924, J.D. Jack 3462 (UC). (x 2.7)
Juglandaceae (Walnut family)

Carya ovata (Will.) Koch. (Hickory).

One leaf studied.

UNITED STATES: Georgia; Dougherty County; near Albany, May 17, 1928, J.W. Gillespie 5046 (GS).

Description. - Broadly ovate. Apex acuminate. Leaflet; if terminal, base symmetrical; if lateral, base very asymmetrical. Teeth apically pointed, 0-3 intersecondary teeth. True camptodromous. Secondaries irregularly spaced along midrib. Externals mostly looped. Many interordinal veins. Tertiaries well developed, simple. Leaf 64 mm. long, 35 mm. wide.

Juglans major (Torr.) Heller. (Walnut).

One leaf studied.

UNITED STATES: Arizona; Yavapai County; near Dewey, July 3, 1940, H.R. Ferris 9900 (GS).

Description. - Long and narrow, elliptical. Leaflet; if terminal, symmetrical; if lateral, highly asymmetrical. Teeth apically pointed; 0-1 intersecondary teeth. Upper two-thirds brochidodromous. Lowest secondary veins 75-85°; secondaries irregularly spaced on midrib. Interordinals common. No externals above lowest one-third of leaf, irregularly distributed. Tertiaries scattered. Leaf 52 mm. long, 20 mm. wide.

Platyclarya strobilacea Sieb. & Zucc.

One leaf studied.
Description. - Lanceolate. Base asymmetrical. Large (3 x 1 mm.), apically directed teeth, with short, pointed, narrow tips; 0-1 inter-secondary teeth. Craspedodromous. Secondary angles 80°; secondaries irregular in course, a few suddenly changing course two-thirds of way to margin, others uniform in direction throughout, irregularly spaced on midrib. Externals irregularly distributed. Many intercostinal veins. Joining tertiaries well developed, irregular in their courses. Leaf 74 mm. long, 29 mm. wide.

5. Salicaceae (Willow family)

POPULUS FREMONTII S.Wats. (Fremont's cottonwood).

Two leaves studied.

UNITED STATES: California; Stanislaus County; near Oakdale, Mar. 31, 1923, L.R.Abrams 2266 (DC).

Description. - L-W ratio 0.9-1.1. Apex acute to abruptly acute. Teeth large, deeply crenate. Prochidodromous. Not loosely arranged. Leaf 25 mm. long, 21 mm. wide.

Remarks. - This or any other cottonwood similar to Betula might have been chosen.

6. Tiliaceae (Linden family)

The species of this family resemble Alnus cordata, and a few species of Corylus and Betula.

Description. - Low length-width ratio, large leaf. Base more often than not strongly asymmetrical, normally cordate, but when asymmetrical, one side cordate, the other flat. Number of intersecondary
teeth small, size large. Five veins radiating from base, sometimes 3, giving leaf a subpalmate appearance, basal segment contracted to 0. Externals departing chiefly as forks rather than branching, thus causing changes in courses of secondaries.

7. Ulmaceae (Elm family)

PLANERA AQUATICA (Walt.) J.F.Come. (Water elm).

One leaf studied.

UNITED STATES: Arkansas; Little Rock, March, 1886, H.F.Hasse s.n. (DS).

Description. - Base asymmetrical. Teeth pointed apically.

Crasspedodromous. Secondaries not parallel and not alternate, irregularly spaced along each side of midrib, each side apparently independent of the other, no pairs developed, angles variable, each secondary at angles independent of secondary above and below, irregular in course, concave, straight. Externals often leaving secondaries as forks. Interordinals common. Net highly developed, Ulmus type. Leaf 50 mm. long, 23 mm. wide.

ULMUS ALATA Michx. (Wahoo elm). (Plate LXXXVIII).

One leaf studied.

UNITED STATES: Oklahoma; Bryan County; Bennington, July 12, 1916, E.J.Palmer 10432 (DS).

Description. - Base very strongly asymmetrical in many cases, a characteristic feature. Margin biserrate, somewhat similar to Acer carpinifolia, large serrations separated from one another by prominent clefts, rounded in outline on basiscopic side; 1-4 smaller serrations,
Plate LXXXVIII. Ulmus alata Kichx.
UNITED STATES: Oklahoma; Bryan County; Bennington, July 12, 1916, E.J. Palmer 10,432 (US) (x 3.0)
apically pointed, lying on basiscopic side of larger serrations, never in cleft between larger serrations. Craspedodromous. Secondaries uniformly distributed, parallel, sometimes bifurcating near margin or near midrib, bending abruptly near margin. One external vein always terminating in cleft between larger serrations, a feature found occasionally in *Carpinus orientalis*. Tertiaries orderly, commonly simple, often sagging midway in their course between secondaries, thus resembling *Carpinus orientalis* and *Acer carpinifolia*. Net rather close and dense, orderly, many vein endings, complex. Leaf 53 mm. long, 23 mm. wide.

ZELKOVA CRRIIATA Spach.

One leaf studied.

UNITED STATES: California; Santa Clara County; a Chinese species cultivated at Stanford University, June 6, 1915, L.E. Abrams s.n. (DS).

Description. - Base asymmetrical, cordate. Teeth large, biconvex, apically directed, with little narrow, pointed tips at ends, very distinctive margin. Craspedodromous, tending toward dictyodromy. Secondary veins sometimes forking close to midrib or to margin as in *Ulmus*, no well-developed secondary veins at top of leaf. Tertiaries poorly developed, blending into rest of net. Net dense, many vein endings, highly complex. Leaf 60 mm. long, 29 mm. wide.
Leaves cleared in sodium hydroxide so that all materials except the veins are removed, are mounted in plastic on large glass slides; collections of such slides comprise slide herbaria. The use of these slide herbaria is the best method developed to date for generic and specific determination of leaves. The method is better than older methods because it enables the investigator to observe at a glance all details of the leaf venation and relationships between each vein. It has always been customary to compare fossil leaves with uncleared herbarium specimens. Thick parenchyma often hides the veins, particularly the lesser veins, so that only the most prominent veins catch the eye for comparison. For this reason, net venation has been almost ignored in leaf identifications. The study of net venation however is possibly the greatest single contribution of the method of slide herbaria to leaf identification.

The best criteria for the identification of betulaceous leaves are: (1) Leaf margin details. The type of margin, whether serrate or biserrate, dentate or doubly dentate, will readily distinguish the species of *Carpinus* and many of the species of *Alnus*. (2) Relationships between basal veins and the leaf base. The relationship of the secondary veins to the leaf base will distinguish most species.
of *Alnus* from the other genera in the family. The highly cordate base which characterized *Corylus* separates it from other genera in the family. The peculiarly distinctive base of *Carpinus turczaninowii* is a certain key to its identification. (3) Angles of the tertiary veins. The intra-angular tertiary angles of *Carpinus* distinguish it from similar leaves of *Betula*, and other tertiary angles are useful in aiding specific determinations throughout the family. (4) Relationships of veins within the net, including net vein endings. The common but complex net vein endings of *Alnus*, *Betula*, *Corylus*, and *Ostryopsis* readily distinguish these genera from all species of *Carpinus* and from most species of *Ostrya*. The development of medials, circumtertiary segments, and tertiary veins are helpful in distinguishing species. (5) External veins. The distribution and type of development of the external veins will aid in generic determinations, particularly between *Alnus* and *Betula*, and *Carpinus* and *Ostrya*.

It is seldom that a single character will readily identify any single specimen. In almost all cases, a combination of characters is necessary for positive determinations. In this connection, the charts accompanying the leaf descriptions will help the determination of any leaf of a species studied in the family. The criteria listed in the charts are the most useful characters for identification, but final identification of all specimens cannot rest upon the charts alone. In a few cases, the charts may limit the specimen to 2 or 3 possibilities, whereupon reference to the descriptions, or careful and detailed microscopic comparisons with known slide specimens will
identify the form positively. In almost cases, however, use of the charts and descriptions will suffice.

Of the 90 species and varieties of extant forms studied (a total of 332 specimens), the majority were readily distinguishable by this method. Only in Corylus were different species difficult, if not impossible, to separate. Species of Alnus, Betula, Carpinus and Ostrya were readily distinguished. In fact, several misidentifications of the specimens were easily discovered. Among these may be mentioned a specimen labeled Betula lutea, which was actually a form of B. papyrifera, two specimens labeled Carpinus turczaninowii which were C. henryana, the various forms of Alnus jorullensis, and a specimen labeled Alnus rubra which in reality was a specimen of A. tenuifolia. No further refinements of existing morphological taxonomic classifications were possible by means of the leaves, but the study did support very closely identifications already made. The study also strengthens views commonly expressed regarding relationships between some of the genera and species, such as those between Alnus and Betula, Carpinus and Ostrya, and Corylus and Ostryopsis. Additional links between the genera were suggested. Among the species, the close relationships between Alnus incana and A. tenuifolia were demonstrated, along with relationships between A. crispa and A. crispa sinuata, the varieties of Betula papyrifera, and the species of Corylus. The difficulty in distinguishing the related forms of Corylus may be ascribed to failure of the method, but may more probably reflect the close genetic relationships existing within this genus.
The use of these slide herbaria may also indirectly benefit
the plant geographer, especially in his studies of fossil floras.
But another phase of this study may be even more helpful to the
plant geographer. The numerical data, such as the length-width
ratio, the measure of leaf taper, and other measurements, may give
"a measure of species stability." For example, the numerical data
for Betula papyrifera are very variable, and this may show that this
species is still in the process of differentiation. On the other
hand, the numerical data of Ostrya virginiana vary only slightly for
any given measurement. This suggests that morphologically the species
is very stable.

It may be mentioned in passing that the majority of the species
of each genus, except Ostrya, occurs in southeastern Asia. This per-
haps indicates that the present center of development of these genera
lies in that area, while the present center of development of Ostrya
lies in southwestern North America.

The creation of slide herbaria is a time-consuming process which
involves more labor than that employed by plant taxonomists in the field.
But the process is no more difficult than the sectioning techniques of
plant study, and is certainly not as time-consuming as genetic studies.
For supplementary data in plant taxonomy, the method is very helpful,
and probably will aid in minimizing errors in identification on the
species level. It is very possible that detailed studies of net vein
endings will produce criteria of great importance to taxonomists. The
differences in vein endings between the genera are often very striking,
and Ostrya is the only genus in which there are greatly variant types
of vein endings.

The benefit for the paleobotanist resulting from this study may prove to be considerable, and the use of this technique by the paleobotanist may ultimately prove to be essential. Though only 7 fossil leaves were studied in detail, several relationships with living forms could be demonstrated. Two specimens labeled Alnus carpinoides (Univ. Cal. Coll. Paleobot. No. 790) and Betula lacustris (Univ. Cal. Coll. Paleobot. No. 567) were found to be referable to the fossil species Alnus corrallina. This fossil species, in turn, was shown to be equivalent to the living A. rhombifolia. Details of the net venation were found to be essential in this determination, as well as details of leaf margin and leaf base. Similarly, two specimens labeled Betula lacustris (Univ. Cal. Coll. Paleobot. Nos. 566 and 568) were shown to be equivalent to B. papyrifera or one of its varieties. One specimen labeled Carpinus grandis (Univ. Cal. Coll. Paleobot. No. 33) was shown to be referable to the genus Ostrya. Finally, two specimens labeled Ostrya proconiana (Univ. Cal. Coll. Paleobot. Nos. 35 and 36) could not be allied conclusively with any living species, either because an insufficient number of specimens of O. baileyi (the living species most similar to the fossil specimen) was studied, or because these specimens have no living equivalent. None the less, the species is clearly related to the O. baileyi - O. knowltonii group within the genus Ostrya. Likewise, Univ. Cal. Coll. Paleobot. No. 33 (labeled Carpinus grandis) is also allied to the O. baileyi - O. knowltonii group.

The degree of preservation of venation below the secondary level in the fossil specimens studied is remarkable. With a hand lens, details
to the quaternary level were discernible, and in the two specimens correctly labeled *Betula lacustris*, details to the external level were visible. These specimens, of course, represent the exceptional cases of fossil preservation, but in many fossil localities, it is possible to find a few specimens of each species represented with a very high degree of venation detail present. Lack of this essential detail in fossil specimens is the greatest single cause for error in identifications. In this study, had not details of minor venation been present, and had not ample study been made beforehand of living specimens by means of slide herbaria, the fossil specimens could not have been determined with complete certainty.

In summary, the possible advantages derived from the use of extensive slide herbaria are many, and by now should be evident. Though this study has been limited to only a very small segment of the plant kingdom, it shows sufficient promise to be applied to the remainder of the plant world.
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APPENDIX A

The following is a translation of Bianconi's venation classification, taken from his work titled Sul Sistema vascolare delle Foglie, Considerato come Carattere distintivo per la Determinazione delle Filii:

Plan for the Distribution of Dicotyledonous Plants
based upon the Venation of the Leaves.

Folia angulinervis De Candolle.

b. Palminervia. Several primary nerves.

Class I, Penninervia.

Order 1. Separated secondary nerves.

Section 1. Simple separated secondary nerves.

Examples: Carpinus ostrya, Ulmus campestris,
Castanea vesca, Fagus sylvatics, etc.

Section 2. Branched separated secondary nerves.

Examples: Quercus robur, . . ., Crataegus
florentina, . . ., Corylus avellana,
Corylus columna, . . ., Betula almus,
Betula alba, etc.

Order 2. Interanastomosing secondary nerves.

Section 1. Shortened secondary nerves joining above
and below.

216
Examples: *Juglans regia*, etc.

Section 2. Shortened secondary nerves joining only above.
Examples: *Philadelphus coronarius*, etc.

Class II. Palminervia.

Order 1. Trinervia.
Examples: *Platanus occidentalis*, etc.

Order 2. Quinquenervia.
Examples: *Acer campestre*, etc.

Examples: *Tilia europaea*, etc.

Order 4. Multinervia.
Examples: *Ricinus communis*, etc.

Order 5. Unnervia (hidden nerves).
Examples: Crassulae, etc.

(Pages 365-367)

Characters relating to the description of the leaves of known dicotyledonous plants, based on the disposition of the nerves:

Nerve: this word is understood to mean the vessel-bundles which emerge from the petiole, and which are spread over the leaf surface in various ways; among them the following:

I. Primary nerve, of which the following:

A. Dorsal nerve (dorsualis), a single nerve emerging from the petiole and proceeding to the leaf apex, giving rise on each side to lesser nerves, for example, *Quercus, Ulmus,*
Castaneae, etc.; of these the following characteristics may be observed:

a. Straight.
b. Sinuous.
c. Thick; longitudinal relationship or massive, spreading relationship.
d. Thin.
e. Vanishing toward the apex.
f. Cylindrical.
g. Pressed flat.
h. Subdued.
i. Angular.
j. Three-cornered.
k. Blunt.

B. Palmate nerves, where all spring from a common point at the leaf base, such as Vitis, Acer, etc., in which, the following:

1. Medial nerve, which varies from straight to sinuous, similar to a dorsal vein, showing possibly these additional characteristics:
   a. Much longer.
   b. Thicker.
   c. Forked.

2. Single lateral primary nerves on either side of the medial nerve. They are described much the same as the dorsal nerve with the following additional characters:
a. Branched, either outwardly, and from midrib, symmetrically, or asymmetrically.
b. Parted or bi-parted.
c. Turned inwards toward midrib.
d. Unobstructed in course, whatever the course.
e. Direct or rectilinear, without deviation.

3. Secondary and tertiary lateral nerves present, radiating from base.

II. Secondary nerves, which originate from the dorsal nerve, or if they originate from palmate nerves, they are joined together by transverse secondary nerves. The following terms may be applied:

a. Separated.
b. Interanastomosing.
c. Simple.
d. Branched: outwardly, symmetrically, from the base, from the middle, from the apex.
e. Parted into two or three nerves.
f. Dichotomous.
g. Short, long, etc.
h. Straight, sinuous, curved.
i. Attached to the apex, middle, base.
j. Equidistant along the primary nerve.
k. Inequidistant along the primary nerve.
l. Closely spaced.
m. Distantly spaced.
n. Turned toward one another.
o. Unobstructed in course.
p. Spread out.
q. Transverse.
r. Convex; i.e. convex downwards or concave upwards.
s. Thick or thin.
t. Prominent or not prominent.
u. Concealed.
v. Forked.

III. Nervules, which originate from the secondary nerves and comprise an interstitial nerve net; there are many of these nervules, variously disposed, between which still others wend their way.

The following terms:
a. Reticulate (A. Brongniart).
b. Areolate (A. Brongniart).
c. Clathrate (grate-like) (A. Brongniart).
d. Transverse (i.e., passing from one large nerve to another).
e. Closely repeated.
f. Loosely arranged.
g. Prominent.
h. Fine.
i. Concealed.

(Pages 383-386)
APPENDIX B

The following is a translation of Leopold von Buch's classification of veins taken from his article titled: Über Blattnerven und die Gesetze ihrer Verteilung:

A. Randläufer: if the nerves run from the midrib straight to the margin and end there.
   a. Simple randläufer: if no tertiary nerves depart from the secondary nerves.
   b. Randläufer with tertiary nerves. Pinnate randläufer if the lower secondary nerves send off tertiary branches toward the margin; the upper secondary nerves send them off only in their outer portions.

B. Bogenläufer: Two adjacent secondary nerves are joined in an arc.

C. Spitzläufer. Two lower secondary nerves run in an arc between the margin and midrib in an attempt to reach the apex of the leaf.
   a. Perfect spitzläufer, if both nerves reach the apex of the leaf.
   b. Imperfect spitzläufer, if both nerves fail to reach the apex of the leaf.

D. Saumläufer. Both basal secondary nerves run at the margin to the apex of the leaf.

(Pages 47-48)
1. Simple randläufer. *Carpinus betulus*. Hornbeam. 14 nerves on each side of the midrib reach the border without sending off tertiary nerves, the fold-line of the parenchyma nerves is quite prominent, from close to the midrib between two secondary nerves to the border and lying closest to the lower of the two secondary nerves. Accordingly, there are 3 or 4 marginal teeth above the point where the crest of the fold reaches the margin, and only one tooth below the fold-line.

2. Randläufer with tertiary nerves. *Corylus avellana*. Hazel-nut. 5 secondary nerves on each side. From the lowest two, there run seven tertiary nerves beneath them to the margin; there are none originating opposite them on the same secondary. Between the secondary nerves, the parenchyma fold may be recognized. As soon as the lower nerve has reached the margin, the next higher nerve likewise sends off several tertiary nerves, still only from the under-side of the secondary nerve. The next higher-lying nerves also follow this pattern.

(Page 148)
APPENDIX C

The following is a translation of part of von Ettinshausen’s *Bericht über das Werk “Physiotypia Plantarum Austriacarum”*, published in 1856. In this work, he describes his type example of craspedodromous nervation, the *Carpinus betulus* type. (Pages 433-434):

1. The *Carpinus Betulus* Linn. type.

Secondary nerves simple, straight or slightly curved, ending in the apices of marginal teeth. Tertiary nerves originating at 90° angles, joining together, circumscribing a fine quaternary net.

This type presents an undivided, commonly rounded to oblong-oval or lanceolate leaf, with a dentate or serrate, seldom entire margin. To this type belong the genera *Fagus, Carpinus, Castanea*, *Alnus*, *Betula* and *Tilia*.

This is the normal nervation structure of the leaf form classified as simple craspedodromous. The secondary nerves often originate close to the base of the leaf at more obtuse angles than the rest of the secondaries, and display more or less prominent external veins, whose character, never the less, has little importance. Those of *Carpinus betulus* itself are close together, while those of *Alnus glutinosa*, and *Betula alba* are more widely separated; in *Castanea vesca* they are often gently curved. In *Fagus sylvatica*, it happens now and then that the secondaries, which are always straight, do not terminate in the insignificant teeth, but double sharply back on themselves, and in a strong, almost marginal tertiary nerve, make a
more or less distinct loop to the next-overlying secondary nerve.

The tertiary nerves, in most cases, enclose a very perfectly
developed net.

In the Alnus-species, they are more prominent and join the
secondary nerves obliquely, so that they may be described as joining.
In these species, the tertiary nerves often grade into external branches
of the secondaries. The tertiary nerves of Carpinus Betulus run a
normal course in which they are endowed with an extraordinary delicacy,
likewise Fagus sylvatica, Castanea vesca, and the Tilia species, etc.
APPENDIX D

The following is a partial translation of a significant part of von Hittingshausen's work titled Die Blattkeleta der Apetalen, eine Vorarbeit zur Interpretation der Pflanzenreste, published in 1858. This work is the prelude to his 1861 work presented in part in Appendix E. (Pages 194-195):

Nervation Relations of the Betulaceae

Nervation forms and types. The leaf forms of this family show throughout simple craspedodromous nervation and in most cases bear the characteristics of Carpinus Betulus.

Primary nerve. In Alnus, this is usually straight, in Betula, often crooked, or sinuous. Occasionally it is considerably thicker than the secondary nerves, as with several Alnus species, i.e., A. jourellensis, etc. In more Betula species, i.e. B. fruticosa, B. glandulosa, it hardly exceeds or only unimportantly so, the thickness of the secondaries.

Secondary nerves. They usually appear relatively thick, are often straight and simple, less often somewhat crooked, as in Betula glandulosa, where they also may frequently be forked. Several Alnus species exhibit weakly curved secondary nerves, i.e., A. jourellensis, Betula lenta, etc. The origin angles are more or less pronouncedly acute. In Betula glandulosa this often amounts to only 25°; in the
greater number of cases the species of this family display origin angles of from $30^\circ$ to $45^\circ$. Cases where the maximum size of the origin angles amount to from $60^\circ$ to $65^\circ$ are not common, as, for example, in *Alnus jourellensis*, and *Betula pumila*. Complete uniformity in the origin angles of secondary nerves occurs in *Betula pumila*; in most *Alnus* and *Betula* species, the lowest secondary nerves originate at somewhat greater angles than the rest. In this connection, the leaves of *Betula glandulosa* are an exception, for the lower secondary nerves originate at predominantly lesser angles than the others. In the majority of the Betulaceae, external veins are attached to the secondary nerves. In *Betula* as a rule, these appear thick in the lowest part of the leaf, in *Alnus* in the middle part. *Betula fruticosa* and *B. Rajpathra* exhibit short, straight external veins, as do some others. *Betula glandulosa* often displays prominent external nerves only on the middle secondary nerves.

The mean distance of the secondary nerves is as a rule not small. It amounts on the average from $1/6$ to $1/5$. In *Betula pumila*, it reaches $1/3$. In *Betula lenta*, on the contrary, the mean distance of the secondary nerves approaches $1/14$.

Tertiary nerves. In most of the Betulaceae, these originate at right angles, and are joining, and appear rather distinctly. As exceptions to the rule are the following cases: in *Betula pumila*, tertiaries which vanish in the net predominate; these are plagiodromous. In an Asiatic *Betula*, they are very fine and close together.

Net nerves of a higher order. Both the quaternary and the quin-ternary nerves, when they are present, originate at right angles, are
usually abundantly developed and build very delicate nets consisting of rounded or U-sided meshes. The net of *Betula lenta* is very delicate, and the mesh is very small, yet clearly developed. The nets of *Betula Rhaipathra* and *B. glandulosa* are built of relatively loose, large meshes. Likewise, *Almus jourellensis* and other species display a nerve net built for the most part of simple, almost plagiodromous and sharply prominent tertiary nerves, and united between by large meshes.
APPENDIX E

Translation of Konstantin F. ritter von Ettingshausen's Die Blatt-Skelete der Dikotyledonen mit besonderer Rücksicht auf die Untersuchung und Bestimmung der fossilen Pflanzenreste:

General Part, I.

Terminology of the nervation of dicotyledon leaves.

Part 1. - Concerning the leaf nerves and their distribution in general.

Those vessel bundles which are spread out in the leaf structure of plants are called ribs, veins, or, commonly nerves, and the distribution pattern of these is designated by the term nervation. In better developed veins, the leaf nerves protrude more or less distinctly from the parenchyma, especially on the underside of the leaf, and these nerves, as well as their finer branches, are easily distinguished in incident light. The finest network of veins is, however, distinctly perceptible in penetrating light only in the leaves of thinner texture. In the leathery leaves, these finest networks of veins cannot be recognized without previous preparation, for as a rule, they do not protrude from the thick parenchyma, and one can obtain an exact knowledge of their forms after one has used the "Natural-self-impression" method. By means of heavy pressure, which is produced on the previously well-dried leaf, the rigid nerves are stamped deeper in the lead plate than the softer leaf parenchyma, and one is convinced by the first glance at the physiotyped impressions that the nervation on those impressions is sharper and more complete than is perceptible on the leaf itself.
The distribution pattern of the nerves in the leaves and the leaf-like organs on the plants is, by no means irregular, accidental, or confused. In these plants, one soon notes the natural law of distribution from comparative investigation and from the determination of their conditions, by which one may consider not only the single nerves by themselves, but also their mutual relationships.

In the study of the nervation, the main attention must be directed to the point of origin of the nerves. Specifically, the nerves appear either as direct extensions of the petiole, or they issue from the other nerves in the form of offshoots. In the first case, the nerves are called nerves of the first order or primary nerves; in the latter case, nerves of second, third, fourth and fifth order, or secondary, tertiary, quaternary, and quinternary may be distinguished.

In the leaves of most dicotyledons, the stele passes into only one primary nerve, whose direction, as well as thickness appears the most striking. The primary nerve is termed connecting if it joins the leaf base with the apex, as is the ordinary case. In the opposite case, the primary nerve is lost in the network below the apex, a more or less short distance about halfway above the base... or, it is at the least, split in two.

If there are several primary nerves present, they will issue radially from the petiole at the base of the leaf, and they are termed basal nerves... The middle one is ordinarily the best developed and is called the basal or median nerve; the others are called lateral basal nerves or lateral nerves.... If several primary nerves of very unequal thickness occur on a leaf, the thicker ones are termed principal nerves;
the finer ones lying between are termed intermediate or adjacent nerves. This is dominantly the case in the leaves of most monocotyledons, but is also the case in the leaf structures of several dicotyledons, for example, *Acacia* leaves.

Those nerves which connect two adjacent primary nerves are called transverse nerves; those nerves which run between two adjacent or secondary, or tertiary nerves, singly or bifurcated, are designated simply as joining nerves.

If lateral basal nerves, or stronger developed tertiary nerves have nerve branches protruding from their outer side toward the leaf margin, these are termed external nerves. Examples: *Ficus populiflora*, *Viburnum Lantana*, *Grewia oppositifolia*. The transverse nerves, like the external nerves, may have either the value of secondary or tertiary nerves.

The nerves of higher order (quaternary and quinternary nerves) form the frequently extremely delicate leaf network, which in some cases is hardly perceptible to the naked eye. Together with the tertiary nerves, one can group these nerves adequately under the term net nerves, in contrast to the primary and secondary nerves which have no part in the construction of the leaf net proper.

In the study of the leaf framework, it is also not unimportant to consider the form, size and attitude of a local segment of the different nerves of a leaf. Thus one may distinguish secondary segments, that is, those portions of a leaf lying between two adjacent secondary nerves; similarly, tertiary and quaternary segments.

The thickness of the nerves is determined by the value of the
diameter of the same. To state its absolute and relative value may, in many cases, be important as a possible characteristic of the nervation. In the Gramineae, Cyperaceae, and many other monocotyledons with parallel-nerved leaves, measurements of the diameter of the parallel nerves taken on the same position on the leaves serves preferentially for the distinction of related nervation forms. In most cases, however, data with respect to the relative size of the nerves are sufficient.

The length of the nerves is of minor importance as a distinguishing character of nervation forms. In most cases, it is sufficient to determine the relative length of two or more equivalent nerves, not only for itself, but also, in relation to the length of the leaf.

The direction of the nerves is expressed through the designation of the origin point and by indicating each region of the leaf to which the nerve extends. The base, the apex, and the margin of the leaf thus give the natural points of reference. Besides, certain points of the thicker nerves can be used to advantage for the designation of the direction.

The course of a nerve, in the case of a constant general direction, can at one time be rectilinear, at another time more or less curved, sometimes curved either to and fro, or in a simuous manner. In many cases, the original direction during the course of a nerve is changed completely. Of special importance is the case where a nerve splits simply at its end or splits repeatedly, by which means it does not touch the leaf margin, but remains always a short distance away from it. Frequently the branches of the fork of this nerve form, with the
neighboring nerve, a more or less strong and prominent curved, acute, or obtuse-angled anastomosis, which I have designated by the term loops....

Aside from the just mentioned conditions which refer to a single leaf nerve, there have to be considered the characteristics resulting from the number, relative position, and connections of all the nerves.

The number of nerves of first and second order of a leaf is ordinarily constant within certain fixed limits. In the case of symmetrical distribution of the nerves, it suffices in most cases to count along one side of a basal or single primary nerve the attached secondary nerves. Only rarely is it necessary to give the number of tertiary nerves.

The relative position of the nerves is measured partly by indicating their distance apart, partly by the angle which the orientation of two nerves will have with each other. The position of two or more nerves may be fixed approximately by the configuration of the leaf segment produced by the above-mentioned bordering nerves. In basal nerves, which run parallel to one another, straight, or faintly curved, it is most expedient to give a distance measurement which is taken from a fixed point in the leaf, usually the center. In secondary nerves, their origin points give a very easy but very important reference point for the judgment of their mean distance apart. Here must be considered whether the distance between all secondary nerves is equally large, or whether they decrease or increase toward the base or apex of the leaf, or whether
toward both ends. These distances are determined on one hand by the
determination of the absolute size, on the other hand by the mean
ratio of the distance apart of the secondary nerve to the length of
the primary nerve or whole leaf. One finds the latter if he expresses
the amount of the distance of the mean secondary nerves of a leaf to
the whole length of the primary nerve and expresses the ratio as a
fraction.

In the measurements of the angle which two nerves make with one
another, one is dealing only with an approximate value where angle sizes
under 5 degrees seldom come into consideration. In many cases, it is
possible to regard the nerves as straight lines; in other cases, one
can, as a rule, consider only the lower part of a nerve which deviates
the least from a straight line.

For the determination of the size of the angle, I make use of a
transparent material, with advantage, of which the best is a semicircle
subdivided in degrees drawn on a varnished straupaper, which is laid on
the object to be measured, and which facilitates the comparison, as well
as the actual reading, of the angle considerably.

The arrangement of nerves of higher order consists of numerous
anastomoses, by which a more or less developed leaf net is produced,
and which, in the leaves of different plant species, are often formed
differently, and as a rule form completely unbroken meshes. In some
plant families, particularly in the Filices, Gramineae, Cyperaceae,
Juncaceae, etc., also in some Trifolium species, in the sepals and
petals of different monocotyledonous and dicotyledonous plants, nerve
networks consisting of closed meshes do not occur. In many monocol-
tyledons, the nerves converge toward the apex of the leaf and often are
The conditions of the nervation presented in the foregoing paragraphs furnishes enough points of reference with which to study the skeleton surface and to obtain from these, on account of their permanency, frequently very important characteristics. But for the characteristics and description of the nervation, it is very helpful to set up a subdivision of the different types and the principle forms to be named. I offer the following as my attempted division of the nervation forms.

1. Craspedodromous nervation (nervatio craspedodroma). A single primary nerve; all, or at least the thicker secondary nerves or their branches running to the leaf margin, where they end. One may distinguish here:
   a. Simple craspedodromous nervation. All secondary nerves strike margins. They are either simple and then run as a rule straight for the margin, or they are bifurcated-branched, and then their branches and external nerves end at the leaf margin (Examples: Ostrya vulgaris, Viburnum Lantana).
   b. Combined craspedodromous nervation. Not all secondary nerves run to margin. The lesser, or smaller intermediate secondary nerves are arcuate, looped, or lose themselves in the nets (examples: Myrica carifera, Myrica quercifolia, Quercus sp., Ficus denticulata).

2. Camptodromous nervation (nervatio camptodroma). A single primary leaf. The secondary nerves do not end at leaf margin. They run in an arcuate or sinuous manner, seldom straight toward the margin, but form, however, prominent loops, or before they reach the margin.
vanish in a fine net, or lose themselves gradually along the leaf margin. This common nervation form falls into three classes:

a. Brochidodromous nervation (*nervatio brochidodroma*). The secondary nerves anastomose beneath one another with distinctly prominent loops (Examples: *Ficus venosa*, *Allamanda verticillata*, *Myrcia multiflora*).

b. Dictyodromous nervation (*nervatio dictyodroma*). The secondary nerves arise at different acute angles, mostly at short distances apart, and after a short lapse, lose themselves in the leaf net without making prominent loops. (Examples: *Myrica aethiopica*, *Leucothoe salicifolia*, *Leucothoe multiflora*, *Copaifera cordifolia*).

c. True camptodromous nervation. The secondary nerves run to the margin, there to anastomose to the next overlying nerve, but without making prominent loops. The secondary nerves are most commonly relatively thicker than the tertiaries, and often originate farther apart (Examples: *Salix riparia*, *Ocotea sp.*, *Diospyros virginiana*).

3. Hyphodromous nervation (*nervatio hyphodroma*). A single primary nerve, the other nerves lacking, or only rudimentary, and so buried in thick, usually leathery mesophyll that they are outwardly not apparent (Examples: *Taxus baccata*, *Galium verum*, *Erica carnea*, etc.).

4. Parallelodromous nervation (*nervatio parallelodroma*). Several primary nerves originating close to one another in usually slight, only little varying distances to the apex of the leaf where then and only then do they converge. (Examples: the leaves of the Graminae, Cyperaceae, etc.).

5. Campylocladodromous nervation (*nervatio campylocadroma*). Several
primary nerves issuing from a point, or originating also adjacent to one another, run in a more or less strongly curved arc to the apex of the leaf, where they converge above and below. The leaf not is either not developed, or consists only of a loose mesh formed from transverse nerves (Examples: the leaves of many Orchidaceae, Smilaceae, Liliaceae, and Colchicaceae).

6. Acrodromous nervation (nervatio acrodroma). Several primary nerves or a single primary nerve. Two or more strongly developed basal nerves or basal secondary nerves run in courses converging at the apex of the leaf. This nervation form is divided thus:

a. Perfect acrodromous nervation. The apex-running nerves are relatively strongly developed, they protrude distinctly and go mostly into the leaf apex (Examples: *Cinnamomum zeylanicum*, *Strychnos* sp., *Gaultheria nummulariodes*, *Davya glabra*).

b. Imperfect acrodromous nervation. The apex-running nerves are mostly fine. They are not prominent and do not reach the apex (Examples: *Celtis* sp., *Cinnamomum Camphora*, *Rignonia* sp., *Crewia bicolor*).

7. Actinodromous nervation (nervatio actinodroma). Three or more primary nerves diverge radially from the end of the petiole. This nervation form falls into four major groups:

a. Marginal actinodromous nervation (nervatio actinodroma marginalis). All or at least the basal nerves next to the median nerve end an almost straight-line course in the apex of an indentation, lobe, or in the teeth of the leaf (Examples: *Cecropia palmata*, *Liquidambar styracifluum*, *Acer monspessulanum*).

b. Retiform actinodromous nervation (nervatio actinodroma retiformis). All the basal nerves, or all excepting the middle one run
sinuously, curving here and there, or branching dichotomously toward the periphery of the leaf without reaching the leaf margin. The lateral basal nerves are well developed, exist in greater numbers (8-16), or they spread with their branches over at least two thirds of the leaf (Examples: *Asarum europaeum*, *Triumfetta* sp., *Tilia* *mexicana*).

c. Imperfect actinodromous nervation (*nervatio actinodroma imperfecta*). The basal nerves are arcuate or sinuous, rarely branching dichotomously, but frequently supplied with external nerves. The lateral basal nerves, existing always in smaller number (3-5) occupy, with their branches, less than two thirds of the leaf surface. The branches of the central basal nerve predominate (Examples: *Ficus superstites*, *Gaultheria coccinea*).

d. Flabelliform actinodromous nervation (*nervatio actinodroma flabelliformis*). Several, or very often, numerous, equally fine basal nerves, originating at a very acute angle, diverge radially, and are repeatedly bifurcated in their course (Examples: the leaves of *Harsilaeae quadrifolia*; the leaflets of *Cassia cultriformia*). (pp.xiii-xvii).

Part 2. Concerning the leaf nerves in particular (partial trans.)

A. Concerning the characteristics of primary nerves:

The properties of the primary nerves are distinguished in relation to the absolute and relative thickness, the direction, the course, and the termination of the same. (p. XVII)

B. Concerning the characteristics of the secondary nerves:

The secondary nerves, that is, the thicker lateral branches of the primary nerves, offer a series of characteristics which are of great permanency, and therefore very important to the characteristics of
the species. These characteristics refer to the origin angle, the thickness, the length, the direction, and the course, to mutual relationships, to location, and to distance apart. Finally, the forms of the secondary segments must be considered. (p. XIX).

C. Concerning the characteristics of the tertiary nerves:

By tertiary nerves, I mean the next finer lateral off shoots from the secondary nerves, and those similarly oriented with respect to the midrib, that is, the nerves branching on both sides of the primary nerve. The tertiary nerves must be distinguished, therefore, on the one hand, from the branches of the secondary nerves which appear most strongly as direct continuations of the secondary nerves; on the other hand, they must be distinguished from nerves of higher order departing on both sides of the secondary nerves. In the tertiary nerves, the origin angle, thickness, length, direction, course and anastomosis, location, number, and finally, the form, size, and attitude of the tertiary segments must be considered. (p. XXIII).

D. Concerning the characteristics of the nerves of higher order:

The next finer nerves originating from the tertiary nerves are called quaternary nerves, and those still finer ones coming from the latter are called quinternary nerves. In both, the absolute and relative thickness, the size, and form of the network built from them is specified, and, finally, the degree of development of the leaf net in general. (p. XXVI).

General Part, II

Methods of investigation of prehistoric plant remains

In water-laid sediments, one finds plant remains confined, mostly leaf fragments, but also whole branches, inflorescences, and
fruit clusters, and often single flowers, seeds, fruits and so forth, wood debris, whose structure is very often so well-preserved that one can examine their anatomic structure exactly.

These plant remains are the props upon which the history of the plant world is based; they are well-preserved letters by which nature documents the past existence of long extinct plant forms, and by which she indicates to us the imposing transformations which the formations of the plant world has undergone in the course of time. Thus it is a law that those vegetable remains enclosed in the rock always belonged to such plants that lived in those times, that the rocks themselves were formed in water.

From this handwriting of nature, we draw our knowledge in a dual way: first directly, through the determination of the fossil plants for which we have specified the place which they occupy in the system, where we do not neglect wherever possible to relate each plant to the present floras which are most alike or equivalent to them; second indirectly, through conclusions from the vegetation conditions of the presently living plants to the vegetation conditions of the analogous fossils, that is, preferably with climatic conditions, then with the character of the habitat.

The direct method in the investigation of fossil plants yields the most important knowledge for Phytopaleontology, for example, that the plants of the oldest period examined belong to the Acotyledons, that is, the most primitive, lowest organized plant life, that these older floras are outstanding because of their poverty of species, by their almost complete uniformity in the widely scattered parts of the
earth where one could find them; that the dicotyledons, therefore, the higher organized plants, first appear in the Cretaceous period, and indeed in very peculiar forms; that the character of the succeeding Eocene flora exhibits a striking conformity with the present day New Holland vegetation, and so forth. The direct determination of fossil remains is, therefore, only useful if it is based on the comprehensive exact comparison of these with the corresponding structures of present day vegetation. The simple naming of the fossils, only conjectural or completely groundless determinations, have no or only very little value for science.

Much certain and worthy knowledge concerning fossil floras, as well as knowledge of their conditions which predominated in early building periods of the earth's body could have been obtained only by an indirect method. In such a manner, the reign of a former tropical climate in our regions could be deduced from the occurrence of fossil remains of certain palms, tree-like ferns, cycads, and other plants in the older sediments of Europe, presently growing only in a hot climate. Likewise, the inclusions of remains of certain Laurineae, Proteaceae, Cupulifereae and many others in the younger rocks permits the hypothesis of a warmer temperate, or at the most, a subtropical climate, which reigned at a later time in the same regions. In like manner, it is permitted to draw conclusions, still with great caution, on the ecology of the habitat of the fossil plants; for such conclusions are only then permissible, if the present living analogies of fossil species show perfectly apparent and peculiar conditions in this respect, but preferably if these conditions are always found in all presently living species of the race, or even of the family. Thus the occurrence of
Chondria and Fucus types in the beds of the Vienna and Carpathian sandstones permits one to conclude the former existence of a sea at the locus of formation of these sandstones; the presence of certain Najadeae in the fossil flora of Fohnsdorf in Steiermark permits one to conclude with certainty the former presence of important freshwater accumulations in this region. From the remains of Taxodium dubium Stern., a characteristic guide plant of the Neogene strata, which is closely related to Taxodium distichum Rich., one can conclude with all probability that we are dealing with a swamp flora, for the above mentioned extant species is encountered in extensive swamps and marshes in Mexico, and in the southern part of the United States of North America. The wealth of ferns, by which the floras of the older Secondary period is characterized, verifies without doubt that these floras inhabited small islands, that they occupied in great numbers each region in which the continent later rose. On the contrary, the occurrence of rich remains of apetalous dicotyledons in the fossil floras of most early Tertiary deposits of Europe assumes the existence of important forests which covered the continent at that time and permits the hypothesis of an even greater former extent of the continent.

But one has yet only to consider the co-occurrence of fossil plant species, and also to apply the principles of plant geography to the past floras. In this way it is possible to progress several steps further in the knowledge of former surface conditions of the earth. I shall illustrate with an example.

In the varied and abundant fossil flora of Radoboj in Croatia, there occur remains of fan and feather palms, tree-like ferns, and more dicotyledons, such as Combretaceae, Myrtaceae, Mimosaceae, Artocarpaceae,
Moreae, etc., which necessarily assume a tropical, or at least a subtropical climate. With these remnants, there occur in the same strata, in fact, in one case, on the same slab of the marl shale, remains of tree species which require only a temperature which is found in temperate or warm temperate climate. The remains of these temperate species are very rare indeed among the fossils of Radoboj, but their interpretation leaves not the slightest doubt. They are remains of beech and oak, and especially of birch and elm. In the collection of the plant families in the K.K. geologischen Reichsanhalt on a piece of the marl shale preserved, which I myself collected near Radoboj, on which the impression of the leaf of a tropical feather palm appears, and over it lies several undoubted catkins and leaves of birch. On another piece may be seen the print of an undoubted elm fruit, immediately beside it the leaves of a subtropical Cinnamomum species. Other local floras of the Tertiary formation produce analogous data, especially in Steiermark, Tirol, and Switzerland. Thus Prof. O. Meer discovered in the Tertiary beds of Switzerland remains of genuine tropical Polypodiaceae, of Gleicheniaceae, among which was an interesting Lygodium species, furthermore, remains of palms, Bromeliaceae, and tropical dicotyledons; but with these are found also species which belong to a temperate climate and species which demand a warmer temperate climate. It is worthy of note that those latter plants occur there more frequently and in greater diversity than in the above mentioned flora from Radoboj in Croatia.

It is impossible that these plants could have lived closely adjacent to one another, for example, in limited space in the forest. Such a supposition contradicts totally the experiences we have found in the present distribution of plants. Moreover, fossils of animals are also
found in the mentioned strata, animals which indicate even more strongly that they did not originate from one and the same place. Likewise in the marl shale of Radoboj, fish and insect remains are often encountered in one and the same piece of rock next to each other. While among the fish some are known to have lived only in salt water, such as *Selotus sardinites* Heck., there were found among the insect species those who live only in the thick and moist forest, then, by contrast, species which inhabit only sunny places covered abundantly with meadow plants, and, furthermore, those species that swarm above the surface of fresh water. Finally the insect fauna of the marl shale of Radoboj contains species which needed for existence a warm climate, such as tropical and subtropical forms of Orthoptera, termites, Homoptera, Cicadidae; then by contrast, species which need a temperate climate, such as many red ants, certain forms of flies and beetles. Likewise, the animal remains of the Radoboj beds surely originate from very different localities of a rather extensive area. Similar results can be concluded from the nature of the fossils of other deposits of the Tertiary.

Is an explanation of these apparently puzzling facts, we can employ the principles of plant geography to advantage. We see exactly the same conditions in the tropics where mountain ranges rise; the regions of vertical plant zonation coincide essentially with the geographical plant zones. Therefore, a much greater vertical zonation of vegetation will be apparent in the mountains the closer one approaches the tropical zone, and in the tropics, the change in elevation according to altitude will be most apparent. Whereas in the low valleys and on the seacoast of the tropical zone, palms, tree-like ferns, *Moraea, Artocarpae*, etc. thrive, in this zone, one sees at an altitude of 2000 feet a strikingly
different vegetation take root, which is characterized by deciduous
trees with shiny leathery leaves, belonging mostly to the families
Myrtaceae and Laurinae. In the flora of the tertiary period, we
have to deal with a tropical vegetation according to the sum total of
its characteristics. If we recognize these as the true valley vegeta-
tion, we can clearly recognize in the flora of the above cited tertiary
localities certain zones of the mountain vegetation. Therefore, the
plants of these deposits did not grow in a restricted area adjacent to
each other, but in the same region over one another, that is, the tropi-
cal species in the valleys, and the temperate ones in a mountain range
adjacent to it; between them now lie the habitats of the subtropical
and warm temperate species. The remains of this mountain vegetation
could be transported easily partly by flowing water, partly by hurri-
canes, often relatively undamaged, into the lower areas, and be deposited
in the reach of the watershed of the valleys, or in the nearby tertiary
sea, where they were deposited, together with the remains of the close-
lying tropical valley vegetation at each place where we still find them
today. (pp. XXVIII - XXX).

Betula alba L. (Europe)

Simple craspedodromous nervation. Primary nerve thick at the
case, straight in its whole course. Secondary nerves feebly curved,
sending off prominent basal outer nerves at angles of 65°-70°, the upper
ones mostly simple, originating at angles of 45°-50°. Mean distance 1/5.
Tertiary nerves fine, joined together, going off from the outer and inner
sides of the secondaries at acute angles. Leaf net rather fully developed,
composed of dominantly oval areoles.
Quaternary nerves building a loose net composed of strikingly large areoles, rounded in outline, which encloses a most imperfectly developed group of quinquenary nerves. (p. 4)

*Betula Rhodopithre* Wall. (East Indies)

Crustedodromous nervation. Primary nerves quite thick at the base, thins toward apex, curves somewhat here and there in its course. Secondary nerves sharply prominent, rectilinear, the average ones supplied with several external nerves, most of them aduncate before their termination in the spines of the teeth. Origin angle of secondary nerves 45-50°. Mean distance 1/7 to 1/6. Tertiary nerves fine, but sharply prominent, simple or bifurcated, originating at right angles, joined together. Quaternary nerves going off at right angles, producing a relatively loose net composed of 4-sided areoles. An average secondary segment including 6-8 tertiary nerves joined to the axis and 10-12 joined to the secondaries. (p. 5)

*Alnus glutinosa* Gaertn. (Europe)

Simple craspedodromous nervation. Primary nerves straight, sharply prominent at the base, thining to almost the thinnest of the secondaries toward the apex. Secondary nerves almost straight, or near the base somewhat diverging, forked at the apex or provided with several prominent external nerves, seldom wholly simple, originating at angles of 50-65°. Mean distance 1/8-1/6. Tertiary nerves going off at acute angles, joined together, curved here and there. Net areoles relatively loose, not prominent. (p. 5)

*Cardium betulius* L. (Europe)

Simple craspedodromous nervation. Primary nerves sharply prominent
to the middle. Secondary nerves sharply defined, rectilinear, the lower ones frequently diverging, alternate, only the lowest are commonly opposite. Origin angle 35°-45°. Secondary segments narrow, the average almost perfectly linear. Mean distance 1/13-1/10. Tertiary nerves on the outer side of the secondaries go off at slightly acute angles, from the inner side at 90° or at slightly obtuse angles. The secondaries from the axis originating predominantly at right angles or slightly obtuse angles; all joined together, the lowest secondary nerves going over frequently into prominent external nerves. Leaf net fully developed. Areoles of the quaternary nets relatively loose, roundish in outline.

*Ostrya vulgaris* Willd. (Southern Europe)

Simple craspedodromous nervation. Primary nerve sharply prominent at the base, gradually thinning toward the apex, reaching the thinness of the secondary nerves, perfectly straight in its course. Secondary nerves rectilinear, the lower often provided with several prominent external nerves, mostly simple, very seldom forked. Origin angles of the secondary nerves 40°-50°. Mean distance 1/14-1/13. Tertiary nerves fine, but distinct, simple and forked, originating at right angles, joined together. Leaf net slightly prominent. An average secondary segment contains 3-4 tertiaries joined to the axis and 15-20 tertiaries joined to the secondaries.

*Corylus colurna* L. (Southern Europe)

Simple craspedodromous nervation. Primary nerve strongly prominent to the middle of the leaf, quite straight. Secondary nerves conspicuous, feeble curved, the lowest originating at angles of 70°-85°.
displaying 4-5 prominent external nerves, the others departing at angles of $35^0-45^0$. Mean distance $1/7 - 1/6$. Tertiary nerves originating on the outer side of the secondaries at slightly acute angles, from the inside at slightly obtuse angles. Quaternary nerves forming a loose, prominent net composed of roundish areoles. (p.9)
APPENDIX F

List of abbreviations used in Charts la, lb, 2, 3, 4, 5, and 6.

Intersec ............................. Intersescondary.
No. ..................................... Number.
#1's ..................................... No. 1 secondary veins.
Sec. ..................................... Secondary.
Seg. ..................................... Segment.
Str. ..................................... Straight.
Tert. ..................................... Tertiary.