Revisions of *Ulmus* and *Zelkova* in the middle and late Tertiary of western North America

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REVISIONS OF *ULMUS* AND *ZELKOVA* IN THE MIDDLE AND LATE TERTIARY OF WESTERN NORTH AMERICA

By TOSHIMASA TANAI[1] and JACK A. WOLFE

ABSTRACT

Examination of previously described and some undescribed leaves of *Ulmus* and *Zelkova* from the later Oligocene, Miocene, and Pliocene of western North America indicates that at least eight species of *Ulmus* and two species of *Zelkova* are represented. Three new species are described: *Ulmus chaneyi, U. knowltoni,* and *Zelkova browni.*

INTRODUCTION

The elms (*Ulmus*) and species of the related genus *Zelkova* are among the most conspicuous elements of temperate broadleaved deciduous forests in the Northern Hemisphere. Judging from the fossil record of both leaves and pollen from the Oligocene and Neogene, members of these two genera were also important constituents of ancient forests. Although foliage of the same basic type also occurs abundantly in many Paleocene and Eocene floras (for example, Brown, 1962; Wolfe, 1968; MacGinitie, 1969), the differences between these earlier leaves and extant leaves of *Ulmus* and *Zelkova* are sufficiently great in many specimens to make generic assignments problematic (Wolfe, 1968). Certainly elmlike foliage and pollen extend back to the latest Cretaceous (Wolfe, 1973), but we have not undertaken the extensive work necessary to unravel the systematics of these earlier occurrences.

Indeed, a flowering specimen of the Eocene *"Zelkova" nervosa* (Newb.) R. W. Br. from the Green River Formation clearly indicates that this species is unassignable to *Zelkova.* The specimen, which is a young shoot, has clusters of conspicuously pedicellate axillary flowers on both upper and lower parts of the shoot, and staminate and bisexual flowers occur in the same clusters. In *Zelkova,* the flowers are sessile or shortly pedicellate, and the staminate flowers are clustered in the lower axils and the bisexual flowers are solitary or few in the upper axils. Moreover, the shoot itself is conspicuously straight, whereas shoots of *Zelkova* are conspicuously zig-zag (see Tanai and Suzuki, 1963, pl. 18, fig. 5). Specimens of shoots of the early Oligocene *"Z." drymeja* (Lesq.) R. W. Br. are also straight. We conclude that neither *"Z." nervosa* nor *"Z." drymeja* can be referred to *Zelkova* and that both species represent some extinct (although certainly ulmaceous) genus. Also assignable to the same genus are the leaves referred by Chaney (1927) to *Ulmus brownellii* Lesq.

The major concern of this report will thus be the later Oligocene, Miocene, and Pliocene species of *Ulmus* and *Zelkova* from western North America. In the process of determining foliage of these genera from the Miocene of Alaska (Wolfe and Tanai, 1977), it became apparent that the taxonomy of middle Tertiary species of these genera was poorly understood. Many epithets have been proposed; however, some authors have erected new species on characteristics of little systematic value, and other authors, who apparently ignored the descriptions of namebearing specimens, have assigned material of widely differing morphology to the same species.

Insofar as we have been able to determine, only one species of *Zelkova—Z. browni*—is represented in the Oligocene and Miocene of conterminous United States. An additional species—the otherwise Eurasian *Z. ungeri* Kovats—is present in the Miocene of Alaska (Wolfe and Tanai, 1977) and is not further treated in this report. Brown (1937) was the first to recognize the presence of *Zelkova* in the Tertiary of North America, although, as discussed below, we do not consider the type of his *Z. oregoniana* to represent *Zelkova.* Nevertheless, some of the nontypic material referred to *Z. oregoniana* by Brown (1937) does indeed represent *Zelkova.*

In contrast to *Zelkova, Ulmus* is represented in the middle and late Tertiary of western North America by at least eight species. Although nine species are discussed in the systematic section of this report, we consider one of these (*U. moragensis*) to be of doubtful validity, that is, this species is probably synonymous with another previously described species. Additionally, the material described as *U. eolaciniata* (MacGinitie, 1937) is considered to be

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Rosaceae and is thus excluded from the enumeration of *Ulmus*. Because of the past confusion in the nomenclature and systematics of Tertiary leaves of *Ulmus*, in western North America, the following key is presented.

A KEY FOR THE IDENTIFICATION OF *ULMUS* LEAVES FROM THE MIDDLE AND LATE TERTIARY

A. A prominent tertiary vein forking without reaching the sinus bottom and extending along each border of sinus.
   1. Principal teeth acutely trigonal. Subsidiary teeth usually 2 and large, having additionally 1 minute tooth each ..... *U. pseudo-americana*
   2. Principal teeth bluntly deltoid, rather apiculate. Subsidiary tooth absent, or sometimes 1 minute tooth ..... *U. knowltoni*

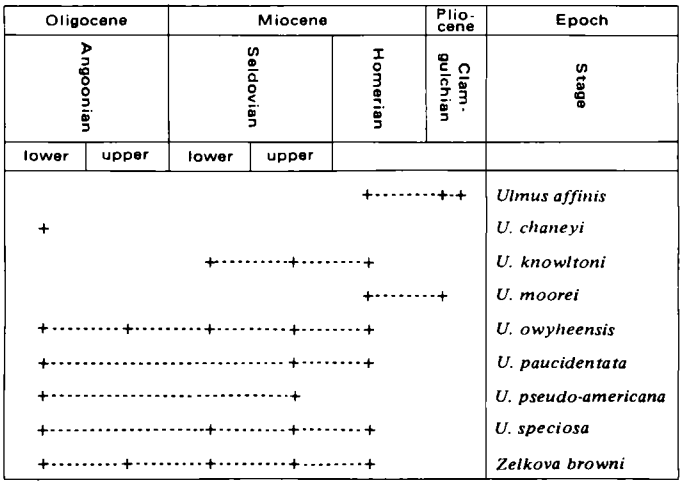
B. A prominent tertiary vein reaching directly the bottom of each principal sinus.
   1. Principal teeth bluntly deltoid.
      (a) Base rounded, slightly asymmetrical.
         (i) Subsidiary teeth 2, small, and nearly equal-sized ..... *U. speciosa*
         (ii) Subsidiary teeth 1 or 2, large, and sometimes absent on the upper margin ..... *U. owyheensis*
      (b) Base asymmetrically cuneate.
         (i) Foliage shape oblong-elliptic; subsidiary teeth 1 or 2, sometimes absent on the upper margin. ..... *U. paucidentata*
         (ii) Foliage shape ovate to orbicular; subsidiary tooth 1 and small, or absent ... *U. moorei*
   2. Principal teeth acutely trigonal. Subsidiary teeth 1 or 2, small ..... *U. affinis*
   3. Principal teeth having subsidiary teeth on both upper and lower sides ..... *U. chaneyi*

We gratefully acknowledge the assistance of H. D. MacGinitie and H. E. Schorn (Museum of Paleontology, University of California, Berkeley) for offering their critical comments on this report. For the loan of specimens, we also express our gratitude to H. F. Becker, J. A. Doyle, L. J. Hickey, and H. E. Schorn.

STRATIGRAPHIC AND AREAL DISTRIBUTION

The two most geologically long-ranging species of *Ulmus* are *U. owyheensis* and *U. speciosa*; both species are known to range from the middle Oligocene (Bridge Creek age) through the late Miocene (table 1). Somewhat shorter ranging are *U. paucidentata* and *U. pseudo-americana*, which range from the middle Oligocene through the middle Miocene, and *U. knowltoni*, which ranges from the early through the late Miocene. Both *U. affinis* and *U. moorei* are restricted to late Miocene and younger horizons, and thus far *U. chaneyi* is known from only one middle Oligocene locality.

TABLE 1.—*Stratigraphic ranges of species of* Ulmus *and* Zelkova *in the late Oligocene and Neogene of conterminous Western United States*



Ulmus knowltoni has the same peculiar relation between the marginal tertiary veins and sinuses as does *U. pseudo-americana*. Although the ranges of the two species overlap during the early to middle Miocene, a phylogenetic relation could be suggested. An undescribed (because of the lack of sufficiently complete material) species from the middle Oligocene (Tsadaka flora) of Alaska is similar to *U. knowltoni*, except that the teeth are pronouncedly attenuated as in *U. pseudo-americana*; this character indicates that probably the lines of *U. pseudo-americana* and *U. knowltoni* had diverged by or during the middle Oligocene.

As well as having long stratigraphic ranges, *Ulmus owyheensis* and *U. speciosa* have broad geographic ranges. During the early to middle Miocene, *U. owyheensis* is known from southeastern Oregon north to lowland southern Alaska (Cook Inlet region), and *U. speciosa* ranged from northeastern Nevada north to Alaska. The somewhat stratigraphically shorter ranging *U. knowltoni* also had a

Miocene distribution from Nevada north to Alaska, as well as occurring in western Montana.

Zelkova browni also has a long stratigraphic range: middle Oligocene through late Miocene. As with long-ranging species of *Ulmus, Zelkova browni* was widely distributed during the early to middle Miocene; occurrences are known from southwestern Nevada north to the Cook Inlet region of Alaska and east to western Montana. The combination of long stratigraphic ranges with wide geographic distribution is, in fact, to be expected. A wide geographic range probably indicates a wide tolerance to different environmental (particularly climatic) factors, and the persistence through a long period of time would also indicate considerable tolerance to changing environmental factors.

SYSTEMATICS

Foliage of *Ulmus* is highly similar to that of *Zelkova,* and such similarity has led to confusion in generic assignments. We cannot agree with Brown (1937, p. 173) that the areoles of *Zelkova* are relatively larger than those of *Ulmus;* from examination of ultimate venation of cleared leaves of all extant species of *Zelkova* and 25 species of *Ulmus,* there is complete overlap between the two genera in size of the areoles. Although most species of *Zelkova* are singly serrate and most species of *Ulmus* are doubly (or more) serrate, some leaves of *Zelkova* possess secondary serrations and some leaves of *Ulmus* are singly serrate. The only feature that consistently separates foliage of the two genera is in the intercostal tertiary venation: in *Zelkova,* the tertiary veins are typically thin, widely spaced, and fork conspicuously midway between the secondary veins, in contrast to *Ulmus* in which the tertiary veins are thick, more widely spaced, and at least half the tertiary veins are unbranched (that is, they are percurrent).

One of the major problems in unraveling the nomenclature for the various species (or rather species concepts) discussed in this report is that many epithets have been founded on poorly preserved or fragmentary (or both) material. In the last decade, increasing emphasis has been placed on details of fine venation and margin for the characterization of leaf species, and such details are in many instances lacking on name-bearing specimens. Other species concepts have been based on one or two fragmentary specimens, and, if no topotypic material is known for such species, circumscription of that particular taxon is uncertain, that is, even certain gross features and their range of variation are unknown in regard to certain specific concepts.

An example of one such problem is the proper name to be applied to the widespread species previously called *Zelkova oregoniana.* Brown (1937) based this species on Knowlton's (1902) *Myrica oregoniana.* Our examination of the type specimen has led us to conclude that it, in fact, represents a species of *Ulmus* (renamed below as *U. knowltoni*), although certain other material synonymized to *Z. oregoniana* by Brown (1937) and other workers does represent *Zelkova.* The next available name for this species of *Zelkova* would be *fernquisti,* based on Knowlton's (1926) *Ulmus fernquisti. Ulmus fernquisti* probably represents *Zelkova,* but Knowlton (1926, p. 39) validly remarks that "finer venation not retained." We thus reject the epithet *fernquisti* because it is based on a poorly preserved specimen, and no comparisons of the finer venation of the type with other fossil or extant species will ever be possible. The next available name would apparently be Brown's (1946) *Z. hesperia.* The only specimen illustrated by Brown (1946) is by inference the holotype; this specimen is very fragmentary, and moreover, the simple line drawing published should not be considered an adequate illustration. In addition, the description offered by Brown (1946) is so vague that it could be applied to leaves of many unrelated genera. Our collections from the topotypic locality do include leaves assignable to *Z. "oregoniana,"* but the fragmentary nature of Brown's holotype combined with the inadequacy of both illustration and description lead us to reject the epithet *hesperia.* Further, if one of Chaney's (1927) specimens, which were placed in *Z. hesperia* by Brown (1946), was selected as the type, this species would become a junior synonym of *"Z." drymeja*; none of the specimens illustrated by Chaney (1927) represents valid *Zelkova.* The next available name for *Z. "oregoniana"* would appear to be Axelrod's (1956) *nevadensis,* based on *Z. nevadensis.* Fully a third of the holotype is lacking, and the paratypes are even more fragmentary. The holotype, moreover, is strongly asymmetrical at the base, which is atypical for *Z. "oregoniana"* and could thus readily be a source for future error. Indeed, it could be argued that a name-bearing specimen that further work reveals is probably highly atypical for that taxon is a monstrosity and can thus be rejected under Article 71 of the International Code of Botanical Nomenclature. In any case, we consider that the fragmentary nature of the type combined with the fact that it is atypical for the definition of the species to which *Z. "oregoniana"* has been previously applied make this specimen an unsatisfactory type. We have, therefore, proposed a new species—*Z. browni*—which is based on several complete (or nearly so) and

well-preserved specimens from the Collawash locality. We suggest that, as workers pay greater attention to more detailed aspects of foliar morphology, more epithets such as *fernquisti, hesperia,* and *nevadensis* will (and should) be relegated to the status of nomina dubia.

For the occurrences of each species, we have cited, where possible, museum catalog numbers pertaining to individual specimens. Specimens that have been previously cited by other authors and that are here considered to be of doubtful systematic status are not cited in this report. The following abbreviations have been used: USNM = U.S. National Museum, UCMP = University of California Museum of Paleontology (Berkeley), UMMP = University of Michigan Museum of Paleontology, NYBG = New York Botanical Garden.

Ulmus affinis Lesquereux

Plate 3B, D, E, G

Ulmus affinis Lesquereux, 1878, Harvard Coll. Mus. Comp. Zoology Mem., v. 6, p. 16, pl. 4, fig. 4 (part).

Rhamnus troutdalensis Chaney, 1944b, Carnegie Inst. Washington Pub. 553, p. 348, pl. 64, figs. 2, 3.

Ulmus californica Lesquereux, 1878 [part, nontypic]. Harvard Coll. Mus. Comp. Zoology Mem., v. 6, p. 15, pl. 4, fig. 2 only.
Condit, 1944a, Carnegie Inst. Washington Pub. 553, p. 46, pl. 8, fig. 4.
Condit, 1944b, Carnegie Inst. Washington Pub. 553, p. 77, pl. 18, fig. 6.
Axelrod, 1944a, Carnegie Inst. Washington Pub. 553, p. 99, pl. 22, figs. 4, 5.
Chaney, 1944a, Carnegie Inst. Washington Pub. 553, p. 318.
Chaney, 1944b, Carnegie Inst. Washington Pub. 553, p. 345, pl. 63, fig. 4.

Ulmus cf. *tanneri* auct. non Chaney, Axelrod, 1944b, Carnegie Inst. Washington Pub. 553, p. 200, pl. 38, fig. 8.

Zelkova oregoniana auct. non (Knowlton) Brown. [Chaney], 1944b, Carnegie Inst. Washington Pub. 553, p. 346.

Ulmus moorei Chaney and Elias, Axelrod, 1964, California Univ. Pubs. Geol. Sci., v. 51, p. 119, pl. 12, figs. 14, 15.

Supplementary description.—Leaves lanceolate-oblong in general outline, gradually narrowed and slightly acuminate at apex, asymmetrically rotund to cordate at base, 4.5–8 cm long and 2–3.8 cm wide; midvein thick, nearly straight; lateral veins distinct, 13–18 subopposite pairs, leaving midrib at angles of 40°–50° at the middle and upper part of blade and at somewhat wider angles near the base, nearly parallel to each other, ending in larger teeth; intercostal tertiary veins forming polygonal meshes that include thrice-branching veinlets; a prominent tertiary vein near the margin ending in the bottom of each principal sinus, margin doubly serrate with large and acute teeth, which are accompanied mostly by a small subsidiary tooth or rarely by two subsidiary teeth on the lower margin; texture thin; petiole rather slender, more than 1.5 cm long.

Discussion.—Despite the previous application of the epithet *californica* to this species of *Ulmus,* we have chosen the epithet *affinis* over *californica* for the following reasons:

(1) The three type specimens illustrated by Lesquereux (1878) came from different localities; the specimens illustrated as plate 4, figure 1 and plate 6, figure 7a came from the early Eocene Chalk Bluffs locality and the specimen illustrated as plate 4, figure 2 came from Table Mountain. The Chalk Bluffs specimens clearly represent *Chaetoptelea pseudofulva* (Lesq.) MacG., whereas only the Table Mountain specimen represents valid *Ulmus.* Hence, discordant elements were included in *Ulmus californica* by Lesquereux (1878), and thus the name must be rejected "unless it is possible to select one of these elements as a a satisfactory type." (Article 70 of the International Code of Botanical Nomenclature). In this instance, it is possible to select a satisfactory type, but this selection has not previously been made.

(2) Lesquereux (1878, p. 15) describes *Ulmus californica* as having "borders irregularly denticulate" and secondary veins "more open towards the base." In these two features, the description clearly applies to the Chalk Bluffs *Chaetoptelea* rather than to the one specimen of *Ulmus* from Table Mountain. Thus, designation of the Chalk Bluffs specimen illustrated as plate 4, figure 1 (Lesquereux, 1878) as lectotype is more consistent with Lesquereux' intention.

(3) All syntypes of *Ulmus affinis* are from the same locality (Table Mountain), and all represent the same species of *Ulmus.*

Insofar as we could determine, the type specimens of the above-cited taxa are synonymous with *Ulmus affinis.* Leaves described as *U. californica* from the upper Tertiary of California and Oregon (Condit, 1944b; Chaney, 1944b; Axelrod, 1944a, b, c) are particularly valid in specific reference, although some of these leaves are more strongly cordate at the base and larger than the types of *Ulmus affinis.*

Ulmus affinis is generally similar to *U. speciosa* Newb. and *U. owyheensis* Smith, particular to some small- and medium-sized leaves. *U. affinis* is distinguishable in marginal characters from *U. speciosa,* as well as in the abaxial tertiary veins of the basal part of the lamina. Among the extant elms, *U. americana* L. is most similar to *U. californica.*

Hypotypes: USNM 208512.

Occurrence.—Table Mountain (USNM 208512; UCMP 1917, 2735, 2736, 5735, 5736, 5737), Remington Hill (UCMP 2408, 2409), Sonoma (UCMP 2804), and Black Hawk Ranch (UCMP 1743-1749), Calif.; Troutdale (UCMP 2601-2604, 2616, 2617), The Dalles (UCMP 2791-2793), and Deschutes, Oreg.; Trapper Creek (UCMP 8420-8425), Idaho.

Ulmus chaneyi Tanai and Wolfe, n. sp.

Plate 4B

Description.—Leaves ovate in general outline, 7 cm wide, to more than 11 cm long; base strongly asymmetrical, obliquely cordate; apex known; midvein thick, nearly straight; secondary veins more than 14 pairs, subopposite to subalternate, departing midrib at angles of 50°-60° one side and 40°-50° another side, nearly straight and parallel each other, ending in primary teeth; intercostal tertiary veins somewhat irregular but convexly percurrent; several tertiary veins branching from the secondaries near the margin, ending in subsidiary teeth; fourth- and fifth-order veins forming polygonal networks that enclose fine veinlets that are twice or more branching; margin compoundly serrate, with triangular primary teeth on the basal side of which are more than four subsidiary teeth, and on the apical side typically one or two; petiole strong, 1.5 cm long.

Discussion.—Three incomplete leaves from Twickenham, Oreg., have a characteristic marginal serration that is distinct from other Tertiary elm leaves previously described from North America. These fossils are closely similar to unlobed leaves of *Ulmus laciniata* Mayer living in northeastern Asia.

Holotype: UCMP 5738

Occurrence.—Twickenham, Oreg.

Ulmus knowltoni Tanai and Wolfe, n. sp.

Plate 1C, F, G; Plate 2A, C, H, I, J

Myrica oregoniana Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 33, pl. 3, fig. 4.

Ulmus speciosa auct. non Newberry. LaMotte, 1936 [part], Carnegie Inst. Washington Pub. 455, p. 124.

Axelrod, 1964,[part], California Univ. Pubs. Geol. Sci., v. 51, p. 120, pl. 12, fig. 13.

Graham, 1965, Kent State Univ. Bull. Research ser. 9, p. 97, pl. 18, fig. 4.

Ulmus paucidentata H. V. Smith, 1941 [part, nontypic], Am. Mid. Naturalist, v. 25, p. 512, pl. 13, fig. 4.

Becker, 1969 [part], Palaeontographica B, v. 127, p. 83, pl. 21, fig. 7.

Zelkova oregoniana auct. non (Knowlton) Brown. Chaney and Axelrod, 1959 [part], Carnegie Inst. Washington Pub. 617, p. 31, pl. 31, figs. 5, 8.

Ulmus newberryi auct. non Knowlton. Graham, 1965, Kent State Univ. Bull. Research ser. 9, p. 96, pl. 18, fig. 3.

Description.—Leaves highly variable in shape and size, oblong to lanceolate-oblong in general outline, 3-15.5 cm (estimated) long and 1.4-6 cm wide; base strongly asymmetrical, obliquely cordate, nearly straight on one side and bulged on the other side into a typically half-circular shape; apex gradually narrowed, attenuate-acuminate; midrib thick, nearly straight; secondary veins opposite to subopposite, 12-20 pairs, diverging at different angles on both sides of midrib, nearly straight or slightly curving up, rarely forking in the lower part of blade, ending in marginal teeth; several prominent branches from a basal secondary vein on the bulged part diverging outward, ending in marginal teeth; tertiary veins in the intercostal area wavy but distinct, irregularly percurrent; fourth-order veins thin, forming quadrangular or pentagonal meshes that include twice- or thrice- branching veinlets; one prominent tertiary vein departing from the secondaries near the margin, forking near the bottom of the principal sinus, then extending along the margin; margin mostly singly serrate with large apiculate teeth that are rarely associated with a minute subsidiary tooth on the lower part of blade; texture thin; petiole thick, more than 1 cm long.

Discussion.—The above description is primarily based on a number of well-preserved leaves from the Miocene Collawash locality, Oregon. Leaves of this species are usually characterized by the principal apiculate teeth, strongly asymmetrical base, and prominent tertiary veins forking near each principal sinus. The leaves having a simply serrate margin could be misidentified as *Zelkova* in some instances but are certainly distinguishable in the marginal serration and venation character of the basal part of the lamina.

The specimens of *Myrica oregoniana* Knowlt. from the Mascall flora (USNM 8532 a, b) were transferred to *Zelkova* by Brown (1937) and are the type specimens of *Z. oregoniana*. These specimens are closely similar to *Zelkova* leaves having an asymmetrical base, which type is sometimes found among the abnormal leaves of the extant *Z. serrata* Makino (especially on the young shoots). However, these Mascall specimens are quite different in marginal serration and tertiary venation of the enlarged part of the lamina and are included in *U. knowltoni* as here established. Although it might seem proper to use the epithet "*oregoniana*" for this new species, this epithet is already occupied by another elm species from the Ashland Eocene (Knowlton, 1900), which is of somewhat doubtful generic status (Wolfe, 1968).

Holotype: USNM 208502.

Paratypes: USNM 208503-208507.

Occurrence.—Mascall (UCMP 3095; USNM 8532, a, b), Rockville (UMMP 44947, 44950), Collawash, Oreg.; Thorn Creek and Trapper Creek (UCMP 8426), Idaho '49 Camp, Nevada (UCMP 797, 3099); Seldovia Point, Alaska; Beaverhead, Mont. (NYBG 601a).

Ulmus moorei Chaney and Elias

Ulmus moorei Chaney and Elias, 1936, Carnegie Inst. Washington Pub. 476, p. 39, pl. 6, figs. 1-5.
Dorf, 1936, Carnegie Inst. Washington Pub. 476, p. 116, pl. 2, fig. 4.
Axelrod, 1956, California Univ. Pubs. Geol. Sci., v. 33, p. 292, pl. 8, figs. 5, 6, 12.
Smiley, 1963, California Univ. Pubs. Geol. Sci., v. 35, no. 3, p. 218, pl. 8, fig. 6b.
?Becker, 1972, Palaeontographica B, v. 141, p. 35, pl. 12, figs. 12, 13.
Ulmus venustula Brown, 1949, Washington Acad. Sci. Jour., v. 39, p. 226, figs. 3-5, 9.
Zelkova nevadensis auct. non Axelrod. Smiley, 1963, California Univ. Pubs. Geol. Sci., v. 35, p. 219, pl. 8, figs. 2, 6a.

Discussion.—This species is represented mostly by small leaves that are ovate to orbicular in shape; the base is slightly asymmetrical and broadly cuneate to slightly cordate. The margin is mostly simply serrate and has large, blunt teeth that may have a minute subsidiary tooth. *U. moorei* closely resembles leaves of the extant *U. crassifolia* Nutt. of eastern United States.

As cited above, *U. moorei* is known in the upper Miocene and Pliocene of California, Washington, and the High Plains, although the specimens are not common everywhere. A single leaf and its counterpart figured as *U. moorei* from the Metzel Ranch locality, southwestern Montana (Becker, 1972), are similar in general outline to some of the original specimens, but the teeth of Becker's specimen are more obtuse. A small leaf figured as *Zelkova nevadensis* Axelr. from the Ellensberg flora, Washington (Smiley, 1963), has serrate teeth on the basal margin, and several tertiary veins from the basal secondaries end in these teeth; this specimen is included in *U. moorei.*

Occurrence.—Beaver County, Okla. (UCMP 5333, 5335-5339, 5350-5353); Logan County, Kans.; Aldrich Station, Nev.; Ellensberg, Washington; (?)Beaverhead basin, Mont.; Weiser, Idaho (UCMP 1202, 1203); Cache Valley, Utah.

Ulmus owyheensis H. V. Smith

Plate 2B, D, E, F; plate 3A

Ulmus owyheensis H. V. Smith, 1939, Michigan Acad. Sci. Papers, v. 24, p. 113, pl. 6, fig. 4.
Graham, 1965, Kent State Univ. Bull. Research ser. 9, p. 97, pl. 18, fig. 1.
Ulmus speciosa auct. non Newberry. Chaney and Axelrod, 1959, Carnegie Inst. Washington Pub. 617, p. 174, pl. 32, figs. 1-3 (part).
Ulmus paucidentata auct. non Smith. Chaney and Axelrod, 1959, Carnegie Inst. Washington Pub. 617, p. 173 (part).
Smiley, 1963, California Univ. Pubs. Geol. Sci., v. 35, p. 219, pl. 8, figs. 4, 5.
Ulmus plurinervis auct. non Unger. Heer, 1869, Flora Fossilis Arctica, v. 2, pt. 2, p. 34, pl. 5, fig. 1.

Discussion.—This species was established for a single, nearly complete leaf from Sucker Creek of Oregon (Smith, 1939a). The species is characterized by an ovate shape, slightly asymmetrically rounded base, simply serrate teeth, and the lowest secondary pair having 3 or 4 abaxial tertiary veins that end in small teeth on the basal margin. Several specimens collected from the Eagle Creek and Bridge Creek (Twickenham) localities add the following characters to this species: principal teeth are rather bluntly trigonal and sometimes accompanied by one or two small subsidiary teeth, especially below the middle of blade; foliar shape is somewhat variable from ovate to oval; base is rotund to slightly cordate, nearly symmetrical to slightly asymmetrical; a prominent tertiary vein near the margin ends in the bottom of each principal sinus; intercostal tertiary veins irregularly crossed with the secondaries and never percurrent. *Ulmus owyheensis* is not similar to any living species of North American elms but seems rather to be related to the extant *U. pumila* L. of east Asia.

Several specimens figured as *Ulmus speciosa* Newb. from the Mascall and Stinking Water floras of Oregon (Chaney and Axelrod, 1959) are included in *U. owyheensis* by the above-noted characters. Although not figured by Chaney and Axelrod, a specimen (UCMP 3091) identified as *U. paucidentata* from the Mascall is also referred to *U. owyheensis.* A single incomplete leaf of *U.* cf. *tanneri* Chaney from the Pliocene Sonoma flora of California (Axelrod, 1950) was later referred to *U. owyheensis* in marginal serration and basal character.

Hypotypes: USNM 208508-208511; UCMP 5733.

Occurrence.—Sucker Creek (UMMP 20017), Mascall (UCMP 3080, 3082, 3083, 3091), Stinking Water (UCMP 3084), Collawash, Fish Creek, Eagle Creek, Twickenham, Oreg.; Seldovia Point, Alaska; Ellensburg, Wash. (UCMP 5346, 5349).

Ulmus paucidentata H. V. Smith

Plate 2G

Ulmus paucidentata H. V. Smith, 1939, Torrey Bot. Club Bull., v. 66, p. 478, pl. 13, figs. 2-4.
Smith, 1941 [part], Am. Midland Naturalist, v. 25, p. 512, pl. 10, fig. 2; pl. 13, fig. 9.
Chaney and Axelrod, 1959 [part], Carnegie Inst. Washington Pub. 617, p. 173, pl. 31, figs. 9-12.

Becker, 1969, Palaeontographica B, v. 127, p. 83, pl. 21, figs. 4-6 (part).

Ulmus speciosa auct. non Newberry. Newberry, 1898 [part, nontypic], U.S. Geol. Survey Mon. 35, p. 80, pl. 45, figs. 5, 8.
Dorf, 1936 [part], Carnegie Inst. Washington Pub. 476, p. 116.
Becker, 1961, Geol. Soc. America Mem. 82, p. 64, fig. 4.
Axelrod, 1964 [part], California Univ. Pubs. Geol. Sci., v. 51, p. 120.

Discussion.—Leaves of this species are typically small and elliptic to ovate-elliptical; on the margin the primary teeth are large and obtusely trigonal, in most instances accompanied by one or two small subsidiary teeth. The base is typically asymmetrically cuneate or obtuse; narrowly cuneate or obliquely straight on one side and rounded on the other. The intercostal tertiary veins are irregularly but prominently percurrent, and a tertiary vein from the secondaries near the margin ends in the bottom of the principal sinus.

Ulmus paucidentata closely resembles *U. owyheensis* and *U. knowltoni* in marginal characters, especially in having large blunt teeth that may resemble a simply serrate margin. However, *U. paucidentata* is distinguishable from these two species in the basal shape and character of the tertiary venation character of the basal part, without any intergradation of characters. Considering the foliar shape and marginal serration, *U. paucidentata* may be related to the extant *U. parvifolia* Jacq. living in Japan and China, but there are some differences in the percurrent tertiary venation.

Hypotype: UCMP 5734.

Occurrence.—Mascall (UCMP 3086, 3088, 3089, 3090), Bridge Creek (USNM 7064, 201872), Twickenham, Oreg. (UCMP 5734); Thorn Creek (UMMP 20016), Trapper Creek (UCMP 8427), Weiser, Idaho (UCMP 1204); Ruby basin (UMMP 38249), Beaverhead basin (NYBG 602a, 603, 604), Montana.

Ulmus pseudo-americana Lesquereux

Plate 1A, B, D, E, H

Ulmus pseudo-americana Lesquereux, 1883, U.S. Geol. Survey Terr. Rept., v. 8, p. 249, pl. 54, fig. 10.

Ulmus speciosa Newberry, 1898 [part, typic], U.S. Geol. Survey Mon. 35, p. 80, pl. 45, fig. 2.
Knowlton, 1902, U.S. Geol. Survey Bull. 204, p. 53 (part).
Chaney and Axelrod, 1959 [part], Carnegie Inst. Washington Pub. 617, p. 174, pl. 32, fig. 5.
Axelrod, 1964, California Univ. Pubs. Geol. Sci., v. 51, p. 120 (part).

Ulmus newberryi Knowlton, 1902 [part], U.S. Geol. Survey Bull. 204, p. 54, pl. 9, fig. 4.
Wolfe, 1964, U.S. Geol. Survey Prof. Paper 454-N, p. N22, pl. 3, figs. 4, 6.

Discussion.—The larger leaves of elm from the middle Tertiary have usually been referred to *Ulmus newberryi* Knowlt., *U. pseudo-americana* Lesq., or *U. speciosa* Newb.; most of these specimens have been compared to extant *U. americana* L. by many authors. These three species have, however, been frequently confused, although the criteria for specific distinction have been discussed by various authors. For example, LaMotte (1952) placed *U. newberryi* in synonymy under *U. speciosa,* whereas Knowlton (1902) and Chaney and Axelrod (1959) separated these two species and included *U. pseudo-americana* in *U. speciosa*. One of the reasons for such confusion is that foliar shape and size are not consistently valid criteria for the discrimination of these elm species, although *U. newberryi* is generally more slender in shape and more oblique (strongly asymmetric) at the base than *U. speciosa*. Another reason for confusion is that most original specimens from the Oligocene or Miocene of Oregon were not always correctly illustrated by Newberry (1898) and Knowlton (1902).

From examination of large suites of these larger elm leaves, including name-bearing specimens, we find that these specimens include divergent morphologic characters in marginal serration and venation. These leaves typically have a doubly serrate margin, as noted by various authors, but are separable into three types. The first type has somewhat longer primary teeth, between which there are typically two large subsidiary teeth, accompanied in many instances by a single minute tooth (Lesquereux, 1883, pl. 54, fig. 10; Knowlton, 1902, pl. 9, fig. 4). The second type typically has two small teeth (rarely three) of nearly equal size between the primary apiculate teeth that the secondary veins enter (Newberry, 1898, pl. 45, fig. 2; Knowlton, 1926, pl. 18, fig. 4). The third type has blunt dentate primary teeth, between which there is typically one blunt tooth, accompanied rarely by one minute tooth (Newberry, 1898, pl. 45, figs. 5, 8). In leaves of the second and third types, one of prominent tertiary veins that departs from the secondaries near the margin ends in or near the principal sinus; in the first type the tertiary vein never reaches the sinus but forks and extends along the margin of sinus. Generally leaves of the first type are linear-oblong, leaves of the second type are lanceolate. Although Chaney and Axelrod (1959) relied on foliar shape and basal form, these characters may intergrade between these three types.

Judging from the original description and the above-noted characters, the first morphologic type contains the nomenclatorial type of *U. pseudo-americana* and some of the nomenclatorial types of *U. newberryi;* the second morphologic type contains the type specimens of *U. speciosa* and *U. newberryi.*

The third morphologic type is included in the *U. paucidentata* H. V. Smith as discussed above. Thus, owing to priority, we reject *U. newberryi* and we retain *U. pseudo-americana* for leaves having the characters of the first morphologic type.

Hypotypes: UCMP 5731, 5732.

Occurrence.—Bridge Creek (UCMP 1758; USNM 7065, 9217, 9367, 8493a), Twickenham (UCMP 5731, 5732), Mascall (UCMP 3735), Oreg.; Fingerrock (USNM 41942; UCMP 8642, 8643), Nev.

Ulmus speciosa Newberry

Plate 3C, F

Ulmus speciosa Newberry, 1898 [part, typic], U.S. Geol. Survey Mon. 35, p. 80, pl. 45, figs. 3, 4.
Knowlton, 1902, [part], U.S. Geol Survey Bull. 204, p. 53.
Chaney, 1920, Walker Mus. Contr., v. 2, p. 171.
Knowlton, 1926, U.S. Geol. Survey Prof. Paper 140, p. 39, pl. 18, fig. 4.
LaMotte, 1936 [part], Carnegie Inst. Washington Pub. 455, p. 124.
MacGinitie, 1962, California Univ. Pubs. Geol. Sci., v. 35, p. 110, pl. 4, figs. 1, 4, 5; pl. 10, fig. 4.
Becker, 1969, Palaeontographica B, v. 127, p. 84, pl. 21, figs. 1, 2.
Ulmus tanneri Chaney, 1920, Walker Mus. Contr., v. 2, p. 172, pl. 15, figs. 1, 2.
Ulmus newberryi auct. non Knowlton. Smiley 1963, California Univ. Pubs. Geol. Sci., v. 35, p. 218, pl. 8, fig. 3.

Discussion.—This species has been discussed in detail in connection with *Ulmus pseudo-americana* Lesq. *U. speciosa* is distinguishable in marginal serration and venation characters from other elm species of the middle Tertiary of North America. The name has been misused by various authors for oval leaves that have a less asymmetrical base. We here designate as the type specimen of *U. speciosa* USNM 7067, which is one of the original specimens figured from the Bridge Creek locality by Newberry (1898). *Ulmus speciosa* as here circumscribed is generally ovate to oblong in outline and is less asymmetrical and rounded in the base (as many authors have pointed out). Because some leaves of *U. pseudo-americana* have a less asymmetrical base, these two species are not consistently distinguishable only by foliar shape and basal form.

On the basis of ovate-oblong and small leaves from the Eagle Creek locality, *Ulmus tanneri* Chan. was separated from *U. speciosa* (Chaney, 1920). Unfortunately, these type specimens of *U. tanneri* were lost after being moved to the University of California at Berkeley from Chicago, and we cannot definitely determine the status of this species. However, judging from the original illustration and description, *U. tanneri* seems to represent only the ovate-oblong leaves of *U. speciosa*.

Lectotype: USNM 7067.

Hypotype: USNM 208513

Occurrence.—Bridge Creek (USNM 7066, 7067), Eagle Creek, Oreg.; Latah, Ellensberg (UCMP 5340), Wash.; Kilgore (UCMP P-746, P-808), Nebr.; Upper Cedarville (UCMP 836), Calif.; Beaverhead (NYBG 605, 844), Mont.; Seldovia Point, Wrangell Mts., Healy Creek (USNM 208513), Alaska.

Zelkova browni Tanai and Wolfe, n. sp.

Plate 4A, C-G

Zelkova oregoniana auct. non (Knowlton) Brown. Brown, 1937 [part], U.S. Geol. Survey Prof. Paper 186, p. 173, pl. 51, figs. 11-15.
Lakhanpal, 1958, California Univ. Pubs. Geol. Sci., v. 35, no. 1, p. 29.
Chaney and Axelrod, 1959 [part], Carnegie Inst. Washington Pub. 617, p. 174, pl. 31, figs. 6, 7.
Becker, 1961, Geol. Soc. America Mem. 82, p. 64, pl. 18, figs. 13-18.
Smiley, 1963, California Univ. Pubs. Geol. Sci., v. 35, p. 219, pl. 8, fig. 1.
Wolfe, 1964, U.S. Geol. Survey Prof. Paper 454-N, p. N23, pl. 3, figs. 2, 3, 5.
Axelrod, 1964, California Univ. Pubs. Geol. Sci., V. 51, p. 120, pl. 12, figs. 8, 10-12.
Graham, 1965, Kent State Univ. Bull. Research ser. 9, p. 97, pl. 18, fig. 2.
Becker, 1969, Palaeontographica B, v. 127, p. 84, pl. 21, figs. 14-21.
Becker, 1972, Palaeontographica B, v. 141, p. 36, pl. 6, figs. 1-9.
Zelkova ungeri auct. non Kovats. Becker, 1969, Palaeontographica B, v. 127, p. 85, pl. 21, figs. 11a, b.
Fagopsis longifolia auct. non (Lesquereux) Hollick. Berry, 1929, U.S. Geol. Survey Prof. Paper 154, p. 245, pl. 50, fig. 7.
Quercus mccanni auct. non Berry. Axelrod, 1964, California Univ. Pubs. Geol. Sci., v. 51, p. 118, pl. 11, figs. 10, 11.
?*Ulmus fernquisti* Knowlton, 1926, U.S. Geol. Survey Prof. Paper 140, p. 39, pl. 19, fig. 2.
?*Zelkova nevadensis* Axelrod, 1956, California Univ. Pubs. Geol. Sci. v. 33, p. 292, pl. 8, figs. 3, 8.
Smiley, 1963, California Univ. Pubs. Geol. Sci., v. 35, no. 3, p. 219, pl. 8, figs. 2, 6a.

Description.—Leaves variable in shape and size, mostly lanceolate-oblong to oblong, rarely linear-oblong or ovate, 2.4-10.5 cm long and 1.7-4.9 cm wide; base nearly symmetrical to asymmetrical, obtuse to rotund, frequently slightly cordate; apex gradually narrowed, attenuate-acuminate, some slightly tapered; midvein thick, nearly straight; secondary veins 9-17 pairs, opposite to subopposite, angles of divergence variable, nearly straight or gently curving apically, very rarely forking on the way, ending in marginal teeth; intercostal tertiary veins wavy or forking but crossing to the secondaries; the fourth- and fifth-order veins forming irregular quadrangular or pentagonal areoles, which include veinlets that branch twice or more; margin

mostly singly dentate with large apiculate teeth, and sinus usually widely opened; large teeth rarely accompanied by a minute subsidiary tooth, or in some instance an additional tooth between two principal teeth on the lower half of the margin; texture firm; petiole stout, more than 3 mm long.

Discussion.—Axelrod (1956) distinguished *Z. nevadensis* from *Z. oregoniana* because of size differences, but his small leaves of *Zelkova* fall well within the variation of size and shape displayed by leaves of *Z. browni* from the Collawash locality. Chaney and Axelrod (1959) transferred *Castanea atavia* Ung. (Lesquereux, 1883, pl. 52, fig. 2) and *Quercus horniana* Lesq. (Knowlton, 1902, pl. 8, fig. 1) to the genus *Zelkova,* but these two fossils do not have the marginal serrations of *Z. browni.*

Zelkova browni, though highly variable in foliar shape and size, typically has large, blunt teeth and is easily distinguishable from *Z. ungeri* Kovats, which has been invalidly reported from the Tertiary of Western United States, excluding Alaska. Though many authors have compared *Z. oregoniana* with the extant *Z. serrata* Mak. of Japan or *Z. sinica* Schn. of China, *Z. browni* is rather related to the extant *Z. carpinifolia* Spach. of the Caucasus region in the shape of the teeth. Many specimens of *Z. browni* have a minute subsidiary tooth on the basal side of the primary teeth, a feature uncommon in extant *Zelkova.*

Holotype: USNM 208514

*Paratypes:*USNM 208515-208518.

DOUBTFUL SPECIES OF *ULMUS*

Ulmus moragensis Axelrod

Ulmus moragensis Axelrod, 1944, Carnegie Inst. Washington Pub. 553, p. 283, pl. 48, figs. 5, 7-9.

Discussion.—This species, established on material from the middle Pliocene of California (Axelrod, 1944c), is not based on well-preserved specimens; they are particularly poorly preserved in marginal character. Chaney (1944b, p. 346) emphasized the smaller average leaf size for separating this species from other Tertiary elms, as did Axelrod (1944c) in his original description. As far as we can determine from the type specimens of *U. moragensis,* this species seems to be characterized by a strongly asymmetrical base and bluntly trigonal teeth that have in some instances a small subsidiary tooth; this species thus is difficult to distinguish from some leaves of *U. affinis.* Furthermore, owing to the poor preservation of the type specimens, *U. moragensis* may be better considered a nomen dubium.

Occurrence.—Alturas, Calif.

REJECTED CITATIONS OF *ULMUS*

Ulmus borealis auct. non Heer. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 106, pl. 57, figs. 1, 2 = *Alnus adumbrata* (Holl.) Wolfe (see Wolfe, 1966, p. B21).

Ulmus braunii auct. non Heer. Hollick, 1936 [part], U.S. Geol. Survey Prof. Paper 182, p. 105, pl. 58, figs. 6, 12 = *Alnus* sp. indet. This material probably represents *A. evidens* (Holl.) Wolfe, but it is too fragmentary for specific determination. The other material assigned to *U. braunii* by Hollick (1936) is of pre-Oligocene age and is thus not further considered.

Ulmus brownellii auct. non Lesquereux. Dorf. 1930, Carnegie Inst. Washington Pub. 412, p. 92, pl. 10, figs. 1-3, 10 = genus and species indetermined. Although Axelrod (1944c, p. 283) assigned these leaves to *U. moragensis,* we consider that the preservation is too poor to permit determination.

Ulmus californica Lesquereux, 1878 [part, typic], Harvard Coll. Mus. Comp. Zoology Mem., v. 6, p. 15, pl. 4, fig. 1, pl. 6, fig. 7a = *Chaetoptelea pseudofulva* (Lesquereux) MacGinitie, 1941, Carnegie Inst. Washington Pub. 534, p. 108. Above, we designated a lectotype for *Ulmus californica* that is clearly *Chaetoptelea.* Thus, it would be possible for someone at a later date to consider *californica* as a senior synonym of *pseudofulva* if one epithet were not chosen in preference to the other at this time.

Ulmus carpinoides auct. non Goeppert. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 105, pl. 51, figs. 1, 2 = *Alnus evidens* (Holl.) Wolfe, 1966, U.S. Geol. Survey Prof. Paper 398-B, p. B18.

Ulmus diptera auct. non Steenstrup. Hollick, 1936, U.S. Geol. Survey Prof. Paper 182, p. 107, pl. 48, fig. 4a = *Alnus evidens* (Holl.). Wolfe, 1966 U.S. Geol. Survey Prof. Paper 398-B, p. B18.

Ulmus eolaciniate MacGinitie, 1937, Carnegie Inst. Washington Pub. 465, p. 126, pl. 5, fig. 3 = *Rubus eolaciniata* (MacG.) Tanai and Wolfe, n. comb. The sharply acute teeth that are irregualrly spaced and the tertiary veins that are conspicuously not perpendicular to the secondary veins exclude this species from *Ulmus.* On the other hand, these features are typically found in the rosaceous *Rubus.* The asymmetry of MacGinitie's material is interpreted as indicative of a leaflet; this character would also fit with an assignment to *Rubus.*

Ulmus montanensis Becker, 1961, Geol. Soc. America Mem. 82, p. 63, pl. 18, fig. 5 = *U. tenuinervis* Lesquereux, 1883, U.S. Geol. Survey Terr. Rept., v. 8, p. 188. Comparison of Becker's specimen with

a suite of *U. tenuinervis* from Florissant indicates that some leaves of *U. tenuinervis* have the characters that Becker (1961) thought characterized his *U. montanensis* and distinguished it from *U. tenuinervis*.

Ulmus paucidentata auct. non H. V. Smith. Becker, 1961, Geol. Soc. America Mem. 82, p. 63, pl. 18, fig. 3 = genus and species indetermined. The specimen has glandular teeth and is hence clearly not *Ulmus*. Otherwise, the specimen is poorly preserved, and we doubt if a reliable assignment can be made.

Ulmus pseudofulva Lesquereux, 1878, Harvard Coll. Mus. Comp. Zoology Mem., v. 6, no. 2, p. 16, pl. 4, fig. 3 = *Chaetoptelea pseudofulva* (Lesquereux) MacGinitie, 1941, Carnegie Inst. Washington Pub. 534, p. 108. LaMotte (1952) transferred MacGinitie's (1941) combination back to *Ulmus*, and this transfer still remains in effect. Although some systematists consider the extant *Chaetoptelea* to be a member of *Ulmus*, other systematists maintain these genera as distinct. Because the foliage of *Chaetoptelea* can be distinguished from that of *Ulmus*, we prefer to recognize the combination proposed by MacGinitie (1941).

Ulmus sorbifolia, auct. non Goeppert. Hollick, 1936 [part], U.S. Geol. Survey Prof. Paper 182, p. 106, pl. 57, figs. 4, 5 = *Spiraea hopkinsi* Wolfe (see Wolfe, 1966, p. B24). Although *Spiraea hopkinsi* is being transferred to *Sorbaria* (Wolfe and Tanai, 1977), it would confuse nomenclature to introduce the new combination in the current report.

Ulmus speciosa auct. non Newberry. Axelrod, 1964 [part], California Univ. Pubs. Geol. Sci., v. 51, p. 120 [unfigured specimen registered as UCMP 8463] = *Betula ashleyi* Axelrod, 1964, California Univ. Pubs. Geol. Sci., v. 51, p. 116.

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[Italic page numbers indicate both major references and descriptions]

PLATES 1-4

Contact photographs of the plates in this report are available, at cost, from U.S. Geological Survey Library, Federal Center, Denver, Colorado 80225.

PLATE 1

FIGURES A. *Ulmus pseudo-americana* Lesquereux. Bridge Creek, Wheeler County, Oreg.: UCMP 1758 (original specimen by Lesquereux, 1883: pl. 54, fig. 10).

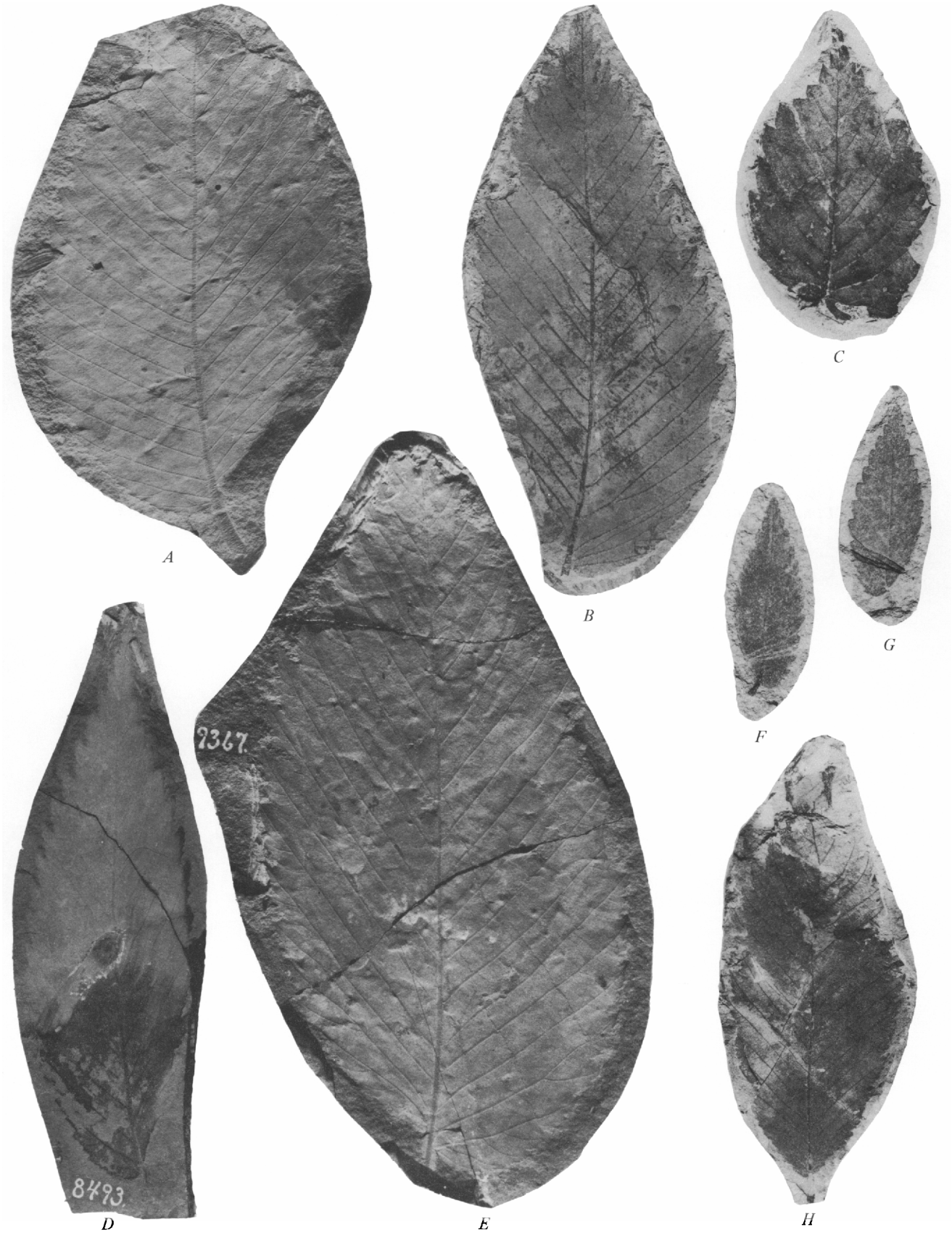
B, H. *Ulmus pseudo-americana* Lesquereux. Twickenham, Wheeler County, Oreg.: hypotypes UCMP 5731, 5732.

C. *Ulmus knowltoni* Tanai and Wolfe, n. sp. Collawash, Clackamas County, Oreg.: paratype USNM 208503.

D. *Ulmus pseudo-americana* Lesquereux. Bridge Creek, Wheeler County, Oreg.: USNM 8493a (Knowlton, 1902: pl. 9, fig. 2).

E. *Ulmus pseudo-americana* Lesquereux. Bridge Creek, Wheeler County, Oreg.: USNM 9367.

F, G. *Ulmus knowltoni* Tanai and Wolfe, n. sp. White Hill, Belshaw Ranch, Grant County, Oreg.: USNM 8532a, b (Knowlton, 1902: pl. 3, fig. 4). These specimens were originally described as *Myrica oregoniana*.



LEAVES OF *ULMUS PSEUDO-AMERICANA* AND *U. KNOWLTONI*

PLATE 2

FIGURES A. *Ulmus knowltoni* Tanai and Wolfe, n. sp. Collawash, Clackamas County, Oreg.: holotype USNM 208502.

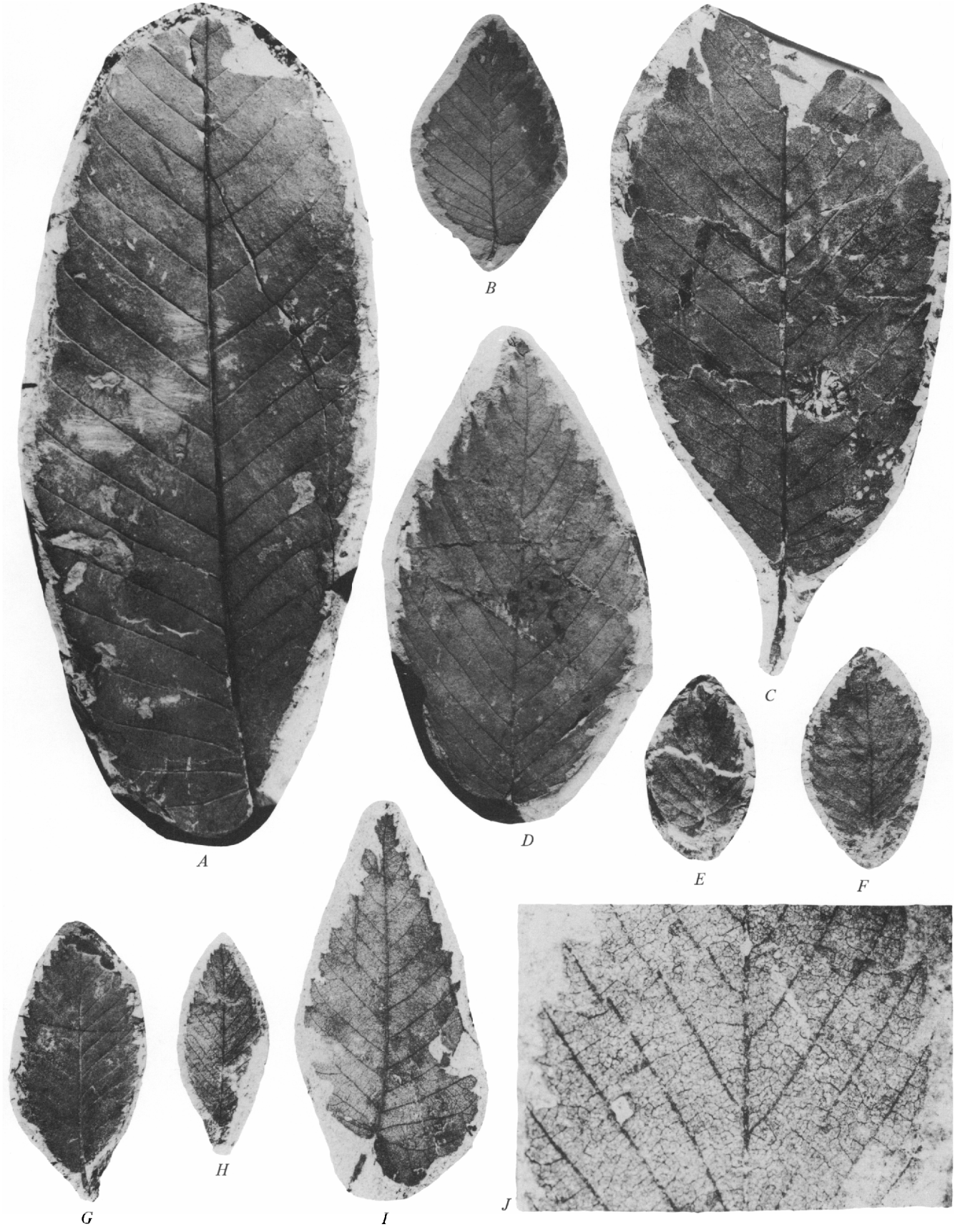
B. *Ulmus owyheensis* H. V. Smith. Twickenham, Wheeler County, Oreg.: hypotype UCMP 5733.

C, H, I. *Ulmus knowltoni* Tanai and Wolfe, n. sp. Collawash, Clackamas County, Oreg.: paratypes USNM 208504-208506.

D, E, F. *Ulmus owyheensis* H. V. Smith. Collawash, Clackamas County, Oreg.: hypotypes USNM 208508-208510.

G. *Ulmus paucidentata* H. V. Smith. Twickenham, Wheeler County, Oreg.: hypotype UCMP 5734.

J. *Ulmus knowltoni* Tanai and Wolfe, n. sp. Collawash, Clackamas County, Oreg.: paratype USNM 208507. Showing margin and fine venation (about X 5.8).



LEAVES OF *ULMUS KNOWLTONI*, *U. OWYHEENSIS*, AND *U. PAUCIDENTATA*

PLATE 3

FIGURES A. *Ulmus owyheensis* H. V. Smith. Collawash, Clackamas County, Oreg.: hypotype USNM 208511.

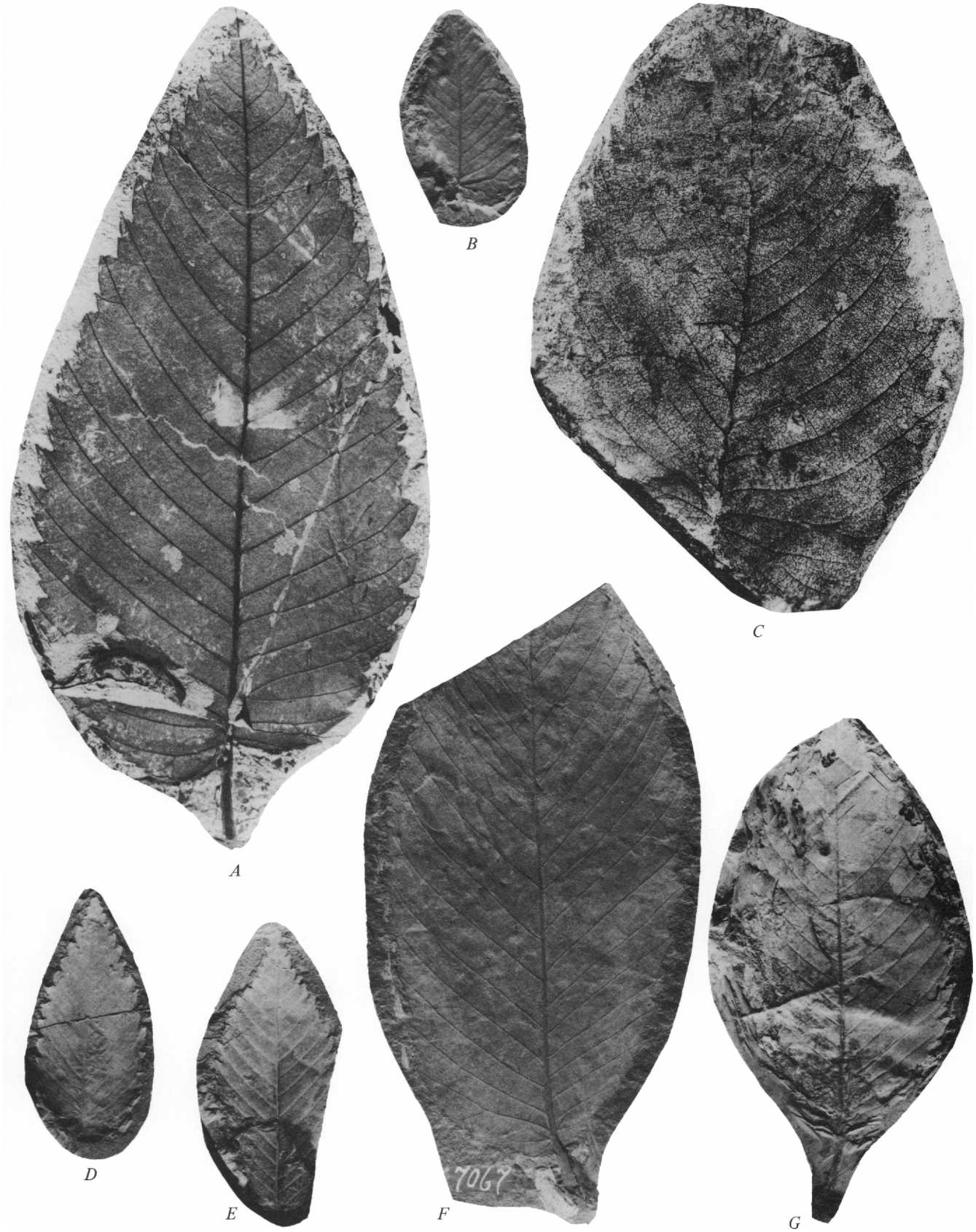
B. *Ulmus affinis* Lesquereux. Table Mountain, Tuolumne County, Calif. (USGS loc. 6902): hypotype USNM 208512.

C. *Ulmus speciosa* Newberry. Healy Creek, west of Suntrana, Alaska (USGS loc. 9925): hypotype USNM 208513.

D, E. *Ulmus affinis* Lesquereux. Table Mountain, Tuolumne County, Calif.: UCMP 5735, 5736. These are unfigured specimens assigned to *U. californica* by Lesquereux (1878).

F. *Ulmus speciosa* Newberry. Bridge Creek, Wheeler County, Oreg.: USNM 7067 (original specimen by Newberry, 1898: Pl. 45, fig. 2).

G. *Ulmus affinis* Lesquereux. Table Mountain, Tuolumne County, Calif.: UCMP 5737 (original specimen by Lesquereux, 1878: pl. 4, fig. 4).



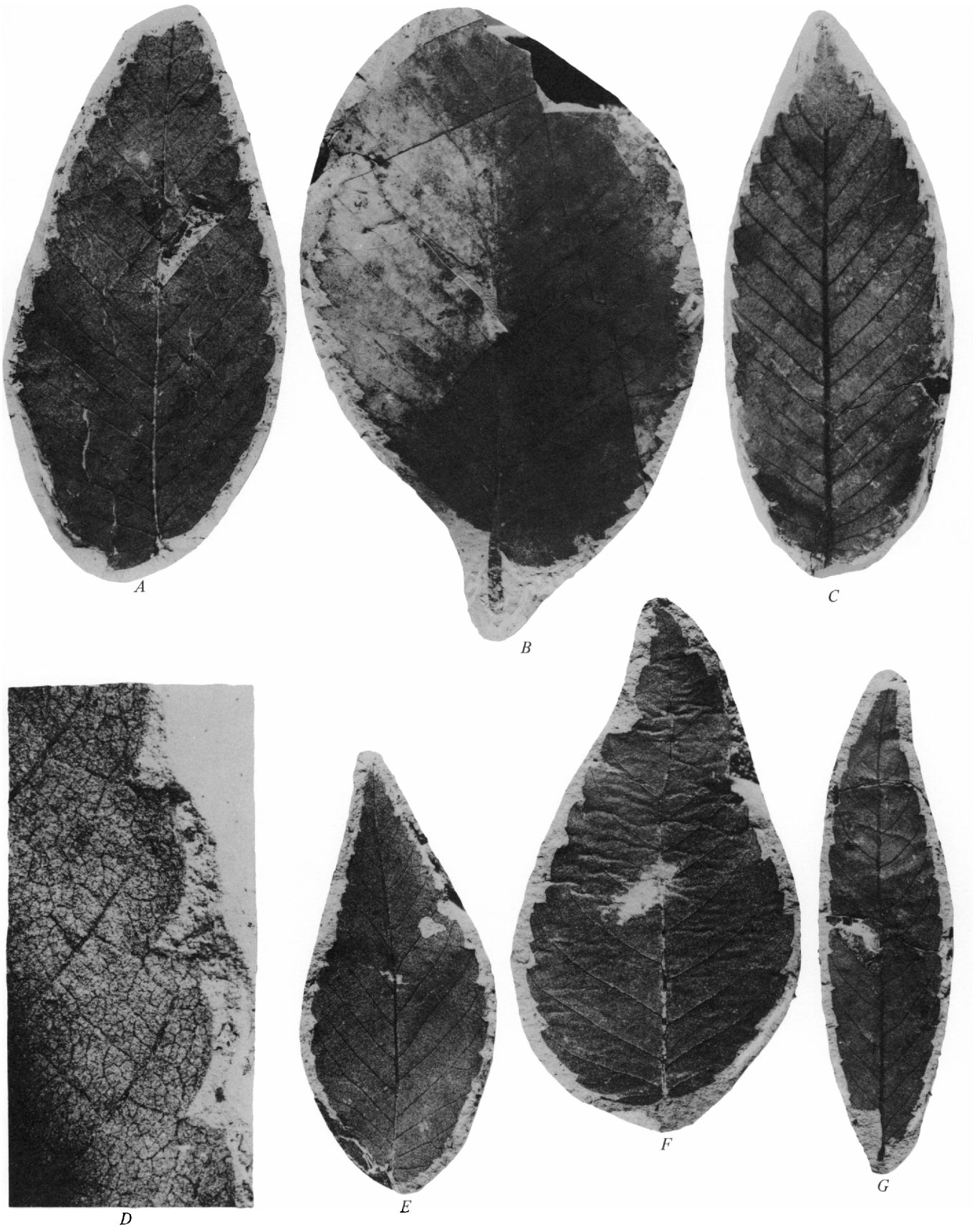
LEAVES OF *ULMUS OWYHEENSIS, U. AFFINIS,* AND *U. SPECIOSA*

PLATE 4

FIGURES A, D. *Zelkova browni* Tanai and Wolfe, n. sp. Collawash, Clackamas County, Oreg. *a,* holotype USNM 208514. X 1. d, Enlargement of holotype specimen showing margin and fine venation. Approximately X 4.

B. *Ulmus chaneyi* Tanai and Wolfe, n. sp. Twickenham, Wheeler County, Oreg. Holotype UCMP no. 5738. X 1.

C, E-G. *Zelkova browni* Tanai and Wolfe, n. sp. Collawash, Clackamas County, Oreg. Paratypes USNM 208515-208518. X 1.



LEAVES OF *ULMUS CHANEYI* AND *ZELKOVA BROWNI*

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