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A NEGLECTED CHARACTER IN WESTERN ASHES (FRAXINUS)

PHILIP A. MUNZ and J. D. LAUDERMILK*

On coming to the Rancho Santa Ana Botanic Garden in 1946, the senior author was impressed by the fact that his predecessor, Dr. Carl B. Wolf, had assembled so large a collection of growing plants of the California species of *Fraxinus*, particularly of *F. oregona* and *F. velutina* var. *coriacea*. Many of these trees were just beginning to produce fruits and it seemed desirable to make some study of them. In his Manual of Southern California Botany (p. 374, 1935) the senior author included *F. oregona*, although other recent treatments, such as that of Jepson (Fl. Calif. 3: 79-80, 1939) limited it to the area from Tulare County northward. Jepson said that the best distinction between this species and *F. velutina* "resides in the fruit. The wing of the fruit in *F. oregona* extends to the base of the body, much narrowed to be sure, often almost obsolete, but still observable. The fruit in *F. velutina* is winged only at the summit; the body is unwinged and rounded or cylindrical in a way which *F. oregona* never is." Then under his discussion of *F. velutina*, Jepson gave both the species and the var. *coriacea* as occurring in California and separated the two by the former being villous or puberulent on rachises and young shoots, villous-tomentulose or puberulent on the under side of the leaves, by having 5 leaflets, and samaras 25-37 mm. long, the wing 2-7 mm. wide, not decurrent or only weakly so on the cylindrical body. The latter ash he characterized as having shoots of the season and rachises glabrous, leaflets glabrous or slightly puberulent beneath, and samaras 22-28 mm. long, the wing 4-5.5 mm. wide. In the variety the petiolules are supposed to be more pronounced and the lateral nerves of the leaflets straighter, more regular and more sharply defined than in the species. In southern California Jepson had both *velutina* and *coriacea* rather widely distributed.

General practice has been about that outlined above. The last complete treatment of the genus seems to be that by Lingelsheim (Das Pflanzenreich, IV. 243 (1): 9-65, 1920). He separated *F. velutina* and *F. oregona* on the basis of the samara-wings. Sargent (Trees of North America, ed. 2, pp. 834-853, 1922) put both species in the group with decurrent wings and separated them on the basis of number of leaflets, *F. velutina* being given 3-5 and *F. oregona* 5-7, usually 7. Under the latter was given var. *glabra* as occurring in Los Angeles and San Bernardino counties and at Ash Creek, Inyo County. McMinn and Maino (Illustrated Manual of Pacific Coast Trees, 335-340, 1935) keyed out *F. oregona* by its having sessile or subsessile leaflets, while *F. velutina* was put in the group with stalked leaflets. Both species and the var.

*Claremont, California.

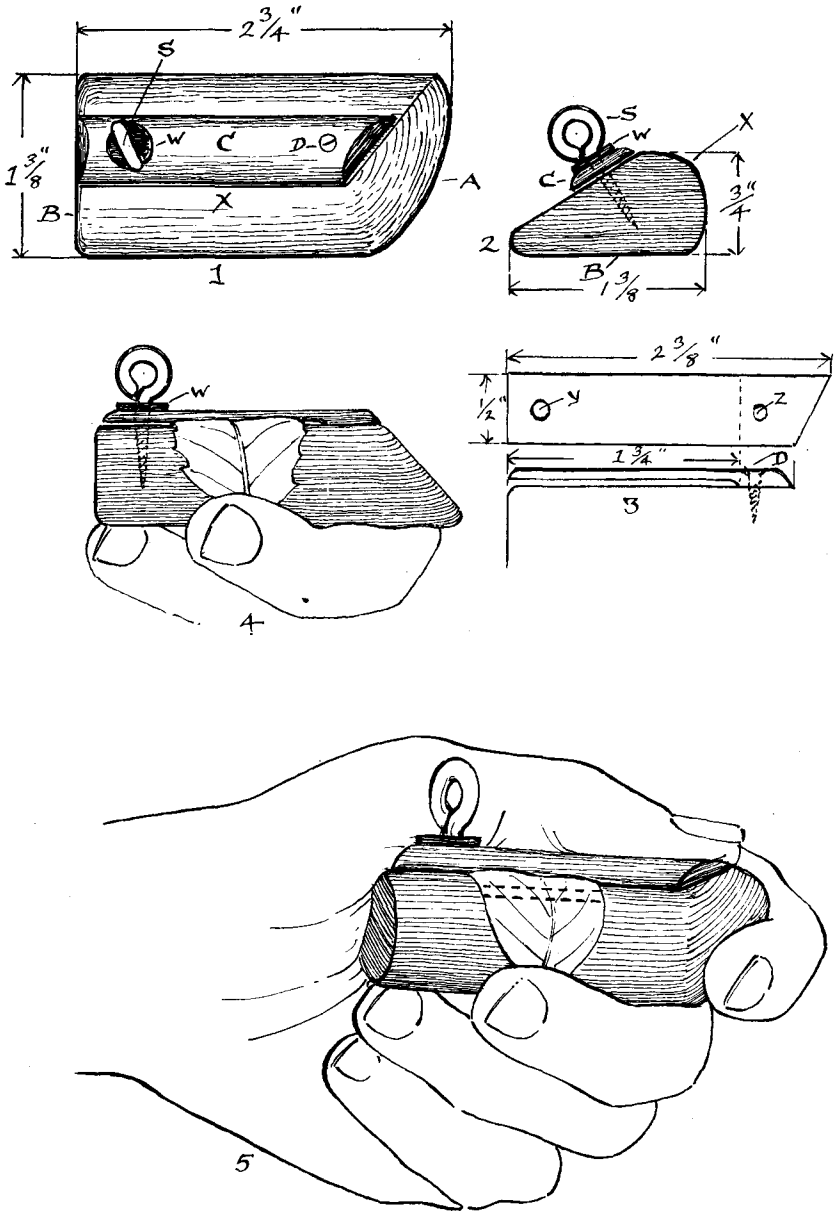


PLATE IX.

Simple clamp and block device for obtaining rapid sections. See description on page 53.

coriacea were said to be in southern California. Rehder (Manual of Cultivated Trees and Shrubs, 767-774, 1940) placed both species in the group with wing of fruit decurrent to or below the middle, and then separated them on the basis of fruit length, *F. oregona* having fruits 3-5 cm. long, the wing decurrent nearly to the base and *F. velutina* with fruit 1-1.8 cm. long, the wing decurrent scarcely to the middle. He gave *F. oregona* as occurring in southern California.

It is evident from the above discussion that writers vary widely in their concept regarding these trees and as to the range that they occupy. Having living trees available in the Garden and with the hope of discovering something that might throw light on the whole question, a microscopic study of the epidermis of the leaves has been undertaken. Since it was hoped that some characters might turn up in connection with size and shape of stomates, the lower surface particularly was examined. The most obvious fact at once was that the lower epidermis in both species is very elaborately patterned with ridges or sculpturing, lines of which radiate out from the stomates and usually from the glandular peltate hairs so characteristic of the Oleaceae (Boodle and Fritsch, Solereder's Systematic Anatomy of the Dicotyledons, 1: 523, 1908). It was thought that some diagnostic characters might be discovered which might help in determining specific lines and distribution.

MICROTECHNIQUE USED IN PREPARING MATERIAL FOR EXAMINATION OF LEAF EPIDERMIS

In these investigations both fresh and dry (herbarium) specimens were used. Fresh material was placed directly into absolute alcohol and allowed to remain until ready to be examined. The chlorophyll was extracted by this treatment and fresh leaves were bleached to a yellowish white color.

Examination was largely confined to epidermal tissue from the under-side of the leaves. Freehand sections were cut from the leaves clamped in the block shown in Plate IX. By this method it was possible to cut sections rapidly; a matter of considerable importance in view of the large number of mounts that had to be made. Sections averaged 2 millimeters wide and generally included a strip from the margin of the leaf to the midrib. Sections were removed from the razor with a wet camel's hair brush and placed directly in the stain which was prepared as follows: Eighty milligrams of safranin were dissolved in 30 cubic centimeters of absolute alcohol. For use equal parts of the stock solution and distilled water were taken. Sections were allowed to remain in the stain for ten minutes, then transferred to distilled water to remove loose stain, and examined as water-mounts.

In the case of herbarium and other dry specimens the leaves were boiled in distilled water until soft, then drained on filter paper and sectioned while still moist. Subsequent treatment was the same as for material that had been preserved in alcohol. Specimens prepared by these methods can be preserved for later examination by being allowed to dry on the slide. For re-examination the sections are irrigated with water flowed in under the cover. In about ten minutes the section is in precisely the same condition as upon first examination.

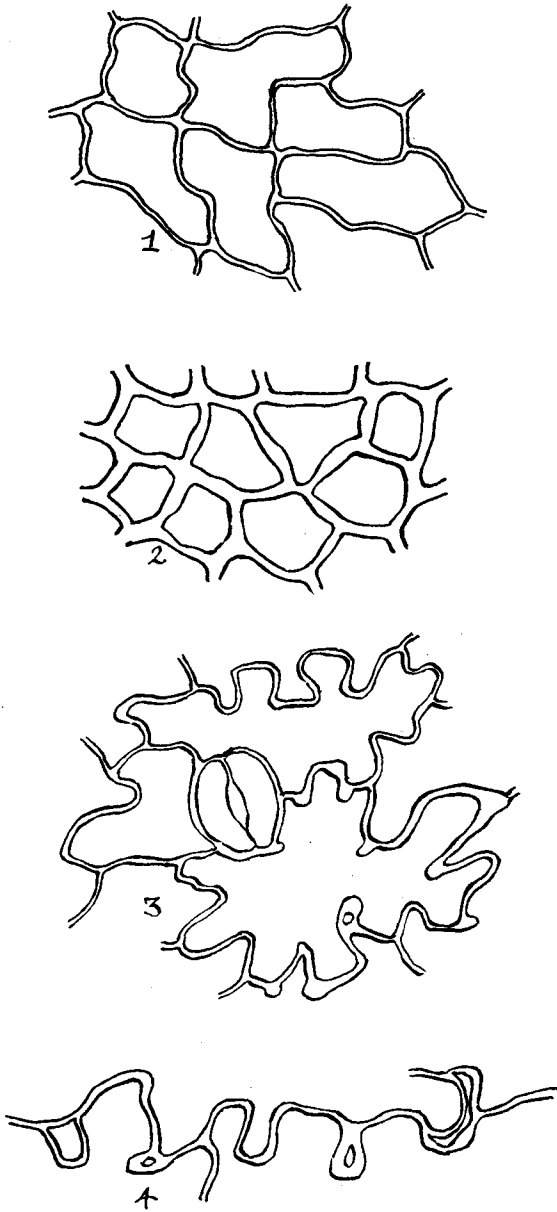


PLATE X.

Cells of lower epidermis of leaves of *Fraxinus*, all drawn to same scale.

Fig. 1. *F. oregona* showing rather thin-walled irregular cells which average 39.26η in length.

Fig. 2. *F. velutina* var. *coriacea*, with thick-walled regular cells, averaging 16.38η in length.

Fig. 3. *F. anomala*, with very irregular cells, which run from $50-60\eta$ in length.

Fig. 4. *F. anomala*, detail of wall to show air-spaces in loops of the walls.

CLAMP AND BLOCK DEVICE FOR RAPID SECTIONS OF LEAF EPIDERMIS

For rapid making of sections to show leaf epidermis a simple device was constructed which is pictured in Plate IX.

A block of hard wood B, of dimensions given in Figs. 1 and 2 was trimmed to the shape shown. End A was curved to the shape shown so as to afford a comfortable grasp with the finger, see No. 5; all edges were sandpapered smooth.

The Clamp C is a slip of hard wood $\frac{1}{8}$ inch thick and of dimensions shown. One face of the slip was scraped to half its thickness for about $1\frac{3}{4}$ inches as shown in Fig. 3. Two holes Y and Z were drilled as shown to accommodate the countersunk screw D which fastens the clamp to the block and a screw-eye S, which works against a washer W and tightens the clamp while holding the leaf being sectioned.

In use, one end of the leaf is pinched beneath the clamp and the free end then bent over the rounded side of the block marked X in No's 1 and 2; the leaf is then held against the lower edge of the block with the middle finger as shown in Figs. 4 and 5.

Fig. 5 shows position of block as grasped. Sections of epidermis are cut from the surface of the leaf bent over the rounded edge X. Sections should include a strip about 2 mm. wide across the leaf or to the midrib as shown by the heavily dashed lines in Fig. 5.

EPIDERMAL CHARACTERS

No attempt has been made to make a general study of western species of *Fraxinus*, but to discover whether the features examined were general or confined only to *F. oregona* and *F. velutina*, the leaves of *F. dipetala* and *F. anomala*, both of which are also growing in the Botanic Garden, were also investigated. In Lingelsheim's treatment *F. dipetala* was placed in a separate subsection *Dipetalae* in the subgenus *Fraxinaster*. It was not surprising, then, to find that its lower epidermis has no sculpturing. But *F. anomala* was included in the same subsection (*Melioides*) with *F. velutina* and *F. oregona*, coming in the key very near the latter species since its fruits have the wings strongly decurrent. It was interesting, then, to find no sculpturing in *F. anomala*. The species is further characterized by exceedingly large epidermal cells, those on the under surface being 50-60 microns long. Furthermore, it differs from the other two species by the remarkable loops on the strongly infolded walls, these "loops" often containing intercellular air spaces, (see Plate X, Figs. 3 and 4). Judging from these two species as compared with *F. oregona* and *F. velutina* the microscopic anatomy of the leaves in other species is well worth study.

SCULPTURING

Boodle and Fritsch (Solereder's Systematic Anatomy of the Dicotyledons, 2: 982, 1908) say: "Papillose differentiation of the lower epidermis of the leaf (coronulate papillae united by a network of ridges) occurs only in three cases

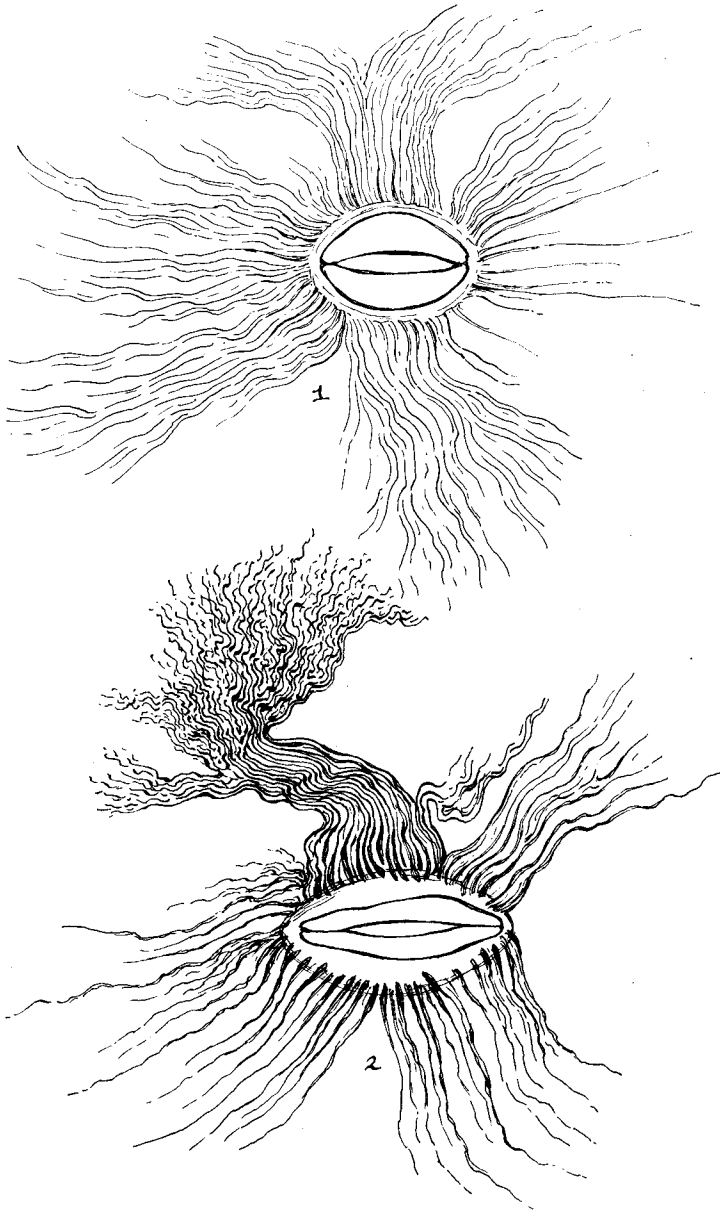


PLATE XI.

Ridges radiating out from stomates on the lower surface of ash leaves as seen under high power.

Fig. 1. *F. oregona*.

Fig. 2. *F. velutina* var. *coriacea*.

among the different species of ash, viz. in *Fraxinus americana*, L., *F. juglandifolia*, Lam. (non Willd.) and *F. texensis*, Sarg. (Koehne)." Since these three names refer to plants included in *F. americana* in Lingelsheim's treatment, they fall in the same section with *F. oregona* and *F. velutina*. This comment on the ridges is the only reference seen pertaining to the sculpturing discussed in the present paper.

On the lower epidermis of *F. oregona* and *F. velutina* occurs a very elaborate series of microscopic ridges or sculpturing forming a pattern which is much alike in the two species. These lines radiate out from the stalked glands, as well as from the guard cells of the stomates, in such abundance as often to make it difficult to follow closely the walls of the epidermal cells themselves. The stomates seem to be of two types, one with the ridges more prominent and the radiating pattern more distinct, the other having the pattern less so. In the more striking examples of stomates these ridges in *F. velutina* var. *coriacea*, as seen under oil immersion, form a continuous series beginning inside the outer margin of the guard cells and running out over surrounding cells to a distance equal to about the width of the guard cells, then beginning to branch in dendritic fashion so as to form a sort of network. Under ordinary high power the series does not seem so continuous (Pl. XI, Fig. 2). In *F. oregona*, on the other hand, these ridges are not in a continuous series as viewed under high power in any given focus, although changing the focus may reveal some intermediate ones in a slightly different plane. Thus the ridges seem to be somewhat fascicled and tend to run out perhaps as far as the entire width of the stomate (both guard cells) before anastomosing. Furthermore, they are less pronounced than in the other species (Pl. XI, Fig. 1) and begin at the outer margin of the guard cells. By looking about on slides of the two species it is soon possible to find stomates that reveal these differences, although at first glance somewhat similar ones may be found in both species. With a little experience, however, the investigator can see a real difference. A study made of leaves from different parts of the same tree and of different portions of a given leaflet and of different leaflets of a given leaf showed no appreciable variations.

STOMATES

An examination of the stomates of both species, *F. oregona* and *F. velutina* var. *coriacea*, was undertaken to ascertain whether there might be any notable size-differences in the stomate as a whole or differences in relative length of the stomatal opening as compared with the length of the guard cells. For this purpose only living material was used and mounted in water. Each lot was taken from a tree of known origin and represented a different collection. Twenty stomates for each lot were measured as to length of the entire stomatal apparatus (guard cells), width of same, and length of opening. The mean was found for each set of measurements and the results put into tabular form. All such measurements were made under oil immersion. Leaves selected from different exposures on a given tree showed no appreciable differences, but to make the study all leaves used were taken from the northeast side of the tree, in order to get as uniform an exposure as possible.

Table I, for *F. oregona*, shows six lots, that is, measurements for six propagation numbers, the origin of which can be ascertained by reference to the data for collections of *F. oregona* studied (see page 60). It will be seen that the average for the six lots, meaning data for 120 stomates, is 29.08 microns for length of stomatal apparatus, 17.72 for width, and 20.78 for length of opening. The mean for length of opening as compared with total length of guard cells is 70.8 per cent. These figures give some indication as to the means about which the stomates of the species fluctuate. For *coriacea* more figures are available, Table II showing measurements for 12 different propagation numbers. It can be seen that the stomates are slightly longer than in *oregona*, considerably wider, and that the stomatal slit as compared with the length of guard cells is greater so that the stomates are organized on somewhat different proportions in the two species. However, the fluctuation for both is so great that measurements of a given tree of one species may completely overlap those of the other species. Obviously, identification can not be based on these measurements.

TABLE I. STOMATAL MEASUREMENTS FOR *F. oregona**

Propagation Number	Guard-cell length	Width of both guard-cells	Length of opening	Length of opening to length of guard-cells %
3860	28.50	20.85	20.78	72.8%
3861	31.84	19.43	21.25	69.8
3863	29.52	18.42	18.95	64.2
3865	31.35	20.12	24.64	77.2
3866	29.40	19.55	20.92	71.1
3870	25.88	16.98	18.15	70.1
Average for all six	29.08 _η	17.72 _η	20.78 _η	70.8%

*Each measurement given is the mean, in microns, for 20 stomates.

TABLE II. STOMATAL MEASUREMENTS FOR *F. velutina* var. *coriacea**

Propagation Number	Guard-cell length	Width of both guard-cells	Length of opening	Length of opening to length of guard-cells %
3834	31.57	19.17	27.26	82.4%
3836	33.31	23.84		81.9
3839	32.44	20.48	22.74	70.1
3841	29.09	19.46	20.63	70.9
3843	30.76	18.44	22.02	71.5
3844	28.07	18.22	20.56	73.2
3846	30.42	20.99	23.98	78.9
3848	35.50	23.47	30.84	87.2
3851	30.84	20.85	27.93	87.0
3852	31.05	19.32	21.80	70.1
3853	31.70	20.41	27.70	87.6
3882	31.93	19.61	22.31	69.8
Mean	31.39 _η	20.36 _η	24.47 _η	77.5%

*12 lots, 20 stomates measured for each lot. Lengths in microns.

SHAPE AND SIZE OF EPIDERMAL CELLS

The most significant epidermal character observed by which the two species can be differentiated is the size and shape of the epidermal cells. In *F. oregona* the epidermal cells have thin cell walls which are sinuous so that the cells have a very irregular shape (Pl. X, Fig. 1). *F. velutina* var. *coriacea*, by way of contrast, has very thick-walled cells, the walls being relatively straight so that the cells are quite regular in shape, (Pl. X, Fig. 2). A glance at a slide reveals the difference between the two species. Moreover, the size tends to be quite different in the two. In *F. oregona* the epidermal cells are mostly from 35 to 51 microns long, with occasional cells below 30. The mean for a number of measurements was 39.26 microns. In *F. velutina* var. *coriacea* the cells measured ran from 14.58 to 29.16 microns, the mean being 16.34. Thus, size, shape and wall-thickness of cells of lower epidermis of leaves are markedly different in these two ashes. It should be mentioned in this connection that all data given are for cells away from the veins, since those on or near the veins tend always to be small and rather elongate and regular in shape.

INTERGRADATION BETWEEN SPECIES

When the traditional characters are used for separating *F. oregona* and *F. velutina* var. *coriacea* in California, there is, as has been pointed out in the first part of this paper, considerable difference of practice among botanists. Decurrence of wing on the body of the fruit and width of the wing vary, although both are useful tendencies. Number and shape of leaflets likewise vary. The coriaceous character is not always easy to determine in dried specimens, but when these are intermediate in gross characters, the microscopic anatomy is very suggestive. The following specimens, all of which except No. 5 are in the Garden Herbarium, are of interest in this connection:

(1) *Wolf 9772* (Propagation Number 3859), Nov. 4, 1940, from 1.5 miles below entrance to Sequoia National Park, Kaweah River, Tulare County, California. Leaflets 5-7, relatively thin, slightly pubescent beneath. Fruits 26-30 mm. long, rather flat, with the wing 6-7 mm. wide, decurrent about three-fourths the length of the body. Based on these characters the collection was called *F. oregona*. The epidermal characters show stomate length with a mean of 31.20 microns, width 22.31 microns and length of opening 20.56. The opening mean is 65.7 per cent of the total length, hence near to *oregona*. But the ridges that radiate out from the stomates begin well inside the outer wall of the guard cells and form a continuous series as in *coriacea*. Moreover, the walls of the ordinary epidermal cells are relatively straight and the cells run from about 22 to 26 microns in length, as in *coriacea*.

(2) *Wolf and Stark 5446* (Propagation Number 1931), Sept. 19, 1933, from Kaweah River, 1.8 miles below entrance to Sequoia National Park, Tulare County, California. Also classified as *F. oregona*. Leaflets mostly 5, quite pubescent and coriaceous. Fruits 30-38 mm. long, the wings 6-7 mm. wide and decurrent about one-third the length of the subterete body. The microscopic ridges are those of *coriacea* and the epidermal cells range from 26 to about 36 microns in length, have heavy walls and regular shape.

(3) *Wolf 9771* (Propagation Number 3858), Nov. 4, 1940, from St. Johns

River at Cutter Park, east of Visalia, Tulare County, California. Classified as *F. oregona*. Leaflets mostly 5, rather coriaceous, quite pubescent. Fruits 28-33 mm. long, with the wings 7-8 mm. wide and decurrent about one-third the way on rather a flattened body. Microscopic ridges beginning at margin of guard cell, separated in distinct groups and branching at about the width of whole stoma from their base. Epidermal cells thick-walled, regular in shape and about 17.5 to 21.9 microns long. Stomate length 24.38 microns, width 19.99 and length of opening 21.43 microns; opening 65.7 per cent of whole.

(4) *Wolf 4714*, May 15, 1933, St. Johns Bridge at Cutter Park, near Visalia, Tulare County, California; classified as *F. oregona*. Leaflets relatively thin, pubescent, mostly 5 in number. Fruit very immature, but wings already 7-8 mm. broad. Microscopic ridges in discontinuous series and long, beginning to branch at about the width of the stomate from their base which is along outer edge of guard cells. Epidermal cells somewhat irregular and wavy, from 26 microns to 44 microns long.

(5) *Johnston 2097*, July 28, 1918, from San Gabriel River at El Monte, Los Angeles County, California; classified as *F. oregona*, specimen at Pomona College. Leaflets 5-7, pubescent beneath, not very coriaceous. Fruits not very mature, and some of them not well formed, but apparently mostly 20-25 mm. long, the wings 4-5 mm. wide and decurrent only on the upper third or half of the rather cylindrical body. Ridges interrupted, fasciculate, branching at about two thirds the stomatal width from their base which is well within the outer wall of the guard cells. Epidermal cells relatively thin-walled, very irregular and wavy, about 37 microns long.

(6) *B. D. Stark 729* (Propagation Number 287), Sept. 9, 1927, from Cajon Pass, San Bernardino County, California, classified as *F. velutina* var. *coriacea*. Leaflets 5, coriaceous, glabrous. Fruits 35-40 mm. long, the wings 7-8 mm. wide and decurrent on about the upper third of the terete body. Microscopic ridges mostly in a continuous series, beginning about half way between the slit and the outer walls of the guard cells and branching at about as far from their base as the width of one guard cell. Epidermal cells, on the other hand, irregular and with sinuous thin walls, the cells from 26 to 44 microns long.

TABLE III. ANALYSIS OF 6 SPECIMENS CITED ABOVE, COMBINING *oregona* AND *coriacea* CHARACTERS

Specimen	Number leaflets	Thickness leaflets	Wing of fruits	Body of fruits	Microscopic ridges	Epidermal Cells	
						Size	Shape
(1)	oregona	oregona	oregona	oregona	coriacea	coriacea	coriacea
(2)	coriacea	coriacea	coriacea	coriacea	coriacea	oregona	coriacea
(3)	coriacea	coriacea	coriacea	oregona	oregona	coriacea	coriacea
(4)	coriacea	oregona	coriacea	oregona	oregona	oregona	oregona
(5)	oregona	oregona	coriacea	coriacea	mixed	oregona	oregona
(6)	coriacea	coriacea	coriacea	coriacea	coriacea	oregona	oregona

It can readily be seen that these six collections are quite intermediate and combine characters of the two species. It seems perfectly obvious that in the southern part of the range of *F. oregona*, that is, in Tulare County and in parts of southern California, there are trees that combine in various fashion

genes from both species. In Table III specimens 1 and 2 are from the same general groves, so are 3 and 4. In line with Mendelian segregation it is of course possible for individual trees to have different combinations. Thus, while in general, trees in Tulare County are most like *F. oregona* they may bear some genes of *coriacea*. In southern California there seems to be no pure *F. oregona*. Most trees which have in the past been referred to that species have been so classified because of pubescent leaves or somewhat wider wings or other character. Re-examination of most such specimens, especially with the new epidermal criteria, throws them pretty much into *coriacea*, especially when the validity of pubescence is questioned. But a few collections such as numbers 5 and 6 above do show considerable *oregona* in their make-up. Here again it seems feasible that *F. oregona* at one time occurred in the southern part of the state, but that during recent times with the drying climate and the northward withdrawal of many species, this ash has disappeared from its former southern territory, to leave only occasional trees with some *oregona* genes.

TAXONOMIC VALUE OF PUBESCENCE

In the past, presence or absence of hair has been one of the leading criteria for recognition of varieties in both *F. oregona* and *F. velutina*. Thus a variety *glabra* has been proposed in both species. It was interesting, therefore, to learn that in making his collections Wolf sometimes found about half the trees in a given grove hairy and half of them glabrous. Thus at Keyes' Ranch in the Little San Bernardino Mountains, he collected from nearby trees two numbers of *F. velutina* var. *coriacea*: 9761 hairy and 9760 glabrous. They seem alike except for this single character. Seeds were taken from the glabrous form and grown at the Garden as Propagation Number 3846. From these seeds four trees are now growing; two of them are glabrous, one almost so but with some hair along the midrib on the lower surface, and one with the hair quite general on the under surface. Otherwise the characters are much alike. Such a situation makes highly questionable the use of presence or absence of hair unless accompanied by other characters.

RELATIONSHIP OF CORIACEA TO VELUTINA

Fraxinus velutina was originally described by Torrey (Emory, Mil. Recon., 149, 1848) from specimens taken between the Rio Grande and the Gila rivers in New Mexico. The typical form has copiously pubescent leaves and the leaflets are nearly or quite sessile. It has been ascribed to a range from western Texas to southern California and northern Mexico.

Fraxinus coriacea was proposed by Watson (Am. Nat. 7: 302, 1873) for material from Ash Meadows, Nye Co., Nevada. It is supposed to differ from *F. velutina* by having the leaves more coriaceous and more reticulate, less pubescent or even glabrescent, the leaflets distinctly petioluled and with more or less serrate margin. It has been given as ranging from southwestern Utah to southern California, where it reaches its northern limit in Kern and Inyo counties.

In recent years *coriacea* has been reduced to varietal rank under *F. velutina* by most authors and even to synonymy by Benson and Darrow (Manual of

Southwestern Desert Trees and Shrubs, p. 260, 1944). Examination of a series of specimens in connection with the present study reveals that the sculpturing (microscopic ridges) of the lower epidermis is very near that of *F. velutina*. In the latter the ridges tend to be almost a network from their very origin well inside the outer walls of the guard cells, forming a sort of elliptical pattern surrounding the stomate, but smaller and less diffuse than in *coriacea*. The epidermal cells themselves are regular in shape and thick-walled as in *coriacea*, and range in size from about 12 to 35 microns. In other words, the epidermal characters are much alike in the two ashes. California material which has been referred to *F. velutina* seems to have been so treated largely because of pubescence. However, its thicker leaves, microscopic ridges, petiolules, etc. throw it into *coriacea*. On such a basis, *F. velutina* occupies a more southeasterly range and *coriacea* is to the north and west. The whole situation seems to justify the recognition of *coriacea* as a variety of *F. velutina*.

Rehder's *F. oregona* var. *glabra*, on the basis of plants so identified and of characters used and range given, seems to be a synonym of *F. velutina* var. *coriacea* as treated by Jepson (Fl. Calif. 3: 80, 1939).

CITATION OF SPECIMENS STUDIED

FRAXINUS OREGONA NUTT., Sylva 3: 59, 1849.

Ranging from British Columbia to Tulare County, California.

Specimens studied*: WASHINGTON. Chehalis Co.: Satsop, July 8, 1898, *A. A. & E. G. Heller 4024* (POM). OREGON. Oregon without definite locality, *J. Howell*, June, 1876 (POM); Rogue River, *Mrs. Austin & Bruce 1491* (POM). Multnomah Co.: Portland, July 19, 1911, *M. E. Jones* (POM). Wasco Co.: near The Dalles, July 29, 1897, *M. E. Jones* (POM). CALIFORNIA. Del Norte Co.: Darlingtonia, Smith River, August 1941, *H. E. Parks 24188* (POM,RSA). Humboldt Co.: Junction east of Arcata, July 16, 1931, *M. E. Jones 28864* (POM); Mattole River, 3 miles below Upper Mattole P. O., *C. B. Wolf 9784*, Prop. No. 3870 (RSA). Mendocino Co.: 9 miles southwest of Ukiah, *L. S. Rose 39195*, May 30, 1939 (RSA); $\frac{3}{4}$ mile south of Ukiah, *C. B. Wolf & B. D. Stark 5511*, Prop. No. 1972, September 27, 1933 (RSA); Lane's Redwood Camp, South Fork Eel River, *E. R. Johnson 1136*, Prop. No. 436, (RSA). Siskiyou Co.: Walker, Klamath River, Siskiyou Mts., at 1,700 ft., September 15, 1934, *L. C. Wheeler 3262* (POM,RSA); Klamathon, July 4, 1903, *E. B. Copeland*, distr. by *Baker 3559*, (POM); Klamath River, 3.5 miles below mouth of Shasta River, *C. B. Wolf 9781*, Prop. No. 3867, (RSA). Sonoma Co.: Cazadero, June 16, 1897, *W. A. Setchell* (POM). Lake Co.: 3 miles east of Hough's Mineral Springs on road to Williams, *C. B. Wolf 2084*, (RSA); Eel River, 1 mile below Hullville, *Heller 6029*, August 4, 1902, (POM); Clear Lake, July 3, 1924, *J. W. Blankinship* (RSA); Allen Springs, *D. Cleveland*, June 21, 1882 (RSA). Napa Co.: near Napa River, north of St. Helena, April 14, 1907, *H. P. Chandler 7514*, (POM); Samuel Springs above Monticello, Pope Valley Grade, *Ewan 8860* (RSA). Marin Co.: Mt. Tamalpais, July 11, 1887, *V. K. Chestnut* (POM). Alameda Co.: Greek Theatre, Univ. Calif. Campus, Berkeley, *Ewan 10121* (RSA). San Mateo

*In citing herbarium specimens POM stands for the herbarium of Pomona College, RSA for that of the Rancho Santa Ana Botanic Garden. We take pleasure in expressing our gratitude to Dr. Lyman Benson for his kindness in letting us use the facilities of Pomona College. The number indicated after the collection number as "Prop. No." is the Propagation Number under which the plants are grown in the Botanic Garden.

Co.: Crystal Springs Lake, June 30, 1903, *C. F. Baker 3355* (POM); San Mateo Creek, July 1903, *A. D. E. Elmer 4615* (POM). Santa Clara Co.: Stanford Univ., May 1898, *L. R. Abrams* (POM), *C. F. Baker in 1903* (POM). Butte Co.: Little Chico, *Mrs. C. C. Bruce 1789* (POM). Nevada Co.: 2.2 miles east Smartsville, on road to Grass Valley, *C. B. Wolf & B. D. Stark 5501*, Prop. No. 1963 (RSA). San Joaquin Co.: Peters, March 20, 1928, *E. E. Stanford 833* (POM); 1 mile north of Lodi, on Mokelumne River, *C. B. Wolf 9780*, Prop. No. 3866 (RSA); 1 mile west of Farmington, *Wolf 9779*, Prop. No. 3865 (RSA). Tuolumne Co.: Iron Canyon, Stanislaus River, *R. S. Ferris 1663*, (POM). Merced Co.: Merced River about 5.5 miles from Snelling on road to Merced, *C. B. Wolf 9776*, Prop. No. 3863 (RSA). Madera Co.: North Fork of San Joaquin River, at bridge between North Fork and South Fork, *C. B. Wolf 9774*, Prop. No. 3861 (RSA). Fresno Co.: Mermontia on Grant's Park road, May 11, 1929, *C. H. Quibell 1192* (POM); San Joaquin River, 1 mile above Friant, April 17, 1930, *C. H. Quibell 1450* (POM); Kings River Canyon below Trimmer, April 28, 1930, *C. H. Quibell 1599* (POM); Kings River Canyon 1 mile below Trimmer Springs, November 5, 1940, *C. B. Wolf 9773*, Prop. No. 3860 (RSA). Tulare Co.: Eshom Creek, August 2, 1910, *Mrs. J. Clemens* (POM).

FRAXINUS VELUTINA TOFF. var. *CORIACEA* (Wats.) Rehder,
Proc. Am. Acad. 53: 206, 1917.

F. coriacea Wats., Am. Nat. 7: 302, 1873.

F. oregona var. *glabra* Lingelsh., Engler, Pflzr. IV. 243(1): 43, 1920.

F. oregona Authors, for southern California references, not Nutt.

Specimens studied: NEVADA. Upper Cane Springs, May 1, 1902, *L. N. Goodding 684* (POM). Clark Co.: north of Wilson's Ranch, Charleston Mts., *I. W. Clokey 8454* (POM, RSA). CALIFORNIA. Inyo Co.: 2.5 miles north of Olancho, *C. B. Wolf 9765*, Prop. No. 3853 (RSA), *5371*, (RSA); Ash Creek, west side of Owens Lake, 3,700 ft., June 5, 1906, *H. M. Hall & H. P. Chandler 7322* (POM); Cartago, 4,000 ft., Oct. 9, 1948, *Munz 12727* (RSA). Ventura Co.: roadside tree, 1.5 miles southeast of Newbury Park, *Morehouse 1* (POM), *Morehouse 2* (POM). Los Angeles Co.: creek bank, Los Angeles Co., *H. E. Hasse*, August 1890 (POM); Kings Canyon, Liebre Mts., *Dudley & Lamb 4376* (POM); between Oakgrove Canyon and Elizabeth Lake, Liebre Mts., *L. R. Abrams & E. A. McGregor 400* (POM); Santa Monica Mts., 0.25 mile up Triunfo Canyon Road off Malibu Lake, *C. B. Wolf 9794*, Prop. No. 3882 (RSA); Lobo Canyon, Santa Monica Mts., *B. D. Stark 4370* (RSA); 0.5 mile below Pine Canyon Dam, San Gabriel Canyon, *L. C. Wheeler 2091* (RSA, POM); West Fork of San Gabriel River at 1,700 ft., *J. A. Ewan 10968* (POM). San Bernardino Co.: Keyes Ranch, near 29 Palms, *B. D. Stark 1438*, Prop. No. 626, (RSA); Keyes' Ranch, 4,300 ft., *C. B. Wolf 9761*, hairy (RSA), *9760*, glabrous, Prop. No. 3846, (RSA); 5 miles south of Victorville, along Mojave River, *C. B. Wolf 9764*, Prop. No. 3852 (RSA); 3 miles north of Victorville, along Mojave River, *I. M. Johnston 6516* (POM); Victorville at "Narrows," *I. M. Johnston*, May 17, 1920 (POM); Lytle Creek Canyon, at 2,500 ft., *L. R. Abrams 2741* (POM); North Fork of Lytle Creek, 0.3 mile below Scotland, *P. C. Everett 6212*, Prop. No. 2166 (RSA); Lytle Creek at Picnic Ground, 0.3 mile above Ranger Station, San Gabriel Mts., *C. B. Wolf 9763*, Prop. No. 3851 (RSA); 1.5 miles below U. S. Forest Service Camp at Glenn Ranch, *C. B. Wolf 2501*, Prop. No. 1360 (RSA, POM); Lytle Creek Canyon, *L. Street 226* (POM); Cajon Station, 3,000 ft., *I. M. Johnston*, May 17, 1920 (POM); side canyon, Cajon Canyon, at 2,200 ft., *P. A. Munz* (POM); Hawes Ranch, Horsethief Canyon, *J. Ewan 5179* (POM); Lone Pine Canyon, San Gabriel Mts., October 1, 1933, *L. C. Wheeler 2157* (POM). Riverside Co.: Pipe Creek, Ken-

worthy at 5,000 ft., *P. A. Munz 5810* (POM), *Munz & Johnston 5487* (POM); Penrod Canyon, southeast of Kenworthy Guard Station, *C. B. Wolf 9758*, Prop. No. 3848 (RSA); Santa Ana River, northwest of Corona, *J. M. Johnston 1804* (POM); San Gorgonio Canyon, north of Banning at 3,700 ft., *Munz & Johnston 8869* (POM); San Gorgonio Canyon, north of Banning at 4,500 ft., *Munz & Johnston 8866* (POM). Orange Co.: Rancho Santa Ana, Santa Ana River southwest of Mexican Village, *E. R. Johnson 7781* (RSA), *5170* (RSA). San Diego Co.: Cottonwood Creek, 2.8 miles above Barrett Store on road to Barrett Dam, *C. B. Wolf 9745*, Prop. No. 3834 (RSA); 2 miles south of Barrett Dam, *F. F. Gander*, April 15, 1934 (RSA); between Campo and Jacumba, *L. R. Abrams 3705* (POM); 5 miles west of Jacumba, *C. B. Wolf 9747*, Prop. No. 3836 (RSA); Warners Hot Springs, 0.12 mile east in Cañada Agua Caliente, *C. B. Wolf 9757*, Prop. No. 3844 (RSA); Spencer Valley, 0.3 mile east of Wynola, *Wolf 9756*, Prop. No. 3843 (RSA); 5.5 miles north of Jim McCain Ranch, 11.8 miles north of Live Oak Springs, *C. B. Wolf 9750*, Prop. No. 3839, (RSA); Noble Canyon, northeast of Pine Valley, Laguna Mts., *Wolf 9753*, hairy, Prop. No. 3841 (RSA). *9752*, glabrous, (RSA). LOWER CALIFORNIA. Northern Lower California, *M. E. Jones*, April 8, 1882 (POM).

CONCLUSIONS AND SUMMARY

Recent writers have not agreed as to the treatment of *Fraxinus oregona* and *F. velutina* var. *coriacea*. Some have used primarily fruit characters, others leaves and pubescence. Some have shown *oregona* as reaching its southern limit in Tulare County, California, others as extending to San Diego County. In the same way, some have placed the Arizona Ash (*F. velutina*) in southern California, others not. And some have recognized in the San Gabriel and San Bernardino Mountains of southern California an entity called *F. oregona* var. *glabra*.

In studying the microscopic anatomy of the lower epidermis of the leaves the present writers have concluded that *F. oregona* and *coriacea* can be separated by the size and shape of the cells, by the thickness of the cell walls, by the microscopic ridges (sculpturing) of the epidermal cells. These same characters indicate the possibility of some hybridization between these two ashes, and force the conclusion that true *oregona* does not now occur south of Tulare County, California, although it seems to have done so in recent geological time. Pubescence alone seems to be a very unreliable character. *F. oregona* var. *glabra* is to be reduced to synonymy under *coriacea*. The latter is a recognizable variety of *F. velutina* with enough characters and distinct range, *F. velutina* itself not being known from California.