

RESURRECTION OF THE MIOCENE FLANNELBUSH AS *FREMONTODENDRON LOBATUM* (MALVACEAE)

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ABSTRACT

Miocene fossil leaves from California can bear a resemblance to *Acer*, *Fremontodendron*, and *Ribes*. Leaves originally described in 1939 as *Fremontia lobata* Axelrod were transferred in 1950 to *Acer* and then in 1987 to the form genus *Dicotylophyllum*. These all have malvoid teeth and bear similar primary, secondary, and tertiary venation and are here recognized as **Fremontodendron lobatum** (Axelrod) Fields, **comb nov.** Based on an understanding of variation in modern *Fremontodendron californicum*, the Miocene leaves from three California floras (and possibly a fourth) represent a single fossil species.

Axelrod (1939) recognized Miocene fossil leaf impressions from southern California as ancestral to the modern flannelbush, *Fremontodendron californicum* (Torr.) Coville. Newly collected fossils caused Axelrod (1950) to change his mind and assign the original and additional fossils to the genus *Acer*. He also determined that a true flannelbush ancestor co-occurred with this newer material, but he did not provide a valid name for it. Wolfe & Tanai (1987) determined that the collections of so-called *Acer* were not maple and transferred the taxon to the form genus *Dicotylophyllum*. All of the material in question is recognized here as a flannelbush, under the generic name currently used for those plants.

Fremontodendron lobatum (Axelrod) Fields, **comb. nov.** *Fremontia lobata* Axelrod, Carnegie Inst. Wash, Publ. 516: 123. 1939. *Acer arida* Axelrod, Carnegie Inst. Wash., Publ. 590-5: 209. 1950. *Dicotylophyllum lobata* (Axelrod) Wolfe & Tanai, Hokkaido Univ. (Japan), Fac. Sci., J. 22-1: 210. 1987. **LECTOTYPE** (designated here): **California**. Tehachapi fossil flora, *UCMP 1506* (University of California Museum of Paleontology, Fig. 2).

Fremontia coriacea Axelrod, Carnegie Inst. Wash., Publ. 590-5: 210. 1950 [nomen nudum].

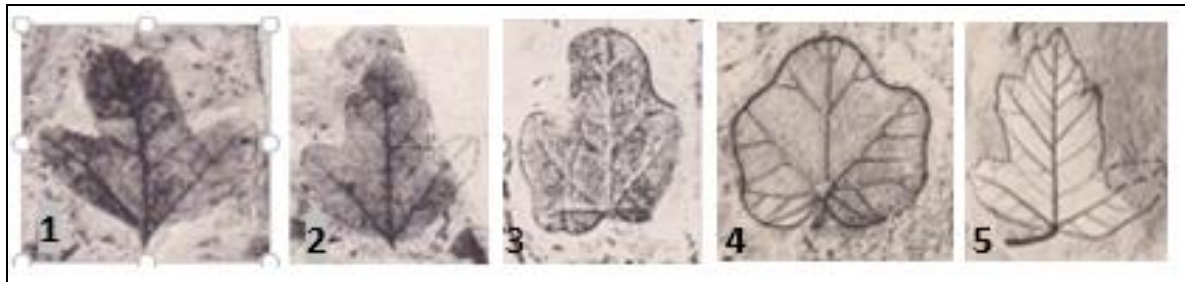
Leaves orbicular, trilobed, or rarely five lobed, the tips of the lobes obtuse; the central and laterals may have additional smaller lobes; base subcordate; petiole heavy, 2-7 mm preserved; leaves 1.6 to 2.7 cm. wide; midrib heavy, straight or curved; the two basal secondaries departing at 45⁰ to nearly 60⁰, heavy; tertiaries departing from the basal side at rather constant angles and looping upward near the margin; secondaries departing from the midrib at 45⁰ to 50⁰, arching upward to the tip of the lateral lobes or to the margin; tertiaries enclosing a polygonal mesh; margins appearing entire with occasional lobes, teeth are malvoid and generally fine, occasionally prominent; texture thick (modified from Axelrod 1939, p. 123).

Discussion

Axelrod (1939) placed fossils from the Miocene Tehachapi, California, flora in the new species *Fremontia lobata* and stated that they were related to the modern *Fremontia californica* (Torrey) Coville, which at that time was placed in Sterculiaceae (see Figs. 1-2 in the present paper). He mentioned that *F. lobata* also occurred in the as yet undescribed Mulholland, California, fossil flora (referred to as "... Pliocene sediments near St. Mary's College, in the hills west of Berkeley,

California”), and he later (Axelrod 1944) included the Mulholland material within *F. lobata* (Fig. 3, this paper).

In a preliminary statement about the undescribed Mint Canyon fossil flora, Axelrod (1940) referred to fossils only by their “living equivalents” and twice referred to fossils related to *Fremontia californica*. However, in the same year Wallace (1940, pp. 17–20) paraphrased a written communication from Axelrod that specifically mentioned *Fremontia lobata* as being present in the newly discovered Mint Canyon fossil flora. Mount (1971) listed *Fremontia lobata* as being present in the Mint Canyon flora.



Figures 1-5. Fossil *Fremontodendron* leaves. 1 & 2. From the Miocene Tehachapi flora (Axelrod 1938, p. 123, plate 11, figs. 8 & 10, UCMP 1507 & 1506, respectively). 3. From the Miocene Mulholland flora (Axelrod 1944, p.144, plate 31, f. 4 (UCMP 1674). 4 & 5. From the Miocene Piru Gorge flora (Axelrod 1950, p. 209-211, plate 6, f. 5-6, UCLA 12341 & 12540, respectively).

Axelrod (1950) transferred *Fremontia lobata* to the genus *Acer* and included a specimen from the fossil flora of Piru Gorge, California (Fig. 5, this paper) to the known collections. As support for this transfer, he referred to a “large suite” of specimens from the Mint Canyon assemblage that represented the maple species, as well as others that were *Fremontia*. Since “*Acer lobata*” would have been a later homonym, he established the replacement name *Acer arida* for his new combination. In tacit evaluation of Axelrod's taxonomy, Mount (1971), while recognizing *Fremontia*, did not find or list any *Acer* from the Mint Canyon assemblage.

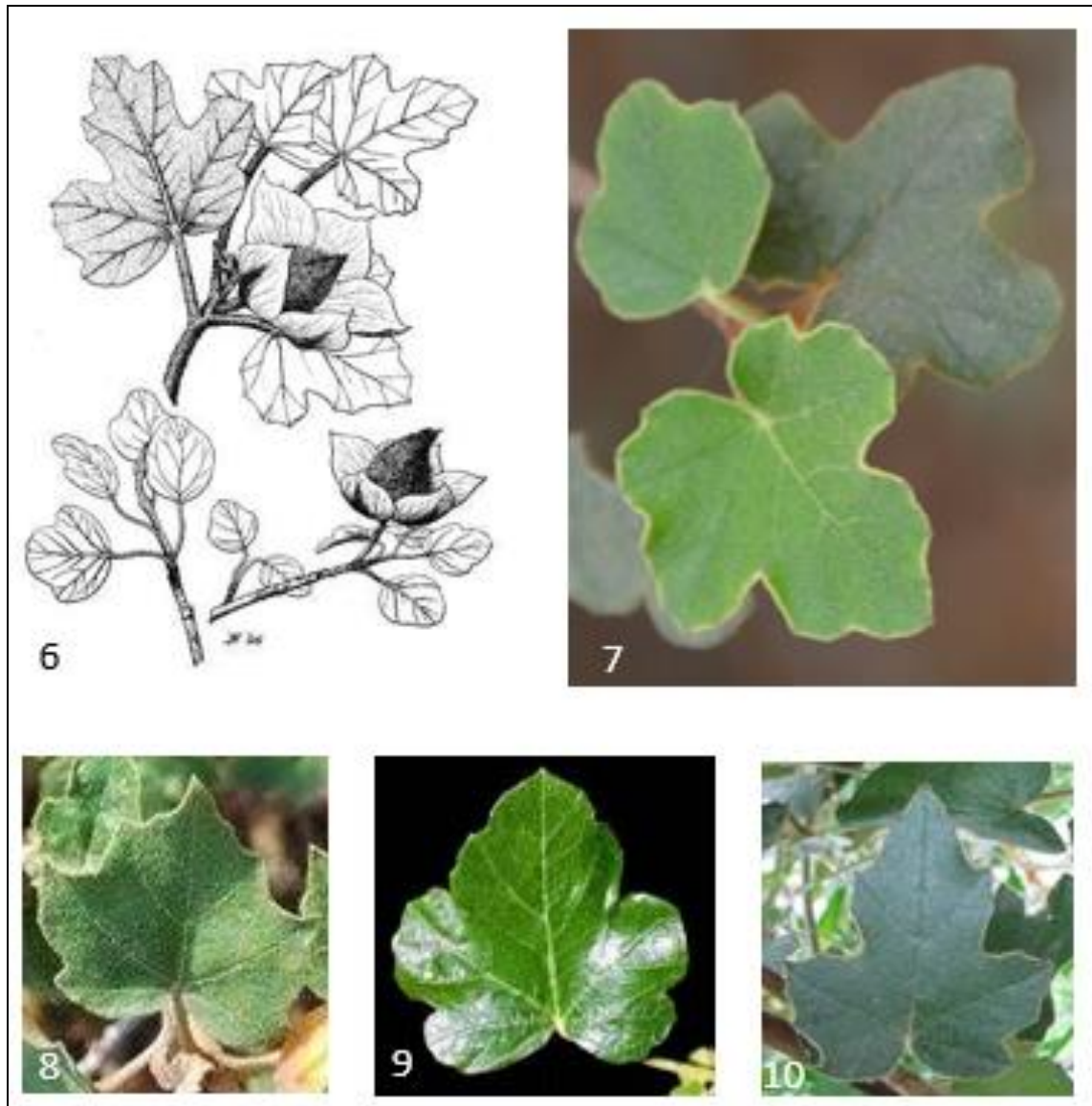
Axelrod (1950) stated that true *Fremontia* occurs in the Mulholland flora and in the Piru Gorge flora as well (Figs. 3 and 4 of this paper). Since both leaves from Tehachapi were then considered to represent *Acer*, a new species was required — Axelrod referred to *Fremontia coriacea* as a “new name” but provided neither description nor type specimen and the name is considered here as invalid.

In reviewing the Western North American fossil maples, Wolfe & Tanai (1987) rejected Axelrod's Piru Gorge and Tehachapi material from *Acer* and transferred the species to the form genus *Dicotylophyllum lobata* Wolfe & Tanai, commenting that “Although the specimens are poorly preserved, the teeth appear to be malvoid. Axelrod (1939) was possibly correct in referring this species to Sterculiaceae, although a reference to Malvaceae might also be valid.” They were essentially stating that since the material was not *Acer*, and because of the confusion over affiliation between Malvaceae and Sterculiaceae, they were placing the material into a form genus, rather than returning it to *Fremontia* (now considered *Fremontodendron*, see below). Subsequently, Sterculiaceae has been included within the Malvaceae (for example see Preston et al. 2012).

A further complication is that the genus *Fremontia* was first established in 1845 for a plant presently assigned to *Sarcobatus vermiculatus* in the Chenopodiaceae (Harvey 1943). Thus, eight years later, when *Fremontia californica* Torrey (1851) was described for the modern California taxon in the Sterculiaceae, it was a homonym and invalid. In 1893, Coville resolved the problem by

establishing the genus *Fremontodendron* and making the new combination *Fremontodendron californicum* (Torrey) Coville, which is currently accepted (Preston et al. 2012).

As presently recognized, modern *Fremontodendron* consists of three species, two of which are extremely local in distribution. *Fremontodendron decumbens* R. Lloyd is restricted to gabbro-rich volcanic soils, nearly all of which occur in the Pine Hill Ecological Reserve, El Dorado Co. *Fremontodendron mexicanum* Davidson is known from only about ten populations in southern San Diego Co. and adjacent northern Baja California, Mexico.



Figures 6-10. Variability in modern *Fremontodendron californicum* leaves. 6. Line drawing showing variation from orbicular to five lobed leaves on same branch (source: California Flannel Bush). 7. Photograph showing three morphological forms varying from five lobes (in back) through nearly orbicular (top foreground) all on same branch, showing moderate amount of adaxial indumentum (source: Urban Ecosystem Institute). 8. Toothed leaf with minimal lobes, but highly hairs (source Kapsenberg 2010). 9. Nearly circular (almost crenulate margined) leaf with minimal teeth and very little hair (source: Hinsley 2003). 10. Toothed, three-lobed leaf with moderate indumentum (source: Top Tropicals).



Figure 11. Geographic distribution of *Fremontodendron californicum* (Torrey) Coville (shaded region), from Map 84 of Little (1976) and approximate location of the fossil floras mentioned in this paper (stars): northernmost star – Mulholland flora; easternmost star – Tehachapi flora; westernmost middle star – Piru Gorge flora; southernmost star – Mint Canyon flora.

The third modern species, *Fremontodendron californicum*, consists of three subspecies that are variable in leaf shape, degree of toothiness, degree of adaxial surface hairiness, and texture (Figs. 6-10). The leaves generally bear a single lobe on each side of the lamina, thus taking on the appearance of some trilobed maples (Figs. 6, 7, 10) or bear few to many very shallow secondary lobes, so as to be orbicular in appearance (as in some species of *Ribes*; Figs. 6, 7, 9). Tooth types can readily distinguish these three genera, as *Acer* bears platinoid teeth, *Fremontodendron* bears malvoid teeth, and *Ribes* bears rosoid teeth (see Hickey & Wolfe 1976). Some individuals bear a high degree of pronounced teeth along the margins (Figs. 8, 10, and Kapsenberg 2010), while others may appear

nearly toothless (Figs. 7, 9). The foliage is hirsute on the abaxial surface but varies in degree of hairiness adaxially so as to be leathery or flannel looking (hence the common name “flannelbush”; cf. Fig. 8 vs. Fig. 9). It is this variation between individuals that apparently led Axelrod (1950) to segregate some forms as *Acer* while assigning others to what has become *Fremontodendron*.

Fremontodendron californicum geographically exceeds the other two species’ ranges (Fig. 11). It occurs along the margins of the Sacramento-San Joaquin Valley of California and the south-facing sides of the transverse and coastal ranges in southern California, and it also occurs in isolated populations in western to central Arizona and northern Baja California, Mexico (Fig. 11, adapted from Map 84 in Little 1976). It ranges in elevation from 180-2320 meters and occurs in chaparral and oak/pine woodland, yellow pine forest, and pinyon-juniper woodland habitats (Preston et al. 2012).

Fremontodendron lobatum is known from three middle to late Miocene floras of California (Fig. 11). Geographic and morphological similarity of the fossil leaves to modern *Fremontodendron californicum* suggests that they are the same species or at least directly ancestral.

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