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PHENETIC ANALYSES AND REVISED CLASSIFICATION OF THE *PTELEA TRIFOLIATA* COMPLEX (RUTACEAE)

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ABSTRACT.—The current classification of *Ptelea* divides the widespread and highly variable *Ptelea trifoliata* L. into 5 subspecies and 11 varieties, while additionally terming many specimens "intermediate." Although there are visually observable differences among regional variants, principal component analyses of quantitative characters failed to separate subspecies or to even incompletely separate most varieties within subspecies. Some recognized subgroups are also not well distinguished by discontinuous qualitative characters. Where multiple varieties appear to be part of a single continuum of variation or are extremely similar, it is suggested that a reduction in the number of infraspecific taxa would improve the utility of the classification. An alternative classification recognizing 5 subspecies and 7 varieties is accordingly proposed.

RESUMEN.—La actual clasificación de *Ptelea* divide a *P. trifoliata* L., que tiene una amplia distribución y es muy variable, en cinco subespecies y once variedades, además de denominar a muchos ejemplares "intermedios." Aunque existen diferencias visualmente observables entre las variantes regionales, el análisis de componentes principales de los caracteres cuantitativos no funcionó para separar subespecies o incluso separar de forma incompleta la mayoría de las variedades en subespecies. Algunos subgrupos reconocidos tampoco son bien distinguidos por caracteres cualitativos discontinuos. Cuando múltiples variedades parecen ser parte de un continuo único de variación o son extremadamente similares, sugiere que una reducción en el número de taxa infra-específicos mejoraría la utilidad de la clasificación. En consecuencia, se propone una clasificación alternativa que reconozca cinco subespecies y siete variedades.

HERBARIA.—ARIZ – University of Arizona, Tucson; MO – Missouri Botanical Garden, St. Louis; OKL – Robert Bebb Herbarium, University of Oklahoma, Norman; UNM – Museum of Southwestern Biology, University of New Mexico, Albuquerque; US – United States National Herbarium, Smithsonian Institution, Washington DC.

Ptelea L. (Rutaceae) is a distinctive North American genus characterized by woody habit, alternate trifoliolate leaves, and winged samaras (Kubitzki et al. 2011), which has a long history of medicinal use (Bailey 1960). The most recent treatment, by Bailey (1962), recognizes 3 species. Two of these, *Ptelea aptera* Parry and *Ptelea crenulata* Greene, are limited in range to Baja California and California, respectively. The third, *Ptelea trifoliata* L., ranges across most of eastern, midwestern, and southwestern North America and displays a taxonomically problematic level of morphological diversity. Even within the eastern to mid-American populations placed within subsp. *trifoliata* in Bailey's (1962) treatment, 14 species-level synonyms exist. Overdescription was greatly exacerbated by Greene, who published several dozen species-level names within *Ptelea* (mostly in Greene 1905, 1906). Greene (1906) recognized a conspicuously excessive 59 species within western and southwestern populations of *Ptelea*, of which no less than 50 were later treated by Bailey (1962) as synonyms of *P. trifoliata*.

Bailey (1962) observed that morphological variation within the *Ptelea trifoliata* complex was substantial but complex, with numerous and widespread intermediate forms seen; hence "it does not seem possible to recognize well-delineated taxa above the rank of subspecies" (Bailey 1962:7). She therefore recognized 5 subspecies and 10 varieties within *P. trifoliata*, with all but 1 subspecies being divided into 2 or more varieties (see Table 1 for a summary). These frequently overlap in range and are often defined largely by characters that frequently vary within taxa (e.g., leaflet size, shape, color and/or indument). Several comments in Bailey (1962) and later works indicate that the delimitation and relationships of these taxa were often considered uncertain and that geography may have played a major role in their circumscription. For

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TABLE 1. Bailey's (1962) classification of *Ptelea trifoliata*. Important morphological characters and distributions are derived from Bailey's (1962:5–7) key and specimen citations, with the order rearranged and characters that do not characterize single taxa or have little informative value omitted for clarity.

Taxon	Selected key characters	Putative distribution
subsp. *pallida* (Greene) V.L. Bailey	Orange to whitish bark; seed usually oval to oblong rather than round, sometimes below midpoint of fruit	
var. *confinis* (Greene) V.L. Bailey	Leaves short-tomentose, margins often revolute, appearing entire	Rio Grande, CO and TX, also to NM [no cited specimens]
var. *lutescens* V.L. Bailey	Twigs and leaves glabrous; terminal leaflets mostly less than one-third as broad as long	Tributary canyons of Colorado River, NW AZ, rarely to S UT
var. *pallida* (Greene) V.L. Bailey	Twigs finely pubescent; leaf indument sparse or absent; margins usually crenate-serrulate	W AZ to New Mexico, also S CO and W TX [no cited specimens]
subsp. *coahuilensis* (Greene) V.L. Bailey	Terminal leaflets <5.5 cm long, subcoriaceous; margins crenulate to revolute; xerophytic habitats	
var. *coahuilensis* (Greene) V.L. Bailey	Leaflets dark green above, the terminal over half as broad as long	Mexico from Nuevo León and Coahuila to Puebla and Oaxaca
var. *pumila* (Greene) V.L. Bailey	Leaflets paler and thinner, glaucous, the terminal <3 cm, less than half as broad as long	Small area of SE Coahuila
subsp. *trifoliata*	Leaf glands <0.1 mm; fruits usually 2-carpellate; seed usually <1 mm thick and at or above midpoint of fruit; largely eastern to southern	
var. *mollis* Torr. & A. Gray	Twigs pubescent; leaves densely villous beneath	VA to N FL and TX
var. *trifoliata*	Twigs glabrous; leaves glabrous to finely pubescent beneath	Ontario to WI, N FL to TX
subsp. *polyadenia* (Greene) V.L. Bailey	Leaf glands >0.15 mm, usually visible; fruits often 3-carpellate, the seed often thick and sometimes below midpoint of fruit; lateral leaflets often strongly asymmetrical	TX to OK, CO, and AZ
subsp. *angustifolia* (Benth.) V.L. Bailey	Leaf glands >0.15 mm, usually visible; fruits often 3-carpellate, the seed often thick and sometimes below midpoint of fruit; lateral leaflets nearly symmetrical	
var. *angustifolia* (Benth.) M.E. Jones	Leaflets paler beneath with whitish veins, attenuate to acuminate apex; terminal leaflet with attenuate base, petiolule <2 mm; blade villous; base and apex of fruit wing retuse	Mexico [intermediates, NM to AR]
var. *cognata* (Greene) V.L. Bailey	Leaflets paler beneath with whitish veins, attenuate to acuminate apex; terminal leaflet with attenuate base, petiolule >(3–)5 mm; blade glabrous to sparsely pubescent; base and apex of fruit wing rounded to cuneate	SE AZ, adjacent NM and Mexico
var. *persicifolia* (Greene) V.L. Bailey	Leaflets pale and "lustrous" with inconspicuous veins, acute to obtuse apex, cuneate to sessile [*sic*] base	Edwards Plateau to central TX, OK

example, Bailey and Bailey (1965:41) say of one group of chromatographically intermediate populations that they "are recognized as subsp. *pallida* var. *confinis* north of the Mexican boundary . . . and as subsp. *coahuilensis* in northeastern Mexico."

As an example of one of the most obvious problems within this species, Bailey's (1962) key (see Table 1) stated that subsp. *polyadenia* had strongly asymmetrical lateral leaflets, with the angle between the lower margin and the midvein up to 90° and the margins crenulate to subentire, whereas subsp. *angustifolia* had more symmetrical leaflets with the angle between the lower margin and the midvein usually under 50(–60)° and the margins serrulate to serrate-dentate. Bailey (1962) claimed that the villous-leaved subsp. *polyadenia* occurred only in the United States, while problematically identifying some Mexican specimens as crosses between subsp. *polyadenia* and subsp. *angustifolia* or *coahuilensis.* Meanwhile, she said that subsp. *angustifolia* was found from Mexico to the southern United States; however, the villous-leaved var. *angustifolia* was said to occur in pure form only in Mexico, with only intermediate specimens in the United States.

Bailey's (1962) taxonomy thus would give the impression that villous-leaved populations in this group consisted of U.S. populations with broad strongly asymmetrical leaves (subsp. *polyadenia*) and Mexican populations with moderately asymmetrical leaves (var. *angustifolia*). In fact, there are relatively numerous U.S. specimens with narrow, moderately asymmetrical leaves (and often crenulate leaf margins), which have been collected from many areas where classic *polyadenia* has also been collected. Several of those seen in this study were treated by Bailey under subsp. *angustifolia,* var. *cognata* (which normally has glabrous to glabrate leaves) as "intermediate" toward subsp. *polyadenia.* The range of variation in leaf shape and symmetry in the western U.S. appears to be continuous; smaller leaves on a single specimen are often narrower and less asymmetrical than larger leaves, so leaf maturity may affect interpretation of this character. Certain Mexican specimens determined by Bailey as var. *angustifolia* also actually had strongly asymmetrical leaflets, as did an illustrated specimen of var. *cognata* (Bailey 1962:17).

However, specimens identified as var. *angustifolia* from Mexico (the region from which the type specimen was collected) actually do appear distinctive relative to U.S. specimens that key out to that variety. Mexican specimens have usually large, yet usually not very asymmetrical, lanceolate leaflets; the leaf venation is more prominent and conspicuous than in U.S. specimens of *angustifolia* or *polyadenia,* and the pubescence is more variable, being more frequently sparse to moderate. It was therefore a preliminary hypothesis of the present study that the Mexican var. *angustifolia* is distinct from villous-leaved U.S. populations that would key out to var. *angustifolia,* as Bailey (1962) believed, but that the latter populations are not distinct from subsp. *polyadenia* and have been wrongly excluded from that subspecies or treated as "intermediates" thereof by a circumscription that placed inappropriate weight on the variable character of leaf shape.

Bailey and Bailey (1965) conducted limited chromatographic studies and collected data on selected leaf and fruit morphological characters that were used for the production of scatter plots and maps showing the frequency of distribution of selected character states. Those analyses did show geographically correlated variation in the frequency of many character states; on the other hand, they also depicted substantial variation within geographic areas. On the basis of morphological and chromatographic similarities, Bailey and Bailey therein suggested transferring var. *cognata* (Greene) Kearney and Peebles from subsp. *angustifolia* to subsp. *pallida.* (They indicated that this created a new combination that changed the authority for the name from "(Greene) Kearney and Peebles" to "(Greene) Bailey and Bailey," but this is not correct under the International Code of Nomenclature [McNeill et al. 2012; see Art. 49.1 Ex. 6].)

Additionally, chemotaxonomic studies (Bailey et al. 1971) reported substantial variation in content of secondary metabolites, primarily alkaloids, within *Ptelea trifoliata.* However, the distribution of alkaloids was of little or no taxonomic value because the variation within subspecies was so great that no consistent differences among them could be seen. In fact, it was much more common for a given alkaloid to be found in <33% or 33%–66% of samples of a single subspecies from a single geographic

region than to be found in >66% of such a group of samples. The one notable result from this study was that samples of subsp. *pallida* consistently contained the coumarin marmesinin, whereas other subspecies rarely (subsp. *polyadenia*) or never contained this compound. It is relevant that subsp. *pallida* (not including var. *cognata*) is distinguished by the consistent qualitative character of orange to white bark, rather than greenish to brown bark, making it also better differentiated by morphology than most subspecies. Bailey et al. (1971:382) stated that marmesenin was present only in subsp. *pallida* and "related forms of subsp. *polyadenia*," again suggesting that the circumscription of subspecies might have been considered doubtful.

Since Bailey's (1962) treatment, one further nomenclatural complication has been added. She noted some specimens of subsp. *trifoliata* from Florida that had unusually small and narrow leaflets, and Bailey et al. (1970) reported that narrow terminal leaflets occurred in about 11% of specimens from peninsular Florida. However, she did not assign any taxonomic status to this variation. Ward (2001), believing that these populations should be formally recognized, has published the combination *P. trifoliata* var. *baldwinii* (Torrey & A. Gray) D.B. Ward.

The present study was motivated by the suspicion that *Ptelea trifoliata* remains overdescribed at the subspecies and varietal levels, and that overly narrow circumscriptions of infraspecific taxa have needlessly identified a substantial fraction of specimens as intermediates. As discussed above, and below under Methods, many specimens cannot be placed unambiguously using Bailey's key. Unquestionably, a huge range of genetically mediated variation can be observed within this species. However, when patterns of variation are extremely complex and many intermediates are seen, it may be better to recognize a single highly variable taxon rather than multiple taxa that encompass smaller portions of the range of variation but are of uncertain biological significance. Bailey's taxon circumscription is treated as a series of hypotheses to be at least informally tested; the corresponding null hypothesis is that some of the taxa currently recognized are not well enough distinguished by quantitative or qualitative characters to merit recognition.

METHODS

Specimens and Taxon Assignments

A total of 368 fruiting herbarium specimens of *Ptelea trifoliata,* emphasizing southwestern populations, were obtained from ARIZ, MO, OKL, UNM, and US (see Appendix 1 for a list of fruiting specimens used). Specimens were assigned a subspecies and, as appropriate, a variety, largely using Bailey's (1962) key and taxon circumscriptions, except as noted below; Florida specimens with unusually small or narrow leaflets were labeled as var. *baldwinii.* Some specimens bore Bailey's determination labels; her determinations of these specimens were usually accepted unless plainly incorrect according to her own key (a rare event), except that many specimens she labeled as intermediates were assigned to what appeared to be the most appropriate taxon. Leaf gland size was not as reliable a character as suggested by Bailey's key (as was also shown by data reported by Bailey et al. 1970): some Western specimens had glands small enough that they keyed out as subsp. *trifoliata,* though they were well outside the stated range of that subspecies and sometimes morphologically inconsistent with it in other ways. That character was therefore ignored as necessary to avoid clearly inappropriate assignment of specimens to subsp. *trifoliata.*

Some consistent means of assigning names to specimens in subspp. *polyadenia* and *angustifolia* was necessary. Bailey's illustrations and specimen determinations suggested that the primary defining feature of var. *cognata* (versus var. *angustifolia* or subsp. *polyadenia*) was glabrous to glabrate leaves rather than other features such as leaflet base shape, leaflet margins, or the presence of a long petiolule (which is an uncommon feature, far from consistent). Following that implicit view, glabrous to glabrate specimens in this group that were not identifiable as var. *persicifolia* were treated as var. *cognata* regardless of leaf shape. Following Bailey's key, villous-leaved specimens from the United States were assigned to subspecies according to the shape of a majority of the largest lateral leaflets on the specimen. Those that keyed to subsp. and var. *angustifolia* because they had moderately asymmetrical leaflet bases, which Bailey had treated as intermediates, were coded as subsp. *angustifolia,* var. *angustifolia* "northern," to distinguish them from

the qualitatively distinctive Mexican form, which was coded as var. *angustifolia* sensu stricto.

For some specimens, the combination of morphological characters, geographic origin, and/or variation within the specimen were such that, even using lenient criteria for taxon assignment, they seemed genuinely intermediate between var. *angustifolia* (Mexican or otherwise), var. *cognata,* var. *persicifolia,* and/or subsp. *polyadenia.* Those specimens were coded as subsp. *angustifolia,* var. "intermediate." Rarely, a similar varietal coding was used for specimens assigned to other subspecies. Fourteen specimens seemed to be best identified as hybrids or intermediates among subspecies other than *angustifolia* and *polyadenia.* Of those, 6 had previously been determined by Bailey as intermediate between 2 or more subspecies. Five others were specimens from Arkansas or the Oklahoma Territory that had been determined by Bailey as subsp. *polyadenia* but that had small glands or large leaves that, together with their geographic origin, would allow them to be at least equally well identified as var. *mollis.* These and similarly ambiguous specimens were coded as subsp. "intermediate," var. "intermediate."

Separately, 129 flowering sheets (corresponding to 125 distinct collections; see Appendix 2) were qualitatively examined to evaluate previous suggestions that flowers were not useful for delimitation of infraspecific taxa. For this purpose, a number of intermediate specimens were deliberately excluded in order to maximize any observed contrasts between flowers of different subspecies or varieties.

Data Collection and Statistical Analyses

A suite of 18 quantitative characters (Table 2; see Fig. 1 for illustration of leaf characters) were measured or calculated from specimen measurements, using the largest leaves and fruits from each specimen, and 5 qualitative characters were recorded. These characters were selected because Bailey's descriptions or preliminary study of herbarium specimens suggested that they were potentially informative. The character of seed thickness, used in her key to help differentiate subspecies, was omitted, both because of the difficulty of measuring this character accurately without damaging some specimens, and because it was apparent that Bailey's reliance on the character was questionable. She stated that the thickness of the seed-body, or central portion of the fruit, was seldom >1 mm in subsp. *trifoliata,* versus often 2 (3) mm in subspp. *angustifolia* and *polyadenia;* however, in fact many Eastern specimens of undoubted subsp. *trifoliata* have seed-body thickness of well over 2 mm. Some fruits said to have very flat seed-bodies perhaps were not fully mature; it appears that the wing develops to its mature size before the seed is fully developed. In addition to collection of quantitative data, all specimens were qualitatively examined consistent with typical procedures for taxonomic revisionary studies of herbarium material.

Principal component analyses (PCAs) of quantitative data were conducted using the statistical software package R (R Development Core Team 2005). The function "prcomp" with "scale = T" was used to perform analyses, and skewplots were examined visually using Cattell's (1966) scree test (see Cangelosi and Goriely 2007) to determine how many axes should be examined (usually 3 or, rarely, possibly 4). Analyses conducted included (1) all measured specimens (both as subspecies and as varieties); (2) specimens assigned to subsp. *angustifolia,* vars. *angustifolia* (both including and excluding "northern" populations), *cognata,* and *persicifolia;* (3) specimens assigned to subsp. *coahuilensis,* vars. *coahuilensis* and *pumila;* (4) specimens assigned to subsp. *pallida,* vars. *pallida, confinis,* and *lutescens;* (5) specimens assigned to subsp. *trifoliata,* vars. *trifoliata, mollis,* and *baldwinii;* (6) specimens assigned to all taxa other than the qualitatively distinctive subsp. *pallida* or var. *trifoliata;* (7) specimens assigned to subsp. *polyadenia,* subsp. *angustifolia,* and var. *mollis* (which appeared possibly to intergrade with *polyadenia*); (8) specimens assigned to subsp. *polyadenia* and var. *angustifolia* "northern"; (9) specimens assigned to subsp. *polyadenia* and var. *mollis;* and (10) specimens assigned to subsp. *polyadenia,* var. *angustifolia* "northern," and var. *mollis.* Additionally, *ex post facto* analysis of all specimens was conducted in which specimens were identified according to the simplified classification proposed in this paper.

RESULTS

Principal Components Analyses

No clear separation of subspecies was observed in principal component analyses of all

TABLE 2. Quantitative and qualitative characters recorded or calculated from fruiting specimens of *Ptelea trifoliata*. (See Fig. 1 for an explanatory illustration of leaf characters.)

Character
QUANTITATIVE CHARACTERS
Petiole length (cm)
Terminal leaflet length (cm)
Ratio of terminal leaflet length : breadth
Ratio of terminal leaflet length from base to broadest point : total length
Terminal leaflet petiolule length (mm)
Ratio of terminal leaflet length : lateral leaflet length
Ratio of lateral leaflet length : breadth
Ratio of lateral leaflet length from base to broadest point : total length
Lateral leaflet angle between midrib and proximal margin (degrees)
Leaf gland diameter (mm, to 2 decimal places)
Pedicel length (mm)
Fruit length (mm)
Ratio of fruit length : breadth
Lateral fruit wing depth (mm)
Apical fruit wing depth
Ratio of apical fruit wing depth : basal fruit wing depth
Seed length (mm)
Ratio of seed length : breadth
QUALITATIVE CHARACTERS
Bark color (greenish to brown, orange to white)
Leaflet indument on abaxial surface (glabrous, sparsely pubescent, short-pubescent throughout; strongly villous)
Petiole indument (glabrous, sparsely pubescent, short-pubescent throughout, strongly villous)
Margin of terminal leaflet (subentire, sharply toothed, crenate/crenulate, revolute)
Shape of base of fruit wing (rounded, cordate, cuneate, attenuate)

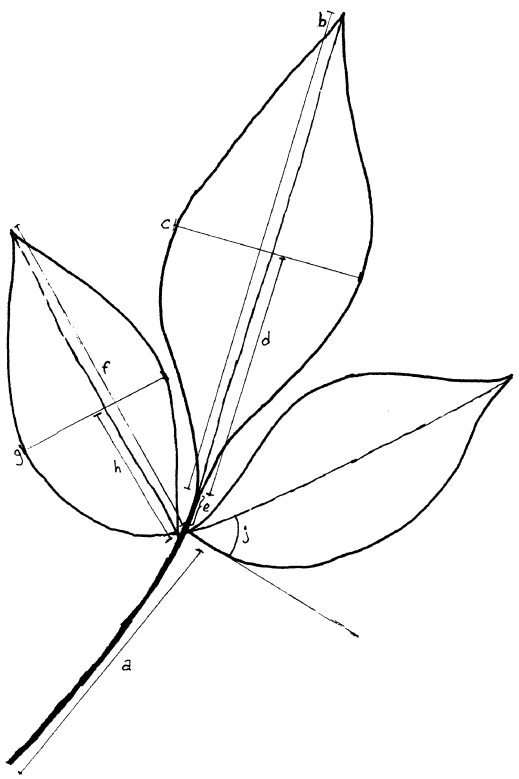

Fig. 1. Illustration of macroscopic leaf characters measured quantitatively: a = petiole length; b = terminal leaflet length; c = terminal leaflet breadth at broadest point (b/c calculated); d = measurement from broadest part of terminal leaflet to its base (d/b calculated); e = petiolule length, if present; f = lateral leaflet length (b/f calculated); g = lateral leaflet breadth at broadest point (f/g calculated); h = measurement from broadest part of lateral leaflet to its base (h/f calculated); j = angle between midrib and proximal margin of lateral leaflet.

included specimens (Fig. 2; all figures show the first 2 axes unless otherwise noted). Outlying points included some specimens of vars. *lutescens* and *trifoliata* (Fig. 3), but neither these nor any other individual varieties were fully separated from others. Identification of points according to the simplified classification proposed below did not change that outcome (not shown).

In none of the analyses of subsets of the specimens or of single subspecies having multiple varieties were any subspecies or varieties within a subspecies clearly distinguished (most not shown). The best separation of varieties was within subsp. *coahuilensis,* where the few specimens identified as the small-leaved var. *pumila* were found toward one extreme of the third axis (Fig. 4); most of the most important components of that axis were related to leaf size and narrowness, including lateral leaflet basal angle. With villous U.S. specimens and intermediates excluded, var. *angustifolia* sensu stricto appeared somewhat, though not fully, distinct within subsp. *angustifolia* (Fig. 5). In separate and combined analyses, subsp. *polyadenia* was not distinct from either villous U.S. specimens keying to "var. *angustifolia,*" which had been hypothesized to represent small-leaved individuals of subsp. *polyadenia,* or from var. *mollis* (Fig. 6), while var. *mollis* was also not separated from var. *trifoliata* when these alone were analyzed (not shown).

Additionally, the proportion of the variability in the PCA models that was explained by the first 3 principal components was relatively small. In the analysis including all specimens, the

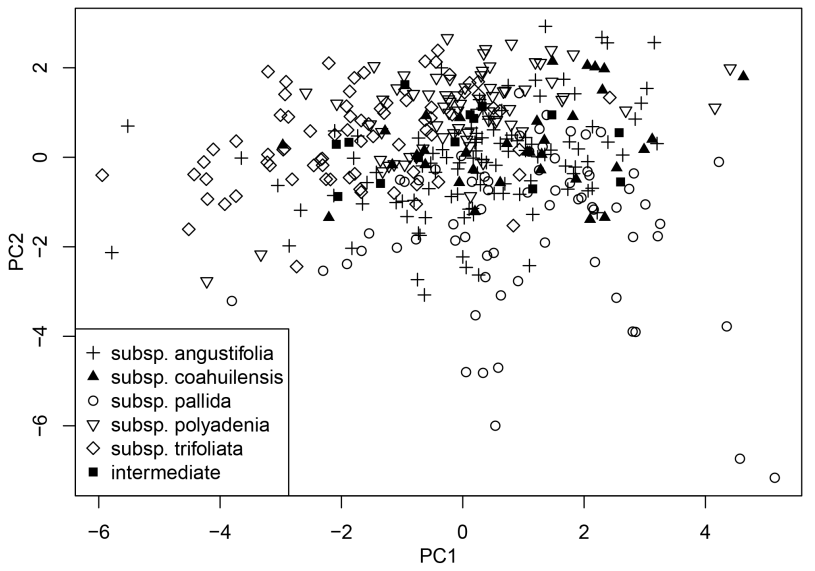

Fig. 2. Principal components analysis of all included specimens of *Ptelea trifoliata,* labeled according to assigned subspecies.

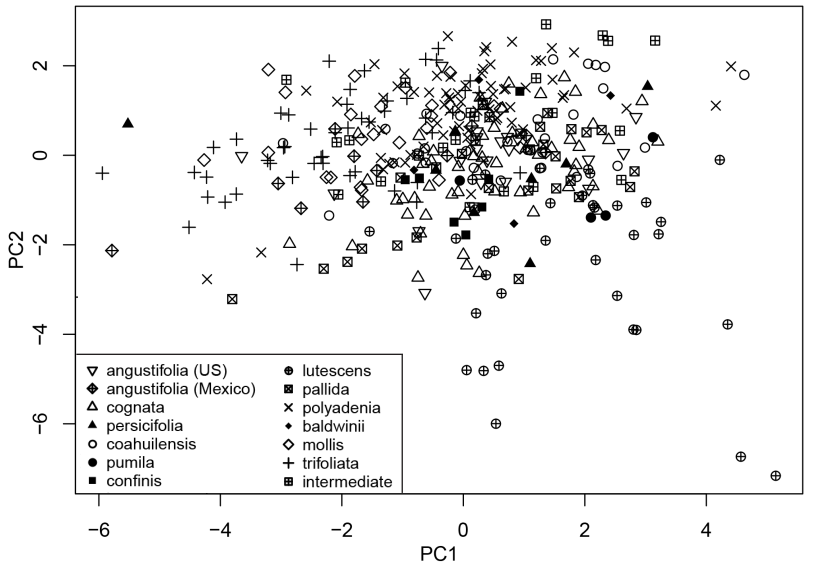

Fig. 3. Principal components analysis of all included specimens of *Ptelea trifoliata,* labeled according to assigned variety.

proportions of variability represented by the first 3 axes were respectively 0.1865, 0.1224, and 0.0896; thus, these together explained 39.84% of the total variation. In analyses of varieties within a subspecies (strictly defined in the case of *angustifolia*), the first 3 axes explained from 40.66% to 51.06% of total variation, being markedly higher in subsp. *coahuilensis* than in others. Thus, in regard to quantitative characters, variation appeared to be continuous and overlapping, and PCA analysis provided no meaningful basis for infraspecific classification.

Qualitative Observations

Qualitative characters recorded from fruiting specimens included bark color, leaf and

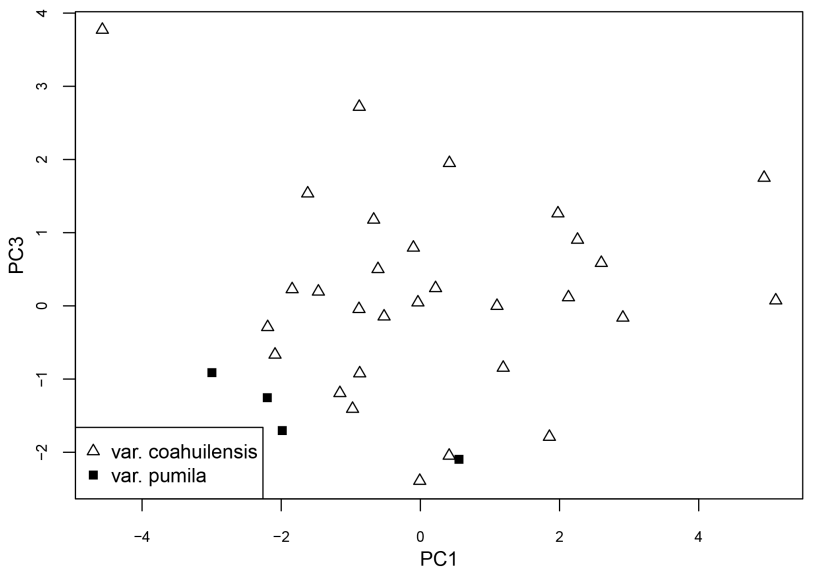

Fig. 4. Principal components analyses of specimens assigned to *Ptelea trifoliata* subsp. *coahuilensis.*

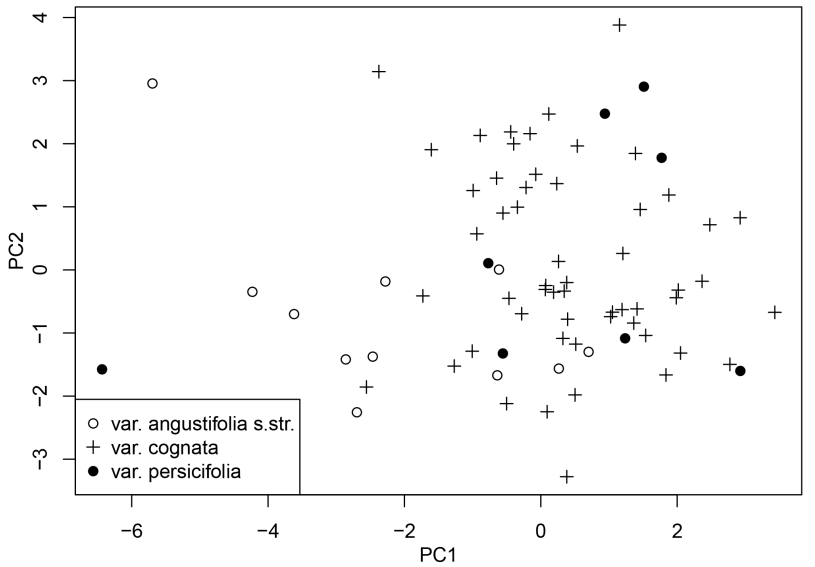

Fig. 5. Principal components analyses of specimens assigned to *Ptelea trifoliata* subsp. *angustifolia,* excluding villous U.S. specimens keying out as var. *angustifolia* and intermediates.

petiole indument, leaf margin, and the shape of the base of the fruit wing. Bark and indument characters affected or controlled taxonomic assignment for many specimens (e.g., specimens were placed into subsp. *pallida* if they had orange to whitish bark, and densely pubescent versus glabrous specimens then keyed out as different varieties). Thus, the question of whether the distribution of bark color or indument varied among infraspecific groups could not be independently examined. However, the difference in bark color between subsp. *pallida* and other subspecies seemed meaningful. Varieties *mollis* and *trifoliata* were

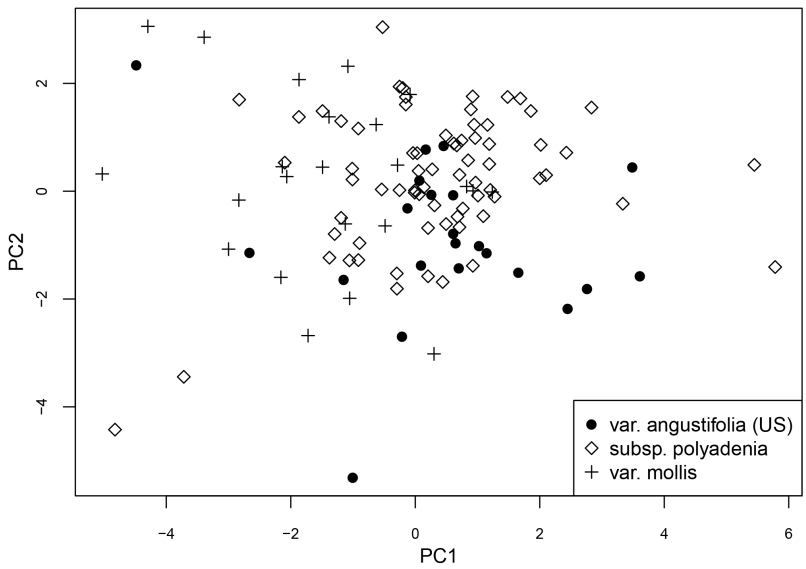

Fig. 6. Principal components analyses of specimens assigned to *Ptelea trifoliata* subsp. *polyadenia,* var. *mollis,* and villous U.S. specimens keyed as var. *angustifolia.*

generally distinguishable; however, some specimens that might be assigned to var. *mollis* have relatively sparse leaf trichomes borne mostly along veins, though the trichomes are usually longer than those present on sparsely pubescent specimens of var. *trifoliata.* There was also substantial variation in indument density in the *angustifolia–polyadenia* group.

In 2 subgroups, leaf margins varied from crenulate to (much less often) serrulate-dentate without consistently coinciding with other characters. Fruit shape did not appear useful. Bailey (1962) did not discuss fruit shape for all subgroups, but stated that fruit wing bases were usually rounded to cordate in var. *trifoliata,* versus cuneate in var. *mollis.* Cuneate fruit bases in mature fruits were relatively uncommon in var. *trifoliata,* where they were seen in a minority of southeastern specimens. However, most of the observed specimens of var. *mollis* also had rounded to cordate fruit bases. Similar variation can also be seen within other subgroups.

Observation of flowering specimens, most of which had male flowers, generally supported the belief that flowers are of limited utility, as flowers of both sexes (where available) were in most ways similar in morphology across all groups. Petals were more likely to be relatively broad in southern varieties, particularly in subsp. *coahuilensis,* but narrow petals were common in all groups. Characters that varied among, but also to a greater or lesser extent within, groups included indument, especially of the sepals and pedicels, and the presence, size, and conspicuousness of glands on the abaxial surface of the petals and sometimes also the sepals. Ovary development in "male" inflorescences, usually a rare aberration, appeared relatively common in subsp. *pallida*, but too few flowering specimens were available to determine its true frequency.

Sepals and pedicels were usually glabrous in var. *trifoliata,* but some specimens had pubescent sepals and pedicels; most of these were specimens with at least slightly pubescent leaves that might be thought intermediate with var. *mollis,* but one had glabrous leaves. Sepals and pedicels of specimens assigned to var. *mollis* ranged from glabrous to densely pubescent, and this was not clearly correlated with leaf and stem pubescence. These organs were consistently glabrous or sparsely pubescent in subsp. *pallida* and in var. *cognata,* but usually at least moderately pubescent (rarely to glabrous) in specimens keying out to subspp. *coahuilensis* and *polyadenia* and to var. *angustifolia* (either Mexican or northern).

Petal glands were usually absent or inconspicuous and small in specimens of subsp. *trifoliata* and Mexican var. *angustifolia,* but were usually large and conspicuous in subsp. *polyadenia*, northern specimens keying to var. *angustifolia,* subsp. *pallida,* and var. *cognata.* The latter groups also relatively often bear conspicuous glands on the sepals. Glands were variable in subsp. *coahuilensis;* only one flowering specimen of var. *persicifolia* was seen, which had relatively inconspicuous glands. Pubescence on the abaxial surface of the petals is usually confined to portions near the margins, but in Mexican var. *angustifolia,* pubescence on the central portion of the petal was unusually common.

Discussion

The lack of discontinuities in the variation seen within *Ptelea trifoliata* in principal component analyses supports Bailey's (1962) choice to lump Greene's (1905, 1906) many overdescribed species into a single species. On the other hand, PCAs proved to be inadequately sensitive for purposes of infraspecific classification. It is not expected that subspecies and varieties should be totally separated in such analyses, since they are not genetically isolated. However, quantitative analyses failed to even incompletely separate some groups of populations that by visual inspection are easily distinguished, while partially separating, on the basis of size variations, groups of populations that appear dubiously distinguished. Still, the inability to quantitatively differentiate subspecies and varieties makes it more plausible to argue that *Ptelea* remains overdescribed at infraspecific levels.

There are 2 potentially conflicting goals to consider in making recommendations regarding infraspecific classification. First, it is desirable to recognize disjunct populations of a species that are particularly genetically distinctive, especially if they have unusual ecological preferences, as these populations may be of conservation concern and obscuring their distinctiveness may impede conservation efforts. However, it is not necessary to formally recognize every local morphological variant. Second, it is desirable not to recognize variants as distinct that actually intergrade continuously, because it will be impossible to key out some or many specimens, reducing the utility and convenience of the classification. The status of each of the currently recognized taxa will be briefly considered with these criteria in mind.

Ptelea trifoliata subsp. *pallida* is probably the subspecies that is best differentiated from others. It is characterized both by distinctive orange to whitish bark (and usually pale leaves) and by distinctive chemistry (Bailey et al. 1971). A case might even be made for its recognition as a distinct species. A few apparent hybrid specimens involving other subspecies are known. Bailey (1962) distinguished 3 varieties of subsp. *pallida* by variations in indument, leaf breadth and leaf margins; they were said to be geographically separated, although the map provided was confusing and 2 occurrences mentioned in the key had no supporting specimens. Of these 3 varieties, var. *lutescens,* confined to northwestern Arizona and southern Utah, is most distinctive. It has narrower, sometimes extremely narrow leaflets, and the twigs and foliage are completely glabrous. Some of its specimens were notable outliers in overall PCAs (Figs. 1, 2).

Varieties *pallida* and *confinis* are distinguished primarily by the degree of pubescence on the leaves; the stated difference in leaf margins is not consistent, and the two are otherwise indistinguishable. Variety *pallida* occurs in northwestern Utah and has been collected in some of the same localities as var. *lutescens*, where the two appear usually distinct. Varieties *pallida* and *confinis* were not easily differentiated even by Bailey, who wrongly determined at least one specimen, and the leaf pubescence of specimens she determined as var. *confinis* is sometimes quite inconspicuous. The two are not sympatric, but their broader geographic distributions seem less distinct than previously reported. These 2 varieties are much more similar to one another than either is to var. *lutescens* (which is even reflected to some extent in PCAs; Fig. 3). Formal taxonomic recognition of minor differences among groups of populations may obscure the significance of larger differences that are recognized at the same level (e.g., the difference between var. *lutescens* on the one hand and vars. *confinis* plus *pallida* on the other). Thus, it is suggested that var. *confinis* be lumped into var. *pallida,* reducing the complexity of the classification.

The southern subsp. *coahuilensis* also is usually qualitatively distinguishable from the

remaining 3 subspecies; it has usually small and relatively coriaceous leaves with rounded to acute apices (rather than usually short-acuminate to cuspidate apices) and margins that are usually crenulate and, at least in mature fruiting specimens, revolute. Although var. *pumila* was closer to being separated from var. *coahuilensis* by PCA analysis than varieties of most subspecies (Fig. 4), this is because var. *pumila* is morphologically distinguished entirely by quantitative characters, specifically by having smaller, narrower, thinner leaves than is typical of var. *coahuilensis.* While var. *coahuilensis* is relatively widespread, var. *pumila* occurs only in a small part of Coahuila, and var. *coahuilensis* is known from some of the same exact localities. Coahuila is drier than much of the subspecies' range, and an unusually harsh local environment may restrict growth. It appears probable that var. *pumila* represents only one extreme of the subspecies' size range rather than a distinct taxon; thus, its continued recognition is not recommended. Though subsp. *coahuilensis* is normally restricted to Mexico, a single older flowering specimen consistent with this subspecies was seen from the Chisos Mountains in extreme southern Texas.

The remaining 3 subspecies and associated varieties seem to intergrade to a considerable extent. It is very clear that subsp. *polyadenia* intergrades into northern material that keys out as var. *angustifolia*, as defined by the combination of villous leaves and only moderately asymmetrical leaflet bases. Bailey (1962) considered true var. *angustifolia* to occur only in Mexico, terming the U.S. plants "intermediates" between subsp. *polyadenia* and var. *cognata,* and considered true subsp. *polyadenia* not to occur in Mexico, though recognizing some "hybrids." This was a problematic explanation for the observed variation because, for example, the U.S. "intermediates" are much more widely distributed than var. *cognata.* In the United States, specimens keying to var. *angustifolia* occur in most of the same range as specimens identified as subsp. *polyadenia,* though narrow near-symmetrical leaves are rare in the eastern part of the range, and there are many areas where both morphologies have been collected (e.g., the Jemez, Sandia, Magdalena, Sacramento, and Organ Mountains in New Mexico and the Hualapai and Sierra Ancha Mountains in Arizona). Study of herbarium specimens suggests that there is a continuous range of variation in leaflet development that may depend not only on genetics but on leaf maturity (on a given specimen, the largest leaves are usually broader and more asymmetrical) and perhaps local environment. Nor are there consistent differences in density of pubescence or leaf margin that appear correlated with either geography or leaf shape. Bailey (1962) noted that subsp. *polyadenia* could have extremely large glands, but gland size is not consistently correlated with leaf shape and extremes are rare. Hence, it seems clear that villous-leaved northern specimens keying as *angustifolia* must be placed within subsp. *polyadenia.*

The eastern subsp. *trifoliata* is distinguished from subspp. *polyadenia* and *angustifolia* by having sometimes very large and broad leaflets and usually small leaf glands. As a caveat, Bailey et al. (1970) reported that relatively large glands were common in the "oak-pine forest region" of its distribution, whereas rare individuals of western subspecies do have small glands. Within subsp. *trifoliata,* the varieties *trifoliata* and *mollis* are distinguished largely by indument and are both widespread, with ranges that overlap to a large extent. They do not seem to intergrade continuously in the regions where they co-occur, although both do display a range of variation in trichome density and length. The distinction between them is therefore justifiable.

It is not clear that the recognition of Florida specimens with small narrow leaflets as var. *baldwinii,* as favored by Ward (2001), is necessary; these may simply represent an extreme form of var. *trifoliata* that is unusually common in a portion of Florida. The relatively numerous narrow-leaved Florida specimens noted but not named by Bailey (1962) were said to have a terminal leaflet breadth-to-length ratio of (0.3–)0.35–0.45(–0.5). In this study, the upper part of that range was seen in some specimens of var. *trifoliata* from states other than Florida. Bailey et al. (1970) reported that 11% of individuals of var. *trifoliata* from Florida had a terminal leaflet breadth-to-length ratio of <0.35. Though that morphology was absent or very rare in most other populations, it did occur outside Florida: in particular, Bailey et al. reported that 8% of specimens from the "oak-hickory, interior highlands" subregion, including most of southern Missouri

and small portions of Arkansas and Oklahoma, had similarly narrow leaflets. In this study, a comparable breadth-to-length ratio was seen in a specimen of var. *mollis* from Illinois and approached in a specimen of var. *trifoliata* from Iowa. Too few narrow- or small-leafleted Florida specimens were available for this study to allow meaningful conclusions to be drawn from quantitative analyses. Nevertheless, formal recognition of this variety seems questionable simply because the only character that supports it also does appear at times in quite distant populations, while not appearing in all individuals from the putative range of var. *baldwinii.*

The range of var. *mollis* overlaps with that of subsp. *polyadenia*, which also often has densely villous leaves, but usually has larger leaf glands and larger and more conspicuous petal (and sometimes sepal) glands. Their distributions may be contiguous or overlapping in Oklahoma and Texas, with var. *mollis* extending far to the north and east and subsp. *polyadenia* west to western Arizona. Three specimens seen from Arkansas and the Oklahoma Territory, treated here as intermediates, had been determined by Bailey as subsp. *polyadenia,* though in fact, most glands were small enough to qualify them as var. *mollis.* No unambiguous specimens of subsp. *polyadenia* were seen from Arkansas. Some specimens of subsp. *polyadenia* seen from Oklahoma had huge leaf glands, but a few specimens from Arizona and New Mexico, far outside the range of var. *mollis,* had very small glands. The leaves of var. *mollis* are on average larger, but rare individuals of subsp. *polyadenia* do have leaflets to 11 cm. Meanwhile, var. *mollis* may have a smaller maximum leaf size toward the western edge of its range and could be seen as intergrading with subsp. *polyadenia.* Bailey (1962) suggested that var. *trifoliata* might have arisen as an intermediate between var. *mollis* and a narrow-leaved glabrous form (such as var. *baldwinii*), but it also seems possible that var. *mollis* is intermediate between var. *trifoliata* and subsp. *polyadenia.* PCAs incompletely separate subsp. *polyadenia* from both var. *mollis* and northern "var. *angustifolia*" (Fig. 6) and suggest (Fig. 2) that var. *trifoliata* might be the outlier relative to subsp. *polyadenia* and var. *mollis.*

There is, however, contrary evidence that *polyadenia* might be the most distinct of the three. In flowering specimens from Oklahoma and Texas, where the ranges of subsp. *polyadenia* and var. *mollis* abut, specimens with large leaf glands (identified as subsp. *polyadenia*) rather consistently have large floral glands, typical of *polyadenia,* while those with small leaf glands (identified as subsp. *mollis*) have absent or small and inconspicuous floral glands, suggesting that there is some real discontinuity between the 2 forms. Meanwhile, the relatively common specimens of var. *trifoliata* whose leaves are sparsely to moderately short-pubescent might be viewed as intermediates between glabrous or glabrate var. *trifoliata* in the purest sense and villous-leaved var. *mollis* (though it should be noted that sparsely pubescent specimens of var. *trifoliata* are known from areas where var. *mollis* does not occur). Detailed population genetic studies would be required to clarify the true relationships among these forms. The present classification, which implies that var. *mollis* has closer affinities to var. *trifoliata* than to subsp. *polyadenia,* is tentatively maintained for lack of evidence to the contrary.

Though northern specimens that are suggested by Bailey's (1962) key to have affinities to var. *angustifolia* are herein identified as subsp. *polyadenia,* villous-leaved Mexican specimens identified as var. *angustifolia* do appear to represent a distinct endemic form. These specimens often have large, yet usually not greatly asymmetrical lanceolate leaves and usually prominent leaf veins at maturity. The petal glands are absent or small, and the petals are unusually often sparsely hairy along the midvein, in contrast to the usually highly glandular petals of subsp. *polyadenia.* As the type of *P. angustifolia* Benth. is from Mexico, the Mexican populations represent "true" var. *angustifolia.* When the northern "*angustifolia*" specimens and intermediates that are herein transferred to subsp. *polyadenia* are excluded from PCA analysis of subsp. *angustifolia*, var. *angustifolia* sensu stricto appears somewhat different from vars. *cognata* and *persicifolia,* though overlapping in quantitative characters (Fig. 5).

The 2 remaining varieties in subsp. *angustifolia,* vars. *cognata* and *persicifolia,* have narrower distributions. The former is largely confined in the United States to the southeastern quarter of Arizona and the southwestern quarter (rarely to the northern extreme) of New Mexico, and also extends into Mexico. That

TABLE 3. Classification of *Ptelea trifoliata* suggested by the present authors, with synonymy confined to taxa recognized by Bailey (1962) and later authors.

Accepted taxa	Synonyms	Distribution
subsp. *trifoliata*		
var. *trifoliata*	var. *baldwinii*	Ontario to WI, N FL, TX, very rarely to Mexico (Guerrero)
var. *mollis*		VA to MI, IL, N FL, TX
subsp. *angustifolia*		
var. *angustifolia* sensu stricto		Mexico
var. *cognata*		SE AZ, adjacent NM, rarely to CO and Mexico (Sonora)
var. *persicifolia*		TX, OK
subsp. *coahuilensis*	var. *pumila*	Mexico; very rarely to extreme S TX
subsp. *pallida*		
var. *pallida*	var. *confinis*	W AZ to NM, UT, W TX, rarely to CO
var. *lutescens*		NW AZ (to S UT), mostly around Colorado River and its tributaries
subsp. *polyadenia*	= subsp. *polyadenia* sensu Bailey, plus northern populations of "var. *angustifolia*" and many "intermediate" specimens	TX to OK, NM, AZ; rarely to CO

range includes substantial regions where pubescent specimens are scarce, notably the Coronado National Forest. The transfer of var. *cognata* to subsp. *pallida* by Bailey and Bailey (1965) substantially reduced the distinctiveness of that subspecies and does not seem appropriate. Variety *persicifolia* is quite similar to var. *cognata*, but its distribution is quite different and it is usually distinguishable by its often acute leaf apices and crenulate to subentire, often revolute leaf margins. (The character of pale leaves with a "luster," as described by Bailey [1962], does distinguish some specimens but not all.) It is perhaps unclear whether the closest affinities of var. *persicifolia* are to other varieties of subsp. *angustifolia* or to subsp. *coahuilensis*, as the morphology of the leaflet apices and margins often resemble the latter. Thus continued recognition pending resolution of its actual relationships seems justifiable, even though it is not otherwise highly distinctive.

Classifications that recognize both subspecies and varieties are often needlessly cumbersome, but in this case Bailey's placement of varieties into subspecies seems useful both to manage the number of varieties involved and to emphasize the similarities among certain recognized varieties. The infraspecific classification that we recommend for *Ptelea trifoliata* (omitting synonymies other than taxa recognized by Bailey [1962]), with taxa recognized by Bailey but not herein given in synonymy, is presented in Table 3.

KEY TO REVISED CLASSIFICATION

This classification reduces *Ptelea trifoliata* from 5 subspecies and 11 varieties to 5 subspecies and 7 varieties, with, in our opinion, little loss of informative value and indeed a likely gain since the recognition of poorly differentiated taxa increases the difficulty of applying a classification in practice. A revised key to the infraspecific taxa whose recognition is recommended is provided below. Variation among some infraspecific taxa is almost continuous; this key will identify typical specimens, but not intermediate or highly aberrant specimens. See also Fig. 7 for illustration of typical leaf shapes of these taxa.

1a. Young twigs orange to stramineous; bark usually whitish to pale gray (subsp. *pallida*). 2

1b. Young twigs greenish to brown; bark brown. 3

2a. Twigs glabrous (sparsely pubescent at base of new growth only), leaves glabrous (sparsely pubescent when very young); terminal leaflet length at maturity mostly > 3× breadth; NW AZ extending into UT. . . . . subsp. *pallida* var. *lutescens*

2b. Twigs at least minutely pubescent; leaves short-tomentose to glabrous; terminal leaflet length at maturity mostly < 3× breadth; W AZ, S and central NM, S CO to S TX along Rio Grande . . . . . subsp. *pallida* var. *pallida*

3a. Terminal leaflet at maturity (1.5–)2.5–5.5(–7.1) cm, apex rounded to obtuse or acute (seldom partly cuspidate), margins usually crenulate and at maturity revolute; Mexico [very rarely extreme S Texas] . . . . . subsp. *coahuilensis*

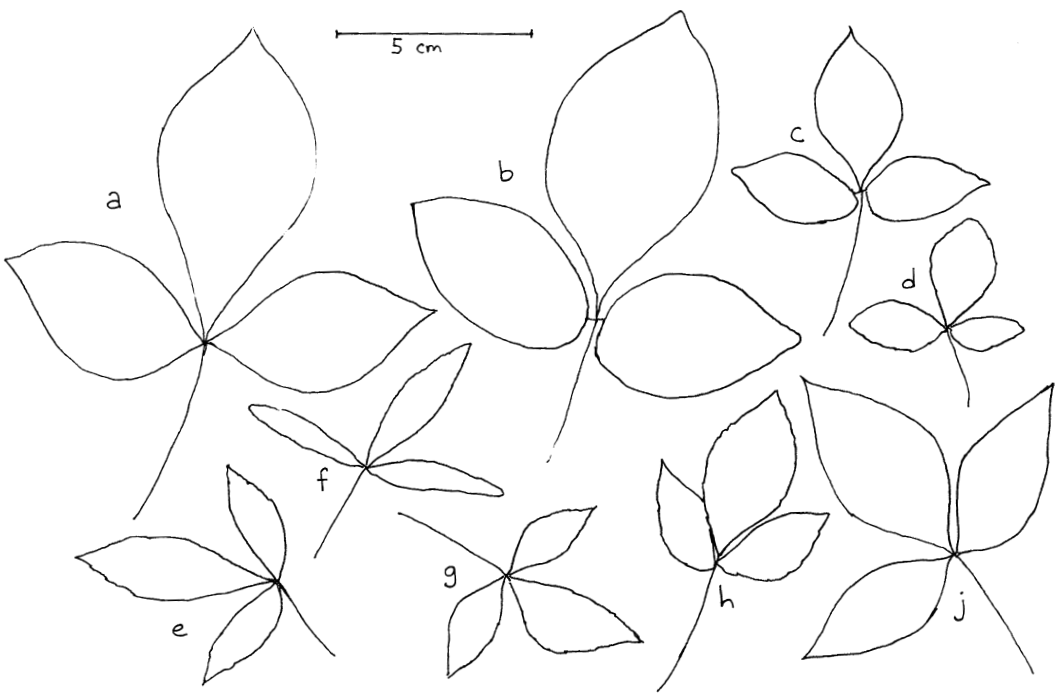

Fig. 7. Representative leaf shapes of infraspecific taxa recognized within *Ptelea trifoliata:* **a,** var. *trifoliata* (*Palmer 7440*); **b,** var. *mollis* (*Demaree 50821*); **c,** subsp. *polyadenia* (*Miller et al. 7528*); **d,** subsp. *coahuilensis* (*Weaver 2053*); **e,** var. *pallida* (*Atwood 5601*); **f,** var. *lutescens* (*Siker 15524*); **g,** var. *cognata* (*Toolin 2264*); **h,** var. *persicifolia* (*Thompson et al. 50453*); **j,** var. *angustifolia* sensu stricto (*Lyonnet 2259*). Scale bar: 5 cm.

3b. Terminal leaflet at maturity (3.5–)4.5–11(–15) cm, apex usually at least slightly short-acuminate to cuspidate with rounded tip (seldom partly acute to rounded), margins crenulate to serrulate-dentate or subentire, not (seldom minutely) revolute; widespread 4

4a. Lower leaf surface and petiole densely to moderately pubescent throughout, usually more or less villous 5

4b. Lower leaf surface and petiole glabrous to sparsely pubescent 7

5a. Leaflets lanceolate (seldom to elliptical); lateral leaflet bases only slightly asymmetrical; venation of mature leaves in fruit usually prominent and pale-colored; Mexico . . . . . subsp. *angustifolia* var. *angustifolia*

5b. Leaflets elliptic to broadly or narrowly elliptic, ovate to lanceolate, or somewhat obovate; bases of large well-developed lateral leaflets moderately to strongly asymmetrical; venation of mature leaves visible but not very conspicuous; E United States to NM, AZ [very rarely Mexico?] 6

6a. Leaves with glands usually <0.1 mm; leaves at maturity variable in size, relatively often large (terminal leaflets 8–12 cm); sepals and petals usually eglandular or with inconspicuous glands (rarely with large glands); SE United States to MI, IL, OK, TX [Mexico?] . . . . . subsp. *trifoliata* var. *mollis*

6b. Leaves with glands usually >0.1 mm; leaves at maturity usually of moderate size (terminal leaflets usually <8.5 cm, rarely to 11.5 cm); conspicuous glands usually present on petals and sometimes on sepals; OK, TX, NM, AZ [rarely CO] . . . . . subsp. *polyadenia*

7a. Leaves variable in size but often large at maturity, the terminal leaflets 4–15 cm, lateral leaflets 3.8–11 cm, petioles 3–12 cm; terminal leaflet length-to-breadth ratio (1.56–)1.7–2.5(–3.3); leaf glands usually <0.1 mm; widespread in E United States to Ontario, IA, TX [very rarely Mexico introduced?] . . . . . subsp. *trifoliata* var. *trifoliata*

7b. Leaves of moderate size, the terminal leaflets (3–)4–9(–10) cm, lateral leaflets 2.3–7.7 cm, petioles 1.5–6.5 cm; terminal leaflet length-to-breadth ratio usually 2.4–3.2(–3.9), rarely or aberrantly <2; leaf glands usually at least partly >0.1 mm; western United States, Mexico 8

8a. Terminal leaflets to 9(–10) cm, often with a distinct petiolule 2–5(–8) mm long; leaflet apices usually consistently short-acuminate; margins most often serrulate, rarely at all revolute; NM, SW AZ, Mexico . . . . . subsp. *angustifolia* var. *cognata*

8b. Terminal leaflets usually <7.5 cm, seldom with a long petiolule; leaflet apices often partly acute

or inconspicuously acuminate; margins usually crenulate to subentire, often minutely revolute; S Texas to OK. . . . . subsp. *angustifolia* var. *persicifolia*

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Appendix 2 on page 426.

APPENDIX 1. Fruiting specimens of *Ptelea trifoliata* included in phenetic analyses. The first name given for each group represents specimens' *a priori* assignment to infraspecific taxa for quantitative analyses in accordance with the treatment of Bailey (1962), except as described above. Subspecies to which varieties were assigned by Bailey are given in brackets, and the present authors' current preferred classification, where different, is given in brackets following the initially assigned name.

Ptelea trifoliata [subsp. *angustifolia*] var. *angustifolia* sensu stricto

MEXICO.—**Jalisco:** Barranca a 5 km de carretera a Barranca de Santa-Clara, Atemajac de Brizuilas, 1800 m, 14 Aug 1987, *Díaz Luna 18850* (MO); road to Yahualica, ca. 20 mi N of Tepatitlan, N side of Rio Verde, 1700 m, 30 Sep 1952, *McVaugh et al. 13273* (US); near El Molino (ca. 25 mi SE of Guadalajara) overlooking Acatlán and basin of Laguna de Atotonilco, 1650 m, 2 Oct 1952, *McVaugh et al. 13305* (US); barranca of Rio Verde, ca. 20 mi N of Tepatitlán on road to Yahualica, 1450 m, 27–28 Aug 1958, *McVaugh et al. 17407* (US, US); summit of ascent 8 mi SE of Jalostotitlán, road to San Miguel el Alto, 1900 m, 30 Aug 1958, *McVaugh et al. 17531, 17532* and *17534* (all US); 1–2 mi E of Tapalpa, 2100–2200 m, 30 Oct 1960, *McVaugh et al. 20511* (US). **Zacatecas:** ridge 2 mi N of Potrero de las Yeguas, 13 mi S of Valparaíso, 2000 m, 5 Sep 1958, *McVaugh et al. 17772* (US); 5 mi NE of Mesquitula near Rio Juchilipa, 3500 ft, 11 Aug 1969, *Taylor & Taylor 6087* (US).

Ptelea trifoliata [subsp. *angustifolia*] var. *angustifolia* "northern" [*Ptelea trifoliata* subsp. *polyadenia*]

UNITED STATES.—**Arizona:** S of Prescott, 2 Jun 1944, *Clark 11774* (UNM); Gila Co., E side of Pine Mt. 8 mi W of Roosevelt, 6000 ft, 17 Jun 1952, *Dickerman 426* (ARIZ); 5 mi W of Chloride, 12 Oct 1909, *Goldman 1767* (US); McMillenville, 4500 ft, 29 May 1916, [*Goldman*] *2674G* (ARIZ); Hualpai Mts., 6300 ft, 5 Oct 1917, *Goldman 2985* (US); Gila Co., Sierra Ancha Mts., near junction of Workman and Reynolds Creeks, 4000 ft, 5 Jun 1947, *Gould 4356* (ARIZ, US); Huachuca Mts., 29 Jun–5 Jul 1903, *Griffiths 4839* (US). **New Mexico:** Torrance Co., Manzano Mts., Priest Canyon, 3.5 mi S and 0.5 mi W of Manzano Peak (1.6 mi NW of windmill and road fork), 7000 ft, 1 Sep 1963, *Bedker 1481* (UNM); Catron Co., Gila Cliff Dwellings National Monument, Cliff Dweller Trail, UTM zone 12, 754681E 3680016N, 1780 m, 19 Jul 2001, *Bennett 900* (ARIZ); Jemez Mts., Lower Frijoles Canyon, 6 Jun 1941, *Castetter "7015"* (UNM); Rito de los Frijoles, Aug 1912, *Cockerell 15* (US); Dona Ana Co., Organ Mts., Dripping Springs, 24 May 1952, *Dunn 2736* (UNM); Catron Co., ravine below Gila Cliff Dwellings, 6000–6500 ft, 5 Jul 1952, *Dunn 8345* (UNM, UNM); Otero Co., Sacramento Mts., Lower Alamo Canyon, S34, T16S, R10E, 5000 ft, 8 Jun 1977, *Fletcher 2090A* (UNM); Rio Arriba Co., near Santa Fe Forest, Abiquiu Cr., 6400 ft, 20 Jul 1967, *Gierisch 3258* (UNM); Bernalillo Co., road to Sandia Peak 1.8 mi N of Sandia Park, 7575 ft, 8 May 1949, *Gordon & Norris 53* (UNM); Bear Cañon, 24 Sep 1897, *Herrick 1042* (US); Sangre de Christo Mts., near Santa Fe Ski Basin, 2 Aug 1961, *Jones s.n.* (UNM); Socorro Co., Magdalena Mts., Sawmill Canyon, 6600 ft, 16 Jun 1973, *Hutchins 4159* (UNM); Santa Fe Co., Santa Fe Ski Basin, 3 Aug 1961, *Lee s.n.* (UNM); Grant Co., S end of Black Range, Devils's Pass, Gallina Creek, 11 Oct 1904, 7600 ft, *Metcalfe 1479* (UNM); Socorro Co., San Mateo Mts., Springtime Canyon, 1 Nov 1958, *Todd 52* (MO); Bernalillo Co., West Sandia Mts., Bear Canyon 1.5 mi E of trailhead, T11N R5E, 7200 ft, 23 Sep 2002, *Vollenweider 26* (UNM); Chisos Mts., 6 Jul 1937, *Warnock 867* (US); Bernalillo Co., Sandia Mts., Cienega Canyon, 8 Oct 1960, *Wright 61* (UNM). **Oklahoma:** N. Laura, 14 Jun 1930, *Clark 2891* (OKL); Muskogee Co., S20, T15N, R20E, 22 May 1927, *Little 2* (OKL, OKL); Greer Co., N of Granite, flood plain of creek near Twin Lakes. 6 Jul 1941, *Sherrill 2985* (OKL); Woods Co., near Alva, 29 May 1913, *Stevens 683* (OKL, US).

Ptelea trifoliata [subsp. *angustifolia*] var. *cognata*

MEXICO. **Sonora:** Tepopa, Sierra Saguaribo, 3000–3500 ft, 16–18 Oct 1961, *Gentry et al. 19334* (ARIZ).

UNITED STATES.—**Arizona:** Verde, canyon, 1 Sep 1937, *Allen 1137* (ARIZ); Black Canyon Rd. 4 mi E of Dewey, 20 Aug 1935, *Benham s.n./1748* (ARIZ, ARIZ); Pima Co., Rincon Mts., along Rincon Peak trail, 6000 ft, 1 Aug 1982, *Bowers & McLaughlin R437* (ARIZ); Graham Co., Santa Teresa Mts., Coronado National Forest, Laurel Canyon, center S21, T6S, R20E, side canyon to E, 4750 ft, 23 May 1998, *Buegge 250* (ARIZ); Pinal Co., Southern Belle Canyon just W and S of stamp mill, 24 Jan 1953, *Caldwell 174* (ARIZ); Santa Cruz Co., Peck Canyon, along cliff base 0.5 mi above last ranch house, 2 May 1972, *Cummins s.n.* (ARIZ); Graham Mts., 5000 ft, 24 Jul 1914, *Goldman 2328* (US); Blue River, 5000 ft, 30 Aug 1914, *Goldman 2398* (US); Santa Catalina Mts., 4500 ft, 22 Aug 1915, *Goldman 2521* (US); Coyote Mts., 4000 ft, 2 Sep 1915, *Goldman 2544* (US); White Mts., Black River, lower crossing, 27 Jul 1910, *Goodding 690* (ARIZ, US); Huachuca Mts., The Reef, 26 Sep 1949, *Goodding 732-49* (ARIZ); Eureka Springs, 18 Jun 1912, *Goodding 1066* (US); Santa Catalina Mts., The Basin, 11 Jul 1916, *Harris C16290* (ARIZ, US); road of north end of [Pinaleno] Mts. from [Klondyke], 16 Jun 1937, *Hinckley 6531* (ARIZ); Gila Co., Sierra

Ancha Wilderness Area in Tonto National Forest, along Trail 144 below spring near Pueblo Mine, NE 1/4, S22, T6N, R14E, 6400 ft, 5 Sep 1993, *Imdorf 1416* (ARIZ); Greenlee or Graham Co., Eagle Creek, 5250 ft, 11 Aug 1935, *Kearney & Peebles 12225* (ARIZ, US); Pima Co., Baboquivari Mts., South Canyon, 3600–4000 ft, 31 Aug 1940, *Kearney & Peebles 14958* (ARIZ, US); Santa Catalina Mts., Mt. Lemmon, Jul 1905, *Lemmon & Lemmon s.n.* (ARIZ); Baboquivari Mts., 9 Jun 1936, *Purchase 3091* (ARIZ); Santa Cruz Co., Sycamore Canyon, Godding Research Natural Area, 3500 ft, 23 Aug 1974, *Reeves & Lehto 1160* (US); Graham Co., Pinaleno Mts., Frye Canyon, 8500 ft, 14 Sep 1914, *Shreve 4327* (ARIZ); Pima Co., Western Ajo Mts., Organ Pipe monument, 1 Apr 1976, *Skaggs & McCarten 2127* (ARIZ); Coronado Trail near Metcalf, 23 Jun 1933, *Taylor s.n.* (ARIZ); Kirkland, 1916, *Taylor 20* (US); Santa Rita Mts., Stone Cabin Canyon, 15 Jul 1903, *Thornber 311* (ARIZ, ARIZ, US); same loc., same date, *Thornber 4207* (ARIZ, ARIZ); Graham Mts., 7–13 Sep 1914, *Thornber & Shreve 7744* and *7934* (ARIZ); Santa Cruz Co., Sycamore Canyon, edge of Ruby Mts. WNW of Nogales near Ruby off Hwy. 289, 3800–4000 ft, 5–6 Sep 1977, *Thorne & Tilforth 59552* (ARIZ); Pima Co., Baboquivari Mts., S24 and S25, R7E, T19S, along road 1.5 mi below ranch house, 4300 ft, 24 Jul 1979, *Toolin 394* (ARIZ). **Colorado:** Cañon City, *Brandegee 1874* (MO). **New Mexico:** Otero Co., Sacramento Mts. 5 mi NE Alamogordo, Fresnal Canyon bottom W of Fresnal Cave, 5500 ft, 4 Jul 1970, *Bohrer 1361* (ARIZ); Catron Co., bank of San Francisco River 2 mi below Frisco Hot Springs, 4000 ft, 10 Jun 1970, *Bostick & Niles 1014* (ARIZ); Catron Co., Frisco, 7 Aug 1952, *Castetter & Dittmer "7012"* (UNM); E of Los Alamos, 3 Jul 1951, *Dittmer & Castetter "7013"* (UNM); Taos Co., 1 mi S Talpa, NW Hwy. 3, 7100 ft, 3 Aug 1961, *Dixon 239* (UNM); Bern[alillo] Co., Cibola Forest, Juan Tabo campground, SE 1/4, S2, T11N, R4E, 13 Sep 1977, *Gordon s.n.* (UNM); Socorro Co., Magdalena Mts., above head of N fork of Water Canyon, 8200 ft, 11 Jul 1959, *Martin 3313* (UNM); Hidalgo Co., Indian Creek Canyon, Animas Peak, 5840 ft, 27 Oct 1960, *Martin 4557* (UNM); Grant Co., summit of Mule Creek Rd., 12 Aug 1935, *Moeller 224* (ARIZ, UNM); sine loc., 17 Jul 1880, *Rusby s.n.* (US); Torrance Co., Manzano Mts., ridge S of Capilla Peak, NW 1/4, S3, T5N, R5E, 2750 m, 7 Jul 1999, *Sivinski 4933* (UNM); Grant Co., 15 mi SW of Silver City in Burro Mts., 11 Sep 1963, *Zarlingo 33* (UNM).

Ptelea trifoliata [subsp. *angustifolia*] var. *persicifolia*

UNITED STATES.—**Oklahoma:** Kingfisher Co., Huntsville, 5 Jun 1896, *Blankinship s.n.* (MO); Comanche Spring, New Braunfels, etc., Jun 1851, *Lindheimer 695* (US); Comanche Co., Quanah Lake, S6, T2N, R13W, 20 May 1989, *Thompson et al. S0453* (MO). **Texas:** Coke Co., Bronte, 1 Jul 1916, *Palmer 10354* (MO); Nolan Co., near Blackwell, 15 Jun 1928, *Palmer 34605* (MO); upper Guadalupe, Jun 1884, *Reverchon 1506* (MO); Bejar Co., Brackenridge Park, 12 Apr 1919, *Schulz 52* (US); McLennan Co., hill near N Bosque River, 14 Jul 1931, *Wolff 3000* (US).

Ptelea trifoliata subsp. *angustifolia* var. "intermediate"

MEXICO.—**Chihuahua:** San Luis Mts., Devil's Cañon, 6200 ft, 12 Aug 1908, *Goldman 1423* (US). **Hidalgo:** Zimapan District, Barranca de San Vicente near km 238 on highway between Zimapán and Jacala, 1800–2000 m, 9 Aug 1948, *Moore & Wood 4420* (US).

UNITED STATES.—**New Mexico:** Bernalillo Co., 3 mi E Albuquerque, Tijeras arroyo, 5400 ft, 24 Aug 1966, *Britt 2* (UNM); Catron Co., Gila National Forest, adj. Whitewater Creek along catwalk National Recreation Trail, S5, T10S, R19W, 5200 ft, 6 Jul 1994, *Huff & Christy 1591* (ARIZ); Gila Co., Sierra Ancha, Workman Creek Falls, 6600 ft, 16 Jul 1958, *Johnson s.n.* (ARIZ); Los Alamos Co., Pajarito Canyon, T19N, R6E, 6500–7000 ft, 17 Jul 1979, *Tierney & Foxx 362* (UNM); Sandoval Co., canyon bottom at W base of Sandia Mts., East Mesa, E of Coronado Airport, 21 Sep 1963, *Walton 4* (UNM); Lincoln Co., vicinity of Gilmores Ranch on Eagle Creek, 27 Jul 1901, *Wooton s.n.* (US). **Texas:** Guadalupe Mts., Culberson Co., Frijole Post Office, 6000 ft, 1 Aug 1930, *Grassl 145* (ARIZ); Bexar Co., 1903, *Jermy s.n.* (MO).

Ptelea trifoliata [subsp. *coahuilensis*] var. *coahuilensis* [*Ptelea trifoliata* subsp. *coahuilensis*]

MEXICO.—**Chihuahua:** Santa Eulalia, 1300 m, 28–29 Apr 1908, *Palmer 126* (MO); Eulalia Hills, 1 Mar 1885, *Wilkinson 23* (US). **Coahuila:** 29 air miles WNW Cuatro Cienegas, N of Sierra de la Madera, ca. 5 mi W Rancho Cerro de la Madera in Cañon Los Pozos, 227°09′ N, 102°30′ W, 1500 m, 13 Aug 1976, *Henrickson & Prigge 15344* (US); Sierra Mojada Mts., 19 Apr 1897, *MEJ 105* (MO); Municipio de Castanos, Puerta de San Lazaro, Sierra de San Lazaro, 30 Aug 1939, *Muller 3052* (US); Carneros, Sierra Madre Oriental, 2100–2300 m, 12 Jul 1934, *Pennell 17301* (US); ravines, battlefield of Buena Vista near Saltillo, 18 Jul 1888, *Pringle 1937* (MO); along Mexico Hwy. 54, Sierra de Carneros, 0.7 mi W of highway, 0.5 mi S of Est. Carneros, ca. 23 mi S Saltillo, 5 Aug 1971, *Reveal et al. 2618* (US); uncertain locality [annotation indicates labels may have been switched], *Wynd & Mueller 384* [or *156*] (US). **Durango:** San Ramón, 21 Apr–18 May 1906, *Palmer 66* (MO). **Nuevo Leon:** near Iturbide, Linares–Galeana Hwy., 13 May 1950, *Hernandez X.*

& Villar B. 5265 (US); San Pedro Iturbide, 1450 m, 12 May 1980, *Hinton et al. 17792* (ARIZ); Sierra Madre above Monterrey, 3000 ft, 2 Jul 1907, *Pringle 10376* (US); Cerro de la Silla, near Monterrey, 5200 ft, 23 Jun 1939, *White 1469* (US). **Oaxaca:** 13 km SW de San Francisco Coixtlahuaca, carretera a San Agustín Atenango, distr. de Silacayoapan, 1890 m, 18 Jun 1982, *Cedillo Trigos & Torres 1446* (US). **Puebla:** Tehuacan (meseta del Riego), 7 Aug 1938, *Lyonnet 2258* (US); N of Tehuacan on Hwy. 150, 0.5 mi N San Lorenzo NW of highway, 7 Aug 1978, *McCarten et al. 2960* (US); near Tehuacan, 2 Sep 1906, *Rose & Rose 11277* (MO, US, US), *11277b* (US) and *11277d* (US). **San Luis Potosí:** 20–35 mi E of San Luis Potosi along road to Rio Verde, 5500–6800 ft, 16–18 Jul 1963, *Gentry et al. 20177* (ARIZ, US); Catorce District, near Santa Ana mine, 9000 ft, 4 Jun 1950, *Robinson 83* (US); San Luis Potosi, Sierra near Villar, 1600 m, May 1932, *von Rozynski 367* (US); near Potrero, 6800 ft, 8 Sep 1939, *Shreve 9349* (ARIZ, US). **Sonora:** Sierra de Alamos, N and below summit of Aduana Peak, 26°58′20″ N, 108°59′30″ W, 1700 m, 27 Nov 1993, *Steinmann & Bertelson 93-452* (ARIZ). **Tamaulipas:** Road between Miquihuana & Doctor Arroyo [Nuevo Leon], 15 Jun 1898, *Nelson 4508* (US).

Ptelea trifoliata [subsp. *coahuilensis*] var. *pumila* [*Ptelea trifoliata* subsp. *coahuilensis*]

MEXICO.—**Coahuila:** Sierra Mojada, Canyon Calabasas, 5500–6500 ft, 7 May 1973, *Gentry & Engard 23235* (US); San Lorenzo Canyon, 6 mi SE of Saltillo, 21–23 Sep 1904, *Palmer 391* (MO); Sierra Pata Galana, Jul 1910, *Purpus 4960* (MO); Buena Vista, battlefield, 22 May 1847, [sine coll.] *745* (US).

Ptelea trifoliata [subsp. *pallida*] var. *confinis* [*Ptelea trifoliata* var. *pallida*]

UNITED STATES.—**New Mexico:** Torrance Co., Manzano Mts., Lower Trigo Canyon, 6700 ft, 20 Jul 1963, *Bedker 1228* (UNM); Socorro Co., N edge of North Oscuro Peak, 7000 ft, 25 Jul 1948, *Dunn & Lint 4042* (UNM). **Texas:** El Paso Co., Franklin Mts. near El Paso, Altura Park, 10 Jul 1911, *Barlow s.n.* (US); El Paso Co., Franklin Mts., 6 mi N of El Paso, 13 May 1946, *Cory 52976* (US); El Paso Co., E side of Franklin Mts., side canyon of Hondo Pass, 4300 ft, 30 May 1964, *Niles 380* (ARIZ); El Paso Co., vicinity of El Paso, canyons of Mt. Franklin, 1911, *Stearns 172* (US).

Ptelea trifoliata [subsp. *pallida*] var. *lutescens*

UNITED STATES.—**Arizona:** Coconino Co., W side of Kaibab Mt., White Pockets Canyon, 29 Jul 1973, *Atwood 5601* (US); Coconino Co., Havasupai Canyon, 12 Jul 1940, *Clover 5044* (ARIZ, US); Mohave Co., rim of canyon Tuweep, N exposure, 4500 ft, 13 Jun 1941, *Cottam 8625* (US); Coconino Co., Kaibab National Forest, Jumpup Canyon near ranger station, 5200 ft, 31 Aug 1945, *Darrow 2984* (ARIZ); Grand Canyon, Bright Angel Trail, 26–28 Sep 1913, *Eastwood 3669* (ARIZ); Grand Canyon, Kaibab Trail to Roaring Springs, 23 Jun 1933, *Eastwood & Howell 1041* (US); same loc., 22 Sep 1938, *Eastwood & Howell 7082* (US); Coconino Co., Big Spring ranger station, Kaibab National Forest, 2100–2500 m, Jul 1914, *Eggleston 10237* (US); Grand Canyon, Bright Angel Trail, 6000 ft, 31 May 1913, *Goldman 2080* (US); same loc., 4800 ft, 19 Aug 1913, *Goldman 2222* (US); Grand Canyon, Jun 1916, *Goodding 46* (ARIZ); Coconino Co., Kaibab Plateau, Jumpup Canyon, 14 Jun 1949, *Goodding 277-49* (ARIZ); Grand Canyon, 1500–2100 m, 30 Jun 1913, *Hitchcock 77½* and *86* (US); Coconino Co., Grand Canyon, Tapeats Creek Canyon, 0.25 mi below Thunder Spring, 30 air mi NW of Grand Canyon Village, 5500 ft, 11 May 1971, *Holmgren et al. 15631* (ARIZ); Coconino Co., Grand Canyon National Park, Hualpai Canyon, 22 May 1940, *Howell 26388* (ARIZ); Nagle's Ranch, 7600 ft, 15 Sep 1894, *Jones 6048* (MO); Grand Canyon National Park, head of Cremation Canyon, 5000 ft, 18 May 1981, *Martin s.n.* (ARIZ); Mohave Co., Grand Canyon National Monument, head of Hack Canyon, tributary to Kanab Creek, 6 Jun 1968, *Mason et al. 2793* (ARIZ); Coconino Co., Grand Canyon, ca. 1 mi up Kwagunt Creek, Mile 56 R, 2920 ft, 12 May 1973, *Phillips s.n.* (ARIZ); Coconino Co., Colorado River, L bank, river mi 19, 31 May 1976, *Suttkus 76-23-23* (ARIZ); Coconino Co., Hualapai switchbacks, 19 May 1976, *Theroux 1696* (ARIZ); Grand Canyon, Grand View Trail, 22 Aug 1907, *Thornber & Hockdoerffer 2948* (ARIZ); Grand Canyon, Bright Angel Trail, 16–18 Aug 1916, *Thornber 8270* (ARIZ); same loc., 17 Aug 1916, *Thornber 8517* (ARIZ); Grand Canyon, Grand View Trail, 14 Aug 1916, *Thornber 8456*, *8468*, *8500*, *8508*, and *8524* (all ARIZ); Grand Cañon, 11 Jul 1892, *Toumey 1083* (ARIZ); Coconino Co., Havasupai Canyon, 22 May 1941, *Whiting 4942* (ARIZ).

Ptelea trifoliata [subsp. *pallida*] var. *pallida*

UNITED STATES.—**Arizona:** Mohave Co., Pigeon Canyon, S2, T33N, R13W, 5200 ft, 24 Aug 1978, *Coombs & Bundy 2700* (ARIZ); Mohave Co., Rattlesnake Canyon, S3, T35N, R13W, 6 Sep 1978, *Coombs & Bundy 2749* (ARIZ); Mohave Co., upper Grand Wash Cliff vicinity, S16, T36N, R16W, 27 Jun 1979, *Coombs & Bundy 2874* (ARIZ); Mohave Co., Hurricane Cliffs, S29, T35N, R9W, 27 Aug 1979, *Coombs & Bundy 2989* (ARIZ); Yavapai Co., Harcuvar Mts., S33, T9N, R10W, 4160 ft, 16 May 1979, *Fischer 6495* (ARIZ); Mohave Co., NW 1/4, SE 1/4, S35, T34N, R10W, Trail Canyon, N end above jct. with Parashant Canyon, 1525 m, 18 May 1993, *Franklin & Atwood 7616* (MO); [Harquahala] Mts., 5000 ft, 14 Oct 1917, *Goldman 3006* (US);

Yavapai Co., N Jerome, 31 May 1947, *Goodding 28-47* (ARIZ); Coconino Co., Kaibab Plateau, Big Springs Canyon, 28 Aug 1948, *Goodding 120-48* (ARIZ); Grand Canyon, 1 Jul 1915, *Hitchcock s.n.* (US); Grand Canyon, 1500–2100 m, 30 Jun 1913, *Hitchcock 87* (US); Mohave Co., Shivwits Plateau, Whitmore Canyon, Paw's Pocket, S35, T33N, R9W, 3900 ft, 21 May 1977, *Leary 1822* (ARIZ); Coconino Co., Kaibab Plateau, Moquitch Canyon, 6400 ft, 12 Jul 1966, *Niles & Reese 818* (ARIZ); sine loc., 1869, *Palmer s.n.* (US, US); Grand Canyon, Bright Angel Trail, 16–18 Aug 1916, *Thornber 8297* (ARIZ); Buckskin Mts., near Ryan, 27 Jun 1909, *Tidestrom 2315* (US); Camp Verde, 18 Aug 1891, *Toumey s.n.* (ARIZ); Yuma Co., Harquahala Mts., Squaw Canyon, 26 Sep 1955, *Wright 66-55* (ARIZ). **Colorado:** Canon City, Grape Creek Cañon, 28 Jun 1876, *Popenoe s.n.* (US); Canyon City, 1 Aug 1896, *Shear 3766* (US). **New Mexico:** Dona Ana Co., Mesilla Valley, Pyramid Peak, 1600 m, 21 Aug 1930, *Fosberg 53810* (US); Dona Ana Co., San Andres Mts., Salt Canyon, 1975, *Sandoval 289* (UNM); Dona Ana Co., S end of Organ Mts., Bishop's Cap, 21 Sep 1974, *Van Devender & Everitt s.n.* (ARIZ); Dona Ana Co., Organ Mts., Bishop's Cap, 21 Oct 1906, *Wooton s.n.* (UNM); Doña Ana Mts., E side, 28 Oct 1906, *Wooton s.n.* (UNM); Dona Ana Co., San Visitas, 22 May 1913, *Wooton s.n.* (US).

Ptelea trifoliata subsp. *polyadenia*

UNITED STATES.—**Arizona:** Chiricahua Mts., main crest W of Paradise, NE aspect, 7500 ft, 16 Aug 1906, *Blumer 1246* (ARIZ); Prescott Forest Reserve, 1901, *Cohoun 1* (US); Gila Co., Matzatzal Mts., Barnhart Pass, 1500–1710 m, 13 May 1935, *Collom s.n.* (ARIZ); Coconino Co., Coconino National Forest, Westfork Canyon of Oak Creek Canyon, 4600 ft, 20 Jun 1959, *Demaree 41223* (ARIZ); Oak Creek, 5400 ft, 24 Jul 1913, *Goldman 2177* (US); Crown King, 6700 ft, 27 Aug 1916, [*Goldman*] *2787* (ARIZ); Mohave Co., Hualpai Mt., 6400 ft, 19 Sep 1935, *Kearney & Peebles 12696* (ARIZ, US); Mohave Co., Hualpai Mt., 6400 ft, 19 Sep 1935, *Kearney & Peebles 12731* (ARIZ, US); Yavapai Co., 10 mi SW of Prescott, 5625 ft, 16 Jul 1938, *Kearney & Peebles 13975* (ARIZ); Pima Co., Baboquivari Mts., South Canyon, 3600–4000 ft, 31 Aug 1940, *Kearney & Peebles 14929* (ARIZ); above Superior, 11 Jul 1926, *Peebles et al. 2329* (ARIZ); Yavapai Co., Schnebly Hill Rd. ca. 5 mi W of Arizona I-17, 29 Jun 1973, *Pinkava et al. 17709* (US); Yavapai Co., Prescott, 29 Jul 1937, *Purchace 420* (ARIZ); 12 mi SW of Jerome, 6000 ft, 19 Aug 1916, *Taylor 95* (US); Flagstaff, in Walnut Canyon, Oct 1912, *Thornber s.n.* (ARIZ); Santa Cruz Co., Atascosa Mts., Romanote Canyon, just above canyon bottom near fork with red rock spire at junction, SW 1/4, S9, T22S, R12E, 1500 ft, 14 Jun 1986, *Toolin 2188B* (ARIZ); Mohave Co., Hualapai Mts., Apr–May 1969, *Whitehead s.n.* (ARIZ); Salt River (Hwy. 60), 26 May 1935, *Whitehead 1283* (ARIZ); Oak Creek Canyon, 5500 ft, 2 Jul 1935, *Whiting & Sanders 756/919* (ARIZ, ARIZ, UNM). **New Mexico:** Jemez Mts., N of Jemez Pueblo, 17 Jul 1936, *Carter G-335* (UNM); Socorro Co., first canyon S of Nogal Canyon on Rt. 85, 18 Jun 1955, *Castetter 8359* (UNM); Sacramento Mts., Cloudcroft & Ruidoso area, Bailey Canyon, 3 Jul 1949, *Castetter & Dittmer "7017"* (UNM); lava break W of Pierce River and N of Rt. 6, 9 Jul 1952, *Dittmar "7010"* (UNM); Otero Co., Cloudcroft, Lincoln Forest, 2300–2700 m, 1–8 Jul 1918, *Eggleston 14538* (US); Harding Co., Canadian River bottom below Mills Canyon Campground, NW 1/4, S35, T21N, R24E, 5050 ft, 30 Jun 1981, *Fletcher 5296* (UNM); Big Hatchet Mountains, 7600 ft, 20 Jul 1908, *Goldman 1326* (US); Organ Mts., 25 May 1898, *Herrick 231* (US); Grant Co., S end of Black Range, Iron Canyon N of Mimbres, 22 Jul 1959, *Jones s.n.* (UNM); Socorro Co., Water Canyon Campground, Magdalena Mts. 20 mi W of Socorro, 28 Oct 1967, *Kimmons 1* (UNM); Bernalillo Co., E side of Sandia Mts., 2 Jan 1965, *Martin & Baca s.n.* (UNM); Mescalero Indian reservation, 10 Jun 1936, *Plumb s.n.* (UNM); Sacramento Mts., Cloudcroft, 8500 ft, 19 Aug 1916, *Rehder 375* (US); Organ Mts., Van Patten's, 11 Jun 1906, *PCS s.n.* (US); Guadalupe Mts., near Sitting Bull Falls, 12–20 Aug 1924, *Standley 40742* (US); Catron Co., White Water Canyon, 14 May 1960, *Martin 3992* (UNM); Grant Co., Hog Canyon, 6000 ft, 2 Jul 1962, *Turner 103* (UNM); Lincoln Co., White Mts., Ruidoso Creek, 6600 ft, 30 Jun 1895, *Wooton s.n.* (UNM, US); Sandoval Co., Sandia Mts., Placitas, 3 Aug 1910, *Wooton s.n.* (US); Lincoln Co., White Mts., 7400 ft, 25 Aug 1907, *Wooton & Standley 3438* (US). **Oklahoma:** Latimer Co., N Laura, 14 Jun 1930, *Clark 2891* (UNM); Woodward Co., 15 mi N of Woodward, bottom of Bent's Canyon, 23 Jul 1934, *Goodman 2188* (OKL); Cimarron Co., N slope of Black Mesa, 1 Jun 1947, *Goodman 4353* (OKL); Roger Mills Co., Antelope Hills 5 mi NE of Durham, S9, T16N, R25W, 18 Jun 1973, *Goodman & Lawson 8407* (OKL); Murray Co., Arbuckle Mts., plateau on E side of Hwy. 77 opposite Turner Falls filling station, 22 Jun 1940, *Hopkins 5193* (OKL); Grady Co., prairie 5 mi E and 2 mi N of Chickasha, 25 Jun 1963, *Pearce 882* (OKL); Cimarron Co., 2 mi N of Kenton, 8 Jul 1947, *Rogers 4713* (US); Kiowa Co., S side of Quartz Mt., 7 Jul 1940, *Smith 2017* (OKL); Cimarron Co., Black Mesa, 3 mi N of Kenton, 29 May 1964, *Taylor & Taylor 2117* (OKL); Murray Co., W of Turner Falls, 15 Jul 1946, *Waterfall 6521* (OKL); Woodward Co., 13 mi N of Mooreland, 18 Jun 1947, *Waterfall 7111* (OKL). **Texas:** Guadalupe Mts., 19 Aug 1901, *Bailey 439* (US); Bexar Co., Camp Bullis, 24 May 1994, *Johnson et al. BUL 206* (OKL); Armstrong Co., Gamble's ranch, 5 Jun 1918, *Palmer 13917* (MO).

Ptelea trifoliata [subsp. *trifoliata*] var. *baldwinii* [*Ptelea trifoliata* var. *trifoliata*]

UNITED STATES.—**Florida:** near Jacksonville, 1 Jun 1894, *Curtiss 4689* (MO); Alachua Co., Alachua sinks, 25 Apr 1937, *Murrill s.n.* (MO); Silver Springs, 25 Jul 1929, *O'Neill s.n.* (MO); ad lac. Monroe, prope Enterprise, Jun 1848, *Rugel 75* (MO).

Ptelea trifoliata [subsp. *trifoliata*] var. *mollis*

MEXICO.—**Guerrero:** Taxco, May 1931, *Lyonnet 1199* (US). [Far outside the native range; possibly introduced or an extremely aberrant form of subsp. *polyadenia*]

UNITED STATES.—**Georgia:** Stephens Co., Curahee Mt. off U.S. Rt. 123–Ga. 13 SW of Toccoa, 580 m, 21 Jul 1975, *Boufford & Wood 17537* (MO); Habersham Co., valley below Wells Shoals (Flat Shoals) along Middle Broad River in extreme SE corner of county, 800 ft, 29 Jun 1950, *Duncan 11155B* (MO). **Illinois:** Peoria Co., Peoria Heights, 20 Jun 1962, *Chase 16984* (MO); sine loc., 1875, *Eggert s.n.* (MO, MO). **Indiana:** Wells Co., Bluffton, 20 Aug 1942, *Demaree 27342* (OKL). **Louisiana:** Ouachita Parish, beside La. 557 at N fork of Cypress Creek, NW 1/4, S15, T15N, R2E, 17 Jun 1970, *Thomas et al. 19377* (MO). **Michigan:** Berrien Co., along Lake Michigan 10 mi N of Benton Harbor, 11 Jul 1941, *Jones 14183* (MO), **Oklahoma:** Marshall Co., 1 mi NW of University of Oklahoma Biological Station, 29 Jul 1959, *Goodman 6948* (OKL); McClain Co., 5 mi E and 2 mi N of Washington, NW 1/4, S15, T7N, R2W, 7 Jul 1970, *Goodman & Lawson 8117* (OKL); Canadian Co., Watery Canyon, S8, T11N, R10W, 25 Jun 1960, *Taylor 281* (OKL). **Texas:** Bexar Co., San Antonio, 22 Apr 1911, *Clemens & Clemens 768* (MO); Sabine Co., Hemphill, Mill Creek, 240 ft, 13 Jul 1964, *Demaree 50821* (MO); Bexar Co., Camp Bullis, 19 Jun 1995, *Johnson et al. BUL 998* (OKL); Bexar Co., San Antonio, Brackenridge Park, 3 Jun 1945, *Lundell & Lundell 13777* (MO); Valverde Co., Devil's River, May 1913, *Orcutt 6007* (MO); Hardin Co., Fletcher, 25 Apr 1916, *Palmer 9546* (MO); Kerr Co., Kerrville, 30 May 1916, *Palmer 9936* (MO); Victoria, 10 May 1904, *Tracy 9251* (MO); Galveston Co., Dickinson, N side of Pine Drive (F.M. 517) on E side of Geisler's Gully, 5 May 1975, *Waller & Bauml 3604* (MO); Williamson Co., 0.5 mi W of Round Rock along Brushy Creek, 13 Jul 1946, *York 46167* (MO). **Cultivated**: Arnold Arboretum, plants received 1928 from C.C. Deam, Bluffton, Indiana, 20 July 1943, *EJP 16351-C* (OKL).

Ptelea trifoliata [subsp. *trifoliata*] var. *trifoliata*

MEXICO.—**Guerrero:** Mazatlán, falda E de cerro Alquitrán, 17°26′1″N, 99°27′54″W, 1425 m, 7 Oct 1968, *Kruse 2040* (MO); 15 km al SW de Xochipala, carretera a Filo de Caballo, 1850 m, 17 Oct 1983, *Nuñez et al. 5672* (MO).

UNITED STATES.—**Alabama:** Etowah Co., near Atalla, 9 Jul 1898, *Eggert s.n.* (MO); Catoma Creek 5 mi SW of Montgomery, 13 Aug 1927, *Harper 29* (MO); Montgomery Co., creek bottoms off U.S. 231, S side Montgomery, 23 Jun 1974, *Kral 53350* (MO). **Arkansas:** Polk Co., Ouachita National Forest, Rich Mt., 2800 [ft], 13 Jun 1942, *Demaree 23182* (MO). **Florida:** Chattahoochee River, 16 Aug 1897, *Bush 198* (MO); Duval Co., S Jacksonville, 21 Apr 1897, *Churchill s.n.* (MO); Lake Co., Eustis, 1–15 Jun 1894, *Nash 976* (MO); east Florida, 1874, *Palmer 70* (MO); Aspalaya, May 1898, [sine coll.] *s.n.* [MO 785697] (MO); **Georgia:** Dade Co., above Mouth of Cloudland Canyon E of Trenton, 800 ft, 8 May 1948, *Cronquist 5157* (MO); Clarke Co., Middle Oconee River, 580 ft, 4 Jul 1900, *Harper 155* (MO); Dougherty Co., Flint River 1 mi above Albany, 170 ft, 26 Aug 1903, *Harper 1949* (MO); Rockdale Co., toward summit of Panola Mt. in State Park, 3 May 1976, *Kral 57801* (MO); Gwinnett Co., banks of Yellow River near Yellow River store, 20 Jul 1893, 850 ft, *Small s.n.* (MO); DeKalb Co., NW slope of Stone Mt., 1000–1400 ft, 3 Jul 1893, *Small s.n.* (MO). **Illinois:** Centerville, 16 Jun 1891, *Douglass s.n.* (MO); French Vill. Sta., 24 Jul 1891, *Douglass s.n.* (MO); St. Clair Co., 9 Aug 1877, *Eggert s.n.* (MO); Pope Co., Golconda, banks of Ohio River, 9 Jun 1919, *Palmer 15449* (MO); Chicago, Jackson Park, cultivated, 1 Oct 1912, *Sherff 2012* (MO); La Salle Co., Starved Rock State Park, Jun–Sep 1921, *Thone 270* (MO). **Indiana:** Tippecanoe Co., SW Lafayette, near N.Y.C. R.R. at stone quarry, 11 June 1942, *Ek s.n.* (MO); Notre Dame, 24 Sep 1912, *Nieuwland s.n.* (MO); Lake Co., Wolf Lake, 26 Jul 1913, *Smith 5731* (MO). **Iowa:** Mt. Pleasant, 1897, *Mills 1850* (MO). **Kentucky:** Camp Nelson, cliffs of Kentucky River, 8 Jun 1923, *McFarland 27* (MO); Bowling Green, Aug 1893, *Price s.n.* (MO). **Massachusetts:** Belchertown, Bay Road, 28 Jul 1928, *Goodale 53871* (MO); Amherst, Massachusetts Agricultural College, 17 Oct 1917, *Thompson s.n.* (MO). **Michigan:** Van Buren Co., between South Haven and Benton Harbor, dunes along Lake Michigan, 19 Jun 1933, *Palmer 40506* (MO). **Missouri:** Jasper Co., Joplin, 19 Jun 1909, *Palmer 2263* (MO). **New York:** Erie Co., Wide Beach near Brant, 1 Sep 1926, *Perkins s.n.* (MO). **Ohio:** sine loc., *Buckley s.n.* (MO); Greene Co., Yellow Springs, John Bryan State Park, 9 Jul 1935, *Demaree 11430* (MO); Huron, 23 Jun 1895, *Starr s.n.* (MO). **Tennessee:** Davidson Co., banks of Little Marrowbone Creek just beyond county line on Marrowbone Road, 21 May 1969, *Kral 34694* (MO). **Texas:** Polk Co., Livingston, 8 Oct 1914, *Palmer 6768A* (MO); San Augustine Co., San Augustine, 10 Sep 1917, *Palmer 12702* (MO). **Virginia:** Clarke Co., crest of Blue Ridge above Shenandoah River, 24 Jul 1946, *Baldwin 5602* (MO); Prince George Co., James River, Windmill Point, Flowerdew Hundred, 19 Jun 1941, *Fernald & Long 13062* (MO); Wythe Co., S of Grahams Forge, 5 Sep 1967, *Harvill 17746* (MO).

Ptelea trifoliata [subsp. *trifoliata*]
var. "intermediate"

UNITED STATES.—**South Carolina:** Pickens Co., Table Rock State Park, Table Rock, trail to summit, N of Rt. 11, elevation mostly 2800–3100 ft, 6 Oct 1993, *Hill & Douglass 25217* (MO).

Ptelea trifoliata subsp. "intermediate"

MEXICO.—**Chihuahua:** south-western Chihuahua, Aug–Nov 1885, *Palmer 152* (US). **Coahuila:** Morillo, Saltillo, 1600 m, May 1942, *Lyonnet 3513* (US).

UNITED STATES.—**Arizona:** Hackberry, 4000 ft, 23 Sep 1917, *Goldman 2969* (US). **Arkansas:** Marion Co., White River, Cotter, 11 Jun 1914, *Palmer 5721* (US); Marion Co., Cotter, White River, 11 Jun 1914, *Palmer 5923* (US); Cleburne Co., Heber Springs, 30 Oct 1914, *Palmer 6957* (US). **Colorado:** Arkansas River, W of Parkdale, 29 Jun 1913, *Jones s.n.* (US). **New Mexico:** Taos Co., Carson Forest, Rio Fernandez de Taos Canyon, 2100–2400 m, 20 Aug 1923, *Eggleston 19107* (US); Florida Mts., 6800 ft, 8 Sep 1908, *Goldman 1483* (US). **Oklahoma:** "Cheyenne Country," Jun 1891, *Carleton 196* (US); Arbuckle Mts. near Davis, 25 Jun 1917, *Emig 740* (MO); chiefly on the False Washita, between Fort Cobb and Fort Arbuckle, 1868, *Palmer 46* (US); Caddo Co., near Binger, 11 Aug 1914, *Phillips s.n.* (US); Osage Co., near Copan, 17 Aug 1913, *Stevens 2126* (US).

APPENDIX 2. Flowering specimens of *Ptelea trifoliata* examined qualitatively, but not included in phenetic analyses. Infraspecific taxa are assigned in accordance with the present authors' preferred classification. Specimens bearing female inflorescences are marked as such; unmarked specimens have only male material at flowering stage (some also include fragments of material in fruit).

Ptelea trifoliata [subsp. *angustifolia*]
var. *angustifolia*

MEXICO.—**Aguascalientes:** Calvillo, 3 km WNW of El Maguey, NE of Colomos, Cerro La Iguana, near 21°55′ N, 102°40′ W, 1982 m [6500 ft], 6 Aug 2002, *Provance 5267* (MO). **Guerrero:** 8.5 mi W of Chilpancingo, 1780 m, 27–28 Jul 1968, ♀, *Anderson & Anderson 4957* (MO); 7 km SE de Taxo, carr. a Iguala, cerca de Minas Viejas, 6 Jul 1982, *Soto Núñez & Martínez S. 3977* (MO). **Jalisco:** 25 mi due S from Guadalajara, Zapotitan de Hidalgo, 1 mi N of Hwy. Mex. 15, Cerro Viejo, 1890 m, 27 Jun 1956, *Gregory & Eiten 224* (MO). **Puebla:** Tehuacán, meseta de Riego, 7 Aug 1938, *Lyonnet 2259* (MO). **Querétaro:** 18 km NE of Landa de Matamoros, La Vuelta, 1500 m, 28 Apr 1982, *Hernández M. & Tenorio L. 7187* (MO).

Ptelea trifoliata [subsp. *angustifolia*]
var. *cognata*

UNITED STATES.—**Arizona:** Chiricahua Mts., Monument Peak, 8000 ft, 24 Jun 1907, *Blumer 1331* (MO); N slope of Santa Rita Mts., 13–21 Sep 1904, *Griffiths 7217* (MO); Mohave Co., S3–4, T37N, R16W, GCPNM, summit of Lime Kiln Canyon, 1800 m, 3 May 2001, *Higgins 22794* (MO); base of cliffs near Massacre Camp, mountains between Ruby and the Tucson–Nogales highway, 12 Apr 1935, *Nelson & Nelson 1489* (MO); Pima Co., Toro Canyon, 8 Apr 1928, *Thackery 52* (MO); Santa Cruz Co., Tumacacori Mts., Rock Corral Canyon, 3700 ft, 10 Aug 1990, *Toolin 2264* (MO). **New Mexico:** Otero Co., Sacramento Mts., Alamo Canon, 5000 ft, 16 Apr 1902, ♀, *Rehn & Viereck 70.76* (MO).

Ptelea trifoliata [subsp. *angustifolia*]
var. *persicifolia*

UNITED STATES.—**Texas:** Gillespie Co., Sandy Creek, s.d., sine coll., *63* (MO).

Ptelea trifoliata subsp. *coahuilensis*

MEXICO.—**Chihuahua:** Santa Eulalia, 1300 m, 28–29 Apr 1908, ♂, ♀, *Palmer 126* (MO). **Coahuila:** 6 air km W of Saltillo, E extremity of the Sierra de la Vega, at and below Estacion Microondas La Vega, 25°25′ N, 101°05′ E, 1800–2000 m, 30 Apr 1973, *Johnston et al. 10504* (MO); Sierra Mojada Mts., 19 Apr 1892, *Jones 105* (MO); Carneros Pass, 29 May 1890, ♂, ♀, *Pringle 3114* (MO); Sierra de Parras, Mar 1905, *Purpus 1035* (MO). **Hidalgo:** Amajac, 7 km N of Atotonilco el Grande, 1900 m, 7 May 1981, *Hernández Magaña et al. 6021* (MO). **Oaxaca:** Tepelmeme, Cerro Verde, Cañada de Carrizalillo, 1600–1820 m, 7 Jul 1984, *Tenorio L. et al. 6981* (MO); Huajuapan de León, 4.2 km W de la desviación a Papalutla, 1720 m, 21 Apr 1983, *Torres C. & Cedillo T. 2646* (MO). **Puebla:** 8 km E de San Luis Atolotitlán, por la terracería rumbo a Caltepec, 18°11′ N, 97°20′ W, 2100 m, 8 Jun 1985, *Chiang C. et al. F2596* (MO); El Riego, Jul 1905, ♂, ♀, *Purpus 1291* (MO); vicinity of San Luis Tultitlanapa, near Oaxaca, May 1908, *Purpus 3170* (MO); Caltepec, Barranca de Los Membrillos, 1860 m, 6 May 1983, ♀, *Tenorio L. et al. 3783* (MO). **San Luis Potosí:** 14.4 km S of Warley, on road to Charcas, 23°28′ N, 100°59′ W, 1600 m, 3 Jul 1972, *Chiang et al. 8238* (MO). **Tamaulipas:** Miquihuana, 15 km N de La Perdida, 1700 m, 18 Apr 1976, *González-Medrano et al. 8760* (MO).

UNITED STATES.—**Texas:** Chisos Mts., 1 Jun 1940, *Tharp s.n.* (MO).

Ptelea pallida [subsp. *pallida*] var. *lutescens*

UNITED STATES.—**Arizona:** Mohave Co., Parashant (Trail) Canyon, 11 mi S of Mt. Trumbull Village, 26 Apr 1974, *Atwood 6013* (MO × 2);

Mohave Co., S of Andrus Canyon, along N rim of Colorado River at Sec. 4, 9, 16, and 17, R10W, T31N, 28 Apr 1974, *Atwood 6076* (MO); Coconino Co., Grand View trail near top of Grand Cañon, 16 Jun 1921, *Ferris & Duncan 2267* (MO); Mohave Co., NE 1/4, S8, T34N, R14W, 1250 m, 27 Mar 1999, ♀, *Higgins et al. 20065* (MO). **Utah:** Salt Lake Co., Salt Lake City, University of Utah campus, State Arboretum of Utah, cultivated, 4600 ft, 29 May 1970, ♀, *Labrum 18* (MO); Garfield Co., 1885, *Siler 15524* (MO); Salt Lake Co., University of Utah campus, cultivated, 4750 ft, 14 May 1959, ♀, *Vickery 2113* (MO).

Ptelea pallida [subsp. *pallida*] var. *pallida*

UNITED STATES.—**Arizona:** Mohave Co., Hidden Canyon, S18, T36N, R13W, 1250 m, 8 Apr 1999, ♀, *Atwood & Furniss 24165* (MO).

Ptelea trifoliata subsp. *polyadenia*

UNITED STATES.—**Arizona:** Fort Whipple, 25 May 1865, *Cours & Palmer 218* (MO). **Colorado**: Cañon City, May 1871, *Brandegee 50* (MO). **New Mexico:** Sine loc., 1847, *Fendler 108a* (MO); Taos Co., Barranca, 6900 ft, 26 May 1897, *Heller & Heller 3583* (MO); Cloudcroft, 2 May 1930, ♀, *Jones 25785* (MO); Grant Co., Burro Mts., 5500 ft, 6 May 1903, *Metcalfe 49* (MO); Sierra Co., S end of Black Range, 1 mi W of Kingston, 18 May 1905, *Metcalfe 1596* (MO); Bernalillo Co., 3 mi S of U.S. Interstate 40 on NM Rt. 233, Cibola National Forest, 35°00′ N, 106°30′ W, 1920 m, 11 May 1992, ♀, *Miller et al. 7528* (MO); Burro Mts., Mar 1880, *Rusby 60* (MO); Santa Fe Co., Water Canyon, road to Rito de las Frijoles, 7000 ft, 3 Jun 1922, *Wiegand & Upton 3733* (MO); Doña Ana Co., Organ Mts., Van Patten's, 3 May 1903, ♀, *Wooton s.n.* (MO). **Oklahoma:** LeFlore Co., 9 mi W of Arkansas state line on Hwy. 1, 19 May 1979, *Buck 1181* (MO); Fort Sill, 9 May 1916, *Clemens 11653* (MO × 2); Woodward Co., 13 mi N of Mooreland, 19 May 1942, *Hubricht B2212* (MO); Kiowa Co., 2 mi E of Snyder, 6 May 1980, *Little 36049* (MO); Roger Mills Co., Antelope Hills, 6 mi NE of Durham, 14 May 1980, ♀, *Little 36123* (MO); Cimmaron Co., Kenton, Black Mesa, 14 May 1913, *Stevens 465* (MO). **Texas**: Briscoe Co., Floyd's Crossing, Swallow Cliff, 9 Jun 1930, ♀, *Demaree 7628* (MO); Brewster Co., Chisos Mts., Boot Spring, 2200 m, 21 Jun 1931, *Moore & Steyermark 3184* (MO); Chisos Mts., 17 Jun 1931, ♂, ♀, *Mueller 8286* (MO); Valverde Co., Devil's River, 26 Mar 1917, *Palmer 11378* (MO); Montgomery Co., Conroe, 15 Apr 1929, *Palmer 33347* (MO); Jeff Davis Co., Davis Mts., 2200 m, 1 Jun 1928, *Palmer 34280* (MO); Jeff Davis Co., Davis Mts., 3 Jun 1928, ♀, *Palmer 34324* (MO); Limpia Canon, 26 Apr 1902, *Tracy & Earle 272* (MO); El Paso, Apr 1881, *Vasey s.n.* (MO); Austin, valley of Shoal Creek, 13 Apr 1918, ♀, *Young 60* (MO).

Ptelea trifoliata [subsp. *trifoliata*] var. *mollis*

UNITED STATES.—**Florida:** Jefferson Co., Lake Miccasukee, 8 Apr 1931, *Palmer 38458* (MO); Liberty Co., Allen Bluff of Apalachicola River, 11 Apr 1931, *Palmer 38550* (MO). **Georgia:** Cobb Co., Kenesaw Mt., 18 Apr 1977, *Kral 59739* (MO). **Illinois:** Peoria, 1 Jun 1917, *McDonald s.n.* (MO × 2); Augusta, s.d., ♀, *Mead s.n.* (MO); Cass Co., 100 m E of Chandlerville water tower, 28 May 1979, *Mibb 34* (MO). **Indiana:** Millers, 2 Jun 1911, *Nieuwland 852* (MO). **Missouri:** Lewis Co., LaGrange, Wyaconda River, 9 May 1912, *Davis 7377* (MO); Jefferson Co., Selma, 30 May 1928, *Steyermark 928* (MO). **New York:** Bronx Co., Bronx, New York Botanical Garden, 40°52′04″ N, 73°52′34″ E, 57 ft, 1 Jun 2006, ♀, *Nee & McClelland 54417* (MO). **North Carolina:** [southeastern], s.d., *Ashe s.n.* (MO). **Pennsylvania:** Berks Co., Wyomissing, cultivated, 13 Jun 1971, ♀, *Brumbach 7591* (MO). **Tennessee:** Lookout Mt., near line between Tennessee & Georgia, 30 Apr 1906, ♀, *Churchill s.n.* (MO); Cheatham Co., Marrowbone Creek by Marrowbone Creek Rd, 0.6 mi E of Tenn. 12, 16 May 1971, ♀, *Kral 42627* (MO). **Texas:** Gillespie Co., Legion Cr., ♂, ♀, sine coll., *62* (MO); Houston, 2 Apr 1899, ♀, *Bush 17* (MO); Houston, 17 Apr 1900, *Bush 39* (MO × 2); Columbia, on the Bernard, 5 Apr 1902, *Bush 1317* (MO); Houston, 20 Apr 1913, *Fisher s.n.* (MO); Bexar Co., San Antonio, 600 ft, 17 Apr 1894, *Heller 1582* (MO); Travis Co., off Webberville Rd. along Walnut Creek, 24 Apr 1941, *Lundell & Lundell 10321* (MO); Guadalupe Co., Cibolo Creek near Selma, 11 Apr 1953, *Rollins 5372* (MO); Harris Co., Lake Houston, N shore of W fork, San Jacinto River, 0.75 mi W of North Shore development section 1001, 47 ft, 7 Apr 1959, *Traverse 1008* (MO).

Ptelea trifoliata [subsp. *trifoliata*] var. *trifoliata*

CANADA.—**Ontario:** Welland Co., Lake Eire, 1.5 mi W of Point Abino, 21 Jun 1941, *Soper 2585* (MO).

UNITED STATES.—**Alabama:** Sine loc., s.d., ♀, *Buckley s.n.* (MO); Montgomery Co., Woodcrest Estates, SW side Montgomery by U.S. 80, Caney Creek, 13 Apr 1975, *Kral 55072* (MO). **Arkansas:** Faulkner Co., Cove Creek, 1925, *Demaree 67* (MO); Carroll Co., Beaver, 13 May 1914, *Palmer 5187A* (MO); Washington Co., limestone barrens near West Fork, 5 May 1925, *Palmer 27023* (MO). **Georgia:** Bartow Co., W side of Allatoona Creek 1 1/8 mi S 20° E of Allatoona Dam, 760 ft, 13 Jun 1948, ♀, *Duncan 8303* (MO). **Illinois:** Cook Co., Jun 1869, *Babcock s.n.* (MO); Peoria Co., Horseshoe Bottom overlook, 27 May 1957, *Chase 14467* (MO); Madison Co., McKinley freight yard of Illinois Terminal RR, N of round-house, 16 May 1979, *Muehlenbach 4322* (MO × 2). **Indiana:** Carroll Co., Deer Creek 0.5 mi W of Rd. 29, 8 Jun 1946, ♀, *Friesner 20376* (MO); Notre Dame (St. Mary's

College), 14 Apr 1916, *Nieuwland 11222* (MO). **Iowa:** Black Hawk County, school garden, 2.8.J.C., 24 Jun 1929, ♀, *Burk 764* (MO); Lee Co., Keokuk, bluffs of Mississippi River, 20 May 1929, *Palmer 35865* (MO); Davenport, 1848, *Parry s.n.* (MO). **Kansas:** Cherokee Co., rocky hills, 1896, *Hitchcock 636* (MO). Kentucky: Livingston Co., Carrsville, old country road bordering Ohio River, 23 May 1971, ♀, *Athey 1361* (MO). **Louisiana:** Matchitoches, 29 Apr 1915, *Palmer 7440* (MO). **Massachusetts:** Dorchester, cultivated, 1883, ♀, *Churchill s.n.* (MO); Amherst, Massachusetts State College grounds, 24 Jun 1916, *Thompson s.n.* (MO). **Missouri**: Carter Co., Big Spring State Park, 17 May 1931, *Christ s.n.* (MO); Franklin Co., Beaufort, 6 Jun 1969, *Christ s.n.* (MO); Marion Co., Hannibal, Riverside Cemetery, 20 May 1913, *Davis 45* (MO); Hannibal, Mark Twain's Cave, 13 Jul 1913, *Davis 164* (MO); Marion Co., Bear Creek Bluffs, 18 May 1915, ♀, *Davis 4439* (MO); Jefferson Co., 8 May 1896, *Eggert s.n.* (MO); Ralls Co., end of Hwy. EE going N off 154, dam construction site, NE 1/4, S26, T55N, R7W, 700 ft, 22 May 1973, ♀, *Hinterthuer 82* (MO); E fork of Black River 9 mi S of Belleview, 27 May 1972, ♀, *Marvin 372* (MO); St. Charles, 1900, *Miller s.n.* (MO); Jasper Co., Oronogo, 23 May 1901, *Palmer 24* (MO); Jasper Co., Joplin, barrens, 20 May 1909, *Palmer 2033* (MO); Benton Co., Osage River near Fredonia, 22 May 1929, *Palmer 35958a* (MO); Jefferson Co., 6.5 mi W of DeSoto, Big River 0.1 mi NNE of confluence with Parker Creek, 38°07′30″ N, 90°40′30″W, 600 ft, 11 May 1986, *Raven 26973* (MO); Boone Co., SE Columbia, Grindstone Park [possibly introduced]; 19 May 2000, ♀, *Smith & McKenzie 3567* (MO); Jefferson Co., St. Peter bluff 6 mi SE of Pacific, 15 May 1927, *Steyermark 294* (MO); Iron Co., 2.5 mi N of Sabula on Hwy. 49, 6 Jun 1993, ♀, *Summer 5773* (MO). **North Carolina:** Madison Co., Hot Springs, 5 Jun 1899, *Churchill s.n.* (MO). **Pennsylvania:** Allegheny Co., Pittsburgh, Nine Mile Run, 40°25′ N, 79°54′ W, 240 m, 19 Jun 1997, ♀, *Thompson 13445* (MO). **South Carolina:** Biltmore, cultivated, 21 Jun 1897, *Biltmore Herbarium 4437* (MO). **Tennessee:** Chattanooga, Wahatchie Creek, 30 May 1911, ♀, *Churchill s.n.* (MO).