# A Synopsis of Persea (Lauraceae) in Central America

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ABSTRACT. During preparation of a treatment of *Persea* for the *Flora Mesoamericana* three new species were recognized. A description of these species (*Persea albiramea* van der Werff, *P. brevipetiolata* van der Werff, and *P. laevifolia* van der Werff) is presented, as well as a key to all the known species in the *Flora Mesoamericana* region including brief notes giving synonyms, distribution, and noteworthy features for these species.

Key words: Alseodaphne, Central America, Lauraceae, Persea.

The genus Persea was described by Miller in his Gardener's Dictionary, ed. 4, in 1754; the type species, P. americana Miller, was described in the 8th edition of the Gardener's Dictionary (1768). Since then, a rather large number of species have been placed in *Persea*, from both (sub)tropical Asia and America. The genus has been variously defined and is consequently quite variable in flower and fruit characters. The American species were last revised by Kopp (1966), who recognized two subgenera in the neotropics. Persea subg. Persea is characterized by having equal or subequal tepals, these reflexed and usually deciduous in fruit, in having quadrilocular anthers, stipitate glands at the base of the stamens of the 3rd whorl, and a pubescent pistil; the subgenus Eriodaphne Nees by its unequal tepals (the inner 3 clearly longer than the outer 3), the tepals persistent and patent in fruit, by its anthers with a variable number of locules (0, 2, or 4), sessile glands at the base of the filaments of the inner three stamens, and the pistil glabrous or pubescent. The main differences between the two subgenera (equal tepals, these reflexed or usually deciduous in fruit vs. unequal tepals patent and persistent in fruit) are easy to observe, and most species can be placed in a subgenus without any hesitation. However, in Kopp's (1966) treatment she also included a few anomalous species, which had equal tepals, persistent and patent in fruit. Some of these species are known from Central America. Finally, there is one species from Suriname, P. julianae van der Werff, with strongly unequal tepals that are deciduous in fruit. The seemingly clear division of Neotropical *Persea* species in two subgenera can no longer be maintained.

Kostermans (1993) added a further complication by describing the new genus *Mutisiopersea*, which differed from *Persea* solely by its persistent and indurate tepals in the fruiting stage, whereas the tepals in *Persea* s. str. are persistent or deciduous, but never indurate. I do not accept *Mutisiopersea* because I find the distinction between indurate and non-indurate tepals vague; in some species the tepals are clearly hardened and swollen in fruit, in others slightly so or not at all. A few Central American species of *Persea* were transferred by Kostermans (1993) to *Mutisiopersea*.

Two of the species described in this contribution (P. albiramea and P. laevifolia) differ in several characters from the other Persea species and warrant further comment. Both species have the leaves clearly clustered at the tips of the branches, their leaves have a glaucous lower surface, and the tepals are small, not exceeding 3 mm, and deciduous or persistent in fruit. If persistent (in P. albiramea), the tepals are not enlarged and are visible as small bracts at the base of the fruit. If deciduous (in P. laevifolia), the tepals are united at the base and dehisce as a unit, together with the stamens, unlike the situation in *P. americana*, where the tepals initially persist in young fruits and later break off individually. Mature fruits of P. albiramea are seated on a swollen pedicel, and fruits of P. laevifolia are not yet known. This combination of characters is also found in Alseodaphne Nees, an Asian genus closely related to Persea (Chanderbali et al., 2001), and these two species would very likely be included in Alseodaphne had they been collected in tropical Asia (van der Werff, 2001). Because of the great variation in floral characters present among the Neotropical species placed in Persea, it would be very difficult to separate the new species from Persea and I prefer to include them in Persea while realizing that a modern study might well radically change generic concepts in Persea s.l.

Type and density of indument are important characters in the species delimitation of Lauraceae. While density of pubescence is in general fairly 576 Novon

Table 1.	Species	groups o	of F	Persea	in	Central	America.

	Tepals of whorl 1 and 2	Tepals in fruit	Length of tepals	Position of leaves
Group 1	equal	deciduous	4–6 mm	evenly distributed
Group 2	unequal	persistent	3-5 mm	evenly distributed
Group 3	equal	persistent	2.5-5  mm	clustered
Group 4	(sub)equal	persistent or deciduous	2-3 mm	clustered

constant within a species, I have found that sometimes this character is much more variable in Persea species than in species of other genera of Lauraceae. One example is the case of Persea bullata Kopp. This species is only known from southern Ecuador and was described as having densely pubescent twigs and pilose leaves. Subsequent collections have shown that this species can be entirely glabrous, and I have found glabrous plants growing almost side by side with pubescent ones. A comparable situation exists with P. boldufolia Mez. Kopp (1966) cited only the type, collected near Molinapampa, Dept. Amazonas, Peru. Around Molinapampa large areas occur covered by a shrubby vegetation growing on poor, sandstone-derived soils. In this scrub I found not only plants exactly matching the type, which is glabrous, but also plants that are moderately pubescent and plants that are densely pubescent. The densely pubescent plants are similar to *P. ferruginea* HBK. Plants ranging from glabrous to densely pubescent grow less than 100 m apart in the same vegetation, and thus it seems reasonable to consider P. boldufolia as a glabrous form of *P. ferruginea*. These examples led me to identify specimens from Costa Rica with a moderate to sparse, erect indument as the much more densely pubescent P. donnell-smithii Mez; describing a new species based only or largely on the density of indument in this case seemed unwise.

**Persea** Miller, Gard. Dict. ed. 4, 1754. TYPE: Persea americana Miller.

Mutisiopersea Kostermans, Rheedea 3: 133. 1993. Syn. nov. TYPE: Mutisiopersea mutisii (HBK) Kostermans.

Trees and shrubs. Leaves alternate, evenly distributed along the twigs or clustered, pinnately veined, axillary tufts of hairs or domatia lacking. Inflorescences in the axils of leaves or cataphylls, paniculate-cymose, lateral flowers of a cyme always strictly opposite. Flowers bisexual; tepals 6, equal or unequal; if unequal, outer 3 tepals smaller than the inner 3; tepals deciduous in fruit or persistent;

if persistent, usually remaining entire, rarely with the tips of the inner tepals breaking off; stamens 9 or 6; if 6, stamens of whorl III staminodial; anthers usually 4-celled, rarely 2-celled; inner 3 stamens with 2 glands at the base; staminodia of whorl IV present, each with a sagittate or triangular apex. Fruit with or without persistent tepals at the base, but never with a cupule. 80–90 species in the neotropics, 1 species on the Canary Islands, ca. 100 species in tropical and subtropical Asia.

The altitudinal range given under the species is taken from Central American specimens and may vary in other parts of its distribution.

The Central American species of *Persea* can be placed in the following species groups (Table 1):

- Species with equal tepals, these ultimately deciduous in fruit; tepals rather large (4–6 mm long): subgenus Persea with P. americana and P. schiedeana Nees. Restricted to Central America, but P. americana widely cultivated.
- Species with unequal tepals, these persistent in fruit (part of the longer tepals sometimes breaking off and tepals appearing equal in fruit); tepals usually 3–5 mm long; subgenus *Eriodaphne* (including species placed in *Mutisiopersea*) with 12 species. An additional 50–60 species in South America.
- Species with equal tepals, these persistent in fruit; tepals 2.5–5 mm long. No name has been proposed for this group; it includes 4 species, P. albida Kostermans with leaves evenly distributed, and P. brevipetiolata, P. rigens C. K. Allen, and P. silvatica van der Werff, with leaves clustered at the swollen tips of the branches. Also a few species from South America and P. indica (L.) Sprengel from the Canary Islands.
- Species with small (2–3 mm long), equal or subequal tepals, these persistent or deciduous in fruit; pedicel swollen in fruit; leaves clustered, glaucous below. Similar to Asian Alseodaphne, including P. albiramea, P. laevifolia, and possibly P. perglauca Lundell. Also in South America

(P.	sphaerocarpa (Winkler) Kostermans from Bo-		ly pubescent on the outer surface, the differ-
	ia and an undescribed species from Ecuador).		ence in indument between inner and outer
11 V	ia and an undesembed species from Beaudory.		surface readily visible P. povedae
V	Concern of Benefit in Central America	13'.	Indument, if any, on inner and outer tepals
KEY 1	TO THE SPECIES OF PERSEA IN CENTRAL AMERICA	14/19)	similar
	m 1 1 2	14(13).	Leaves sessile, the base cordate or rounded
1.	Tepals equal or nearly so	14'.	Leaves petiolate, the base never cordate 15
1'.	Tepals unequal, the outer 3 clearly shorter (not more than ½ the length of) than the inner		Twigs densely tomentose, the surface com-
	tepals	19(14).	pletely covered; lower leaf surface moderate-
2(1).	Pistil pubescent; pedicels 5–15 mm long 3		ly to densely tomentose, the indument dis-
2'.	Pistil glabrous; pedicels to 5 mm long 4		cernable to the touch P. donnell-smithii
3(2).	Pedicels 5–8 mm long; bracts surrounding ter-	15'.	Twigs glabrous or variously pubescent, but
	minal buds uniformly pubescent; pistil sparse-		not densely tomentose; lower leaf surface
	ly to densely pubescent P. americana		usually glabrous or appressed pubescent; if
3'.	Pedicels 10–25 mm long; bracts surrounding		hairs ascending, then straight, not curly or
	the terminal buds with a scarious margin; pis-		crisped
	til densely pubescent P. schiedeana	16(15).	Lower leaf surface covered by a short, dense,
4(2).	Lower leaf surfaces glaucous; tepals 2–3 mm		felt-like indument, this sometimes difficult to
4'.	Lower leaf surfaces not glaucous; tepals 3 mm		discern; individual hairs not or scarcely vis-
4.	or longer ( <i>P. brevipetiolata</i> with tepals 2.5 mm		ible
	long)	16'.	Lower leaf surface glabrous or with ap-
5(4).	Leaves 15–30 cm long; petioles 15–40 mm		pressed or ascending hairs; if pubescent, in-
0(1).	long P. albiramea		dument not felt-like and individual hairs vis- ible 17
5'.	Leaves to 15 cm long, petioles to 16 mm long	17(16)	Leaves, twigs, and terminal buds glabrous;
		17(10).	leaves longer than 10 cm P. standleyi
6(5).	Bark of twigs whitish; midrib impressed and	17'.	Plants vegetatively with some indument (oc-
	reticulation raised on the upper leaf surface;	14.	casionally specimens of <i>P. obtusifolia</i> may be
	terminal buds sparsely to moderately ap-		glabrous, but this species has leaves gener-
61	pressed pubescent		ally less than 10 cm long) 18
6'.	Bark of twigs dark brown; midrib and reticu- lation immersed on the upper leaf surface; ter-	18(17).	Leaves and twigs initially pubescent, the
	minal buds densely white pubescent		hairs erect or ascending, but soon becoming
	P. laevifolia		glabrous; leaves coriaceous, rarely exceeding
7(4).	Leaves whorled, clustered near the tips of the		10 cm in length P. obtusifolia
(-)	branches; branches with thickened nodes from	18'.	Indument of twigs and leaves when present,
	which multiple branches emerge 8		strictly appressed; leaves coriaceous or char-
7'.	Leaves evenly distributed; tips of branches not		taceous, usually exceeding 10 cm (to 10 cm
	swollen, without multiple branches P. albida	10(10)	long in <i>P. brenesii</i> )
8(7).	Inflorescences and flowers densely white pu-	19(18).	Leaves elliptic, to $10 \times 3.5$ cm, petioles 1–
	bescent, the surface of the flowers completely covered		1.5 cm; indument on twigs and lower leaf surface dense, consisting of coarse, ap-
8'.	Inflorescences and flowers sparsely pubescent		pressed hairs
ο.	or if densely pubescent, the indument brown	19'.	Leaves elliptic to broadly elliptic or ovate,
	9	19.	generally longer and/or broader than 10 ×
9(8).	Petioles to 8 mm long; tertiary venation raised		3.5 cm; indument variable; if dense, then
	on the upper leaf surface, forming a coarse		hairs fine
	reticulum; flowers sparsely pubescent to	20(19).	Inner tepals 3-4 times longer than the outer
	subglabrous P. brevipetiolata	, ,	tepals; flowers with a distinct, slender pedi-
9'.	Petioles 8–25 mm long; tertiary venation im-		cel; distal part of the inner tepals breaking
	mersed or raised on the upper leaf surface; if raised, forming a fine reticulum; flowers mod-		off in fruit, thus fruit seemingly subtended
	erately to sparsely pubescent 10		by 6 equal tepals P. caerulea
10(9)	Leaves 3–6 cm wide, the base slightly decur-	20'.	Inner tepals twice as long as the outer ones;
10(5)	rent on the petiole; flowers moderately pubes-		flowers sessile or nearly so, without slender
	cent, the hairs ascending to erect P. rufescens		pedicel; distal part of inner tepals not break- ing off in fruit, thus fruit subtended by 6
10'.	Leaves 7–12 cm wide, the base not decurrent		unequal tepals
	on the petiole; flowers sparsely pubescent; the	21(20).	anequal repuis
	hairs appressed	21(20).	sonal growth or near the tip of the twigs, in
	Flowers with nine 2-celled stamens P. cuneata		the axils of bracts or leaves, about as long as
11'.	Tiowers with six of time I cented stanted		the leaves
12(1	1). Flowers with six 4-celled stamens	21'.	Inflorescences ± evenly distributed along
12'.	Flowers with nine 4-celled stamens 13		the seasonal growth, mostly in the axils of
	2). Outer tepals glabrous or nearly so on the out-		leaves, rarely more than half as long as the
(	er surface; inner tepals moderately to dense-		subtending leaves P. liebmannii

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Persea albida Kostermans, Reinwardtia 7: 511. 1969. Replaced name: Persea pallida Mez & Pittier, Bull. Herb. Boissier, ser. 2, 3: 231. 1903, non (Nees) Oliver, Hooker's Icon. Pl. 14: 11. 1880. TYPE: Costa Rica. Valle de Coto, Pittier 11111 (isotype, G).

Persea guatemalensis Lundell, Wrightia 5: 37. 1974. Syn. nov. TYPE: Guatemala. Contreras 10943 (isotype, MO).

Distribution. Guatemala, Honduras, Costa Rica; possibly Chiapas (*Breedlove 31306*, CAS, a fruiting specimen), from 1200 to 2100 m altitude.

Best recognized by its densely pubescent flowers, equal tepals, and evenly distributed (not clustered) leaves. Differs from *P. americana* in its glabrous (not pubescent) pistil and shorter tepals (to 4.5 mm long in *P. albida*, to 6 mm long in *P. americana*).

**Persea albiramea** van der Werff, sp. nov. TYPE: Costa Rica. Puntarenas: Canton de Osa, Rancho Quemado, Aug. 1991, *J. Marin 128* (holotype, MO; isotype, INB). Figure 1.

A congeneris foliis magnis, subtus glaucis, ad apices ramulorum aggregatis, floribis parvis, glabris, tepalis subaequalibus diversa est.

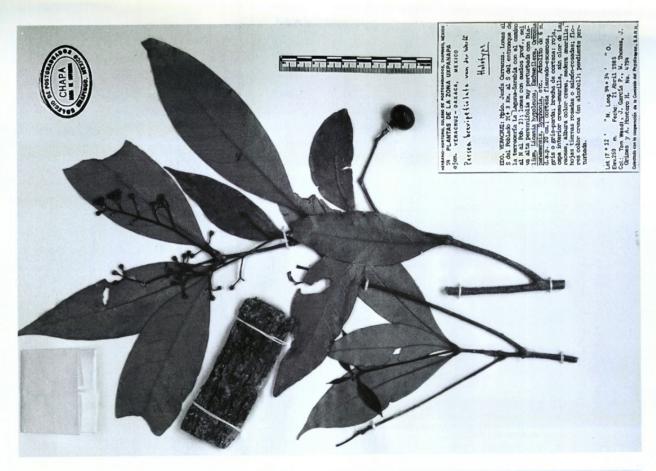
Trees, to 30 m. Twigs thick, ridged or angular, with pale gray bark, glabrous or with a few appressed hairs near the apex, grouped toward the tip of leafless shoots, clusters of bract scars lacking: terminal buds densely pubescent, the hairs brownish, ascending, completely covering the surface, not protected by bracts. Leaves  $15-30 \times 5-10$  cm, elliptic, chartaceous, grouped along the distal parts of seasonal shoots, the base and apex acute, the margin thickened, glabrous on both surfaces, or minutely puberulous along the major veins on the lower surface, the lower surface glaucous, midrib immersed or slightly raised, lateral veins and tertiary venation immersed on the upper surface, midrib and lateral veins raised, tertiary venation immersed on the lower surface; lateral veins 10-16 on each side; petioles 1.5-4 cm, ridged, glabrous, dark brown and contrasting in color with the light-colored twigs. Inflorescences 7-15 cm, paniculate-cymose, sparsely puberulous, in the axils of bracts immediately below the tip of seasonal flushes. Flowers 2.5–3 mm diam., white, pedicels slightly longer than the flowers. Tepals ca. 2 mm, the outer 3 slightly shorter than  $(\frac{1}{3})$  to  $\frac{1}{5}$  the length of) the

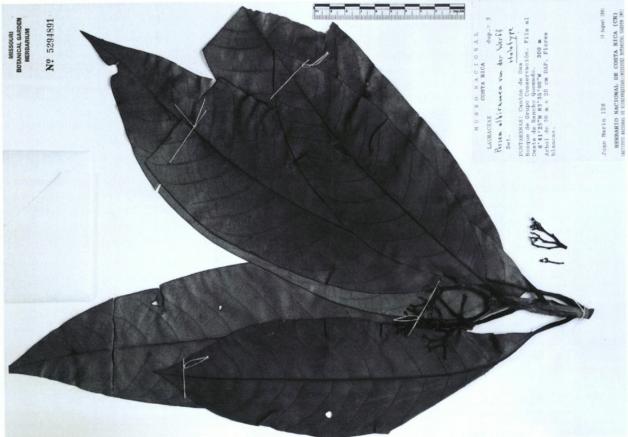
inner 3, erect at anthesis, sparsely puberulous or glabrous on the outer surface, puberulous on the inner surface; stamens 9, 4-celled, ca. 1.5 mm, the filaments pubescent, about as long as the anthers, slightly narrower than the anthers; outer 6 anthers with the cells introrse, inner 3 with the cells extrorse, filaments of the inner 3 stamens with 2 globose glands at the base; staminodia 0.8 mm, broadly triangular, with a cordate apex, abaxially pubescent, adaxially pubescent near the base only: pistil 1.5 mm, glabrous, the style distinct and about as long as the ovary; receptacle cup-shaped, densely pubescent inside. Fruits 1.4 × 1.9 cm, wider than long, tepals persisting at the base of the fruits, reflexed, not enlarged or thickened; pedicel thickened toward the fruit, at the base 4 mm diam., near the tip 8 mm diam.

Distribution. Costa Rica, Panama, from 200 to 600 m.

Persea albiramea is a very distinctive species and is easily recognized by the combination of large, glaucous leaves grouped near the tips of the branches, the thick, pale twigs, and the long petioles. As is the case with P. laevifolia, it does not fit well in any of the proposed infrageneric taxa of Persea due to its small flowers with subequal tepals and the persistent, but not enlarged tepals in fruit. It strongly resembles Asiatic species placed in Alseodaphne or Dehaasia and is likely closely related to these species. An unusual feature, shared with P. laevifolia, is the impressed tertiary venation on the upper leaf surface. Most Persea species have the tertiary venation raised and forming a fine reticulum. A related species from Bolivia is P. sphaerocarpa (Winkler) Kostermans with large, clustered leaves, these glaucous below, and thick twigs with pale bark; it differs from P. albiramea in its erect indument on the lower leaf surface and along the major veins. Persea sphaerocarpa is only known from the fruiting type collection. Several collections from Ecuador also show the combination of clustered, glaucous leaves and thick twigs with pale bark. These collections are either sterile or in bud, and additional collections are needed for their identification.

The Panamanian specimen included here differs from the Costa Rican specimens in its glabrous flower buds; vegetatively, it is a good match with the Costa Rican specimens.





Paratypes. COSTA RICA. Puntarenas: Canton de Osa, G. Herrera & J. Marin 4980 (INB, MO), B. Hammel & J. Marin 18315 (INB, MO), G. Herrera 5019 (INB, MO), K. Thomsen 491 (MO). PANAMA. Darién: Rio Tuquesa, T. Croat 27170 (MO).

- Persea americana Miller, Gard. Dict. ed. 8. 1768. Laurus persea L. TYPE: Plate 222, fig. 2 in Sloane (1725; lectotype, designated here).
- Persea americana var. angustifolia Miranda, Anal. Inst. Biol. Mexico 17: 129. 1946. TYPE: Mexico. Puebla, Miranda 3482 (UNA not seen).
- Persea drymifolia Schlechtendal & Chamisso, Linnaea 6: 365. 1831. Persea americana var. drymifolia (Schlechtendal & Chamisso) Blake, J. Wash. Acad. Sci. 10: 15. 1920. Persea gratissima var. drymifolia (Schlechtendal & Chamisso) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 147. 1889. TYPE: Mexico. Schiede & Deppe 1140 (isotype, MO).
- Persea edulis Rafinesque, Sylva Tell. 134. 1838. Nom. superfl. for Persea americana Miller.
- Persea floccosa Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 148. 1889. TYPE: Mexico. Liebmann 85 (holotype, C).
- Persea gigantea L. O. Williams, Ceiba 4: 39. 1953. TYPE: Honduras. Williams & Molina 12629 (holotype, EAP not seen).
- Persea gratissima Gaertner, Fruct. Sem. Pl. 3: 222. 1807. Nom. superfl. for Persea americana Miller.
- Persea gratissima var. oblonga Meissner, DC. Prodr. 15(1): 53. 1864. TYPE: Mexico. Aschenborn 110 (syntype, not seen), Galeotti 7010 (syntype, not seen); Peru. Ruiz & Pavon s.n. (syntype, not seen); Brazil. Riedel 106 (syntype, not seen), Martius s.n. (syntype, not seen); Java, Zollinger 457 & 3101 ex parte (syntype, not seen).
- Persea gratissima var. praecox Nees, Syst. Laurin. 129. 1836. Persea gratissima var. macrophylla Meissner, DC. Prodr. 15(1): 53. 1864. TYPE: Peru. Poeppig 2446 (not seen).
- Persea leiogyne Blake, J. Wash. Acad. Sci. 10: 19. 1920. TYPE: U.S.A. Florida: Popenoe 219 (holotype, US not seen).
- Persea nubigena Williams, Ceiba 1: 55. 1950. Persea americana var. nubigena (Williams) Kopp, Mem. New York Bot. Gard. 14: 19. 1966. TYPE: Guatemala. Williams & Molina 16833 (isotype, MO).
- Persea paucitriplinervia Lundell, Wrightia 5: 146. 1975. TYPE: Guatemala. Lundell & Contreras 19177 (isotype, MO).
- Persea steyermarkii Allen, J. Arnold Arbor. 26: 286. 1945.
  TYPE: Guatemala. Steyermark 37061 (holotype, F).

Distribution. Widely cultivated in tropical and subtropical countries for its edible fruits.

Persea americana is morphologically a variable species and is closely related to P. schiedeana. It can be separated from this species by its shorter pedicels (to 8 mm long), the uniformly pubescent bracts protecting the terminal buds, and its narrower leaves. Smith (1966) reported that Persea americana cotyledons were found in cave deposits approximately 10,000 years old; thus the species has been cultivated for a long period. Much of the variation in fruit shape and size as well as variation in indument and leaf shape can be attributed to the process of cultivation. A classification based on these characters (for instance, the one proposed by L. O. Williams in 1977) will only lead to the recognition of cultivars; I prefer to accept Persea americana in a wide sense and ignore the cultivated races of this species. It seems likely that P. americana originated in the highlands of Central America (Kopp, 1966). However, I would not know how to recognize the "wild" P. americana and include all specimens matching the description given above in P. americana, regardless of whether they come from obviously cultivated or seemingly native trees.

The type of *P. leiogyne* is from a cultivated tree; I assume that the types of *P. americana*, *P. gratissima*, and *P. edulis* also come from cultivated trees, based on their origin outside the Central American highlands or their specific epithets.

Two invalidly published names, Persea tolimanensis (Zentmyer & Schieber, 1990) and P. zentmyerii (Schieber & Berg, 1987), have been applied to P. americana s.l. These names were published without a Latin diagnosis, and no type specimens were designated.

Kopp (1966) designated the description in Clusius (1601: 2) as the lectotype of *Laurus persea*, but because descriptions cannot serve as lectotypes according to Article 8.1 of the St. Louis Code (Greuter et al., 2000), a new one had to be chosen. The illustration in Sloane (1725) is quite adequate, has a brief description as well, and is backed by a specimen (no. 965) in the Sloane herbarium at BM. Therefore, I designate here the illustration in Sloane (1725) as the lectotype of *Laurus persea* L. and therefore of *Persea americana* Miller.

Persea brenesii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 458. 1937. *Mutisiopersea brenesii* (Standley) Kostermans, Rheedea 3: 134. 1993. TYPE: Costa Rica. La Palma de San Ramon, *Brenes* 4451 (holotype, F; isotype, CR not seen).

Distribution. Costa Rica, from 900 to 1200 m altitude.

A poorly known species, best recognized by its dense indument, consisting of coarse, appressed hairs on twigs and lower leaf surface.

Persea brevipetiolata van der Werff, sp. nov. TYPE: Mexico. Vera Cruz: Mpio. Jesus Carranza, Apr. 1985, T. Wendt, J. García, W. Thomas, J. Grimes & A. Montero 4794 (holotype, CHAPA; isotype, MO). Figure 2.

Perseae rufescentis similis, sed floribus inflorescentiisque glabris vel subglabris, reticulatione subtus elevata et petiolis brevioribus recedit.

Small trees, to 8 m. Twigs smooth, terete, solid, glabrous, thickened at nodes, from which multiple branches may emerge, a few bracts or bract scars present at the base of seasonal growth; terminal buds small, glabrous, protected by a few bracts. Leaves  $10\text{--}16 \times 2.5\text{--}5$  cm, elliptic, clustered near the tips of seasonal growth, coriaceous; the base acute or somewhat decurrent on the petiole, apex gradually acute, glabrous on both surfaces, midrib, lateral veins, and tertiary venation weakly raised on the upper surface, the tertiary venation forming a coarse reticulum, midrib, lateral veins, and tertiary venation raised on the lower surface; lateral veins 7-10 pairs; petioles 5-8 mm, glabrous, flat above, with the same color as the twigs. Inflorescences 10-15 cm, paniculate-cymose, glabrous or nearly so, often with a few bracts or bract scars at the very base, in the axils of leaves or bracts at the nodes. Flowers 4 mm diam., green-yellow, pedicels 5 mm. Tepals equal or subequal, with the outer tepals slightly shorter, 2.5 mm, broadly elliptic, erect or weakly spreading at anthesis, the outer surface glabrous or very sparsely and minutely pubescent, the inner surface glabrous or nearly so, stamens 9, 4-celled, ca. 2 mm, the anthers as long as the filaments, anthers glabrous, filaments pubescent, filaments half as wide as the anthers; outer 6 stamens with introrse cells, inner 3 with extroselateral cells, filaments of the inner stamens with 2 globose glands near the base; staminodia present, 1.3 mm, broadly triangular, abaxially pubescent; pistil 2 mm, glabrous, the ovary 1.2 mm, distinct from the narrow style; receptacle shallowly cupshaped, glabrous inside. Fruits globose, ca. 2 cm diam., tepals persistent in fruit, but not enlarged, spreading, the pedicel a little thickened and warty.

Distribution. Persea brevipetiolata is only known from three collections from Mexican lowland forests (200–250 m altitude) on the Isthmus of Tehuantepec. It is closely related to *P. rufescens* Lundell (Fig. 3), which occurs in montane forests be-

tween 1500 and 2500 m in Chiapas and Oaxaca, Mexico; it differs from this species in its glabrous (or nearly so) flowers and inflorescences, in the raised reticulation on the lower leaf surface, and in its shorter (to 8 mm long vs. 15–25 mm in *P. rufescens*) petioles. *Persea brevipetiolata* is also close to the Costa Rican–Panamanian *P. rigens* C. K. Allen and *P. silvatica* van der Werff. The former can be recognized by its dense, white indument on flowers and inflorescences; the latter differs in its larger and wider leaves and longer inflorescences. All four species in this group are rarely collected, and more collections are needed for a better understanding of this group.

Paratypes. MEXICO. Oaxaca: Mpio. Matías Romero, Hernandez & Sanchez U-16 (CHAPA). Vera Cruz: Mpio. Hidalgotitlan, T. Wendt & I. Navarrete 3252 (MO).

Persea caerulea (Ruiz & Pavón) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 171. 1889. *Laurus caerulea* Ruiz & Pavón, Fl. Peruv. 4: t. 350. 1802. TYPE: Peru. *Ruiz & Pavón s.n.* (MA not seen).

Persea petiolaris HBK, Nov. Gen. Sp. 2: 159. 1817. TYPE: Colombia. Humboldt & Bonpland s.n. (B not seen).

Persea laevigata HBK, Nov. Gen. Sp. 2: 157. 1817. TYPE: Colombia. Humboldt s.n. (B not seen).

Persea lignitepala Lasser, Bol. Soc. Venez. Ci. Nat. 9: 177. 1944. TYPE: Venezuela. Pittier 7541 (holotype, VEN not seen).

Persea skutchii C. K. Allen, J. Arnold Arbor. 24: 289. 1945. TYPE: Costa Rica. Skutch 4812 (holotype, GH not seen).

Distribution. Honduras, Nicaragua, Costa Rica, Panama, South America, from 500 to 1800 m altitude.

A common species characterized by its strongly unequal tepals, with the outer ones ½ to ¼ the length of the inner ones and small (1 cm diam.), greenish blue fruits. Vegetatively, it resembles *P. americana*, which has equal tepals and much larger fruits.

Persea cuneata Meissner, DC. Prodr. 15(1): 46. 1864. Beilschmiedia cuneata (Meissner) Kostermans, Bol. Técn. Inst. Agron. N. 28: 59. 1959. Mutisiopersea cuneata (Meissner) Kostermans, Rheedea 3: 134. 1993. TYPE: Colombia. Jervise (K not seen).

Distribution. Costa Rica, Panama, northern South America, from 1000 to 1900 m altitude.

The only species of *Persea* with nine 2-celled stamens in Central America. Vegetatively very sim-

ilar to *P. povedae* Burger, but this species has larger leaves, flowers (with 4-celled stamens), and fruits.

Persea donnell-smithii Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 113. 1892. Mutisiopersea donnell-smithii (Mez) Kostermans, Rheedea 3: 134. 1993. TYPE: Guatemala. Alta Verapaz, J. Donnell Smith 1718 (syntype, MO); Mexico. Liebmann Laurac. 11 (syntype, C not seen).

Distribution. Chiapas, Guatemala, Honduras, Nicaragua, Costa Rica, from 900 to 2400 m altitude.

A rather common, montane species characterized by its unequal tepals and dense, erect indument on twigs and lower leaf surface. Collections from Costa Rica placed here have a sparser indument than the collections from Nicaragua northward. It is similar to *Persea chamissonis* Mez from Mexico in indument, but the latter has narrower leaves. It is also possible that *P. donnell-smithii* is conspecific with *P. chamissonis*; the fact that a syntype of *P. donnell-smithii* was collected in Veracruz, Mexico, lends support to this idea.

Persea laevifolia van der Werff, sp. nov. TYPE: Costa Rica. Heredia: Chilamate de Sarapiqui, May 1989, B. Hammel & M. Grayum 17334 (holotype, MO; isotypes, BM, BO, CANB, F, HBG, INB, KUN, L, LE, MEXU, MO, NY, P, PMA, TI, US, XAL). Figure 4.

Perseae perglaucae similis, sed ramulis fuscis, gemmis terminalibus dense pubescentibus costisque immersis recedit.

Trees, to 20 m. Twigs slightly ridged, glabrous or nearly so, dark brown, the branching not clustered. clusters of bract scars lacking; terminal buds densely white pubescent, not protected by bracts. Leaves  $7-15 \times 2-4$  cm, chartaceous, elliptic to slightly obovate, alternate and clustered near the tips of the branches; base narrowly cuneate and somewhat decurrent on the petiole, the margin thickened, the apex acute or shortly acuminate, glabrous on both surfaces, midrib immersed or weakly raised, lateral veins and tertiary venation immersed on the upper surface, midrib raised, lateral veins and tertiary venation immersed on the lower surface, lower surface glaucous; lateral veins 7-10 on each side, poorly visible; petioles 7-14 mm, glabrous, canaliculate. Inflorescences 4-12 cm, panic-

ulate-cymose, sparsely pubescent when immature, glabrous in young fruiting stage, near the base of seasonal flushes. Flowers unknown; description of floral parts based on remnants at the base of young fruits. Tepals 1.7 mm, broadly elliptic, equal, the outer surface sparsely to moderately, the inner surface moderately to densely pubescent; stamens 9, all 4-celled, but often only 2 or 3 cells opening. the inner 3 stamens sometimes with the upper 2 cells vestigial, the outer six 1 mm, the anther clearly wider than the filament, the cells introrse, anther about as long as the basally pubescent filament; inner 3 stamens as long as the outer 6, anther slightly wider than the filament, filament as long as the anther, densely pubescent, with large glands near the base, staminodia 0.8 mm, broadly triangular, pubescent on both surfaces, pistil glabrous. Young fruits globose, the largest seen 6 mm diam., tepals in very young stage persisting, but ultimately dehiscing as a unit with the stamens attached or, less frequently, individually.

Distribution. Costa Rica, only known from the lower Atlantic slope, 100–200 m.

Persea laevifolia is an unusual Persea species because of its small, equal tepals, which are dehiscent in the fruiting stage. Thus, it does not fit well in the previously recognized infrageneric taxa of Persea. Most Neotropical species of Persea have unequal tepals or equal, persisting tepals or equal, deciduous tepals that are not basally united. Nearly all have clearly larger flowers. Persea laevifolia resembles P. perglauca from Guatemala vegetatively, but differs in having dark brown (not very pale to whitish) twigs, a densely pubescent (not sparsely pubescent) terminal bud, immersed (not raised or slightly raised) lateral and tertiary veins on both surfaces, the leaf bases slightly decurrent on the petioles and the midrib immersed (not impressed) on the upper leaf surface. These differences are slight, but constant, and I expect that when good flowering collections become available floral differences will be found as well.

Paratypes. COSTA RICA. **Heredia:** Chilamate, B. Hammel & I. Chacon 16055 (INB, MO), B. Hammel et al. 14135 (MO), G. Herrera 4987 (INB, MO); Sarapiqui, Rancho El Bejuco, H. van der Werff et al. 14045 (INB, MO).





Persea liebmannii Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 166. 1889. *Mutisiopersea liebmannii* (Mez) Kostermans, Rheedea 3: 135. 1993. TYPE: Mexico. Oaxaca: *Liebmann 115* (syntype, C not seen), *Liebmann 116* (syntype, C not seen, photo MO).

Persea flavifolia Lundell, Contr. Univ. Michigan Herb. 6: 17. 1941. TYPE: Mexico. Matuda 1821 (isotype, MO).

Persea petenensis Lundell, Wrightia 4: 109. 1969. Syn. nov. TYPE: Guatemala. Contreras 903 (isotype, MO).

Persea podadenia Blake, Contr. Gray Herb. 52: 62. 1917. TYPE: Mexico. Palmer 119 (isotype, MO).

Distribution. Mexico, Guatemala, from 2000 to 2500 m.

Can be recognized by its rather large (to 16 cm long and 8 cm wide) leaves, inflorescences evenly distributed along the twigs, and appressed indument. Vegetatively similar to *P. veraguasensis* Seemann from Panama and Costa Rica, which has longer inflorescences clustered near the tips of the branches.

**Persea obtusifolia** Kopp, Mem. New York Bot. Gard. 14: 81. 1966. TYPE: Panama. Chiriquí: Cerro Copete, *Allen 4883* (isotype, MO).

Distribution. Costa Rica, Panama, from 2500 to 3300 m.

Best recognized by its rather small (to 10 cm long), coriaceous leaves, which have, when young, an erect or ascending indument, but which become quickly glabrous with age.

Persea perglauca Lundell, Wrightia 5: 147. 1975. TYPE: Guatemala. Baja Verapaz, Lundell & Contreras 19217 (isotype, MO).

Distribution. Guatemala; altitudinal distribution not known.

Typical are the whitish twigs contrasting with the dark petioles, clustered leaves, which are glaucous on the lower surface, the impressed midrib, and the small flowers with tepals 2 mm long. Similar to *P. laevifolia*, which has darker twigs and an immersed midrib. It is possible that *P. perglauca* is only a small-flowered variety of *P. americana*.

**Persea povedae** Burger, Fieldiana Bot., n.s. 23: 105. 1990. TYPE: Costa Rica. Alajuela: *Poveda 740* (isotype, MO).

Distribution. Costa Rica, Panama, Ecuador, Venezuela, from 700 to 1100 m.

Readily recognized by the indument on the te-

pals (inner 3 tepals much more densely pubescent than the outer 3) and its 4-celled stamens. Similar to *P. cuneata*, which has 2-celled stamens.

Persea pseudofasciculata Kopp, Mem. New York Bot. Gard. 14: 85. 1966. TYPE: Bolivia. La Paz, *Krukoff 11283* (isotype, MO).

Distribution. Costa Rica (1 collection), South America, at 500 m.

The only species of *Persea* with six fertile stamens and whorl III staminodial in Central America. The inflorescences are short, branched, and densely pubescent.

Persea rigens Allen, J. Arnold Arbor. 26: 297. 1945. TYPE: Panama. Chiriquí: Little 6058 (isolectotype, MO).

Distribution. Costa Rica, Panama, probably Colombia, from 1360 to 1600 m.

A poorly known species with clustered leaves, thickened branch tips, and densely white-pubescent flowers. Similar to P. silvatica, which has less pubescent flowers. Kopp (1966) discussed the problems with the type designated by Allen. She concluded that the holotype (Little 6075, F) was a mixed collection consisting of a sterile twig of Little 6075 and a flowering twig of Little 6058 and selected the flowering twig of Little 6058 in F as the lectotype. On labels of duplicates of *Little 6075* (for instance, in MO) it is clearly mentioned that no flowers or fruits were in evidence, while labels of Little 6058 state that immature flowers were present. Allen (1945) described flowers of P. rigens and thus must have seen material of Little 6058. Both Little 6058 and 6075 were collected in Panama. Allen's statement that Little 6075 was collected in Costa Rica is incorrect.

Persea rufescens Lundell, Wrightia 5: 38. 1974. TYPE: Mexico. Chiapas: *Matuda* 5394 (isotype, MO).

Distribution. Oaxaca, Chiapas, from 1500 to 2550 m.

A poorly known species with clustered leaves, thickened branch tips, and moderately brown-pubescent flowers, with spreading to ascending hairs. See under *P. brevipetiolata* for differences with that species.

Persea schiedeana Nees, Syst. Laurin. 130. 1836. Persea gratissima var. schiedeana (Nees) Meissner, DC. Prodr. 15(1): 53. 1864. TYPE: Mexico. Misantla, Schiede 1141 (holotype, B not seen). Persea pittieri Mez, Bot. Jahrb. Syst. 30, Beibl. 67: 15. 1901. TYPE: Costa Rica. Pittier 1156 (holotype, BR not seen).

Distribution. From Mexico to Panama, at 800–2500 altitude.

Readily identifiable by its large flowers (tepals 6–8 mm long) and long pedicels (10–25 mm long). Its leaves are somewhat clustered and to 20 cm broad.

Persea sessilis Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 115. 1944. TYPE: Guatemala. Zacapa, Steyermark 42487 (holotype, F).

Distribution. Guatemala, at 2100-2400 m.

Rarely collected, but easily identified by its sessile leaves. Flowers and fruits poorly known, but definitely a *Persea* species. Only known from the type collection.

Persea silvatica van der Werff, Fieldiana Bot., n.s. 23: 107. 1990. TYPE: Costa Rica. Heredia: Schatz & Young 964 (holotype, MO).

Distribution. Costa Rica, at 80-300 m.

Best recognized by its clustered leaves, swollen branch tips, and sparsely pubescent flowers. Close to *P. rigens*, which has densely white-pubescent flowers.

Persea standleyi Allen, J. Arnold Arbor. 26: 301. 1945. *Mutisiopersea standleyi* (Allen) Kostermans, Rheedea 3: 135. 1993. TYPE: Guatemala. Sololá: *Steyermark 47130* (holotype, F).

Distribution. Guatemala, Honduras, from 1500 to 2100 m.

Poorly known and best recognized by its glabrous leaves, twigs, and vegetative buds.

Persea veraguasensis Seemann, Bot. Voy. Herald 193. 1854. *Mutisiopersea veraguasensis* (Seemann) Kostermans, Rheedea 3: 135. 1993. TYPE: Panama. Veraguas: Volcan Chiriquí, *Seemann 1578* (BM, photo MO).

Distribution. Costa Rica, Panama, from 1200 to 2000 m.

Similar to *P. liebmannii*, but differs in having the inflorescences about as long as the leaves and clustered at the base of seasonal growth. Meissner (1864) erroneously used the name *P. veraguensis* for this species.

Persea vesticula Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 116. 1944. Mutisiopersea vesticula (Standley & Steyermark) Kostermans, Rheedea 3: 135. 1993. TYPE: Guatemala. San Marcos, Steyermark 36207 (holotype, F).

Persea chiapensis Lundell, Wrightia 1: 150. 1946. TYPE: Mexico. Chiapas: Matuda 5498 (isotype, MO).

Persea popenoei L. O. Williams, Ceiba 1: 57. 1950. TYPE: Honduras. Williams & Molina 13692 (isotype, MO).

Distribution. Chiapas, Guatemala, Honduras, El Salvador, from 1800 to 2500 m.

Characterized by a short, dense, felt-like indument on the lower leaf surface, which may be difficult to discern. Specimens from Costa Rica previously identified as *P. vesticula* are here placed in *P. obtusifolia*. These specimens lack the dense, felt-like indument on the lower leaf surface and instead have longer, straighter hairs, which may wear off with age.

#### EXCLUDED SPECIES

Persea primatogena Williams & Molina = Beilschmiedia riparia Miranda (Nishida, 1999).

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