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Author(s): Louis O. Williams

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The Avocados, a Synopsis of the Genus *Persea*, subg. *Persea*¹

LOUIS O. WILLIAMS²

The larger American genera of the Lauraceae are notoriously difficult taxonomically and *Persea* is no exception. *Persea* can be separated into two subgenera, subg. *Persea* and subg. *Eriodaphne*, and these are about as distinct as some of the genera in the Lauraceae. The type of the genus *Persea* is *Persea americana* Miller, *Gardners Dictionary*, ed. 8. 1768. Miller's rather full account indicates that he was discussing the ordinary "West Indian" avocado for he wrote: "The fruit is as large as one of the largest Pears, enclosing a seed with two lobes, included in a thin shell." The plant was said to grow in the "Spanish West-Indies, as also in the island of Jamaica, and has been transplanted into most of the English settlements in the West-Indies. . . ."

This plant with the pyriform fruits was the only one that Linnaeus knew and was included in the *Species Plantarum* 370. 1753, as *Laurus Persea*.

The "West Indian" avocado was the first one known to Europeans although there is no record of the tree in the West Indies at the time of discovery. The name "West Indian" avocado or, in this century, "West Indian" race has been applied to this plant—unfortunately.

Since *Persea americana* Miller is the type of the genus it is also the type of the subgenus *Persea*. Miss Kopp in her "A taxonomic revision of the genus *Persea* in the western hemisphere," *Mem. N.Y. Bot. Gard.* 14:1-117. 1966, apparently accepted Nees' *Persae Propriae* (Linnaea 8:49. 1833) as a basionym for the subgenus *Persea*. Since none of the species given by Nees is a synonym, or even a relative, of *Persea americana* and only one of them belongs in the genus *Persea* the basionym chosen by Miss Kopp is incorrect and does not agree with her correct statement

that *P. americana* is the type of the genus *Persea*.

There were at least three kinds of edible avocados known to the pre-Columbian peoples of America. The oldest of these is the little Mexican avocado (*P. americana* var. *drymifolia*). Dr. Smith³ has detailed the archeological evidence for the use and selection of the Mexican avocado by pre-conquest peoples in the Tehuacán valley in the state of Puebla, Mexico. These fruits apparently were in use as long ago as 8000-7000 B.C. Data presented by Dr. Smith indicates that the Indians did select the Mexican avocado for size. Later studies⁴ based on archeological materials found in caves near Mitla, state of Oaxaca, indicates that these small Mexican avocados were in use there perhaps as long ago as 7800 B.C. and as recently as 1300 A.D. Dr. Smith believed that selection was not practiced by these Indians nor that they received the selected forms from the Tehuacán valley.

In addition to the Mexican avocado there were two others, and more important ones, selected and grown by pre-conquest peoples in Mexico and Guatemala—the "West Indian" avocado (*P. americana* var. *americana*) and the Guatemalan avocado (*P. nubigena* var. *guatemalensis*). Unfortunately, I know of no archeological evidence to indicate the approximate time of origin and how long these fruits may have been used by pre-conquest peoples in Mexico and Guatemala. Both were in cultivation in essentially their present forms at the time of discovery and doubtless had been for many centuries. It is possible that plants of hybrid origin, between the Mexican (or a derivative of it) and the Guatemalan avocados, may

³ Smith, C. Earle Jr., Archeological evidence for selection of avocados. *Econ. Bot.* 20:169-175. 1966.

⁴ Smith, C. Earle Jr., Additional notes on pre-conquest avocados in Mexico. *Econ. Bot.* 23:135-140. 1969.

¹ Submitted for publication September 23, 1975; accepted for publication August 6, 1976.

² Route 6, Pointe Clear, Rogers, Arkansas.

have existed pre-conquest. I know of no evidence for this but hybridization could have occurred over a long period of time.

The "West Indian" avocado (*P. americana* var. *americana*) most probably originated by selection from the Mexican avocado (*P. americana* var. *drymifolia*). I believe that the place of origin must have been along the mountains and the lowlands of eastern central Mexico. The time perhaps as much as 4,000–5,000 years ago for these avocados. Presumably *P. americana* var. *americana* must have gotten into Peru at least as early as 1800 B.C. Dr. Pozorski⁵ excavated two sites in the Moche valley, one dating from 2000–1500 B.C. and the other 1500–1200 B.C. and found abundant remains of the avocado. Margaret A. Towle⁶ brought together the published data on the avocado in Peru and found at least eight references to discoveries of avocado remains in pre-Columbian archeological sites. The evidence indicating the presence of avocados in pre-Columbian Peru is clear.

We may assume that avocados were in northern and eastern South America in pre-Columbian times but I have no evidence to support this thesis. Why avocados did not get into the West Indies, at least were not reported there until post-conquest times, is a curious circumstance. They must have been there!

The Guatemalan avocado (*Persea nubigena* var. *guatemalensis*), in my opinion, is the best avocado known to have appeared in pre-conquest America. The presumed progenitor, *P. nubigena*, is or was native in the montane forests all the way from Puebla and Vera Cruz in Mexico to Costa Rica. I see no reason not to believe that the Guatemalan avocado was a selection, or a series of selections by the Indians from the widely distributed and still abundant *Persea nubigena*. Selection of the Guatemalan avocado could have taken place anywhere along the range of the wild species. The most logical places are in the high interior valleys of Guatemala

where, at least from conquest times to the present the tree was and is so abundant. Whether the Guatemalan avocados were in or were carried into the highlands of Mexico before conquest times I do not know. If the place of origin was in Guatemala, as I believe, then it may have been carried to Mexico post-conquest and hybridization with the Mexican avocado (or a derivative of it) may have occurred to produce the "Fuerte-like" cultivars discovered toward the beginning of this century—not that they may not have been there long before they were recognized.

The limited distribution of the Guatemalan avocado pre-conquest argues for a relatively recent origin. Ecological barriers southeastward from Guatemala, low hot regions extending from the Atlantic to the Pacific, may have inhibited the spread of this plant which is native of cool interior valleys. Why such a valuable food plant did not get into the mountains of Costa Rica, Panama and on into the South American highlands with early man is not easy to explain otherwise.

THE SPECIES OF PERSEA SUBG. PERSEA

There have been published two taxonomic accounts of *Persea* in America since 1945. The first of these by Dr. Allen⁷ contains a basic account of the *Perseas* and covers both subgenera without distinguishing them. The second publication is Dr. Kopp's⁸ formal revision of *Persea*. Miss Kopp's revision is quite good. She had no field experience and did not mention some of the important cultivated avocados so my concepts of these are often quite different from hers.

A KEY TO AND MY CONCEPT OF THE TRUE AVOCADOS AND THEIR RELATIVES

Fruits round to ovoid or obovoid, not much longer than broad.

Fruits with thin green covering, stone cells absent or not obvious; rare species of eastern Mexico.

⁵ Pozorski, Shelia G., Prehistoric subsistence patterns and site economics in the Moche Valley, Peru. University of Texas Ph.D. thesis. Austin, Texas, May 1976.

⁶ Towle, Margaret A., The ethnobotany of pre-Columbian Peru. Aldine Publishing Co., Chicago, pp. 40–41. 1961.

⁷ Allen, Caroline K., Studies in the Lauraceae, VI. Preliminary survey of the Mexican and Central American species. Journ. Arn. Arb. 26:280–434. 1945.

⁸ Kopp, Lucille E., A taxonomic revision of the genus *Persea* in the Western Hemisphere. Mem. N.Y. Bot. Gard. 14:1–117. 1966.

- Young growths and leaves floccose pubescent3. *P. floccosa*.
 Young growths and leaves glabrous
7. *P. parvifolia*.
 Fruits with thick shell-like covering with abundant stone cells, usually green when mature but sometimes blackish; both rare and abundant species represented.
 Fruits less than 4 cm in diameter, the flesh scant and less than 5 mm thick; trees of the montane forest.
 Secondary nerves of leaves widely divergent, 45–75 degrees; leaves glabrous, not glaucous; rare species
4. *P. steyermarkii*.
 Secondary nerves of leaves not widely divergent, mostly 20–40 degrees; leaves glaucous and/or fulvous pubescent; abundant species
2. *P. nubigena*.
 Fruits more than 4 cm in diameter, usually much more, the flesh abundant and often 2–3 cm thick; cultivated, or spontaneous trees of door yards and road sides
2a. *P. nubigena* var. *guatemalensis*.
 Fruits obviously longer than broad, the covering or shell thin and without large stone cells, black, brown or green when mature.
 Bud scales scarious margined and large; flesh of mature fruits usually brownish; brown pubescence of fruits persisting at least on young fruits; large native or spontaneous trees
5. *P. schiedeana*.
 Bud scales not scarious margined nor large; flesh of fruits predominantly green; fruits glabrous or soon glabrous; small to large native or spontaneous trees.
 Mature fruits almost always black (purple-black), rarely more than 5–6 cm long; flesh scant, mostly less than 5 mm thick.
 Fruits 3–4 cm long, obovate, not anise flavored; leaves oblong-obovate, coriaceous, lateral veins diverging at 40–50 degrees; rare species in montane forests of Nicaragua ...
6. *P. primatogena*.
 Fruits mostly less than 5 cm long,

anise flavored; leaves mostly submembranaceous, lateral veins diverging usually at less than 40 degrees; common species native and cultivated in Mexico, rare in Guatemala as a cultigen
 1a. *Persea americana* var. *drymifolia*.

Mature fruits almost always green, commonly 10–15 cm long, commonly pyriform; flesh abundant, commonly more than 1 cm thick; cultivated or spontaneous trees of relatively low elevations
1. *Persea americana* var. *americana*.

1. PERSEA AMERICANA var. AMERICANA. *Persea americana* Miller, Gard. Dict. ed. 8. 1768. *Laurus Persea* L. Sp. Pl. 370. 1753. *Persea gratissima* Gaertn. Fruct. & Sem 3: 22. 1805. *Persea leiogyna* Blake, Journ. Wash. Acad. Sci. 10:19. 1920.

This botanical name should be applied to all the commonly cultivated and spontaneous avocados which are called “West Indian” and have relatively large mostly pyriform fruits usually with a thin green peel. The flesh of the fruit is usually more than 1 cm thick. The seed is customarily not quite round, often somewhat elongated.

1a. PERSEA AMERICANA var. DRYMIFOLIA (Schlecht. & Cham.) Blake, Journ. Wash. Acad. Sci. 10:15. 1920. *Persea drymifolia* Schlecht. & Cham. Linnaea 6:365. 1831.

I use this varietal name for the little avocado, commonly called Mexican avocado, that is so abundant in many of the towns of the Orizaba valley and adjacent regions of Mexico. Fruits from this tree were used as food by the Indians in the Tehuacán valley, Puebla, Mexico as long ago as 8000–7000 B.C. I have seen it in Guatemala and it was, or perhaps still is to be found in door-yards in other Central American countries. The only way that I know to distinguish the var. *drymifolia* from the var. *americana* is to see the small ovoid, usually black fruits which are mostly less than 5 cm long. The leaves of the tree are usually if not always anise scented and the thin pulp of the fruits is anise flavored, often so strongly so as to make it unpalatable. The anise scent is not distinctive of this variety but may be noticed in the

crushed leaves of other avocados and even of unrelated trees of the Lauraceae.

There is an isotype of *Persea drymifolia* in the Missouri Botanical Garden herbarium. Chamiso and Schlechtendahl say, following the field label of *Schiede 1140*, "Aguacate oloroso Papantlensium a *Persea gratissima* differe videtur: Folia trita odorem aromaticum spargunt; . . . fructus minores, saporisque minus grati ac ellius." The description applies very well to the small black-fruited Mexican avocado.

2. *PERSEA NUBIGENA* L. Wms. var. *NUBIGENA*. *Persea nubigena* L. Wms. Ceiba 1:55. 1950. *Persea gigantea* L. Wms. Ceiba 4:39. 1953. *Persea americana* var. *nubigena* Kopp, Mem. N.Y. Bot. Gard. 14:19. 1966. *Persea paucitriplinervis* Lundell, Wrightia 5:146. 1975 (*ex char.*). *Persea perglauca* Lundell, l.c. 147 (*ex char.*).

This is the common and often abundant montane or cloud forest species that extends from the mountains of Puebla and Vera Cruz in Mexico to all of the high mountains where I have collected in Guatemala, Honduras, and Nicaragua. I found the species only one time in Costa Rica. No other species similar to this is found in the montane forests of this region except the somewhat related *P. steyermarkii*, a very rare species. The fruits are always small, perhaps 3–4 cm in diameter, globose or rarely subpyriform and green. The flesh is sparse and rarely more than 5 mm thick. The types of the two names proposed by Lundell, who apparently overlooked Dr. Kopp's and my own earlier works, have not been available. I find nothing in the descriptions to indicate differences from *P. nubigena*.

2a. *PERSEA NUBIGENA* var. *GUATEMALENSIS* L. Wms. var. nov. Habitu et textura *P. nubigena* L. Wms. et affinibus similis et nullo dubio his specibus proxima, praecipue differt fructibus grandiores.

Similar in habit and texture to *P. nubigena* L. Wms. and without doubt closely related and perhaps derived from it. The plant is known only in cultivation or as an escape from cultivation. It differs principally in having much larger fruits with the flesh often as much as 2–3 cm in thickness; the fruit is round or nearly so, the "shell" durable and

usually 2–3 mm thick and with prominent stone cells, usually rough but sometimes quite smooth outside, usually green in color but sometimes almost black; the flesh is usually quite good, rich in fats and flavorful; rare seedlings have the flesh quite prominently flavored with anise; the leaves of most trees, when crushed are scented with anise, often faintly so.

This is the avocado which is known to horticulturists as the Guatemalan type, Guatemalan race, or simply as Guatemalans. The variety is best exemplified by perhaps hundreds of thousands of these trees growing in door-yards and plantations near Antigua, Guatemala and other localities in central Guatemala. It is now grown or is spontaneous at middle elevations ($\pm 1,500$ m), possibly from Guatemalan seeds, in other Central American countries and in Mexico.

TYPE: Guatemala: from a door-yard tree in Antigua, Dept. Sacat pequez, alt. 1,600 m, *Williams and Molina*, Dec. 1973 (F; EAP).

3. *PERSEA FLOCCOSA* Mez, Jahrb. Bot. Gard. Berlin 5:148. 1889.

A relatively rare montane species related to *P. nubigena*, but distinguished by the floccose pubescence of the young growths and leaves, and by the small fruits which have a thin "shell." The fruits are ovoid to obovoid and about 5 cm long. I have seen this species but once, near Aquila, Vera Cruz, Mexico at 1,800 m. It was reported from Puebla and Chiapas by Dr. Kopp in her revision of the genus.

4. *PERSEA STEYERMARKII* Allen, Journ. Arn. Arb. 26:286. 1945.

This rare species of the true avocados is known only from the type locality in western Guatemala and from a limited area in El Salvador. The last of the montane forest has been cut down, possibly exterminating the species in that locality. The relationship of the species is with *P. nubigena* from which it is distinguished by the relatively smaller glabrous leaves with widely divergent secondary nerves. The fruits are obovoid-globose and similar to those of *P. nubigena*. The inflorescences of all specimens seen were lateral.

5. *PERSEA SCHIEDEANA* Nees, Syst. Laur.



Fig. 1. *Persea parvifolia*. Part of the type collection, one fruit cut to show the large round seed.—Photograph by the author, October 17, 1947.

130. 1836. *P. pittieri* Mez, Engler Bot. Jahrb. 30, Beibl. 67:15. 1901.

The most easily distinguished of the avocado relatives. The leaves, young branchlets and inflorescences are much more pubescent than in any other avocado, except the relatively rare *P. floccosa*. The large and scarios bud scales are distinctive. The widely spreading secondary veins of the leaves help to distinguish it. The ovaries and at least the young fruits are densely pubescent. The inflorescences are borne on tender new growths and by the time the fruits have matured the wood is also mature. The tree has undoubtedly been in cultivation, or semi-cultivation, for a long period of time. The fruits are large and much used for food although inferior to the true avocados. The variations in the fruits, in the vegetative structure and in the tree itself are rather great as might be expected in a seedling plant that has been selected for superior fruits over a long period of time. The range of the species extends from Puebla and Vera Cruz south to Chiapas in Mexico, then through Central America to Panama. It is reported from Colombia. How much of this range is natural and how much due to man is impossible to say. The tree is capable of invading a forest situation and does well on open slopes or in

old fields. The altitudinal range in which it does well is also rather great, from near sea level to nearly 2,000 m.

6. *Persea primatogena* Williams & Molina, sp. nov.

Subg. *Persea*. Arbores effusae excelsae usque ad 25 m vel ultrae. Folia oblongo-ovata vel ovata acuta vel vulgo obtusa coriacea glabra; inflorescentiae laterales racemosae pauciflorae; flores ignotae; fructus obovati obtusi viridi vel ad maturitatem negri lustrosi.

Large spreading trees of the montane forest, to 25 m or perhaps taller, the trunk often much branched, smooth or the bark but little fissured, the young branches finely ferruginous puberulent, glabrescent. Leaves oblong-ovate to acute, acute or usually obtuse at the apex, the base rounded to acute, coriaceous, with mostly 6–8 pairs of lateral veins diverging at an angle of 40–50 degrees, the lower surface prominently reticulate, above less so, the blade (6–)9–12 cm long and 5–8 cm broad, the petiole 1–2 cm long, obscurely puberulent; inflorescences lateral, few flowered racemes, in fruiting condition borne below the leaves; flowers not known; fruits at maturity obovate, obtuse, 3–4 cm long and 1.5–2 cm in diameter above the

middle, bright green becoming purple-black at maturity, the seeds almost as big as the fruits, the flesh 1 mm thick.

Nicaragua: tree 15–20 m, mixed forest near hotel Sta. María de Ostuma, Dept. Matagalpa, alt. 1,400 m, Nov. 1, 1968, *Molina* 22952 (EAP; F); “Guaslipe,” wet montane or cloud forest, finca Sta. María de Ostuma, Cordillera Central de Nicaragua, Dept. Matagalpa, alt. 1,300–1,400 m, Nov. 30, 1973, *Williams & Molina* 42575 (type, F; EAP; others).

This is perhaps the most unusual species of the small subgenus *Persea*, being easily distinguished from the other species by the relatively broad, short, and obtuse leaves. The small obovate fruits with thin covering (or “shell”) are the most distinctive of those of the montane species of the subgenus, not only in size and shape, but in color of the mature fruits. The only other avocado relative having fruits with thin black skin is the small Mexican avocado (*P. americana* var. *drymifolia*) of relatively low elevations and known to us only in cultivation.

This species is known from trees on Leo Salazar’s ranch, Sta. María de Ostuma. The plant has a well established common name, “guaslipe,” which is used by the native people. We have called the plant “Salazar’s avocado,” since it is known to us only on don Leo’s ranch, where we have been guests many times.

7. *Persea parvifolia* L. Wms. sp. nov.

Subg. *Persea*. Arbores parvae glabrae. Folia elliptica vel elliptico-lanceolata acuta vel breviter acuminata, ad basem acuta, coriacea; inflorescentiae longe pedunculatae cymosae vel racemosae; tepala similia ovato-

orbicularia obtusa obscure puberula; ovarium glabrum; fructus obovoideo-globosus viridis nitidus; semina globosa.

Small trees to 7 m tall from the cloud forest, glabrous except the inflorescence. Leaves elliptic or elliptic-lanceolate, acute or short acuminate, acute to the base, coriaceous, with 6–8 pairs of inconspicuous lateral nerves diverging at an angle of about 45 degrees, finely reticulate nerved between the lateral nerves, especially below, the blades 4–11 cm long and 1–3 cm broad, the petioles 0.4–2 cm long; inflorescences lateral long pedunculate cymose panicles or racemes to about 10 cm long; the flowers small, greenish; the pedicel as long as the flower; tepals 6, similar, ovate-orbicular, obtuse, about 2 mm long and nearly as broad, obscurely puberulent; outer series of anthers 5–6, almost as long as the tepals, inner series short and sessile, sterile; ovary glabrous, style as long as the tepals; fruits obovoid-globose, broadest above the middle, bright green, lustrous, about 3.5 cm long and 2.5 cm in diameter, the “shell” thin, the seed globose, about 1.7 cm in diameter.

Mexico: “aguacate cimarrón, aguacatillo.” Small tree 7 m, in cloud forest about 2 hours walk above Tetla, municipio Chocomán, Vera Cruz, alt. 7,000–8,000 feet, Oct. 17, 1947, *Williams & Popenoe* 13511 (type, EAP; F).

This is the smallest leafed and one of the most distinctive of all the true avocados, which we found with an Indian guide some 25 years ago. While the species is somewhat related, in fruit characters to *Persea americana* var. *drymifolia*, I do not think that the relationship is close nor that this tree might have had anything to do with the cultivated avocados.

Book Reviews (continued from page 314)

typographical errors not listed. For the price, Academic Press could have provided a product of better quality.

J.F.M.

Cottonseed Chemistry and Technology—In Its Setting in India. K. S.

Murti; edited and partly rewritten by K. T. Achaya. 348 pp. Publications and Information Directorate, Council of Scientific and Industrial Research, New Delhi, India, 1975. \$32.00.

Here is a masterly text, seven years in preparation by the late Dr. K. S. Murti fol-

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