

THE VASCULAR FLORA OF LA SELVA BIOLOGICAL STATION,
COSTA RICA*
LAURACEAE

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BERNARDI, L. 1962. Lauraceae. Universidad de Los Andes, Merida, Venezuela. 355 pp.
MEZ, C. 1889. Lauraceae Americanae. Jahrb. Königl. Bot. Gart. Berlin 5: 1-556.

Usually evergreen, hermaphroditic or dioecious, woody shrubs or trees or very rarely woody vines; usually noticeably and characteristically aromatic; sap watery and often mucilaginous; freshly cut wood usually white but rapidly oxidizing orange to tan. *Leaves* simple, entire, usually both unlobed and usually pinnately veined, stipulate. *Inflorescence* paniculate, usually axillary, few- to many-flowered, the ultimate clusters of flowers often cymose; bracts of the inflorescence soon deciduous. *Flowers* actinomorphic, 3-merous, often sweetly aromatic; perianth segments (tepals) perigynous, usually in 2 similar whorls, the 3 tepals of each whorl erect or spreading at anthesis; fertile stamens 3-9(12) or rarely more; anthers with distinct filaments or nearly sessile, dehiscent by 2 or 4, ovate flaps (valves) hinged at the top, those of the outer 3 whorls (3 + 3) introrse, those of the inner whorl extrorse or lateral; stamens of the inner whorl each usually

3 or lacking, alternating with the stamens of the inner whorl; ovary superior, unicarpellate, unilocular; style single, simple. *Fruit* a 1-seeded drupe or berry, the oily flesh usually green at maturity, the skin green or black; hypanthium often accrescent and then forming a reddish, succulent to woody cupule at maturity.

The Lauraceae, a family of 30 to 50 genera and 2,000 or so species with perhaps 150 in Central America, usually have a characteristic spicy fragrance. Pollination is probably by small bees and beetles. The fruits of most species at La Selva are between 1 and 2 cm in diameter and are eaten by birds, especially parrots and toucans.

The family is mostly tropical in distribution and is particularly abundant in South America. Revisionary work is sorely needed in the neotropics together with careful collection, matching fruiting collections with those in flower, to determine the range of variation within species. Eleven of the 17 New World genera are endemic and 12 genera are known from Central America.

The genus *Aniba*, recently reported in Flora Neotropica No. 31 as restricted to South America, occurs on the forested hills not far from La Selva. It is easily recognized in flower as the nine fertile stamens have only two valves per anther and the small globose perianth, resembling that of many species of *Licaria*, rests upon a relatively long floral tube.

KEY TO THE GENERA

1. Anthers 2-celled.
 2. Flowers with 9 fertile stamens; cupule lacking; leaf apex rounded to broadly acute, occasionally with a short acumen; plants with an unusual sweet, citrus fragrance. 1. *BEILSCHMIEDIA*.
 2. Flowers with only 3 fertile stamens; margin of cupule double; leaf apex with a long acuminate tip; plants usually with a sassafras or sweet laurel fragrance. 2. *LICARIA*.
1. Anthers 4-celled.
 3. Flowers with linear, clavate or no staminodia.
 5. Tepals reflexed at anthesis, oblong, usually 1.5-2 times longer than wide; anther cells in a low wide arch or in 1 horizontal row. 3. *NECTANDRA*.
 5. Tepals erect at anthesis, usually ovoid-triangular, about as long as wide; anther cells in a narrow arch or in 2 columns or nearly vertical rows. 4. *OCOTEA*.

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3. Flowers with conspicuous cordate-stipitate staminodia.
 4. Fruits lacking a cupule, the pedicels sometimes swollen and bearing the withered remains of the tepals, but these not cupulate. 5. *PERSEA*.
 4. Fruits with cupules derived from the persistent, accrescent tepals, the margin thus lobed or dentate. 6. *PHOEBE*.

KEY TO THE SPECIES BASED ON VEGETATION AND FRUIT CHARACTERS

1. Leaf blades conspicuously pubescent, the trichomes erect.
 2. Margin of blade curled under at base, forming two large auricles. *Nectandra reticulata*.
 2. Margin of blade plane or only slightly recurved basally.
 3. Leaves subopposite distally; reticulate venation conspicuous and fine above, the ultimate aeries about 0.5 mm in diameter; fruit lacking a cupule. *Beilschmiedia anay*.
 3. Leaves alternate throughout; reticulate venation obscure and coarse above, the ultimate aeries about 1.5 mm in diameter or larger; fruit with a cupule.
 4. Twigs gray and nearly glabrous (except at apex and in axils); fruits globose, about 1 cm in diameter; cupule subtending rather than covering the base of the fruit. *Ocotea babosa*.
 4. Twigs conspicuously rusty or tan pubescent; fruits ovoid-cylindrical at maturity, ca. 2.5–4 cm long, the basal ¼ to ⅓ covered by the cupule.
 5. Apex of leaf long acuminate; petioles 2–2.5 cm long; prop roots lacking. *Nectandra kunthiana*.
 5. Apex of leaf rounded or acute, sometimes with a short acumen; petioles 0.5–1.5 cm long; prop roots present.
 6. Leaf blades narrowly acute and decurrent basally, nearly 3 times longer than wide, glaucous below. *Ocotea hartshorniana*.
 6. Leaf blades broadly acute and not decurrent basally, less than 2 times longer than wide, not glaucous. *Ocotea mollifolia*.
 1. Leaf blades glabrous or minutely appressed pubescent (trichomes visible with a lens but not detectable by touch).
 7. Lamina widest above the middle, gradually narrowed to the base.
 8. Stem apex hollow and harboring small ants; leaf apex abruptly narrowed to a slender tip (caudate). *Ocotea atirrensis*.
 8. Stem apex solid; leaf apex not caudate.
 9. Leaves whorled; reticulate venation prominent above. *Persea rigens*.
 9. Leaves alternate; reticulate venation inconspicuous above.
 10. Petioles less than 0.5 cm long, 0.5 cm wide at base; base of blade decurrent nearly to the twig; fruits cylindrical or ovoid.
 11. Leaf blades minutely appressed pubescent and glaucous below; trees with prop roots; margin of cupule toothed. *Ocotea caracasana*.
 11. Leaf blades glabrous except for scant trichomes in the axils of lateral veins, not glaucous; trees lacking prop roots; margin of cupule entire. *Ocotea ira*.
 10. Petioles about 1 cm long, 0.2–0.3 cm wide; base of blade merely acute or attenuate but not to the twig; fruits globose.
 12. Leaf blades nearly 4 times longer than wide, basally attenuate; cupule conical, the margin thin; sap with piny fragrance. *Ocotea bijuga*.
 12. Leaf blades less than 3 times longer than wide, basally merely acute; cupule discoid, the margin thick; sap with sweet, nutty laurel fragrance. *Ocotea floribunda*.
 7. Lamina widest at or below the middle.
 13. Leaves glaucous on the lower surface.
 14. Petioles 3–6 cm long, usually red; leaf blades often 30 cm or more long, glabrous throughout; leaf apex broadly acute to rounded; margin of cupule toothed or lobed. *Phoebe chavarriana*.
 14. Petioles 1–2 cm long, green; leaf blades 15–20 cm long at most, pubescent in the axils of lateral veins; apex acuminate; margin of cupule entire. *Nectandra hypoleuca*.
 13. Leaves not glaucous on the lower surface.
 15. Lower surface of leaves with trichomes or pits (domatia) in the axils of lateral veins.
 16. Reticulate venation obscure above; trichomes of the axils dense. *Nectandra hypoleuca*.
 16. Reticulate venation prominent above; trichomes of the axils sparse or lacking.
 17. Lateral veins with conspicuous submarginal loop connections; vein axils sparsely pubescent; leaf buds not spinelike. *Nectandra purpurea*.
 17. Lateral veins lacking conspicuous loop connections; domatia glabrous pits; dormant leaf buds often hard and spinelike. *Ocotea meiziana*.
 15. Lower surface of leaves lacking trichomes or pits in the axils of veins (but see *Ocotea tenera*).
 18. Lamina minutely appressed pubescent below.
 19. Leaf blades 3–4 times longer than wide.

20. Base of blade decurrent and the margin slightly revolute; plants with more or less typical laurel fragrance. *Nectandra membranacea*.
20. Base of blade acute, the margin plane; plants with unusual pungent fragrance. *Ocotea leucoxydon*.
19. Leaf blades 2 times longer than wide or less.
21. Leaves subopposite at least distally; reticulate venation prominent and conspicuous on both surfaces; cupule lacking; plants with unusual, sweet, citrus-like fragrance. *Beilschmiedia mexicana*.
21. Leaves alternate throughout; reticulate venation indistinct above; cupule present; plants with typical laurel fragrance or almost none.
22. Twigs green and glabrous or at most sparsely appressed pubescent; reticulate venation distinct below; fruits elongate-ovoid; trees 5–15 m tall. *Ocotea meiziana*.
22. Twigs brown or golden tan due to a dense covering of short trichomes; fruits globose; trees about 25 m tall. *Nectandra cissiflora*.
18. Lamina glabrous on the lower surface.
23. Stem apex hollow and harboring small ants. *Ocotea dendrodaphne*.
23. Stem apex solid.
24. Leaf blades bearing small round depressions (punctate); cupule with a single margin.
25. Apex of leaf rounded overall but abruptly narrowed to a long (1.5–2 cm) narrow (2 mm) acumen; leaves drying gray green. *Ocotea cernua*.
25. Apex of leaf acute overall with a gradually acuminate tip; leaves drying brownish black. *Ocotea tenera*.
24. Leaf blades not punctate; cupule margin either single or double.
26. Apex of leaf long acuminate; fruits ovoid; margin of cupule double.
27. Leaves mostly 5–7 cm wide; leaf surfaces strongly contrasting, very glossy above, dull below; plants with strong sassafras fragrance. *Licaria sarapiquensis*.
27. Leaves mostly 2.5–3.5 cm wide; leaf surfaces of similar reflectance.
28. Leaf margins undulate; bark gray to dark brown; plants not at all fragrant. *Licaria* sp.
28. Leaf margins plane; bark flaky, orangish tan; plants with strong sweet fragrance. *Licaria triandra*.
26. Apex of leaf rounded to narrowly acute; fruits globose; margin of cupule single.
29. Leaf blades almost 4 times longer than wide, the base attenuate; reticulate venation indistinct and coarse above (aerioles ca. 1.5 cm in diameter); cupule conical, the margin thin. *Ocotea bijuga*.
29. Leaf blades less than 3 times longer than wide, the base merely acute; reticulate venation prominent and fine above (aerioles 0.5 mm in diameter); cupule discoid, the margin thick. *Ocotea floribunda*.

1. BEILSCHMIEDIA Nees

Trees or shrubs. *Leaves* alternate or often subopposite at least distally, ovate-elliptic, pinnately veined, prominently and finely reticulate. *Inflorescences* axillary or appearing terminal, paniculate. *Flowers* yellowish, bisexual; tepals erect at anthesis, deciduous; fertile stamens 9, the anthers 2-celled with the connectives protruding beyond the cells, 2-valved; staminodia 3, cordate and conspicuous. *Fruits* cylindrical-ovoid, lacking a cupule; pedicel not swollen.

The fine, conspicuous reticulation of the leaves characterizes the genus, at least locally. *Beilschmiedia* is similar to *Persea* in its lack of a cupule and in the presence of large cordate stipitate staminodia but it is usually classified together with the other genera having nine fertile stamens with just two valves per anther. The genus is pantropical with approximately 200 species, 23 of them from the New World and of these ten Central American. Only three mature

individuals representing two species are known from La Selva.

KEY TO THE SPECIES

1. Leaf blades erect pubescent on both surfaces; midrib sulcate above; fruit at least 6 cm long. 1. *B. anay*.
1. Leaf blades glabrous above, sparsely appressed pubescent below; midrib prominent above; fruit about 2 cm long. 2. *B. mexicana*.

1. *Beilschmiedia anay* (S. F. Blake) Kosterm.

Trees to 20 m tall and 25 cm in diameter; outer bark dark brown, orange inside. *Leaf* blades broadly elliptic, 15–20 cm long, 8–12 cm wide, membranaceous; major lateral veins arising at an angle of 50–55°; petiole 1–2.5 cm long. *Inflorescences* clustered at the tips of the branches, 11–13 cm long, the rachis pubescent. *Flowers* about 2 mm long; tepals about 1.6 mm long, sparsely pubescent; outer stamens 1.2–1.5 mm

long, the filaments shorter than or nearly equal to the anthers, pubescent; staminodia about 1.1 mm tall, 0.6–0.7 mm wide; floral glands small, about 0.4 mm in diameter, slightly stipitate; ovary about 0.8 mm in diameter, the style about as long as the ovary. *Fruits* at least 6 cm long and 2.5 cm in diameter. Flowering in July, middle rainy season; fruiting by February, early in the dry season. Guatemala, Costa Rica and Colombia.

This species, like the following, is known from only one or two mature individuals at La Selva. The La Selva material differs from the Guatemalan collections in that the leaves are not glaucous. The fact that these apparently isolated individuals at La Selva set fruit and have produced seedlings suggests that the species is either autogamous or more common in the area than presently known. The somewhat acid-sweet fragrance of the sap is characteristic of both species at La Selva.

2. *Beilschmiedia mexicana* (Mez) Kosterm.

Trees to 15 m tall and 15 cm in diameter; outer bark light tan, pink inside. *Leaf* blades broadly elliptic, 14–17 cm long, 6–9 cm wide; midrib prominent above; major lateral veins arising at an angle of 45–50°; leaf surface glabrous above except for scant pubescence on midrib basally, distantly and minutely appressed pubescent below; petioles 1–1.5 cm long. *Inflorescences* axillary, 3–15 cm long, the rachis sparsely appressed pubescent. *Flowers* about 2.8 mm wide, tepals 1.5–1.7 mm long, sparsely pubescent externally; stamens of the outer series about 1.3 mm long, the anthers about twice as long as the filaments, filaments pilose; floral glands sessile; ovary ovoid, about 1 mm long, the style as long, glabrous. *Fruits* 3.5–4 cm long, about 2 cm in diameter, blackish purple at maturity. Flowering at the beginning of the dry season, January to February; fruits maturing by September. Mexico south into Colombia.

The only mature individual of this species known at La Selva grows in primary forest along the Research Trail at the base of the large *Gnetum*-bearing *Hymenolobium*. Several saplings are known from low areas in primary forest in the northern part of the property. The reticulation, prominent on both surfaces even in fresh material and the nearly glabrous leaves distinguishes this species.

2. LICARIA Aubl.

KOSTERMANS, A. J. G. H. 1937. Revision of the Lauraceae. II. The genera *Endlicheria*, *Cryptocarya*

(American species) and *Licaria*. Recueil Trav. Bot. Néerl. 34: 500–609.

Shrubs or trees. *Leaves* usually alternate and narrowly elliptic, pinnately veined, glabrous or pubescent. *Inflorescences* small to large, axillary to subterminal, diffuse, the ultimate clusters umbelloid. *Flowers* apparently perfect, small, campanulate, usually with a distinct floral tube, yellow green; tepals usually erect at maturity, about equal to the floral tube; fertile stamens 3 (the inner series), the anthers with only 2 valves; outer series of stamens reduced to ligulate staminodia or absent; staminodia of the inner series lacking; floral glands stipitate, as long as the filaments. Floral tube accrescent in fruit to a thick (1)2(3)-margined cupule; *fruit* ovoid; pedicels slightly swollen.

Licaria, a neotropical endemic, is the only genus with three fertile stamens. There are apparently 50 described species of which 13 are from Central America. The three species at La Selva all have glabrous, long acuminate leaves with the distinct loop connections of the lateral veins well removed from the margin. In Central America only species of *Licaria* and *Aniba* together with a few species of *Ocotea* have conspicuously double-margined cupules.

KEY TO THE SPECIES

1. Leaves mostly 5–7 cm wide; leaf surfaces strongly contrasting, very glossy above, dull below; whorl of fertile stamens surrounded by 6 ligulate staminodia. 1. *L. sarapiquensis*.
1. Leaves mostly 2.5–3.5 cm wide; leaf surfaces of similarly dull reflectance; staminodia lacking.
 2. Leaf margins plane; bark of trunk and twigs flaky, orange tan; sap with strong sweet fragrance; anther valves apical-extrorse. 2. *L. triandra*.
 2. Leaf margins undulate; bark gray to brown; sap not at all fragrant; anther valves apical-introrse. *Licaria* sp.

1. *Licaria sarapiquensis* Hammel

Trees 6–20 m tall, 5–20 cm dbh; outer bark gray to nearly black, inner bark thin, yellow, with strong, distinctive fragrance of sassafras. *Leaf* blades 16–20 cm long, 4.5–7 cm wide, the narrow caudate tip 1–3 cm long; major lateral veins arising at an angle of 50–75°; reticulate venation prominent on both surfaces but more so below in dried material; upper surface very dark green and shiny, contrasting with the dull and paler lower surface; petioles 0.5–1 cm long. *Inflorescences* 2.5–4 cm long, very slender-branched and sparsely flowered, the ultimate clusters of flowers umbelloid, glabrous. *Flowers* campanulate, 2.3–2.5 mm long, yellowish green, very inconspic-

uous; tepals ligulate, about 1.2 mm long, about as long as the floral tube, patent or curved inward at anthesis; fertile stamens about 1.2 mm long, the anthers much shorter than the filaments, oblate-depressed, the valves opening apically and somewhat extrorsely; filaments about 1 mm long, flanked by 2 stipitate floral glands each as long as the filaments and with a stipe as long as the body of the gland; stamens of the outer series represented by thin ligulate staminodia about the same length as the floral glands; ovary more or less pyriform, acuminate apically into the style, the style and ovary together about 1.8 mm long. *Fruits* ovoid-elliptic, about 2 cm long and 0.8 cm in diameter, black at maturity, the lower third covered by the conical, thinly double-margined, red cupule. Flowering in mid May; fruits maturing towards the end of August. Costa Rica.

Although nowhere abundant at La Selva, this *Licaria* is widespread in the primary forest especially on slopes and ridges. The strong sassafras fragrance of the crushed foliage is most distinctive.

All observed flowering individuals of this species were slender understory trees only about 6 to 12 m tall and 5 to 10 cm in diameter. They are at least partially dependent for support on nearby trees. These individuals apparently do not set fruit. The one fruiting specimen, however, is from a stout mid canopy tree about 20 m tall. Although the flowers appear to be perfect, the plants apparently function only as staminate individuals until reaching a certain size.

2. *Licaria triandra* (Sw.) Kosterm.

Trees 10–15 m tall, 15–20 cm dbh; outer bark of trunk and twigs soft and somewhat flaky, orange-colored, very fragrant; inner bark orange. *Leaf* blades 9–10.5 cm long, 3–3.5 cm wide; major lateral veins arising at an angle of 45–55°; reticulate venation indistinct on both surfaces in dried material; petioles 2.5–10 mm long. *Inflorescences* axillary, clustered near the tips of branches, mostly 5–8 cm long; *flowers* 2–3 mm long, tepals glabrous, anthers 0.8 mm long, 0.8 mm wide, the valves apical and extrorse, filaments hirsute, staminodia lacking; ovary about 1.5 mm long, glabrous. *Fruits* ovoid, purplish black, the lower half covered by the red, warty cupule, the whole structure about 2 cm long and 1.5 cm in diameter. Flowering in the dry season, January to March; fruits mature by late July. Known from Central America; West Indies.

This species is uncommon at La Selva but distinctive especially for its soft, orange, flaky, and very sweetly aromatic bark. Even the twigs on the La Selva material have a distinctive orange

flaking periderm. The few collections known are restricted to ridges in the primary forest.

3. *Licaria* sp.

Slender dioecious(?) shrub about 3 m tall and 3 cm dbh; bark thin and gray without fragrance. *Leaf* blades 11–14 cm long, 3–3.5 cm wide, the caudate tip 1–2 cm long, margins distinctly undulate crisped; major lateral veins arising at an angle of ca. 60°; reticulate venation obscure above, very prominent below, the lower surface somewhat more lustrous than the upper. *Inflorescence* sparsely flowered, somewhat racemose but with ultimate, umbelloid clusters of flowers; *flowers* campanulate, about 1.7 mm long, yellow-green, very inconspicuous, gradually tapering to the slender pedicel; tepals broadly triangular, about 0.65 mm long, slightly shorter than the floral tube, incurved at anthesis; stamens stout, succulent, about 1 mm long and 0.9 mm wide, the anthers hardly if at all distinct from the filaments, valves of the anther opening apically and introrsely; floral glands somewhat external to the stamens, the adjacent pairs apparently connate and forming a small fleshy appendage between the stamens; staminodia lacking; ovary, sterile(?), filiform. Flowering in early December; fruits not seen. Known only from La Selva.

Known from just one individual in gallery forest along the Río Puerto Viejo. Its small undulate-margined, nonfragrant leaves are unusual for the family at La Selva. No other *Licaria* from Central America is reported as having introrse anthers. Although introrse anthers are rare in *Licaria*, the really curious feature of this plant is its apparent unisexuality; dioecy has not been reported for the genus. Further collections are needed.

3. *NECTANDRA* Roland. ex Rottb.

BERNARDI, L. 1967. Emendationes laureae imprimis de Nectandra. et seq. Candollea 22: 49–105.

Trees or rarely shrubs, occasionally dioecious. *Leaves* pinnately veined, alternate or rarely subopposite, glabrous or pubescent. *Inflorescences* axillary panicles, usually densely flowered. *Flowers* small; tepals spreading or reflexed at anthesis, usually ligulate and widest near the tip, usually bright white adaxially; fertile stamens 9, the outer 6 introrse, the inner 3 with the valves extrorse or lateral, the valves 4, those of the outer anthers describing a low arc or nearly straight horizontal row; staminodia linear and inconspicuous or absent. *Fruits* globose or ovoid, usually black at maturity, partially enclosed or sub-

tended by a reddish fleshy cupule merging with the swollen pedicel.

Nectandra is restricted to the neotropics. Only two of the 38 species reported by Allen for Central America were thought to occur outside of that area. Many more are now known throughout tropical America; five of the six species at La Selva are also known from South America. No more than 40 to 50 species of *Nectandra* occur in Central America.

The difficulty in distinguishing *Nectandra* from *Ocotea* is well known. Nevertheless the two groups are currently treated as separate genera by most workers. Both genera are accepted here but the species are also presented together in a combined key which follows the treatment of the genus *Ocotea*. In general, local material can be identified to species without reference to the characters traditionally used to distinguish the two genera.

KEY TO THE SPECIES

1. Flowers densely pubescent and colored by the gray, golden or rusty trichomes; twigs or leaves or both conspicuously pubescent also.
 2. Margin of leaf blade strongly revolute at the acute base and forming 2 large auricles. 6. *N. reticulata*.
 2. Margin of leaf blade plane or only obscurely revolute along the acuminate base.
 3. Leaf blades lanceolate-elliptic, 20–40 cm long, the base acute and with a conspicuous marginal vein; reticulate venation prominent above; pubescence tan. 3. *N. kunthiana*.
 3. Leaf blades ovoid-elliptic, 15–22 cm long, the base decurrent and the marginal vein faint; reticulate venation obscure above; pubescence golden. 1. *N. cissiflora*.
1. Flowers minutely and sparsely pubescent, the trichomes not colored; twigs and leaves glabrous or at most minutely and sparsely pubescent.
 4. Axis of lateral veins bearing tufts of trichomes (domatia) below, leaf blades otherwise glabrous; fruit ovoid.
 5. Reticulate venation prominent above; leaf surface shiny above and not glaucous below; trichomes of domatia sparse; lateral veins distinctly loop-connected marginally. 5. *N. purpurea*.
 5. Reticulate venation obscure above; leaf surface dull above and usually glaucous beneath; trichomes of domatia dense; lateral veins not distinctly loop-connected. *N. hypoleuca*.
 4. Axils without domatia; leaf blades minutely appressed pubescent beneath; fruit globose.
 6. Leaf blades 3–4 times longer than wide; tertiary veins between the secondaries perpendicular to the midvein, twigs nearly glabrous. 4. *N. membranacea*.
 6. Leaf blades about 2 times longer than wide; tertiary veins not perpendicular to the midvein; twigs densely golden pubescent. 1. *N. cissiflora*.

1. *Nectandra cissiflora* Nees (=*Nectandra paulii* C. K. Allen)

Trees to 25 m tall and 30 cm in diameter; outer bark light gray, white inside but rapidly oxidizing orange; sap slimy and fragrant. *Leaf* blades elliptic, 15–22 cm long, 7–9 cm wide, the apex acute, the base decurrent; midrib and lateral veins slightly impressed above, prominent below; lateral veins arising at an angle of 45–50°; leaf surface glabrous and shining above, distantly appressed pubescent below especially on the veins; petioles 1.5–2.5 cm long. *Inflorescences* open panicles, axillary among the distal leaves, 18–25 cm long, many-flowered, the rachis minutely erect pubescent. *Flowers* 4–5 mm broad, white, the tepals 1.8–2 mm long; outer stamens sessile and truncate, wider than long, about 0.6 mm long, the anther valves in a straight line, the outer 2 more or less lateral; staminodia linear with a triangular pointed tip, about 0.5 mm long; ovary globose, the style less than ¼ the length of the ovary. *Fruits*, globose, 1.5–2 cm in diameter, black at maturity, subtended by the shallow, 1.5 cm wide, slightly ribbed cupule. Flowering in the dry season, January to February; maturing fruit by the middle of April. Costa Rica, Panama, and Peru.

Known from just two mature individuals at La Selva growing on ridge tops in primary forest. The large globose fruits and leaf blades narrowly decurrent on the petiole are distinctive. These plants are inconspicuous both in flower and in fruit. Saplings are rather common in forest along the Southwest Trail.

2. *Nectandra hypoleuca* Hammel

Trees 5–15 m tall, 10–30 cm in diameter; bark surface dark brown. *Leaf* blades elliptic, 17–27 cm long, 6.5–10 cm wide; apex acuminate, the base acute; midrib plane to somewhat impressed basally above, prominent below; major lateral veins arising at an angle of 30–60°; leaf surface dull above, drying grayish green, glabrous, usually glaucous below and glabrous except for the densely brown pubescent domatia in the vein axils; petioles 7.5–15 mm long. *Inflorescences* axillary and clustered towards the branch ends, 8–18 cm long, many but rather loosely flowered; rachis sparsely pubescent. *Flowers* about 5 mm wide, sparsely pubescent; tepals ligulate, 2–2.4 mm long, bright white at anthesis; outer stamens nearly sessile, quadrate and somewhat emargin-

ate, 0.6–0.8 mm long, abruptly narrowed to the short filament; anther valves in a line, the outer 2 lateral; staminodia clavate, about 0.4 mm tall; ovary globose-pyriform, about 0.6 mm long, the style slightly shorter. *Fruits* ovoid-elliptic, to at least 1.5–1.7 cm long (immature); cupule conical, about 7 mm long and as wide. Flowering mostly in June but seen in flower also in early November; fruits maturing by October. Known only from La Selva.

Nectandra hypoleuca is frequent in the old secondary woods and alluvial forest along the Río Puerto Viejo. At La Selva it is usually marked by a remarkably silvery white (glaucous) lower leaf surface. The floral morphology and leaf shape are similar to *N. martinicensis* Mez but that species is well marked by a pellucid punctate and glossy leaf surface. The glaucous leaves of *N. hypoleuca* are particularly notable in saplings. The sweet coconut fragrance of the flowers perfumes the air noticeably when these plants burst into flower.

3. ***Nectandra kunthiana*** (Nees) Kosterm.
(=*Ocotea cooperi* C. K. Allen)

Trees dioecious, 20–25 cm tall, 30–40 cm in diameter; bark surface dark gray, marbled white inside, oxidizing orange. Leaf blades oblong-elliptic, 20–40 cm long, 6–15 cm wide (shade and sapling leaves much larger than fertile canopy leaves), the apex long acuminate to rarely rounded, the base acute to rounded; midrib and lateral veins impressed above, prominent below, reticulate venation conspicuous and prominent above; major lateral veins arising at an angle of 40–50°; leaf surface glabrous (midrib pubescent) and shining above, erect pubescent and glaucous (canopy leaves) below; petioles 2–3 cm long. *Inflorescences* large, open panicles, axillary among the distal leaves, 17–26 cm long, many-flowered, the rachis densely tan pubescent. *Flowers* (pistillate not seen at La Selva) campanulate, 4–5 mm wide, densely pubescent; tepals triangular-ovoid, 1.2–1.5 mm long and about as wide; outer stamens nearly sessile, quadrate, 0.6–0.8 mm tall and about as wide; anther valves forming a line or very low arc, the outer valves more or less lateral; staminodia lacking; ovary linear. *Fruits* oblong-elliptic, 3.5–4 cm long, the lower 1/3 covered by the campanulate cup. Flowering in late February; fruits maturing perhaps by late July or August. Costa Rica, Panama and British Guiana.

Occasional in the alluvial forest along the principal rivers. This species can be recognized by its large, oblong, long acuminate leaves and, even in the seedling stage, by the thickened margin at the base of the blade. Although only presumed staminate flowers were examined at La Selva,

their more or less linear gynoecia and failure to produce fruit while near-by plants are known to produce fruit, confirm other reports of dioecy for this species.

4. ***Nectandra membranacea*** (Sw.) Griseb.
(=*N. standleyi* C. K. Allen)

Trees 5–15 m tall, 10–25 cm in diameter; bark surface dark gray, dirty white inside. *Leaf* blades oblong-elliptic, 19–31 cm long, 6.5–13 cm wide, the apex acuminate, the base acute and slightly recurved along the margin; midrib and lateral veins plane or slightly impressed above, drying reddish; lateral veins arising at an angle of 25–45°, cross veins between lateral veins perpendicular to the midrib; surface of the blade glabrous and usually dull above, minutely pubescent near base and shining above, petiole 0.5–1 cm long. *Inflorescences* open panicles, axillary among the distal leaves, 7–20 cm long, many-flowered. *Flowers* 3.5–4.5 mm wide at anthesis, greenish yellow; tepals ligulate, 1.6–2 mm long; outer stamens dome-shaped, wider than long, about 1 mm tall by 1.3 mm wide, with a short but definite filament about 1/2 as wide as the anther, the valves of the anthers in a horizontal line, the outer 2 lateral, the staminodia acicular, 0.4–0.6 mm long. *Fruits* ovoid, 1.2–1.5 cm long, the cupules conical, about 1 cm long. Flowering June and July; fruiting by December. West Indies; Costa Rica south into Brazil and Bolivia.

Common at La Selva in the abandoned pasture and in forest edge along the Sarapiquí River in the front of the Western Annex where apparently restricted mostly to open areas and unknown from the primary forest. The strongly ascending lateral veins and parallel transverse veins perpendicular to the midrib are distinctive.

5. ***Nectandra purpurea*** (Ruiz & Pavon) Mez

Small tree to 5(17) m tall and 15 cm in diameter. *Leaf* blades elliptic, 17–24 cm long, 7–11 cm wide, the apex abruptly short acuminate, the base acute; midrib apically prominent or plane, basally impressed above, prominent below, major lateral veins prominent on both surfaces, more so below; lateral veins arising at an angle of 40–45°, distinctly loop-connected submarginally, leaf surfaces glabrous and shining above, dull below and glabrous except for sparse hairs in the axils of the lateral veins; petioles 0.5–1 cm long. *Inflorescences* axillary but clustered at the tips of branches, 9–17 cm long, densely flowered, the rachis gray pubescent. *Flowers* about 5 mm wide, densely gray pubescent; tepals 1.4–1.8 mm long; anthers quadrate and slightly longer than the filaments, the valves of the an-

thers in a low arc, the staminodia rather large, clavate, 0.4–0.5 mm long; ovary depressed-globose, about 0.3 mm in diameter, the style slightly shorter. *Fruits* globose, about 1.5 cm in diameter, the cupule conical, about 1 cm long including the pedicel. Flowering late May through June. Nicaragua south to Peru and Brazil.

Presently known from only a few immature individuals on the La Selva property, but has been collected fertile nearby. The almost totally glabrous leaves, which are very shiny above both fresh and dry, the distinctly loop-connected lateral veins, and the sparsely pubescent domatia set this species apart from others in the area. This species is treated in the Flora of Barro Colorado Island under the name *Ocotea purpurascens*.

6. *Nectandra reticulata* (Ruiz & Pavon) Mez

Trees 15–30 m tall, 30–70 cm in diameter; surface of bark dark gray. *Leaf* blades lanceolate, 15–27 cm long, 5–10 cm wide, apically long acuminate, basally broadly acute to rounded and the margin markedly recurved below, the lamina bullate between the veins; major lateral veins slightly impressed above, prominent below, arising at an angle of 40–45°; leaf surface pubescent above and below with ferruginous hairs 2–3 mm long, older shade leaves often glabrous and shiny above; petioles 0.7–1.5 cm long. *Inflorescences* axillary among the distal leaves, 9–13 cm long, many-flowered; rachis densely ferruginous pilose. *Flowers* large, 1–1.2 cm broad, ferruginous pubescent; tepals 4–5.5 mm long; outer stamens 1.4–1.6 mm long, the anthers tepaloid, triangular or broadly lanceolate, about 3 times as long as the filaments, the valves of the outer anthers clustered in a low arc in the lower $\frac{1}{3}$ to $\frac{1}{4}$ of anther, the staminodia sessile, deltoid, about 0.5 mm tall; gynoecium densely pubescent, about 2.5 mm long, the ovary turbinate, about equal in length to the style. *Fruits* ovoid, about 13 mm long, the cupule campanulate, covering the lower third of the fruit. Flowering during the rainy season, October to December. Mexico south to northwestern South America.

Along rivers in the Puerto Viejo area. Although it is nowhere abundant, its large white flowers make this species very conspicuous during the rainy season when few other trees are in flower. No other species of Lauraceae at La Selva

has basally recurved leaf margins that form such large auriculate flaps. Some collectors indicate that these pockets harbor small ants.

4. *OCOTEA* Aubl.

Trees, often dioecious. *Leaves* alternate, glabrous to densely pubescent. *Inflorescences* axillary panicles, sparsely to densely flowered. *Flowers* small; tepals erect at anthesis, usually broadly triangular, mostly yellowish green to creamy white; fertile stamens 9, the outer 6 introrse, the inner 3 extrorse or lateral, the 4 valves of the outer anthers describing a narrow arc or essentially in 2 vertical rows; stamens of the inner whorl flanked basally by paired floral glands, the staminodia usually linear and inconspicuous or lacking. *Fruits* globose or ovoid, green or black at maturity, subtended or partially enclosed by a flat to deeply concave cupule, green or red at maturity.

Ocotea is now restricted to the neotropics with most species found in South America. All but two of the 33 species reported by Allen for Central America were considered endemic. Many species are undoubtedly more widespread than previously thought; seven of the 13 species at La Selva are known either from the West Indies or South America or both.

In the dioecious species of *Ocotea*, the staminate flowers have gynoecea that are usually linear compared to the turgid more or less globose ovary of the pistillate flowers. Likewise, the pistillate flowers bear stamens that may appear abortive (smaller) only by comparison to those of the staminate flowers. Thus, it is often difficult to be certain about the breeding system (hermaphroditic vs. dioecious) of a particular species if one examines only a single individual. Even in those species that show some dimorphism in other features (tepals and floral tube), the differences are all in relative size (e.g., floral tube longer in pistillate than in staminate flowers) and therefore cryptic.

As indicated in the generic key, *Ocotea* is distinguished from *Nectandra* by the anther valves arranged in a narrow arc or two vertical rows and by the broadly triangular tepals that are erect at anthesis. These characters are best and perhaps only accurately examined in mature flowers.

KEY TO THE SPECIES

1. Flowers densely pubescent and colored by the gray, golden or rusty hairs; twigs or leaves or both also conspicuously pubescent.
2. Pubescence golden or rusty; inflorescence $\frac{1}{2}$ or more as long as the leaves; fruits ovoid and partially enclosed in the cupule.

3. Base of blade acute, the margin plane; treelets or subcanopy trees usually of stream margins in primary forest. 12. *O. mollifolia*.
3. Base of blade decurrent and the margin slightly revolute; canopy trees of alluvial forest.
 4. Pubescence of lower leaf surface appressed, golden; flowers with linear to clavate and occasionally polleniferous staminodia. 4. *O. caracasana*.
 4. Pubescence of lower leaf surface erect, rusty; flowers lacking staminodia. 8. *O. hartshorniana*.
2. Pubescence gray, inflorescence $\frac{1}{3}$ or less as long as the leaves; fruits always globose and subtended but not enclosed by the cupule.
 5. Leaf blades 3–4 times longer than wide, minutely appressed pubescent below; plants with distinctive pungent fragrance; cupule and pedicel warty with lenticels; small trees of forest edge. 10. *O. leucoxydon*.
 5. Leaf blades about 2 times longer than wide, erectly pubescent below; plants with typical laurel fragrance; cupule and pedicel smooth; canopy trees of alluvial forest. 2. *O. babosa*.
1. Flowers minutely and sparsely pubescent, the hairs not colored; twigs and leaves minutely and sparsely pubescent if at all.
 6. Leaf blades widest above the middle.
 7. Tepals gray green, about 3 mm wide; cupule discoid, thick-margined, green at maturity. 7. *O. floribunda*.
 7. Tepals cream-colored, 1–2 mm wide; cupule campanulate, thin-margined, red at maturity.
 8. Apex of stem hollow and harboring small ants. 1. *O. atirrensis*.
 8. Apex of stem solid; rare canopy or subcanopy trees.
 9. Petioles less than 0.5 cm long, the blade decurrent nearly to the twig; axils of lateral veins sparsely pubescent below; fruits ovoid. 9. *O. ira*.
 9. Petioles about 1 cm long, the blade attenuate basally but not to the twig; leaves glabrous throughout; fruits globose. 4. *O. bijuga*.
 6. Leaf blades widest at or below the middle.
 10. Tepals 5–7 mm long; apex of stem hollow and harboring small ants; common shrubs, usually less than 4 m tall. 6. *O. dendrodaphne*.
 10. Tepals 1.5–2.5 mm long; apex of stem solid.
 11. Reticulate venation very prominent, especially below; axils of basal lateral veins often bearing large domatidial pits. 11. *O. meziana*.
 11. Reticulate venation obscure; axils with or without domatia.
 12. Inflorescence densely flowered; leaf apex abruptly narrowed to a caudate tip; domatia lacking; leaves drying gray green. 5. *O. cernua*.
 12. Inflorescence sparsely flowered; axillary domatia very minute; leaf apex acuminate; leaves drying black. 13. *O. tenera*.

1. *Ocotea atirrensis* Mez

Shrubs or small trees 2.5–3(?) m tall, 2–5 cm in diameter; branch tips angled and hollow, harboring small ants. *Leaf* blades oblong-spatulate, widest above the middle, 25–32 cm long, 9–13.5 cm wide, the tip acute to rounded with an abrupt acumen 0.5–2.5 cm long, the base acute; midrib and lateral veins distinct and prominulous on both surfaces, often drying reddish; lateral veins arising at an angle of 30–40°; surface of the blade glabrous, gray green above (reddish when young), minutely appressed pubescent on the tertiary veins below; petioles 1–1.5 cm long, deeply grooved. *Inflorescences* axillary among the distal leaves, 13–23 cm long, many-flowered; rachis glabrous. *Flowers* about 1.5 mm long; tepals 1.2 mm long, cream-colored; outer stamens 1 mm long, the anthers longer than wide and about as long as the filaments, staminodia lacking; ovary globose, about 0.8 mm in diameter, the style slightly longer. *Fruits* ovoid-cylindric, 2.5–3.5 cm long, black at maturity, the cupule nearly hemispherical, about 1 cm long and 0.7 cm wide, shortly flared at the summit and often bearing

persistent tepals on the margin, red at maturity. Flowering late in February through April; mature fruit developing August through November, often persisting into March. Costa Rica and Panama.

Ocotea atirrensis is one of the most common species of Lauraceae at La Selva. It is a low shrub or treelet found in the understory of primary forest on slopes and ridges, at the edge of trails and in other light gaps. Like *O. dendrodaphne*, it nearly always harbors small ants in its hollow twigs. The short petiolate, elongate leaves widest above the middle, help distinguish this species from others in the area. A closely related species, *O. nicaraguensis* Mez, with very similar though much larger leaves grows in forest nearby along the Río Peje.

2. *Ocotea babosa* C. K. Allen

Trees 15–35 m tall, 30–100 cm in diameter; surface of bark gray, marbled tan and white within; sap slimy. *Leaf* blades elliptic, 16–25 cm long, 8.5–12.5 cm wide, the apex and base acute; midrib and lateral veins plane, reticulate veins pro-

minulous above, all prominent below; lateral veins arising at an angle of 45–55°; leaf surface bullate, glabrous and shiny above, the lower surface pubescent with trichomes to 0.3 mm long; petioles 1.5–3 cm long. *Inflorescences* axillary among the distal leaves, 7–10 cm long; rachis gray pubescent. *Flowers* about 3.5 mm long; tepals to 2.5 mm long; outer stamens about 1 mm long, the anthers more or less quadrate and longer than the filaments, the staminodia lacking; ovary ellipsoid. *Fruits* globose, 0.7–0.8 cm in diameter, dark green at maturity; cupule campanulate-cylindrical, 0.7–1 cm long, about 0.5 cm wide, pink, the tepals often persistent on its margin. Flowering (specimen immature) begins in late November, probably continues to February; fruits maturing by April. Costa Rica (only known from La Selva); Venezuela.

Apparently rare at La Selva where known from only three or four individuals in alluvial soil. The prominent reticulate venation, bullate leaves, pubescence of the lower leaf surface, and small globose fruits distinguish this species from all others at La Selva. Because the only flowering collection from La Selva has immature inflorescences, the identification is based on a close match of the rather unique leaves and fruits to those of type material of *Ocotea babosa*.

3. *Ocotea bijuga* (Rottb.) Bernardi

Trees 25–30 m tall, 45–60 cm in diameter; surface of bark light gray to nearly white, orange inside, rapidly oxidizing brown; sap with faint pine fragrance. *Leaf* blades elliptic, 9–14.5 cm long and 3–5.5 cm wide, apically acute to acuminate, basally acuminate, the midrib and lateral veins plane above, prominent below, the lateral veins arising at an angle of 40–60°; surface of blade glabrous and glossy above, glabrous and duller below; petioles 0.5–1.5 cm long. *Inflorescences* axillary and extra axillary among the distal leaves, 10–15 cm long; rachis glabrous to minutely and sparsely pubescent. *Flowers* 2–2.5 mm long, minutely appressed pubescent, yellowish green to cream; tepals 1.2–1.5 mm long; outer stamens somewhat triangular to ovoid, about 1 mm long, the anthers slightly longer than the filaments, the staminodia lacking; ovary ovoid, about 1 mm long, the style about as long; stigma discoid. *Fruits* globose, 0.8–1.2 cm in diameter; cupules shallow, broadly funnelform in fresh material, discoid when dry. Flowering in October; fruits mature in February to April. Costa Rica, Venezuela, Surinam and Brazil.

Apparently rare at La Selva and known only from ridge tops in primary forest. The glabrous, narrowly elliptic leaves with somewhat decurrent bases are distinctive and serve to distinguish this

rather nondescript species from other Lauraceae. The small globose fruits are hidden, even at maturity, in small infructescences below the clusters of leaves near the branch tips. The species is reportedly dioecious.

The leaves of *Ocotea bijuga* are similar in size and shape to some specimens of *O. floribunda* which also has perfectly globose fruits. The similarities between these two species, however, are only superficial; among those at La Selva the present species is probably most closely related to *O. ira*. As with several other canopy Lauraceae found at La Selva, this species is apparently rarely collected in Central America.

4. *Ocotea caracasana* (Nees) Mez (=*Nectandra hypoglauca* C. K. Allen)

Trees about 30 m tall and 60 cm in diameter, the base provided with prop roots; surface of bark dark gray, inside marbled white and tan. *Leaf* blades obovate, 15–20 cm long, 6–8 cm wide, apically acute to rounded with a short acuminate, basally acuminate-decurrent nearly to the base of the apparent petiole; midrib and lateral veins plane above, prominent below arising at an angle of 40–45°; leaf surface glabrous and shiny above, minutely appressed silvery pubescent and appearing glaucous below; petioles 0.4–0.5 cm long. *Inflorescences* axillary but clustered near the apices of the branchlets, 8–11 cm long, densely flowered; rachis silvery appressed pubescent. *Flowers* about 4 mm long, pubescent, cream-colored; tepals 1.8–2.2 mm long; outer stamens 1.2–1.5 mm long, the anthers trapezoidal, slightly longer than the filaments, arrangement of the valves variable, sometimes approaching a low arc, the staminodia from filiform to anther-bearing, 1–1.5 mm long, often flanked by floral glands; ovary pyriform, about 1.5 mm long, the style $\frac{1}{3}$ as long. *Fruits* large, ovoid, 3–4 cm long, 2–2.5 cm in diameter; cupules hemispherical, about 1.5 cm long and 2.5 cm in diameter, the margin distantly toothed by the persistent remains of the tepals. Specimen with both mature fruit and flower collected in late May. Costa Rica, Panama, Venezuela and British Guiana.

Known at La Selva from just one individual at the base of a steep ridge near the southwest corner of the Western Annex. The presence of prop roots relates this species to *Ocotea mollifolia* and *O. hartshorniana* which it also resembles in details of the flowers, fruits and pubescence.

5. *Ocotea cernua* (Nees) Mez

Dioecious shrubs or trees to 20 m tall; surface of the bark dark gray, white within. *Leaf* blades

oblong-elliptic, 12–17 cm long, 5–8 cm wide, the apex abruptly caudate with a narrow acumen 1–2 cm long, the base acute; midrib and lateral veins plane above, prominent below, reticulate venation indistinct on both surfaces; lateral veins arising at an angle of 40–80°, the lowest veins at the narrowest angle and often extending beyond ½ the length of the blade; leaf surface usually with punctate dots above, glabrous, yellowish green both surfaces, drying grayish green; petioles 1–1.5 cm long. *Inflorescences* racemose-paniculate, 5–7 cm long, axillary and sometimes extra axillary, dispersed among the distal leaves, rather densely flowered; rachis glabrous or with a few minute appressed trichomes. *Staminate flowers* funnel-shaped, 2.2 mm long; tepals 1.2–1.6 mm long, yellowish green to cream; outer stamens quadrate, about 0.8 mm tall, sessile; staminodia lacking; gynoecium clavate-linear, about 0.8 mm long; *pistillate flowers* campanulate, about 2.2 mm long; tepals, stamens, and floral glands ½ the size of those in the staminate flowers; ovary globose, about 1 mm in diameter, the style much shorter; stigma 3-lobed. *Fruits* ovoid, 1.5–2 cm long, black at maturity; cupules crateriform, red, covering the lower ⅓ of the fruit. Flowering in early April; fruits maturing in August. Mexico south into South America.

Uncommon at La Selva where restricted to river and stream banks in the primary forest. The plants apparently have a very short flowering season. The flowers produce a strong sweet fragrance in the morning. Except for the large pistillate plant in the Arboretum, all the known individuals at La Selva are understory treelets. The leaf apex, abruptly narrowed to a definite acumen, is the most distinctive vegetative feature of this species.

6. *Ocotea dendrodaphne* Mez

Shrubs or treelets 3–5 m tall; surface of bark gray; branches sharply angled, hollow and harboring small ants. *Leaf* blades oblong-elliptic, 20–36 cm long, 6.5–13 cm wide, the apex acute to acuminate, the base acute; midrib and lateral veins slightly impressed above, prominent below; lateral veins arising at an angle of 40–70°; surface of blade smooth above, prominently reticulate below, glabrous; petioles 1–3 cm long. *Inflorescences* clustered at the tips of branches, 3–9 cm long, densely flowered; rachis minutely appressed pubescent. *Flowers* large, 5–6 mm long, bright white; tepals 4–5 mm long, narrowly triangular; outer stamens somewhat tepaloid, 1.5–1.7 mm long, sessile, the floral glands sometimes lacking, staminodia lacking; ovary pyriform, about 1 mm tall, stipitate, the style much shorter,

the stigma large, discoid. *Fruits* narrowly ovoid, 2–2.5 cm long, black at maturity; cupules funnel-shaped, covering the lower ¼ of the fruit. Flowering mostly March to June (also seen in September); fruits maturing mostly by July to November (fruits also seen in March). Mexico south into Panama.

Very common at La Selva where found on slopes and ridges throughout the primary forest. Its flowers are much larger and brighter white than other sympatric species of *Ocotea*. It is related to the widespread *O. veraguensis* (Meisner) Mez with which it shares the large flowers and tepaloid stamens.

7. *Ocotea floribunda* (Sw.) Mez

Diocious trees 20–30 m tall, 30–80 cm in diameter; surface of bark dark gray, pale tan and marbled within; branches black. *Leaf* blades elliptic, widest at or slightly above the middle, 10–19 cm long, 4–8 cm wide, the apex almost rounded to acute, the base acute; midrib and lateral veins slightly prominent above, more so below, drying reddish brown, the reticulate venation very finely areolate and prominulous on both surfaces, at least in dried material, the lateral veins arising at an angle of 50–60°; leaf surface glossy and glabrous above, dull, occasionally somewhat glaucous, sparsely pubescent along the veins below; petioles 1–1.5 cm long. *Inflorescences* axillary and extra axillary, scattered among the distal leaves, 7–14 cm long, many-flowered; rachis minutely pubescent. *Flowers* (staminate not seen) large, salverform, 5–7 mm across, grayish green, appressed pubescent; tepals broadly triangular, 2.5–3 mm long and as wide; outer stamens 1 mm long, the anthers triangular and equal in length to the filaments, staminodia lacking; ovary ovoid, about 1.2 mm long, equal in length to the style, the stigma large, discoid. *Fruits* globose 1.5 cm in diameter, glaucous, green at maturity; cupule a thick flat disc about 1 cm wide and 2 mm thick, green, marked by a glaucous ring on the upper surface (seen where the fruit has fallen), the margin smooth and rounded but sometimes adorned with the persistent tepals. Flowering January to February; fruits mature by September. West Indies; Nicaragua south into northern South America.

Widely dispersed at La Selva but apparently nowhere abundant. It is known from just three individuals in the primary forest. The species is quite distinctive and easily recognized as the very fine prominulous reticulation, the discoid cupule and the very broad tepals are unusual in *Ocotea* and set *O. floribunda* apart from all others at La Selva.

8. *Ocotea hartshorniana* Hammel

Trees 20–30 m tall, 40–100 cm in diameter; surface of bark pinkish tan, pink inside; trunk usually with stilt, or prop roots. *Leaf* blades oblong-spatulate, 12–19 cm long, 3.5–7 cm wide, the apex abruptly acuminate, the base cuneate, decurrent on the petiole and the margin often slightly recurved; midrib and lateral veins plane or slightly impressed above, rusty pubescent and prominent below; reticulate venation conspicuous on both surfaces; lateral veins arising at an angle of 30–40°; surface of blade glabrous and shiny above, soft pubescent and glaucous (canopy leaves) below; petioles 0.5–1.5 cm long, flat above. *Inflorescences* clustered among the distal leaves, 12–15 cm long, densely flowered; rachis rusty pubescent. *Flowers* about 3 mm long, rusty pubescent; tepals 1.6–2 mm long; outer stamens about 1.2 mm long, the anthers triangular and slightly longer than the pubescent filaments, staminodia lacking; ovary pyriform, narrowed at the base, about 1.5 mm tall; style about 1 mm long, the stigma peltate and discoid. *Fruits* ovoid-cylindrical, about 2 cm long, 1 cm wide, obtuse and apiculate, green at maturity; cupules urceolate, about 1.5 cm long, brownish, covering the lower 1/3 of the fruit. Flowering and fruiting April to May. Costa Rica and Ecuador.

Quite conspicuous although at La Selva apparently restricted to the alluvial forest near the Río Puerto Viejo. Juvenile plants are commonly encountered and are very distinctive because of their tiered growth and reddish orange new leaves with rusty pubescence. Mature plants are usually provided with stilt roots, apparently an unusual feature in the Lauraceae. *Ocotea hartshorniana* is probably closely related to *O. caracasana* and *O. mollifolia* which also possess stilt roots and are similar in details of venation, pubescence, flowers and fruits.

9. *Ocotea ira* Mez

Trees 20–25 m tall, the trunk with short narrow buttresses; surface of bark dark brown or gray, somewhat roughened and flaky, white but oxidizing orange within; sap with strong resinous fragrance. *Leaf* blades spatulate, 15–23 cm long, 8–10 cm wide, apically broadly acute to rounded, basally gradually tapered, narrowly acute and slightly recurved; midrib and lateral veins plane to slightly prominent above, prominent below; lateral veins arising at an angle of 40–50°, indistinct domatia present in the lower axils; leaf surface more or less shiny above, paler below, glabrous except for sparsely pubescent domatia; petioles very short, 3–5 mm long or lacking. *In-*

florescences clustered at the tips of branches, 15–18 cm long, densely flowered; the rachis glabrous. *Flowers* about 2.5 mm long, cream-colored, minutely and sparsely pubescent; tepals 1.2–1.6 mm long; outer stamens 0.7–0.8 mm long, the pubescent filaments slightly longer than the anthers, staminodia lacking; ovary globose, about 1 mm long, the style 1/2 as long. *Fruits* cylindrical-ovoid, 2–2.5 cm long, 1 cm wide, black at maturity; cupules conical, about 1.5 cm long, only subtending, not enclosing the base of the fruit. Flowering observed in November and July; fruiting observed in October and July. Costa Rica, Panama, and South America.

Apparently uncommon at La Selva where found only in primary forest, most often on ridge tops. The species is easily distinguished from other sympatric Lauraceae by the glabrous, nearly spatulate sessile leaves, which are reddish when young and when dry. Although these features as well as floral and fruit characters ally *Ocotea ira* with *O. atirrensis*, the two species are quite distinct; the latter is a hollow-stemmed, ant-har-boring, understory treelet with much larger, abruptly acuminate leaves.

10. *Ocotea leucoxylo* (Sw.) Lanessan

Dioecious shrubs or treelets, 5–10 m tall; bark surface dark gray-black and warty; crushed herbage foetid. *Leaf* blades oblong-elliptic, 16–27 cm long, 5.5–8.5 cm wide, apically acuminate, basally acute; midrib and lateral veins plane above, prominent below; lateral veins arising at an angle of 40–50°; surface of blade glabrous above, minutely scaly and pubescent below, both surfaces drying dull grayish green; petioles 1–2 cm long. *Inflorescences* axillary, dispersed along the branches, 4–8 cm long; rachis gray pubescent. *Flowers* (pistillate not seen) about 2.5 mm long, yellowish white, pubescent; tepals about 2 mm long; outer stamens 1.2 mm long, the anthers more or less triangular, slightly longer than the filaments, staminodia lacking; gynoecium linear. *Fruits* globose, 1–1.5 cm in diameter, green at maturity; cupules campanulate, about 1 cm long, 0.5 cm wide, warty, brownish red at maturity. Flowering February to July; fruits maturing by May to October. West Indies; Mexico south into Venezuela.

Although found in the primary forest understory, this species occurs most often at forest edges but is nowhere common. The foul smelling fragrance of the crushed leaves is alone enough to distinguish *Ocotea leucoxylo* from all other species at La Selva. The warty cupules, distant rather than clustered inflorescences, gray green leaves and unusual scaly lower leaf surface make

the species very distinctive and easy to recognize even on herbarium sheets.

11. *Ocotea meziana* C. K. Allen

Shrubs or trees 2–15 m tall, 10–30 cm in diameter; surface or bark dark gray; sap not fragrant. *Leaf* blades elliptic, 16–22 cm long by 7–10 cm wide, apically acuminate, basally acute; midrib and lateral veins plane above, prominent below, reticulate venation very distinct and prominent, especially below; lateral veins arising at an angle of 40–60°, often with conspicuous, glabrous pit-domatia in the axils; surface of blade usually shinier below than above, glabrous except often minutely and very sparsely pubescent below; petioles 1–3 cm long. *Inflorescences* axillary and extra axillary among the distal leaves, 8–15 cm long, rather sparsely flowered; rachis glabrous or microscopically and sparsely appressed pubescent. *Flowers* 1.5–2.5 mm long, glabrous or sparsely and minutely appressed pubescent, cream to yellowish green; tepals 1.2–1.6 mm long; outer stamens about 1.5 mm long, the anthers narrowly triangular and slightly longer than the filaments, staminodia lacking; ovary turbinate, about 1 mm long, tapering to the somewhat shorter style. *Fruits* oblong-ovoid, 2.5–3 cm long; cupules campanulate, about 1.5 cm long, enclosing only the very base of the fruit, flaring funnellform in dried material. Flowering February through March; maturing fruit by August to November. Nicaragua, Costa Rica and Panama.

Common at La Selva where found only in primary forest, most often on slopes and ridges. The shining, prominently reticulate lower leaf surface helps distinguish this species from other sympatric species of *Ocotea*. The almost total lack of fragrance to the sap is also unusual. The leaf domatia, when present, are very large and form visible blisters even on the upper surface in fresh material.

12. *Ocotea mollifolia* Mez

Shrubs or trees 4–20 m tall, 15–45 cm in diameter; surface of bark orange tan, pink inside; trunk often provided with prop roots. *Leaf* blades obovoid, 16–23 cm long, 10–13 cm wide, the apex broadly acute to rounded, the base acute; midrib and lateral veins plane above, prominent below; lateral veins arising at an angle of 40–60°; surface of blade usually shiny above, rusty tan pubescent on the veins, pubescent throughout below; petioles 0.5–1 cm long. *Inflorescences* axillary and apparently extra axillary among the distal leaves, 5–15 cm long, many-flowered but

diffuse; rachis reddish tan pubescent. *Flowers* about 3 mm long, reddish tan pubescent; tepals 1.5–2 mm long; outer stamens 1.2–1.5 mm long, the anthers nearly triangular, slightly longer than the pubescent filaments; staminodia lacking; ovary turbinate, the acute tip topped by the small stigma. *Fruits* oblong-cylindrical, about 4 cm long and 1.5 cm wide, globose at early stages and mostly immersed in the cupule; cupules campanulate, about 1 cm long, covering the lower ¼ of the fruit at maturity, the margin often toothed with the persistent and somewhat accrescent tepals. Flowering February to June; fruits maturing by December. Wet lowlands of Costa Rica.

Uncommon at La Selva where usually found as an understory tree in primary forest, most often along streams in the hilly southern part of the property. With *Ocotea hartshorniana* and *O. caracasana* it shares the unusual feature of prop roots as well as many features of venation, pubescence, flowers, and fruits. *Ocotea mollifolia* is easily distinguished among these three by its broader leaf blades that are abruptly acute rather than decurrent on the petiole.

13. *Ocotea tenera* Mez

Shrubs or treelets, dioecious(?), 3–6 m tall, 4–10 cm in diameter; branches tiered with the leaves more or less distichous and horizontal; surface of bark dark grayish brown. *Leaf* blades elliptic, 15–20 cm long, 5.5–8 cm wide, apically acuminate, basally acute; midrib and lateral veins slightly raised above, prominent below, the lateral veins arising at an angle of 50–70°, the axils with small inconspicuous blisters (domatia) opening below; leaf surface glabrous, bullate, dark green and satiny but drying black; petioles 0.5–1 cm long. *Inflorescences* axillary and extra axillary among the distal leaves, 5–12 cm long, many-flowered but the flowers dispersed; rachis glabrous. *Flowers* yellowish green to cream; tepals 1.3–1.6 mm long; outer stamens rectangular or clavate, longer than wide, 0.8–1 mm long, the anthers equal in length and hardly distinct from the wide filaments, the staminodia linear, 0.4 mm long; ovary pyriform, about 1.5 mm long, gradually tapering to the apex; style short or lacking. *Fruits* ovoid, about 2.5 cm long, usually pendent; cupules narrowly conical, not differentiated from the swollen pedicel, about 4 cm long, subtending but not or only slightly enclosing the base of the fruit. Flowering June and July; developing mature fruit by September to November. Costa Rica and Panama.

Usually found in secondary woods or at the edge of forest and apparently restricted to the front of the property. Its growth form with tiered

branching and more or less distichous, horizontal leaves is quite distinctive. The almost black leaves (when dry) make for easy recognition. Although reportedly dioecious, no floral dimorphism was observed in the plants at La Selva.

In stature and in its small, glabrous inflorescences and greenish flowers *Ocotea tenera* resembles sympatric *O. cernua* and *O. meiziana*.

COMBINED KEY TO THE SPECIES OF BOTH NECTANDRA AND OCOTEA

1. Flowers densely pubescent and colored by the gray, golden or rusty hairs; twigs or leaves or both also conspicuously pubescent.
 2. Margin of leaf blade strongly revolute at the acute base and forming 2 large auricles. *Nectandra reticulata*.
 2. Margin of blade plane or only obscurely revolute along the acuminate base.
 3. Pubescence golden or rusty; inflorescence $\frac{1}{2}$ or more as long as the leaves; fruits ovoid and partially enclosed in the cupule (globose and exposed in *Nectandra cissiflora*).
 4. Tepals erect at anthesis; anthers stipitate, triangular-ovoid, the valves in a narrow arc; margin of cupule often toothed with the persistent remains of the tepals; trees with prop roots.
 5. Base of blade acute, the margin plane; treelets or subcanopy trees usually of stream margins in primary forest. *Ocotea mollifolia*.
 5. Base of blade decurrent and the margin slightly revolute; canopy trees of alluvial forest.
 6. Pubescence of lower leaf surface appressed, golden; flowers with linear to clavate and occasionally polleniferous staminodia. *Ocotea caracasana*.
 6. Pubescence of lower leaf surface erect, rusty; flowers lacking staminodia. *Ocotea hartshorniana*.
 4. Tepals spreading at anthesis; anthers sessile, quadrate, the valves in a single horizontal row; margin of cupule entire; prop roots lacking.
 7. Leaf blades lanceolate-elliptic, 20–40 cm long, the base acute and with a conspicuous marginal vein; reticulate venation prominent above; pubescence tan. *Nectandra kunthiana*.
 7. Leaf blades ovoid-elliptic, 15–22 cm long, the base decurrent and the marginal vein faint; reticulate venation obscure above; pubescence golden. *Nectandra cissiflora*.
 3. Pubescence gray, inflorescence $\frac{1}{3}$ or less as long as the leaves; fruits always globose and subtended but not enclosed by the cupule.
 8. Leaf blades 3–4 times longer than wide, minutely appressed pubescent below; plants with distinctive pungent fragrance of hair dye chemicals; cupule and pedicel warty with lenticels; small trees of forest edge. *Ocotea leucoxydon*.
 8. Leaf blades ca. 2 times longer than wide, erect pubescent below; plants with typical laurel fragrance; cupule and pedicel smooth; canopy trees of alluvial forest. *Ocotea babosa*.
1. Flowers minutely and sparsely pubescent, the hairs not colored; twigs and leaves minutely and sparsely pubescent if at all.
 9. Leaf blades widest above the middle.
 10. Tepals gray green, ca. 3 mm wide; cupule discoid, thick-margined, green at maturity. *Ocotea floribunda*.
 10. Tepals cream-colored, 1–2 mm wide; cupule campanulate, thin-margined, red at maturity.
 11. Apex of stem hollow and harboring small ants. *Ocotea atirrensis*.
 11. Apex of stem solid; rare canopy or subcanopy trees.
 12. Petioles less than 0.5 cm long, the blade decurrent nearly to the twig; axils of lateral veins sparsely pubescent below; fruits oblong. *Ocotea ira*.
 12. Petioles ca. 1 cm long, the blade attenuate basally but not to the twig; leaves glabrous throughout; fruits globose. *Ocotea bijuga*.
 9. Leaf blades widest at or below the middle.
 13. Tepals 5–7 mm long; apex of stem hollow and harboring small ants; common shrubs, usually less than 4 m tall. *Ocotea dendrodaphne*.
 13. Tepals 1.5–2.5 mm long; apex of stem solid.
 14. Leaf blades glabrous throughout (sometimes obscurely appressed pubescent in *Ocotea meiziana*); tepals ca. 1.5 mm long.
 15. Reticulate venation very prominent, especially below; axils of basal lateral veins often bearing large domatidial pits. *Ocotea meiziana*.
 15. Reticulate venation obscure; axils with or without domatia.
 16. Inflorescence densely flowered; leaf apex abruptly narrowed to a caudate tip; domatia lacking; leaves drying gray green. *Ocotea cernua*.
 16. Inflorescence sparsely flowered; axillary domatia very minute; leaf apex acuminate; leaves drying black. *Ocotea tenera*.
 14. Leaf blades sparsely appressed pubescent below or at least pubescent in the axils of veins; tepals mostly ca. 2 mm long.

17. Axils of lateral veins bearing tufts of hair (domatia) below, leaf blades otherwise glabrous; fruits ovoid.
18. Reticulate venation prominent above; leaf surface shiny above, not glaucous; hairs of the domatia sparse; lateral veins distinctly loop-connected submarginally. *Nectandra purpurea*.
18. Reticulate venation obscure above; leaf surface dull above, usually glaucous below; hairs of the domatia dense; lateral veins not distinctly loop-connected. *Nectandra hypoleuca*.
17. Axils without domatia; leaf blades minutely appressed pubescent below; fruits globose.
19. Leaf blades 3-4 times longer than wide; tertiary veins between lateral secondaries perpendicular to the midrib; twigs nearly glabrous. *Nectandra membranacea*.
19. Leaf blades ca. 2 times longer than wide; tertiary veins not perpendicular to the midrib; twigs densely golden pubescent. *Nectandra cissiflora*.

5. PERSEA P. Mill.

KOPP, L. E. 1966. A taxonomic revision of the genus *Persea* in the western hemisphere (*Persea*—Lauraceae). Mem. New York Bot. Gard. 14: 1-117.

Trees or shrubs, usually aromatic. *Leaves* alternate or appearing whorled, often glaucous below, pinnately veined, the marginal vein often thickened basally. *Inflorescences* paniculate, axillary to subterminal among the distal leaves, the rachis often conspicuously pubescent. *Flowers* perfect, the tepals subequal or strongly differentiated and then the inner whorl longer, patent or reflexed at anthesis, not forming a perianth tube; fertile stamens 9, each with 4 locules, the 3 of the inner whorl each flanked by a pair of glands; staminodia large, cordate, stipitate. *Fruits* often globose, to pyriform, lacking a cupule but often subtended by the persistent remains of the tepals; peduncle often somewhat thickened.

As usually treated the genus *Persea* is largely restricted to tropical America. Kopp's recent revision of American species recognized 81 species, 20 of them from Mexico and Central America.

Persea is usually distinguished from *Phoebe* by the arrangement of anther valves (analogous to the distinction of *Ocotea* from *Nectandra*). The cupulate fruit of *Phoebe* in contrast to the non-cupulate fruit of *Persea* is probably a more certain distinction.

The two species of Lauraceae at La Selva that were not found in fertile condition (and hence not included since they were not identified) very likely belong to the genus *Persea*. Both unknowns have leaves with relatively long petioles and are large trees from primary forest near the back of the property.

KEY TO THE SPECIES

1. Leaves alternate, the blades elliptic, pubescent below; petioles often 3-6 cm long, pubescent. 1. *P. americana*.
1. Leaves whorled or subopposite, the blades oblanceolate, glabrous throughout; petioles 1-1.5 cm long, glabrous. 2. *P. rigens*.

1. *Persea americana* P. Mill.

Trees to 20(40) m tall. *Leaf* blades elliptic, 6-30 cm long, 3.5-19 cm wide, apically acute to acuminate, basally acute to rounded, the lateral veins plane above, prominent beneath; reticulate venation obscure above, prominent beneath; lateral veins arising at an angle of 40-50°; surface of blade glabrous above, sparsely pubescent and glaucous beneath; petioles 1-6 cm long. *Inflorescences* subterminal, 5-15 cm long; rachis tawny pubescent. *Flowers* about 6 mm long, tawny pubescent; tepals erect at anthesis; outer stamens about 3.5 mm long, the anthers more or less rectangular, slightly longer than the pubescent filaments; staminodia sagittate; ovary globose to ovoid, the style about 3 mm long, the stigma somewhat peltate. *Fruits* large, globose to pyriform, 5-15 cm in diameter. Flowering mostly in the dry season, December to March. Mexico into South America; cultivated worldwide in tropics and subtropics.

Planted near dwellings and perhaps persisting or escaped. Saplings of this species have been found in the primary forest at La Selva.

2. *Persea rigens* C. K. Allen

Trees to 10 m tall (taller elsewhere), 15 cm in diameter; leaves subopposite and whorled. *Leaf* blades oblanceolate, 21-24 cm long, 9-11 cm wide, the apex and base acute; midrib impressed above, at least basally, prominent below, lateral veins prominent above but more so below; reticulate venation prominent and conspicuous on both surfaces; lateral veins arising at an angle of 50-70°; surface of blade glabrous throughout, upper surface shedding a thin cuticular layer when dry, lower surface slightly glaucous; petioles 1-1.5 cm long. *Inflorescences* appearing terminal, congested at the tips of branches, 8-10 cm long; rachis glabrous to sparsely pubescent. *Flowers* about 3 mm long, minutely puberulent; tepals about 2.5 mm long, erect at anthesis; outer stamens 2 mm long, the anthers rectangular or truncate triangular, equal to or slightly shorter than

the pubescent filaments; staminodia 1.5–1.6 mm long, the head cordate and shorter than the stipe; ovary globose, about 1.2 mm in diameter, the style as long, the stigma large, discoid. *Fruits* large, depressed-globose, wider than long, about 2 cm tall by 5 cm wide; cupule lacking, perianth persistent but not accrescent. Flowering July to August. Guatemala, Costa Rica and northern South America.

Known from only two collections at La Selva, both from the primary forest near the south boundary. It has also been seen nearby on steep slopes along the Río Peje. The terminal inflorescences and whorled leaves with blades that are widest above the middle and that have prominent reticulate venation as well as the relatively large globose-depressed fruits distinguish this species from others at La Selva. The La Selva collection differs from that of the type only in having nearly glabrous rather than densely pubescent inflorescences.

The flowers of this species are almost identical to those of *Phoebe chavarriana* and other species of *Phoebe* such as the widespread *P. mexicana*. Placing the present species in *Persea* rather than *Phoebe* depends on accepting a circumscription of those two genera based on fruiting characters. *Phoebe* has persistent accrescent tepals forming a cupule-like structure while *Persea* may have persistent tepals but nothing resembling a cupule of any sort.

6. PHOEBE Nees

Trees or shrubs, aromatic. *Leaves* alternate or appearing whorled; basal pair of lateral veins often opposite and thicker than others, the venation then triplinerved. *Inflorescences* paniculate, axillary to subterminal among the distal leaves. *Flowers* perfect, the tepals usually equal, erect or reflexed at anthesis; fertile stamens 9, each with 4 locules, the 3 of the inner whorl each flanked by a pair of glands; staminodia large, cordate-stipitate. *Fruits* globose-ovoid, subtended by a cupule-like whorl of persistent and ac-

rescent tepals; peduncle often somewhat thickened.

1. *Phoebe chavarriana* Hammel

Small trees 10–15 m tall, 15–25 cm in diameter; surface of bark reddish brown, marked with long horizontal lenticels, warty, the inside marbled tan and white, slowly oxidizing orange, very fragrant. *Leaf* blades coriaceous, elliptic, 25–50 cm long, 10–23 cm wide, usually slightly more than 2 times longer than wide, the base and apex acute to nearly rounded; midrib impressed above, prominent below; venation strictly pinnate, the (6)8–10 major lateral veins borne at an angle of 45–50° and as much as 4–5(12) cm apart; leaf surface satiny above, dull and much paler below, appearing glaucous due to papillose epidermal cells, glabrous throughout; petioles (2)3.5–4.5(6) cm long and 3–5 mm thick, channeled above, distally, reddish. *Inflorescences* narrow and axillary but clustered near the branch tips, 12–23 cm long; rachis nearly glabrous to distantly short appressed pubescent. *Flowers* 2.5–3.2 mm long, nearly glabrous to sparsely appressed pubescent; tepals 2.3–2.4 mm long, the 2 whorls nearly equal, greenish white, the outer stamens 1.7–1.9 mm long, the filaments about ½ the length of the anthers, the staminodia conspicuous, cordate, stipitate, about 1.2 mm tall by 0.8–1 mm wide, the filaments of stamens and staminodia sparsely pubescent; ovary globose, as long as the style, both glabrous. *Fruits* ovoid, 1.5–1.8 cm long, 1–1.2 cm wide, dark green to almost black; cupule thin, shallow and the margin lobed from the persistent and accrescent tepals, mounted on a red and somewhat thickened, conical pedicel 1–1.5 cm long. Flowering April to May; fruits maturing by the end of July. Caribbean coast of Costa Rica.

Widespread in the forest at La Selva especially on slopes and ridges of the primary forest along the river as well as on hills in the south of the property. The huge, entirely glabrous, pale green leaves distinguish *Phoebe chavarriana* from all other Lauraceae in the area.