

Revision of *Piper* (Piperaceae) in the New World

3. The taxonomy of *Piper* sections *Lepianthes* and *Radula*

MARGARET CECILIA TEBBS

c/o Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB

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SYNOPSIS. The paper presents a taxonomic treatment of *Piper* sections *Lepianthes* (formerly the genus *Lepianthes*) and *Radula*, and 53 species are recognized, keyed, and described. There are two new species in section *Radula*, *Piper malpasensis* Tebbs and *P. thomasii* Tebbs.

INTRODUCTION

This third part of a revision of New World species of *Piper* deals with sections *Lepianthes* Raf. and *Radula* Miq. Section *Lepianthes* contains two herbaceous or shrubby species with inflorescences clustered together on a contracted, leafless stem, formally in the genus *Lepianthes* Raf. (*Pothomorphe* Miq.). Section *Radula* contains species with prominent prophylls, petioles mostly with ligule-like structures at the base, minute, often ciliate floral bracts, and small, obovoid, trigonous or round fruits. Most of the species in this section are shrubs or subshrubs; the remainder are scandent or herbaceous.

SECTION LEPIANTHES RAF.

There are only two species in this section, *Piper umbellatum* L. and *P. peltatum* L., separated from the other sections in *Piper* by their unusual stem development. These species were removed from *Piper* and placed in the genus *Lepianthes* by Rafinesque (1838), in *Heckeria* by Kunth (1839), and in *Pothomorphe* by Miquel (1844). Examination of the umbellate inflorescences show that they are not on a common axillary peduncle, but a contracted leafless stem emerging from a sheathing petiole (Burger, 1977). This character is not considered sufficient to maintain *Lepianthes* as a separate genus, and therefore it has been placed into a section within *Piper*. Section *Lepianthes* shares characters with *Piper auritum* Kunth at the end of section *Churumayu* (Tebbs, 1990), such as large membranous leaves with sheathing petioles, triangular, pale-ciliate bracts, and glabrous, trigonous fruits. *Piper marginatum* Jacq. and other species in the early parts of section *Radula* also have large leaves, sheathing petioles, and similar inflorescence characters. Section *Lepianthes* has therefore been placed between sections *Churumayu* and *Radula*.

DISTRIBUTION AND HABITAT

Piper peltatum and *P. umbellatum* both originated from the New World, but have since become widespread throughout the tropics. *Piper peltatum* grows in moist places, usually in fairly open positions, such as road- or track sides, edges of pasture, waste ground, and stream sides. It is a lowland plant, generally occurring from sea-level to about 500 m, although it can be found above these heights. *Piper umbellatum* is a plant of shady clearings in moist forests, cloud forest, and river banks. It is usually found at altitudes over 800 m, and often up to 1600 m.

MORPHOLOGY

Section *Lepianthes* contains herbaceous or shrubby plants with large, strongly veined, peltate or cordate leaves with sheathing petioles. The inflorescences are clustered together and arise at short intervals from a contracted, leafless stem; at the base of each peduncle are two prophylls, which at first enclose the young inflorescence (Blanc & Andraos, 1983). Inflorescences are slender and erect, with minute, white-ciliate floral bracts and glabrous, trigonous fruits.

TAXONOMIC TREATMENT

Section LEPIANTHES Raf.

Type: *Piper umbellatum* L.

Herbs or shrubs, stems glabrous to sparsely or densely pubescent. Leaves large, membranous, petioles sheathing the stems. Inflorescences clustered together, each one at first enclosed in two prophylls, on a leafless stem emerging from a

sheathing petiole. Floral parts densely congested; stamens 2; bracts white-ciliate; fruits obovoid, trigonous, glabrous; stigmas 3.

Open or shady areas, moist secondary forest, cloud forest, road- and stream sides, waste places; 0–2000 m.

Key to the species in section *Lepianthes*

- 1a. Shrub or subshrubs; leaves cordate, not peltate 54. *P. umbellatum*
 1b. Herbaceous or subshrubs; leaves ovate to suborbiculate, peltate 55. *P. peltatum*

54. *Piper umbellatum* L., *Sp. pl.* 1: 30 (1753). Type: Habitat in Domingo. *Plumier*.
 Fig. 1A, a.

Lepianthes umbellata (L.) Raf., *Sylva tellur.*: 84 (1838).

Heckeria umbellata (L.) Kunth in *Linnaea* 13: 566 (1839).

Pothomorphe umbellata (L.) Miq., *Comm. phytogr.*: 36 (1840).

Shrubs or subshrubs, 1–3 m high; stems glabrous to sparsely or densely pubescent, glandular. Leaves 20–40 cm long, 20–40 (–42) cm wide, cordate, membranous, glabrous to minutely puberulent, glandular, apex acute, base deeply lobed. Venation with 3–8 pairs of secondary veins arising from or near the base and 1–2 pairs from the middle part of the midrib, curving to the apex. Petioles sheathing, 10–30 cm long, glabrous to densely puberulent. Prophylls 10–20 cm long, glandular, subtending the peduncles. Inflorescences 4–10 cm long, in clusters of 2–8; peduncles 2–20 mm long, minutely puberulent. Anthers 1–2 mm long. Floral bracts 0.3–0.6 mm wide, triangular, white-ciliate. Fruits 0.5–0.8 mm wide, obovoid, trigonous, glabrous; stigmas 3, sessile.

Shady areas in cloud forest, moist secondary forest, hillsides and riverbanks; (400–) 700–2000 m.

DISTRIBUTION. Pantropical. **Mexico**, Guerrero: *Paxson* et al. 17M833 (BM); Morelos: *Pringle* 6159 (E); Nayarit: *Croat* 45328 (MO); Oaxaca: *Hernández & Torres* 449 (MO); Temascaltepec: *Hinton* 4407 (BM); Veracruz: *Purpus* 2017 (BM). **Guatemala**, Alta Verapaz: *Turckheim* 11258 (E); El Progreso: *King* 3256 (NY). **El Salvador**, Achuachapán: *Croat* 42083 (MO); Santa Ana: *Villacorta* 179 (LAGU). **Honduras**, Cortés: *Hernández* 5295 (BM); Lempira: *Nelson* et al. 0265 (MO); Tegucigalpa: *von Hagen* 1151 (NY). **Nicaragua**, Boaco: *Stevens* 14751 (BM); Esteli: *Grijalva & Araquistain* 614 (BM); Granada: *Araquistain & Moreno* 612 (BM); Madriz: *Moreno* 2771 (BM); Matagalpa: *Moreno* 10209 (MO). **Costa Rica**, Alajuela: *Carvajal* 501 (MO); Cartago: *Holm & Iltis* 118 (NY); Heredia: *Croat* 35840 (MO); Limón: *Burger & Liesner* 6893 (NY); Puntarenas: *Hepper* 34 (BM); San José: *Burger & Stolze* 5382 (NY). **Panama**, Chiriquí: *Croat* 66387 (MO); Coclé: *Hammel* 3875 (MO); Darien: *LeDoux* 2640 (NY); Panama: *Croat* 3373 (NY). **Colombia**, Dryander 2282 (BM). **Venezuela**, Miranda: *Davidse* 4508 (MO). **Peru**, Huanuco: *Mexia* 8254 (BM); Loreto: *Mexia* 6103 (BM). **Bolivia**, Mapiri: *Buchtien* 572 (BM). **Brazil**, Ceará: *Gardner* 1850 (BM); Minas Gerais: *Mexia* 4160 (BM); São Paulo: *Davis* et al. 59843 (E).

55. *Piper peltatum* L., *Sp. pl.* 1: 30 (1753). Type: Habitat in America calidiore.

Fig. 1B,b,c.

P. pruinum Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* 1: 59 (1816). Type: Willd., h.n. 705 (B).

P. speciosum Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* 1: 59 (1816). Type: Willd., h.n. 704 (B).

Lepianthes peltata (L.) Raf., *Sylva tellur.*: 84 (1838).

Heckeria peltata (L.) Kunth in *Linnaea* 13: 565 (1839).

H. scutata Kunth in *Linnaea* 13: 567 (1839). Type: Willd., h.n. 703 (B).

H. speciosa (Kunth) Kunth in *Linnaea* 13: 568 (1839).

Pothomorphe peltata (L.) Miq., *Comm. phytogr.*: 37 (1840).

P. scutata (Kunth) Miq., *Comm. phytogr.*: 37 (1840).

P. speciosa (Kunth) Miq., *Comm. phytogr.*: 37 (1840).

P. almirantensis Trel. in *Ann. Mo. bot. Gdn* 27: 306 (1940). Type: Panama, Bocas del Toro, *Cooper* 170 (F-holotype).

P. baileyorum var. *paucispica* Trel. in *Ann. Mo. bot. Gdn* 27: 306 (1940). Type: Panama, Canal Zone. *Woodson, Allen & Seibert* 1573 (NY!-isotype).

P. tecumensis Trel. in *Ann. Mo. bot. Gdn* 27: 306 (1940). Type: Panama, Canal Zone, *Standley* 26735 (US-holotype).

Herbaceous, sometimes subshrubs, 0.5–1.5 m high; stems glabrous or sparsely puberulent. Leaves 20–40 cm long, 15–30 cm wide, ovate to suborbiculate, membranous, glandular, upper surface minutely puberulent on the veins, apex acute-acuminate, base round to subcordate, peltate. Venation with 10–14 secondary veins arising from or near the petiole attachment, and 1–2 pairs from the middle of the midrib, curving towards the apex. Petioles sheathing, 10–26 cm long, glabrous. Prophylls 10–20 cm long, glandular, subtending the peduncles. Inflorescences 4–10 cm long, in clusters of 2–20; peduncles 3–20 mm long, glabrous. Anthers 0.1–0.2 mm long. Floral bracts 0.3–0.6 mm wide, triangular, white-ciliate. Fruits 0.5–0.8 mm wide, obovoid, trigonous, glabrous; stigmas 3, sessile.

Moist places at edges of forest and pastures, road- and track sides, stream sides and waste ground; 0–500 (–800) m.

DISTRIBUTION. Pantropical. **Mexico**, Chiapas: *Hoover* 159 (MO). **Belize**, Sibun River: *Gentle* 1400 (NY). **Guatemala**, Izabal: *Kellerman* 7411 (NY); Petén: *Molina* 15857 (NY). **Honduras**, Atlántida: *Yuncker* et al. 8449 (NY); Puerto Sierra: *Wilson* 128 (NY). **Nicaragua**, Boaco: *Stevens* 5917 (BM); Chontales: *Stevens* 2836 (BM); Granada: *Grijalva* 1911 (BM); Managua: *Stevens* 5339 (BM); Matagalpa: *Guzmán* et al. 766 (BM); Rivas: *Seymour* 1931 (BM); Zelaya: *Ortiz* 52 (BM). **Costa Rica**, Cartago: *Tonduz* 7332 (NY); Heredia: *Stevens* 13320 (MO); Limón: *Davidson & Donahue* 8269 (LA); Puntarenas: *Kernan* 78 (CR); San José: *Whitmore* 60 (NY). **Panama**, Bocas del Toro: *Woodson* et al. 1875 (NY); Coclé: *Davidse & Hamilton* 23733 (MO); Colón: *Nee* 6979 (MO); Darien: *Antonio* 4579 (MO); Panama: *Hamilton & D'Arcy* 1322 (MO); San Blas: *Hamilton & Stockwell* 1077 (MO). **Colombia**, Antioquia: *Klevens* et al. 17C413 (BM); Barbacoas: *Triana* 754 (BM); Meta: *Philipson* et al. 1672 (BM); Santa Marta: *Smith* 1243 (BM). **Venezuela**, Carabobo: *Alston* 5892 (BM). **Guyana**, Schomburgk 954 (BM). **Ecuador**, Salanga I.: *Barclay* 629 (BM). **Peru**, Loreto: *Mexia* 6102 (BM). **Bolivia**, Isapuri: *Williams* 682 (BM).

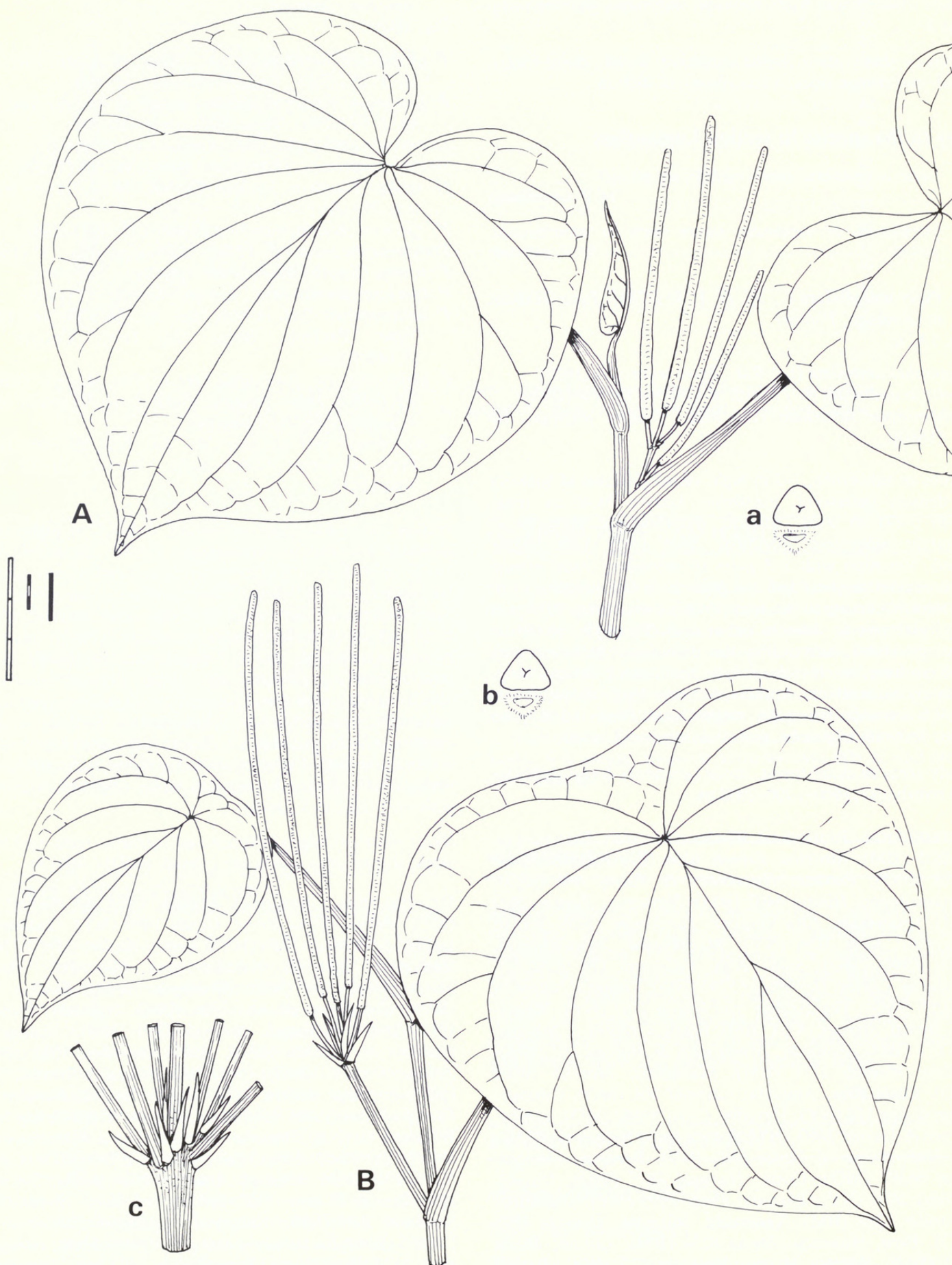


Fig. 1 A: *P. umbellatum*, habit; a: fruit and bract. B: *P. peltatum*, habit; b: fruit and bract; c: peduncles and prophylls.

Brazil, Amazonas: *Mexia* 6067a (BM); Pará: *Moss* s.n. (BM).

SECTION *RADULA* MIQ.

The section, as accepted here, follows Miquel's (1844) *Artanthe* section *Radula*, which he describes as 'Folia plerumque membranacea, elliptica, ovata, oblonga, raro angusta, inaequilatera, acuminata, basi inaequalia, supra pilis rigidis verruculisque scabra, raro glabra, subtus pilosa, pilis in pagina sup. sensim deciduis; costata, costis usque ad 1/3–2/3 alt. a basi ortis, adscendentibus, summa ad apicem ducta. Amenta recta vel curvata. Bractae peltatae, pelta triangulari vel semicirculari ciliata; rarius cucullato-inflexae. Baccae tetra- vel trigono- compressae, subcuneatae.'

Piper section *Radula* contains a number of species which at first glance look very much alike. It is only when characters such as prophylls, bracts, and fruits are examined in detail that differences begin to emerge. The determination of *Piper* to species is facilitated by using both vegetative and inflorescence characters. Many species have been reduced to synonymy, especially under *Piper hispidum* Sw. I have endeavoured to see as many type specimens as possible of these species; where types have not been available, plates and photographs of types have been examined, and original descriptions have of course been carefully studied.

DISTRIBUTION AND HABITAT

Many species in this section are rapid colonisers of cleared land, often forming stands along sides of tracks or in clearings (e.g. *P. aduncum* L., *P. bredemeyeri* Jacq., *P. hispidum*). *Piper marginatum* Jacq., a widespread species, is commonly found in clearings, often in full sunlight. *Piper cinereum* C.DC., found from Panama south to Ecuador, is an early coloniser of disturbed ground such as landslides or unstable cliffs, whereas *P. littorale* C.DC. grows near the sea, often on the strand. Several species are found in wet forest, often at high altitudes (e.g. *P. chamissonis* (Miq.) Steud. of Mexico and Guatemala, *P. holdridgeanum* W.C. Burger from Costa Rica and Panama, and *P. subflavum* C.DC. from Colombia). The climbing *P. multiplinervium* C.DC. grows in moist forest, reaching and spreading over tree tops. *Piper malpasoensis* Tebbs is only found in steep moist ravines in southern Mexico; *P. chrysostachyum* C.DC. grows in seasonally dry evergreen forest, usually on the Pacific side of Nicaragua, Costa Rica, and Panama. *Piper dotanum* Trel. of Costa Rica grows in the deep shade of forest and *P. scalarispicum* Trel. is found in Central American cloud forest.

MORPHOLOGY

Habit

The majority of species in this section are shrubs or small trees, 1–6 (–8) m high. *Piper multiplinervium* and *P. silvivagum* C.DC. are scandent or climbing, ascending by means of adventitious roots at the nodes, while *P. hostmannianum* (Miq.) C.DC. is usually found as a shrub, but may

climb if the opportunity arises. *Piper thomasi* Tebbs is an epiphytic subshrub.

Leaves

Leaves are cordate, oblong to lanceolate, elliptic or ovate, membranous or coriaceous. The bases are usually unequally attached to the petioles, with one side lower than the other. Occasionally one side is slightly lobed, often concealing the petiole. The upper surfaces of the leaves in this section are typically scabrous, often combined with a sparse to dense indumentum (e.g. *Piper aduncum*, *P. hispidum*, *P. villiramulum* C.DC.). Undersides are usually pubescent, especially on the veins. *Piper marginatum* has glossy leaves, with a distinct margin of pale, minute hairs, whereas *P. bredemeyeri* has extremely rough, densely brown-pubescent, bullate leaves. *Piper cinereum* has whitish-pubescent leaves, which are sometimes rugose.

Venation

Several species in this section have palmate venation (actinodromous or campylodromous), with 3–13 secondary veins arising from the base of the leaf and curving towards the apex (e.g. *Piper marginatum*, *P. sanctum* (Miq.) Schltdl.). *Piper flavidum* C.DC. ex Donn.Sm. has 1–2 pairs of veins arising from the lower part of the leaf, running parallel to the apex, with prominent cross-venation. *Piper aduncum* and *P. lanceifolium* Kunth have secondary veins arising from the lower to middle part of the midrib, ascending steeply to the apex. *Piper dotanum* and *P. hirtellipetiolum* C.DC. have distinct brochidodromous venation, whereas *Piper hispidum* and *P. poasanum* C.DC. have curving or arcuate-ascending secondary veins arising from the lower to middle part of the midrib.

Indumentum and pellucid glands

The amount of indumentum is very variable and is often greater in young growth, diminishing as the plant ages. *Piper biauiritum* C.DC. is densely pubescent, often with long multicellular hairs, whereas *P. hispidum* and *P. villiramulum* are covered with short, pale hairs, especially in young growth. *Piper cinereum* has white-puberulent stems and leaves. *Piper villiramulum* has dark, reddish glands visible, especially on the leaf undersides, whereas *P. bisasperatum* Trel. has copious orange glands on both surfaces. The ligule-like structures present at the base of the petioles are often prominently glandular (e.g. *P. chrysostachyum* C.DC.).

Prophylls

The prophylls are generally prominent in this section and usually associated with a ligule-like structure that arises from the base of the petiole. The exceptions are those species with sheathing petioles (*P. marginatum*, *P. cinereum*, *P. multiplinervium*, and *P. holdridgeanum*) where the prophylls are partially or wholly concealed. *Piper bredemeyeri* has prophylls 10–25 mm long, whereas those of *P. terrabanum* C.DC. are up to 30 mm long.

Inflorescences

In this section, the inflorescences are erect, arched or curved and are usually pale in colour. The inflorescences of *Piper*

marginatum are erect for about half their length and then arch gracefully. *Piper multiplinervium* has slender, erect, yellowish spikes with a pleasant fragrance. The inflorescences of *P. bisasperatum* are erect, with pubescent sterile tips up to 4 mm long. Those of *Piper epigynium* C.DC. and *P. biauratum* are coloured pinkish to purple.

Floral bracts

Bracts are triangular or round, usually densely white- or yellow- ciliate with glabrous centres, as in *P. poasanum* or *P. chamissonis*. Some species have a pale basal bulge (e.g. *Piper chrysostachyum*, *P. biauratum*). Bracts of *P. dotanum* and *P. villiramulum* are densely puberulent.

Fruit

Fruits are obovoid, round or trigonous from above, glabrous (e.g. *P. sanctum*, *P. terrabanum*), densely pale puberulent (e.g. *P. cinereum*, *P. flavidum*, *P. hispidum*), or minutely granular (e.g. *P. achoteanum* Trel.). *Piper marginatum* has round, dark fruits with a central depression.

TAXONOMIC TREATMENT

Section RADULA Miq.

Type: *Piper radula* Kunth

Herbs, shrubs or small trees, occasionally scandent or climbing, rarely epiphytic, stems glabrous to densely pubescent. Leaves linear, lanceolate, ovate-elliptic, oblong or cordulate, glabrous, scabrous or pubescent, often glandular. Venation pinnate or palmate. Petioles mostly with ligule-like structures at the base, occasionally sheathing. Prophylls prominent, glabrous or pubescent, sometimes glandular, or occasionally hidden by sheathing petioles. Inflorescences erect or curving, sometimes distinctly arching, rarely pendulous. Floral bracts triangular, round or semilunar, sparsely to densely ciliate, rarely glabrous. Fruits trigonous or round from above, glabrous to pubescent, sometimes granular or glandular, estylose; stigmas 2–4.

Disturbed areas, often along roads or tracks, secondary forest, shady wood or field margins, occasionally by the sea; 0–3000 m.

Key to the species in section *Radula*

- 1a. Petioles partly or completely sheathing the stems:
 - 2a. Plants scandent or climbing 58. **P. multiplinervium**
 - 2b. Plants shrubs or subshrubs:
 - 3a. Leaves with palmate venation; prophylls hidden by sheathing petioles; inflorescences arching or curving:
 - 4a. Leaves glossy above, sparsely puberulent, with distinct ciliate margins; fruits glabrous, drying brown or black 56. **P. marginatum**
 - 4b. Leaves dull above, pubescent, without distinct ciliate margins; fruits densely white-pubescent 57. **P. cinereum**
 - 3b. Leaves pinnately or sub-pinnately veined; prophylls visible, not hidden by sheathing petioles; inflorescences erect 59. **P. holdridgeianum**
- 1b. Petioles not partly or completely sheathing the stems:

- 5a. Fruits trigonous from above:
 - 6a. Epiphytic subshrubs 65. **P. thomasii**
 - 6b. Terrestrial herbs, shrubs, or trees:
 - 7a. Upper surface of leaves glabrous, often glossy:
 - 8a. Leaf bases unequally auriculate, covering the petioles:
 - 9a. Leaves lanceolate, undersides with minute dark glands 70. **P. enganyanum**
 - 9b. Leaves elliptic-ovate, undersides eglandular:
 - 10a. Leaves 14–24 x 6–10 cm; inflorescences 6–12 cm long 68. **P. otophorum**
 - 10b. Leaves 8–12 x 3.5–6 cm; inflorescences 4–6 cm long 69. **P. malpasoensis**
 - 8b. Leaf bases not auriculate, not covering the petioles:
 - 11a. Upper surface of fruits glandular:
 - 12a. Petioles with ligule-like structures 3.5 mm long; upper surface of fruits pubescent 61. **P. via-chicoense**
 - 12b. Petioles with ligule-like structures 0.5–1 mm long; upper surfaces of fruits glabrous:
 - 13a. Leaves membranous; prophylls 20–30 mm long 66. **P. terrabanum**
 - 13b. Leaves subcoriaceous, slightly succulent; prophylls 5–10 mm long 67. **P. littorale**
 - 11b. Upper surface of fruits eglandular 64. **P. dilatatum**
 - 7b. Upper surface of leaves pubescent:
 - 14a. Stems densely covered with long hairs; inflorescences erect:
 - 15a. Leaves narrowly to broadly ovate, upper surface bullate; underside densely covered with yellow-brown hairs 63. **P. bredemeyeri**
 - 15b. Leaves elliptic to obovate or rhombic, upper surface not bullate; underside densely covered with pale yellow hairs 62. **P. pseudofuligineum**
 - 14b. Stems sparsely to densely covered in short hairs; inflorescences arching 71. **P. lanceifolium**
 - 5b. Fruits round or oblong from above:
 - 16a. Upper surface of fruit glabrous, sometimes granular:
 - 17a. Leaves with palmate venation:
 - 18a. Leaves broadly ovate to elliptic, the bases round to shallowly cordate 106. **P. sanctum**
 - 18b. Leaves oblong-lanceolate to elliptic-lanceolate, the bases obtuse to slightly lobed on one side 105. **P. pseudolindenii**
 - 17b. Leaves with pinnate venation:
 - 19a. Inflorescences arching, curving, or pendulous:
 - 20a. Upper surface of leaves scabrous or densely puberulent; inflorescences arching or curving, without sterile tips:
 - 21a. Prophylls 5–8 mm long; peduncles 15–30 mm long 73. **P. mollicomum**
 - 21b. Prophylls 20–25 mm long; peduncles 8–15 mm long 72. **P. aduncum**
 - 20b. Upper surface of leaves glabrous; inflorescences pendulous, with sterile tips 1–3 mm long 99. **P. carpinteranum**
 - 19b. Inflorescences erect:
 - 22a. Leaves ovate-cordate, more or less sessile, often with blunt apices 23
 - 22b. Leaves petiolate, elliptic-lanceolate, ovate, or oblong to obovate, apices acuminate 24
 - 22c. Leaf surfaces distinctly glandular 25
 - 22d. Upper surfaces of leaves bullate 78. **P. pseudoasperifolium**
 - 22e. Upper surfaces of leaves smooth 26
 - 22f. Underside of leaves with red or orange

- glands 94. **P. colonense**
- 26b. Undersides of leaves lacking red or orange glands 27
- 27a. Petioles glabrous, with glabrous ligule-like structures 98. **P. tenuimucronatum**
- 27b. Petioles villous, with ciliate ligule-like structure 96. **P. hirtellipetiolum**
- 24b. Leaf surfaces eglandular 28
- 28a. Ligule-like structures on petioles 2–3 mm long, glandular 93. **P. chamissonis**
- 28b. Ligule-like structures on petioles 0.5–1 mm long, eglandular 29
- 29a. Upper surfaces of leaves glossy, glabrous 30
- 30a. Leaves with prominent cross-venation; inflorescences with sterile tips 31
- 31a. Stems glabrous; inflorescences 2–5 (–6) cm long 97. **P. decurrens**
- 31b. Stems sparsely to densely yellow-pubescent; inflorescences 10–12 cm long 100. **P. hostmannianum**
- 30b. Leaves lacking prominent cross-venation; inflorescences without sterile tips 32
- 32a. Leaves lanceolate to elliptic-lanceolate; prophylls 7–10 mm long, with central line of hairs 101. **P. scalarispicum**
- 32b. Leaves elliptic to ovate or rhombic, prophylls 12–25 mm long, glabrous 84. **P. umbricola**
- 29b. Upper surfaces of leaves moderately to densely yellowish-pubescent 33
- 33a. Leaves narrowly elliptic to oblanceolate; peduncles 14–25 mm long 95. **P. oblanceolatum**
- 33b. Leaves ovate-lanceolate to elliptic-lanceolate; peduncles 3–5 (–10) mm long 60. **P. subflavum**
- 16b. Upper surface of fruit pubescent 34
- 34a. Plants scandent or climbing 77. **P. silvivagum**
- 34b. Plants erect, not scandent or climbing 35
- 35a. Upper surface of leaves glabrous 36
- 36a. Leaves falcate, linear-lanceolate, with 1–2 pairs of secondary veins 76. **P. flavidum**
- 36b. Leaves not falcate, linear-lanceolate, with at least 3 pairs of secondary veins 37
- 37a. Leaves glandular 38
- 38a. Upper surface of leaves bullate, undersides lustrous 104. **P. biritak**
- 38b. Upper surface of leaves smooth, undersides dull 39
- 39a. Ligule-like structures on petioles, 6–18 mm long 81. **P. sancti-felicitis**
- 39b. Ligule-like structures on petioles, not more than 3 mm long 40
- 40a. Fruits 1–1.2 mm wide, densely pale yellow-pubescent 102. **P. curvatipes**
- 40b. Fruits 0.4–0.8 mm wide, minutely white puberulent or glandular 41
- 41a. Leaves with dark glands; prophylls lacking glands; floral bracts densely puberulent 87. **P. dotanum**
- 41b. Leaves with pale glands; prophylls glandular; floral bracts glabrous or minutely ciliate 42
- 42a. Prophylls 14–30 mm long; fruits glandular 86. **P. epigynium**
- 42b. Prophylls 8–15 mm long; fruits eglandular 85. **P. chrysostachyum**
- 37b. Leaves eglandular 43
- 43a. Floral bracts oblong-triangular; fruits minutely white-pubescent or granular 82. **P. poasanum**
- 43b. Floral bracts semi-lunar; fruits densely yellow-brown pubescent 103. **P. jacquemontianum**
- 35b. Upper surface of leaves pubescent, rugose or bullate 44
- 44a. Leaves with dark red, orange or brown glands visible 45
- 45a. Petioles glabrous or pubescent, glandular, with glandular ligule-like structures 4–10 mm long 83. **P. bisasperatum**
- 45b. Petioles densely pubescent, with eglandular ligule-like structures 0.5–1 mm long 46
- 46a. Stems densely whitish-pubescent 79. **P. villiramulum**
- 46b. Stems densely yellow-brown pubescent 92. **P. perhispidium**
- 44b. Leaves eglandular 47
- 47a. Upper surface of leaves covered in long hairs; inflorescences red or purple 91. **P. biauratum**
- 47b. Upper surface of leaves minutely pubescent; inflorescences not red or purple 48
- 48a. Stems shortly white-pubescent; ligule-like structures glandular 80. **P. hispidum**
- 48b. Stems with long yellow to brown hairs; ligule-like structures eglandular 49
- 49a. Floral bracts mostly glabrous, with a few minute hairs at the base 88. **P. polytrichum**
- 49b. Floral bracts yellow-ciliate, with glabrous centres 50
- 50a. Prophylls densely puberulent; inflorescences 3–9 cm long 90. **P. zacatense**
- 50b. Prophylls hirsute only along midrib; inflorescences 10–16 cm long 89. **P. peracuminatum**
56. **Piper marginatum** Jacq., *Icon. pl. rar.* 2: 2, t. 215 (1786). Type: West Indies. *Jacquin* s.n. (G-holotype). Fig. 2A,a,b,c.
- P. caudatum* Vahl, *Eclog. amer.* 1: 3 (1796). Type: Rohr 217 (C!-holotype).
- P. anisatum* Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* 1: 58 (1816). Type: Willdenow Hb. 698 (B-holotype).
- P. catalpaefolium* Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* 1: 58 (1816). Type: Willdenow Hb. 699 (B-holotype).
- P. alare* Ham., *Prodr. pl. Ind. occid.*: 3 (1825). Type: Cayenne. *Hamilton* s.n. (?-holotype).
- Schilleria caudata* (Vahl) Kunth in *Linnaea* 13: 716 (1839).
- S. catalpaefolia* (Kunth) Kunth in *Linnaea* 13: 718 (1839).
- S. marginata* (Jacq.) Kunth in *Linnaea* 13: 718 (1839).
- Piper patulum* Bertol., *Fl. guatimal.*: 407, pl. 36 (1840). See note below.
- Artanthe catalpaefolia* (Kunth) Miq., *Syst. piperac.*: 382 (1844).
- A. caudata* (Vahl) Miq., *Syst. piperac.*: 380 (1844).
- Artanthe marginata* (Jacq.) Miq., *Syst. piperac.*: 381 (1844).
- A. alaris* (Ham.) Miq., *Syst. piperac.*: 406 (1844).
- Piper marginatum* var. *catalpaefolium* (Kunth) C.DC. in DC., *Prodr.* 16(1): 246 (1869).
- P. san-joseanum* C.DC. in *Linnaea* 37: 351 (1872). Type: Costa Rica, *Oersted* 893 (C!-holotype).
- P. pseudo-marginatum* C.DC. in *Bull. Herb. Boissier* 6: 492 (1898). Type: Ecuador, *Sodi* 1/38 (P?-holotype).

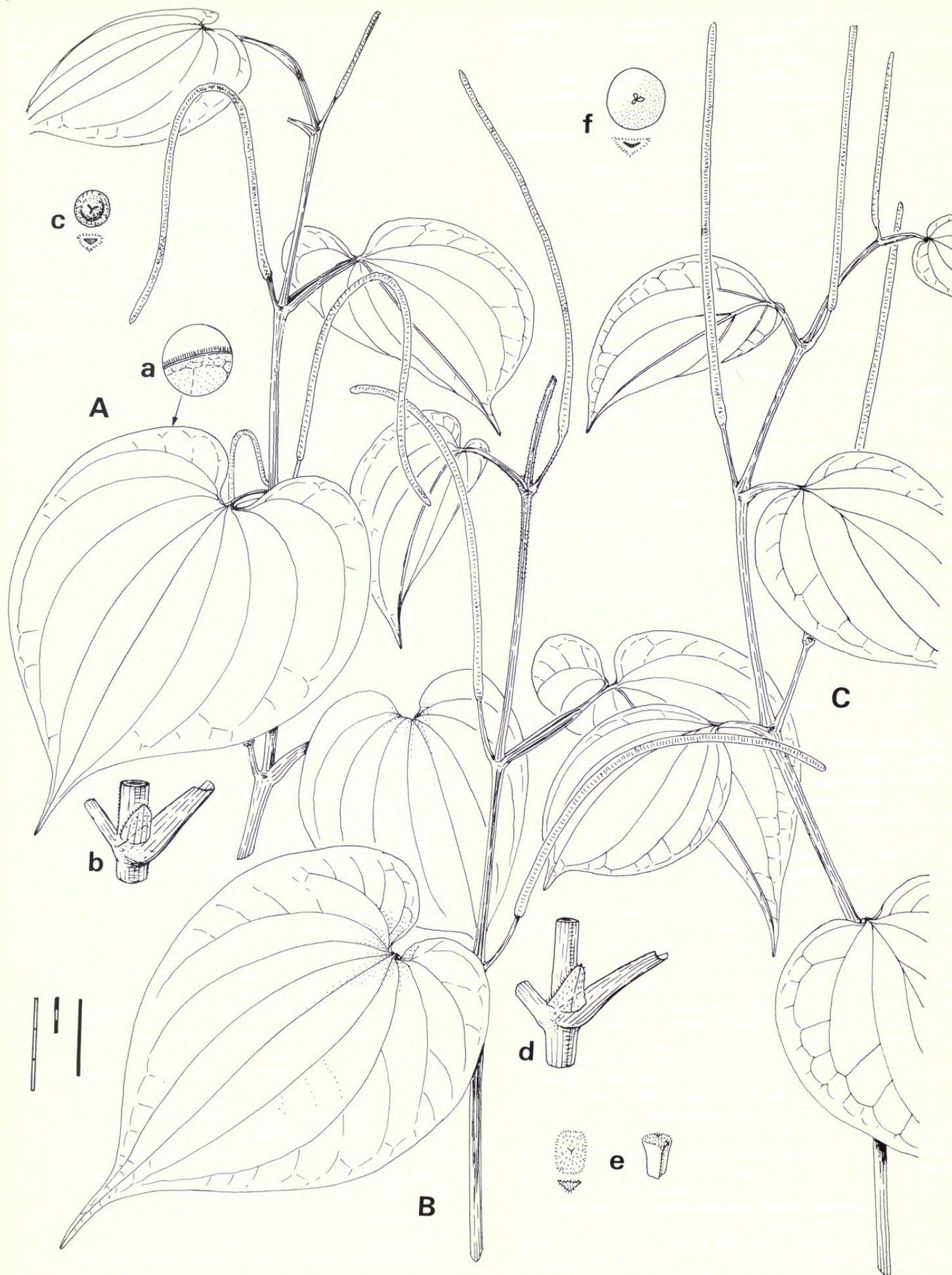


Fig. 2 A: *P. marginatum*, habit; a: section of leaf margin; b: prophyll; c: fruit and bract. B: *P. cinereum*, habit; d: prophyll; e: fruit and bract. C: *P. multiplinervium*, habit; f: fruit and bract.

- P. marginatum* var. *anisatum* (Kunth) C.DC. in Urb., *Symb. antill.* **3**: 172 (1902).
- P. patulum* var. *cordifolium* Trel. in *J. Wash. Acad. Sci.* **13**: 366 (1923). Type: El Salvador, Sonsonate, *Standley* 22046 (ILL!-holotype).
- P. uncatum* Trel. in *J. Wash. Acad. Sci.* **13**: 367 (1923). Type: El Salvador, Tonacatepeque, *Standley* 19435 (ILL!-holotype).
- P. san-joseanum* var. *minor* Trel. in *Contr. U.S. natn. Herb.* **26**: 133 (1929). Type: Costa Rica, Nicoya, *Tonduz* 13695 (US- holotype, photograph!).
- P. san-joseanum* var. *chiriquinum* Trel. in *Ann. Mo. bot. Gdn* **25**: 826 (1938). Type: Panama, Chiriquí, *Woodson* et al. 416 (MO!-holotype).
- P. san-joseanum* var. *kobense* Trel. in *Ann. Mo. bot. Gdn* **27**: 297 (1940). Type: Panama, Canal Zone, *Woodson* et al. 1423 (ILL!-holotype).
- P. san-joseanum* var. *panamanum* Trel. in *Ann. Mo. bot. Gdn* **27**: 297 (1940). Type: Panama, Gorgona Beach, *Woodson* et al. 1690 (ILL!-holotype).
- P. san-joseanum* var. *remediosense* Trel. in *Ann. Mo. bot. Gdn* **27**: 297 (1940). Type: Panama, Chiriquí, *Woodson* et al. 1191 (ILL!-holotype).
- P. san-joseanum* var. *tabogense* Trel. in *Ann. Mo. bot. Gdn* **27**: 297 (1940). Type: Panama, Taboga, *Woodson* et al. 1531 (ILL!- holotype).
- P. niceforoi* Trel. & Yunc., *Piperac. N. South Amer.* **1**: 79 (1950). Type: Colombia, norte de Santander, *Niceforo* 49 (ILL!- holotype).
- P. marginatum* var. *marginatum* forma *catalpaefolium* (Kunth) Steyer., *Fl. Venezuela* **2**: 480 (1984).
- P. marginatum* var. *niceforoi* (Trel. & Yunc.) Steyer., *Fl. Venezuela* **2**: 482 (1984).

Shrubs 2–3 m high, glabrous or slightly pubescent. Leaves 9–20 (–28) cm long, 5–16 (–24) cm wide, broadly ovate, glossy above, membranous, glabrous or with scattered hairs, underside often puberulent on veins, margins densely pale-ciliate, apex acuminate, base shallowly to deeply cordate. Venation palmate, with 7–13 nerves arising from the base. Petioles 2–5 cm long, sheathing the stem. Prophylls hidden by sheathing petioles, 2–4 mm long, glabrous, papery, minutely glandular, apex blunt, sometimes fimbriate. Inflorescences 10–25 cm long, whitish, becoming arched; peduncle 5–12 (–20) mm long, glabrous. Anthers 0.3–0.4 mm long. Floral bracts 0.5–0.8 mm wide, triangular or round, densely ciliate. Fruit 0.5–1 mm wide, obovoid, dark brown, round to oblong from above, glabrous; stigmas 3–4.

Hillsides, pasture, disturbed forest, roadsides, and edges of streams; 0–1300 m.

DISTRIBUTION. Mexico to Brazil. **Mexico**, Campeche: *Gomez-Pompa* 1316 (CAS); Chiapas: *Breedlove* 28606 (MO); Colima: *Ferris* 6219 (DS); Oaxaca: *Chavelas & Perez* 266 (DS); Quintana Roo: *Cabrera* 609 (CAS); Veracruz: *Calzada* 894 (CAS); Yucatan: *Lundell* 1195 (DS). **Belize**, Cayo: *Proctor* 29552 (BM). **Guatemala**, Alta Verapaz: *Croat* 41520 (MO); Escuintla: *Croat* 42051 (MO); Petén: *Ratcliff* 42 (CAS); Retalhuleu: *Ellis & LeDoux* 1128 (DS); Zacapa: *Croat* 41865 (MO). **El Salvador**, Ahuachapan: *Croat* 42067 (MO); La Libertad: *Vicente & Villacorta* 151 (BM); Santa Ana: *Villacorta* 180 (BM). **Honduras**, Comayagua: *Soto* 41 (BM); Copan: *Croat* 42518 (MO); Olanchito: *Carvajal* 25

(BM); Santa Barbara: *Croat* 42759 (MO). **Nicaragua**, Boaco: *Stevens* 14708 (BM); Carazo: *Moreno* 10732 (BM,MO); Chinandega: *Fonseca* 80 (BM); Granada: *Baker* 66 (DS); Managua: *Stevens* 2917 (BM); Masaya: *Zelaya* 149 (BM); Matagalpa: *Stevens* et al. 21424 (BM). **Costa Rica**, Alajuela/ Heredia: *Grayum* et al. 4134 (BM,MO); Guanacaste: *Williams* et al. 26596 (DS); Puntarenas: *Grayum* 4192 (BM,MO). **Panama**, Canal Zone: *Croat* 12875 (MO); Chiriquí: *Hamilton* et al. 938 (BM,MO); Colón: *Sytsma* 1611 (BM,MO); Darien: *Hammel* 1084 (MO); Panama: *Hamilton* 540 (BM,MO); Perlas Is.: *Knapp* 3276 (BM,MO); San Blas: *Nevers & Herrera* 4524 (MO); Veraguas: *Antonio* 2325 (BM,MO). **West Indies**, Trinidad: *Breedlove* 18992 (CAS). **Colombia**, Boyaca: *Lawrance* 194 (BM); Los Llanos: *Haught* 2472 (BM); Santa Marta: *Smith* 1239 (BM); Sur de Santander: *Haught* 1421 (BM). **Venezuela**, Apure: *Davidse & Gonzalez* 21632 (BM,MO); Aragua: *Williams & Alston* 173 (BM); Lara: *Davidse & Gonzalez* 20947 (BM,MO); Miranda: *Davidse* 4108 (BM,MO); Monagas: *Croat* 54330 (BM,MO); Portuguesa: *Davidse* et al. 21466 (BM,MO); Táchira: *Davidse & González* 22441 (BM). **French Guiana**: *Sagot* 533 (BM). **Ecuador**, Esmeraldas: *Barclay* s.n. (BM); Guayas: *Camp* 3547 (BM,NY). **Brazil**, Pará: *Ducke* 3494 (BM); Pernambuco: *Pickel* s.n. (DS).

Piper marginatum is one of the most widespread species in this section and also one of the easiest to identify. It can be recognized by its glossy, palmately-veined leaves with ciliate margins, sheathing petioles, and white, curving inflorescences. *Piper auritum* Kunth also has leaves with ciliate margins and sheathing petioles, but these are oblong-cordate, without palmate venation, and the fruits are trigonous rather than round, as in *P. marginatum*. Both *Piper auritum* and *P. marginatum* have a pleasant, aniseed-like odour when the stems or leaves are crushed. *Piper cinereum* is closely related to *P. marginatum*, with cordate leaves, sheathing petioles concealing the prophylls and palmate venation. The leaves, however, are whitish pubescent, the fruits are densely white-puberulent, and the stems, petioles, and peduncles are often streaked with red.

In his original description of this species, Bertoloni mentioned only vegetative characters, failing to describe bracts or fruits which he presumably did not see. He described the leaves as ovate-oblong to cordate-ovate, thin, entire, with a rounded, somewhat unequal base, acuminate apex, 7–9 reticulate nerves arising from the base, with dorsal nerves slightly thinner and puberulent. The immature spike was described as being some 5–6 inches (12–15 cm) long, spreading, with flowers small and crowded. The specimen from which his description was made was collected from Esquintla in Guatemala. As the type has been presumed lost in the Second World War (Duncan, 1983), only Bertoloni's coloured illustration has been seen, which lacks the important details of the inflorescence. Standley & Steyermark (1952) noted in the description of *P. patulum* that 'this is presumably the *Piper* that has been reported from Guatemala as *P. marginatum* Jacq.', but did not go into more detail. This account of *P. patulum* matches the description of *P. marginatum*. Burger (1971) placed *P. patulum* Bertol. as a synonym of *P. marginatum* Jacq. One of the characters of *P. marginatum* is the distinct white-ciliate margin of the leaves, which is curiously not mentioned by Bertoloni in his original description. All the specimens seen by the present author, originally annotated as *P. patulum*, are actually *P. sanctum* (Miq.) Schltdl.

As the type specimen is missing and the original description and plate are inadequate, it may never be possible to prove the true identity of *P. patulum*; therefore, for convenience, the name has been retained in the synonymy of *P. marginatum* Jacq.

57. ***Piper cinereum*** C.DC. in *J. Bot., Lond.* 4: 214 (1866). Type: Colombia, prov. de Chocó, *Triana* s.n. (G-holotype; BM-isotype?).

Fig. 2B,d,e.

- P. candicans* Sodiro, *Sertula fl. ecuad.*: 13 (1905). Type: Ecuador, Esmeraldas, *Mille* s.n. (?-holotype; ILL!-isotype).

Straggling shrubs or subshrubs 1–2 m high, pubescent, with pink or red streaks on stems. Leaves 9–17 cm long, 8–14 cm wide, ovate-cordate, dull green above, paler beneath, whitish pubescent, occasionally rugose, apex acute-acuminate, base deeply cordate. Venation palmate, with 9–13 nerves arising from the base and curving towards the apex, with prominent cross-veins. Petioles 2–7 cm, sheathing, often marked with red. Prophylls hidden beneath sheathing petioles, 3–5 mm long, whitish, papery, pubescent, apex acute. Inflorescences 8–11 cm long, erect or slightly curved; peduncles 12–25 mm long, white pubescent. Anthers 0.1–0.2 mm long. Floral bracts 0.2–0.4 mm wide, triangular, covered with white hairs. Fruit 0.5 mm wide, obovoid, round to trigonous from above, upper surface white pubescent; stigmas 3–4.

Coloniser of disturbed ground, often found on landslide areas or sides of cliffs; 0–700 m.

DISTRIBUTION. Panama to Ecuador. **Panama**, Darien: *Whitefoord & Eddy* 107 (BM). **Colombia**, Cauca: *Haught* 5368 (BM); Chocó: *Luteyn* et al. 10495 (G); El Valle: *Killip & Garcia* 33360 (BM).

58. ***Piper multiplinervium*** C.DC. in *J. Bot., Lond.* 4: 214 (1866). Type: Colombia, Barbacoas, *Triana* 27 (G-holotype; BM!-isotype).

Fig. 2C,f.

- P. aragonense* Trel. in *Contr. U.S. natn. Herb.* 26: 146 (1929). Type: Costa Rica, Aragon near Turrialba, *Tonduz* 9021 (US-holotype).

Scandent or climbing up to 10 m high, glabrous or minutely puberulent. Leaves 6–16 cm long, 5–12 cm wide, glossy, upper leaves ovate-elliptic, lower leaves ovate-cordate, apex acute-acuminate, base obtuse to cordate. Venation with 3–4 secondary veins arising from or near the base, and 1–2 pairs arising from the middle of the midrib, ascending to apex. Petioles 1–3 cm long, sheathing. Prophylls not apparent — if present hidden by the sheathing petioles. Inflorescences 6–16 cm long, erect, yellow-white, lemon-scented; peduncles 1–2 cm long, glabrous or minutely pubescent. Anthers 0.1–0.2 mm long. Floral bracts 0.4–0.6 mm wide, triangular to round, yellow-white ciliate. Fruits 1–1.5 mm wide, obovoid, round from above, glabrous; stigmas 2–3.

Moist forest; 0–1000 m.

DISTRIBUTION. Nicaragua to Peru. **Nicaragua**, Zelaya: *Miller & Sandino* 1206 (BM,MO). **Costa Rica**, Cartago: *Taylor* 11429 (NY); Heredia: *Burger* 8083 (NY); Limón: *Whitmore*

102 (F); Puntarenas: *Greig* 174 (F). **Panama**, Bocas del Toro: *McPherson & Allen* 9626 (BM); Canal Zone: *Gentry* 5765 (F); Chiriquí: *Werff & Hardeveld* 6527 (BM,MO); Coclé: *Croat* 67106 (BM,MO); Darien: *Mori* 7087 (BM,MO); Panama: *Garwood* 1856A (BM); San Blas: *Croat* 69237 (BM,MO); Veraguas: *Croat* 25546 (NY). **Colombia**, Antioquia: *Shepherd* 740 (F); Bogota: *Triana* 50 (BM); Chocó: *Gentry & Fallen* 17875 (F); Santander: *Haught* 2177 (BM). **Ecuador**, Esmeraldas: *Madison* et al. 5030 (F); Imbabura: *Solís* 12525 (F); Los Ríos: *Dodson & Gentry* 6337 (F). **Peru**, Huánoco: *Schunke* 1421 (F); Madre de Dios: *Smith & Condon* 1070 (F).

A vigorous and attractive species, often sprawling over the crowns of trees, and producing many slender, fragrant, yellow-white flowering spikes. The younger leaves are often a different shape from older, lower leaves, a feature noted in other species of *Piper*, such as *P. schiedeana* Steud. *Piper multiplinervium* has similar leaves, venation, and petioles to the climbing *P. nigrum* L., an old world species widely cultivated for its fruit, known as the culinary peppercorns. However, *P. nigrum* has a pendulous inflorescence, dioecious flowers, glabrous bracts and large red to black fruits.

59. ***Piper holdridgeianum*** W.C. Burger in *Fieldiana Bot.* 35: 144 (1971). Type: Costa Rica, Heredia, *Burger & Stolze* 5776 (F!-holotype; BM!-isotype).

Fig. 3A,a,b.

- P. picardae* var. *pilinervium* Trel. in *Feddes Reprium Spec. nov. veg.* 23: 309 (1927). Type: Haiti, *Ekman* 1769 (ILL!-holotype).

Shrubs 1–2 m high, stems glabrous or minutely puberulent. Leaves 10–22 cm long, 3.5–13 cm wide, ovate-elliptic to ovate-lanceolate, upper surface glabrous, glossy, dark green, underside glabrous or minutely pubescent, apex acuminate, base round to deeply cordate on older, lower leaves. Venation with 2–4 pairs of secondary veins arising from the lower part of midrib, ascending to apex. Petioles 1–5 cm long, deeply vaginate, appearing to sheath the stems, glabrous or minutely puberulent. Prophylls 4–10 mm long, blunt, glabrous, drying dark brown or black. Inflorescences 6–10 cm long, erect; peduncles 10–18 mm long. Anthers 0.2–0.3 mm long. Floral bracts 0.2–0.4 mm wide, triangular or round, white ciliate, with dark, glabrous centres. Fruits 0.7–0.8 mm wide, obovoid, glabrous, fleshy; stigmas 3, sessile, in slight depression.

Deep shade in wet forest; 0–1000 m.

DISTRIBUTION. Costa Rica, Panama. **Costa Rica**, Heredia: *Raven* 20999 (F). **Panama**, Coclé: *Hammel* 3598 (BM,MO); Panama: *Croat* 14775 (MO); Veraguas: *Croat* 27617 (MO).

Piper holdridgeianum occurs in moist to wet forest, often near streams or rivers. It can be identified by its deeply vaginate petioles, slightly uneven, cordate lower leaves, and upper leaves with little or no basal lobing. This variation of leaf shape on the same plant is quite common in *Piper*.

60. ***Piper subflavum*** C.DC. in *J. Bot., Lond.* 4: 210 (1866). Type: Colombia, prov. Pasto Ortega, *Triana* 23 (G-holotype; B!-isotype).

Fig. 3B,c,d.

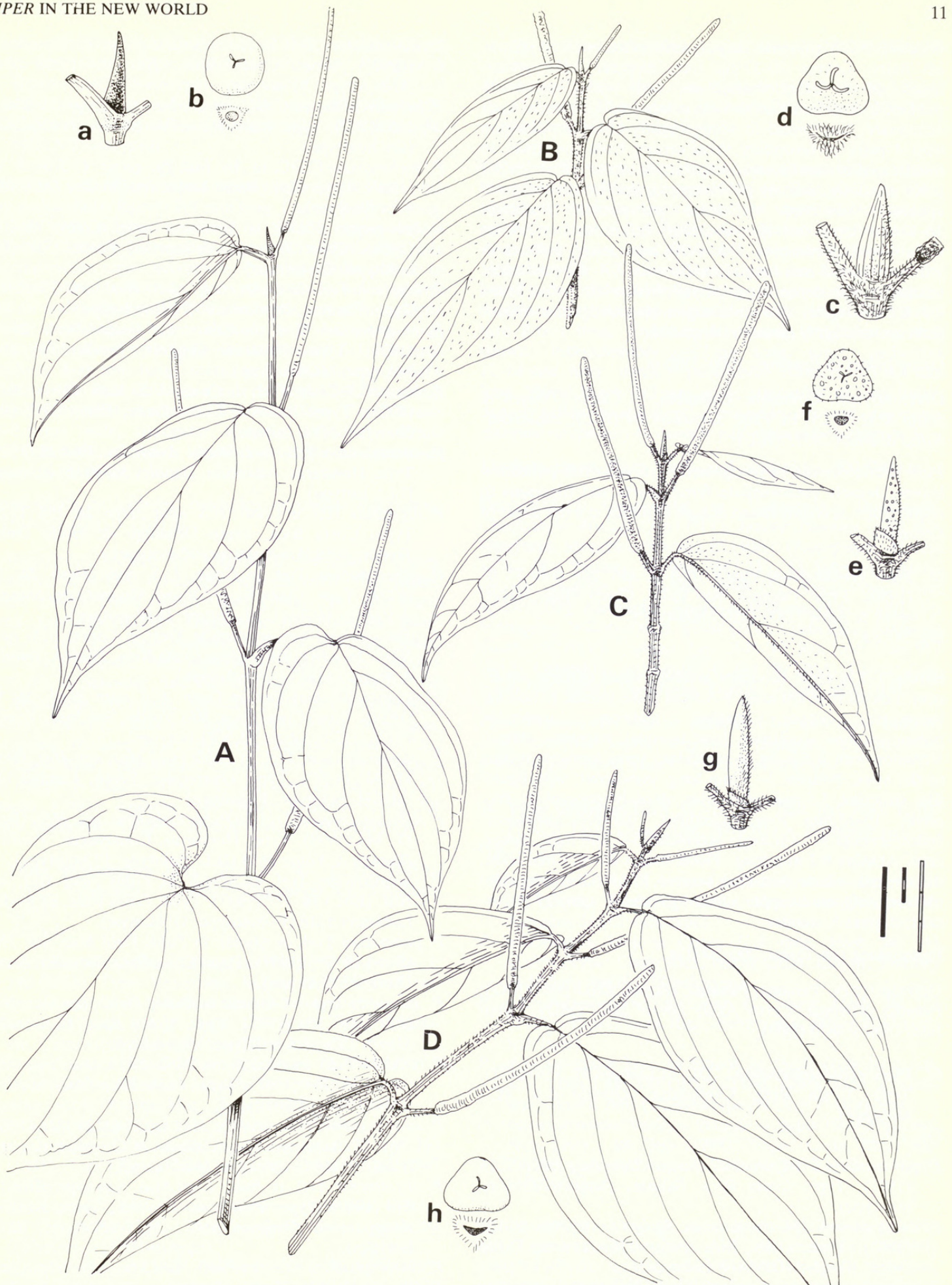


Fig. 3 A: *P. holdridgeianum*, habit; a: prophyll; b: fruit and bract. B: *P. subflavum*, habit; c: prophyll; d: fruit and bract. C: *P. via-chicoense*, habit; e: prophyll; f: fruit and bract. D: *P. pseudofuligineum*, habit; g: prophyll; h: fruit and bract.

Shrubs 2–3 m high, stems densely soft-pubescent with yellowish hairs. Leaves 10–17 cm long, 4–8 cm wide, ovate-lanceolate to elliptic-lanceolate, both sides yellowish-pubescent, lower surface densely so especially on veins, apex acuminate, base round to acute, slightly unequal. Venation with 4 pairs of secondary veins arising from the lower to middle part of midrib, ascending sharply to apex. Petioles 3–7 (–10) mm long, densely pubescent, ligule-like structure not apparent, obscured by dense pubescence. Prophylls 10–12 mm long, densely pubescent. Inflorescences 7–9 cm long, erect; peduncles 3–5 (–10) mm long, pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.7–0.9 mm wide, triangular with dense fringe of yellowish-white hairs. Fruits 0.9–1.2 mm wide, obovoid, trigonous-round from above, glabrous or slightly granular; stigmas 3.

Damp places in clearings; 1000–2300 m.

DISTRIBUTION. Colombia. **Colombia**, El Cauca: *Pennell & Killip* 8232 (ILL); El Valle: *Dryander* 64 (ILL); Santander: *Killip & Smith* 20331 (ILL).

Piper subflavum can be recognized by its yellowish-pubescent leaves, densely yellow-ciliate floral bracts and trigonous to round fruits. It is only found at high altitudes in a few areas of Colombia.

61. ***Piper via-chicoense*** Yunck. in *Ann. Mo. bot. Gdn* **37**: 67 (1950). Type: Panama, Río Indio, Chico Trail, *Steyermark & Allen* 17431 (MO!-holotype).

Fig. 3C,e,f.

Shrubs 1–2 m high, branches arching, stems densely pubescent. Leaves 9–16 cm long, 3–5.5 cm wide, elliptic to oblong-lanceolate, upper surface glabrous, underside pubescent, apex acuminate, base unequal, narrowly obtuse. Venation with 3–5 pairs of secondary veins loop-connecting to the apex. Petioles 2–5 mm long, pubescent, with ligule-like structure 3.5 mm, glandular, densely pubescent. Prophylls 10–13 mm long, glandular, densely pubescent. Inflorescences 3–7 cm long; peduncles 5–7 mm long, pubescent. Anthers 0.2 mm long. Floral bracts 0.4–0.5 mm wide, densely pale-ciliate, with dark centres. Fruits 0.8–1 mm wide, obovoid, trigonous, upper surface glandular, sparsely pubescent; stigmas 3, slender.

Premontane rain forest; 200–1000 m.

DISTRIBUTION. Panama. **Panama**, Darien: *Duke* 8061 (MO); Panama province, Cerro Azul: *Dwyer* 2085 (MO); Cerro Jefe: *Gentry* 4870 (MO).

62. ***Piper pseudofuliginum*** C.DC. in *Linnaea* **37**: 355 (1872). Type: Costa Rica, Candelaria, *Oersted* s.n. (C!-holotype).

Fig. 3D,g,h

- P. salinasanum* C.DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 214 (1892). Type: Costa Rica, Salinas, *Pittier* 2775 (G!-holotype).
- P. domingense* C.DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 161 (1897). Type: Costa Rica, Santo Domingo de Golfo Dulce, *Tonduz* 10034 (G!-holotype).
- P. salinasanum* var. *subscabrifolium* C.DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 164 (1897). Type: Costa Rica, Virilla, *Tonduz* 10126 (G!-holotype).

- P. dumeticola* C.DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 164 (1897). Type: Costa Rica, Boruca, *Pittier* 4490 (G!-holotype; F!-isotype).
- P. pseudo-dilatatum* C.DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 165 (1897). Type: Costa Rica, Punta Mala, *Tonduz* 6797 (G!-holotype).
- P. verbenanum* C.DC. in *An. Inst. fís.-geogr. C. Rica* **9**: 165 (1897). Type: Costa Rica, Alajuelita, *Tonduz* 8867, 8870 (G!-syntypes).
- P. taboganum* C.DC. in *Smithson. misc. Collns* **71**(6): 4 (1920). Type: Panama, Taboga Is, *Pittier* 3529 (US-holotype; G!-isotype).
- P. bigelovii* Trel. in *Contr. U.S. natn. Herb.* **26**: 23 (1927). Type: Panama, *Bigelow* s.n. (NY!-holotype).
- P. chagresianum* Trel. in *Contr. U.S. natn. Herb.* **26**: 37 (1927). Type: Panama, Chagres, *Fendler* 268 (US-holotype; MO!-isotype).
- P. breve* C.DC. ex Trel. in *Contr. U.S. natn. Herb.* **26**: 38 (1927). Type: Panama, Canal Zone, *Pittier* 3787 (US-holotype; NY!-isotype).
- P. atlantidanum* Trel. in *J. Wash. Acad. Sci.* **19**: 329 (1929). Type: Honduras, Atlántida, *Standley* 56739 (F!-holotype; ILL!-isotype).
- P. nigricaulis* Trel. in *Contr. U.S. natn. Herb.* **26**: 158 (1929). Type: Costa Rica, Santo Domingo de Golfo Dulce, *Tonduz* 9959 (US-holotype; F!-isotype).
- P. griseo-pubens* Trel. in *Contr. U.S. natn. Herb.* **26**: 176 (1929). Type: Costa Rica, Líbano, Guanacaste, *Standley & Valerio* 44879 (US-holotype; ILL!-isotype).
- P. griseo-pubens* var. *revocabile* Trel. in *Contr. U.S. natn. Herb.* **26**: 176 (1929). Type: Costa Rica, Tilarán, *Standley & Valerio* 44943 (US-holotype).
- P. squali-pelliculum* Trel. in *Contr. U.S. natn. Herb.* **26**: 178 (1929). Type: Costa Rica: Río Virilla, San José, *Tonduz* 10126 (US-holotype; F!, NY!-isotypes).
- P. quadratilimum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **17**: 233 (1937). Type: Guatemala, Petén, *Lundell* 1488 (MICH!-holotype; F!-isotype).
- P. deltoideocarpum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **17**: 344 (1938). Type: Honduras, Comayagua, *Yuncker, Dawson & Youse* 5654 (ILL!-holotype; F!-holotype).
- P. clavulispicum* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 337 (1937). Type: Costa Rica, El Rodeo, *Lankester* 1318 (F!-holotype; G!-isotype).
- P. ponendum* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 355 (1937). Type: Costa Rica, Heredia, *Brenes* 13244 (F!-holotype).
- P. salutatrix* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 359 (1937). Type: Costa Rica, El General, *Skutch* 2504 (US-holotype; MO!-isotype).
- P. vitabile* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 369 (1937). Type: Costa Rica, Buenes Aires, *Valerio* 894 (F!-holotype).
- P. canyazasense* Trel. in *Ann. Mo. bot. Gdn* **25**: 826 (1938). Type: Panama, between Cañazas & Cordillera Central, *Allen* 185 (ILL!-holotype; MO!-isotype).
- P. coyolesense* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **9**: 278 (1940). Type: Honduras, Coyoles, Yoro, *Yuncker, Koepfer & Wagner* 8147 (ILL!-holotype; F!, G!-isotypes).
- P. elasmophyllum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **9**: 278 (1940). Type: Honduras, Atlántida, *Yuncker, Koepfer & Wagner* 8461 (ILL!-holotype; F!, G!-isotypes).

- P. subaequilaterum* Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* **9**: 280 (1940). Type: Honduras, Yuncker, Koepper & Wagner 8565 (G!-isotype).
P. amphibium Trel. in *Ann. Mo. bot. Gdn* **27**: 288 (1940). Type: Woodson, Allen & Seibert 1222 (ILL!-holotype; MO!, NY!-isotypes).

Shrubs 1–2 (–3) m high, stems densely yellow pubescent, with long multicellular hairs 0.2–1 mm long. Leaves 8–23 cm long, 3–14 cm wide, elliptic to obovate to rhombic, upper surface scabrous, densely long-pubescent, underside densely pale long-pubescent, apex acuminate, base unequally obtuse to rounded. Venation with 4–5 pairs of secondary veins, prominent on underside, arising from the lower part of the midrib, arcuate-ascending to apex. Petioles 5–15 (–20) mm long, densely pubescent, with ligule-like structure 0.5–1 mm long. Prophylls 8–16 mm long, acute, puberulent along midrib. Inflorescences 3–11 cm long, erect; peduncles 5–12 mm long, densely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.2–0.5 mm wide, triangular, densely pale-ciliate. Fruits 0.7–1 mm wide, obovoid, obpyramidal-trigonal, glabrous; stigmas 3, recurved.

Partial shade on hillsides, roadsides, secondary vegetation, and forest edges; 0–1200 m.

DISTRIBUTION. Mexico to Venezuela. **Mexico**, Chiapas: *Breedlove* 9959 (F); Escuintla: *Matuda* 16719 (F). **Belize**, Belize: *Dwyer* 11488 (MO); Cayo: *Gentle* 2261 (F); Stann Creek: *Spellman* 1607 (F). **Guatemala**, Alta Verapaz: *Standley* 91745 (F); Escuintla: *Standley* 64176 (F); Jutiapa: *Standley* 77560 (F); Petén: *Ortiz* 1368 (MO); Santa Rosa: *Standley* 79270 (F). **El Salvador**, San Vicente: *Standley & Padilla* 3598 (F). **Honduras**, Atlántida: *Standley* 56600 (F); Comayagua: *Molina* 7036 (F); Olancho: *Standley* 18175 (F). **Nicaragua**, Matagalpa: *Williams et al.* 24010 (F); Zelaya: *Seymour* 3262 (F). **Costa Rica**, Guanacaste: *Daudenmire* 114 (F); Puntarenas: *Burger & Liesner* 6534 (F); San José: *Burger* 7618 (F). **Panama**, Colón: *Antonio* 1789 (MO); Panama: *Greig* 204 (BM). **Venezuela**, Táchira: *Berti & Sanchez* 982–132 (G).

63. *Piper bredemeyeri* Jacq., *Ecl. pl. rar.* **1**: 125 (1815). Type: Venezuela, Caracas, *Bredemeyer* s.n. (W-holotype).

Fig. 4A,a,b

- P. radula* Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* **1**: 148 (1816). Type: Venezuela, habitat in Provincia Caracas, *Humboldt & Bonpland* s.n. (B-holotype).
P. flexuosum Jacq., *Ecl. pl. rar.* **1**: 139 (1816). Type: Venezuela, Caracas, *Bredemeyer* s.n. (W-holotype).
Steffensia flexuosa (Jacq.) Kunth in *Linnaea* **13**: 644 (1839).
S. radula (Kunth) Kunth in *Linnaea* **13**: 650 (1839).
Artanthe radula (Kunth) Miq., *Syst. piperac.*: 426 (1844).
A. flexuosa (Jacq.) Miq., *Syst. piperac.*: 454 (1844).
Piper pseudopsis C.DC. in *An. Inst. fis.-geogr. C. Rica* **9**: 164 (1897). Type: Costa Rica, San José, *Tonduz* 1088, 2847 (G!-syntypes).
P. villibracteum C.DC. in *Annu. Conserv. Jard. bot. Genève* **21**: 233 (1920). Type: Colombia, Santa Marta, *Smith* 384 (G holotype; BM!-isotype).
P. pelliticaule Trel. in *Contr. U.S. natn. Herb.* **26**: 157 (1929). Type: Costa Rica, Alajuela, *Standley & Torres* 47539 (US-holotype).
P. alveolatifolium Trel. in *J. Wash. Acad. Sci.* **19**: 329 (1929).

Type: Honduras, Comayagua, *Standley* 56344 (F-holotype; ILL!-isotype).

- P. copacabanense* Trel. in *Caldasia* **1**: 88 (1940). Type: Colombia, Copacabana, near Medellín, *Daniel* 279 (US!-holotype; ILL!-isotype).

Shrubs 1–3 m high, stems densely pubescent with yellowish hairs 0.5–1 mm long. Leaves 10–26 cm long, 4–10 cm wide, broadly to narrowly ovate-lanceolate, upper surface bullate, scabrous, hirsute, underside densely brown-pubescent on veins, dark green, apex acuminate, base unequally rounded. Venation with 4–7 pairs of secondary veins arising from the lower part of the midrib, ascending steeply to apex. Petioles 8–18 mm long, densely puberulent, with a ligule-like structure 8 mm long. Prophylls 10–25 mm long, drying dark brown. Inflorescences 6–12 cm long, erect; peduncles 12–24 mm long, densely pubescent. Anthers 0.3–0.4 mm long. Floral bracts 0.8 mm wide, triangular to semi-lunar, densely yellow-ciliate. Fruits 1 mm wide, obovoid, trigonal, glabrous or sparsely to densely pale-puberulent; stigmas 3.

Thickets, forest edges, track- and creek-sides; 800–2000 m.

DISTRIBUTION. Guatemala to Venezuela. **Guatemala**, Chiquimula: *Molina* 25163 (NY); Jalapa: *Standley* 76781 (F). **Honduras**, Morazan: *Sanchez* 83 (BM); Ocotepeque: *Molina* 22387 (F); Paraiso: *Molina* 7667 (F). **El Salvador**, Ahuachapán: *Standley & Padilla*: 2698 (F); Santa Ana: *Croat* 42284 (MO). **Nicaragua**, Jinotega: *Williams et al.* 27491 (F); Matagalpa: *Williams et al.* 23464 (NY). **Costa Rica**, Alajuela: *Smith* 1692 (NY); Cartago: *Lent* 3646 (F); San José: *Utley* 917 (MO). **Colombia**, Antioquia: *Archer* 780 (BM); Cauca: *Lehmann* 3807 (BM). **Venezuela**, Trujillo: *Alston* 6488 (BM).

Piper bredemeyeri can be identified by its rough, bullate, ovate-lanceolate leaves, long hairs, triangular to semi-lunar, yellow-ciliate floral bracts, and trigonal fruits.

64. *Piper dilatatum* Rich. in *Act. Soc. Hist. nat. Paris* **1**: 105 (1792). Type: Guadalupe, *Bertero* s.n. (G-holotype). Fig. 4B,c,d.

P. argillicola C.DC. in *Annu. Conserv. Jard. bot. Genève* **21**: 37 (1920). Type: Colombia, Cordillera Occidentale, *Langlass* 52 (G!-holotype).

P. subsericeum Trel. in *Contr. U.S. natn. Herb.* **26**: 141 (1929). Type: Costa Rica, below Cairo, Limón, *Standley & Valerio* 48636 (US-holotype).

P. echeverrianum Trel. in *Contr. U.S. natn. Herb.* **26**: 172 (1929). Type: Costa Rica, Echeverria, *Pittier* 2547 (US-holotype).

P. obiter-sericeum Trel. ex Standl. in *Publ. Field Mus. nat. Hist. (Bot.)* **18**: 350 (1937). Type: Costa Rica, El General, *Skutch* 2865 (US-holotype; MO!, NY!-isotypes).

P. triquetrofructum Trel. ex Standl. in *Publ. Field Mus. nat. Hist. (Bot.)* **18**: 366 (1937). Type: Costa Rica, Río Pejivalle gorge, *Dodge & Thomas* 4431 (GH-holotype; MO!-isotype).

Spindly shrubs 1–3 m high, stems sparsely to densely puberulent. Leaves 11–20 cm long, 4–8 (–10) cm wide, narrowly ovate to elliptic, upper surface smooth or slightly scabrous, underside puberulent, dark green, apex acute-acuminate, base unequally obtuse to rounded. Venation with 3–4 pairs of secondary veins arising from the lower part of the midrib,



Fig. 4 A: *P. bredemeyeri*, habit; a: prophyll; b: fruit and bract. B: *P. dilatatum*, habit; c: prophyll; d: fruit and bract. C: *P. thomasi*, habit; e: prophyll; f: fruit and bract.

arcuate ascending to apex. Petioles 4–15 mm long, glabrous to puberulent, with ligule-like structure 0.5–2 mm. Prophylls 8–20 mm long, acute, puberulent along midrib. Inflorescences 6–10 cm long, erect; peduncles 5–10 mm long. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.7 mm wide, triangular to semi-lunar, pale ciliate. Fruits 0.6–0.8 mm wide, obovoid, trigonous, usually glabrous; stigmas 3, in slight depression.

Forest edges, roadsides, river and stream sides; 0–1700 m.

DISTRIBUTION. Mexico to Paraguay, W. Indies. **Mexico**, Cordoba: *Bourgeau* s.n. (G). **Honduras**, Atlántida: *Yuncker* et al. 8461 (MO). **El Salvador**, Sonsonate: *Tucker* 1360 (F). **Costa Rica**, Guanacaste: *Williams* et al. 26609 (F); Puntarenas: *Lent* 3068 (MO). **Panama**, Chiriquí: *Croat* 22469 (MO); Colón: *Antonio* 1940 (MO); Los Santos: *Lewis* et al. 1549 (MO); Panama: *Croat* 6997 (MO). **Brazil**, Bahia: *Beto & Hage* 219 (K); Mato Grosso: *Berg* et al. P18507 (K). **Paraguay**, Sierra de Amambay: *Hassler* 11039 (K).

65. ***Piper thomasi*** Tebbs, *sp. nov.* Type: Panama, south of El Cope sawmill, Coclé, 1700 m, *Hammel* 4157 (MO!-holotype).

Fig. 4C,e,f.

Fruticulus epiphyticus, caulibus rubris glandulosis pilosis. Folia elliptica coriacea glandulosa petiolis glandulosis, basi pilis flavidis longiusculis induta.

Epiphytic subshrubs 1–1.5 m high, stems reddish, glandular, young stems with yellowish-white multicellular hairs. Leaves 5–9 cm long, 2–5 cm wide, elliptic to elliptic-lanceolate, coriaceous, underside glabrous or minutely pubescent, with brown or black glands, apex acuminate, base acute to cuneate. Venation with 2–3 pairs of secondary veins arising from the lower to middle part of the midrib, curving to the apex. Petioles 4–8 (–10) mm long, glandular, usually with long yellowish hairs clustered at the base, obscuring a ligule-like structure 0.5 mm long. Prophylls 5–8 mm long, glandular, glabrous to sparsely pubescent. Inflorescences 2.5–5 cm long, erect; peduncles 6–10 mm long, glabrous to sparsely pubescent, glandular. Anthers 0.1–0.2 mm long. Floral bracts 0.8–1 mm wide, broadly triangular or crescent-shaped, densely yellowish white ciliate. Fruits 1–1.2 mm wide, obovoid, trigonous from above, glabrous, glandular; stigmas 3.

Cloud forest, forested slopes, along trails and ridges; 800–1700 m.

DISTRIBUTION. Panama. **Panama**, Bocas del Toro: *Croat* 69205 (BM,MO); Chiriquí: *Hampshire & Whiteford* 161 (BM); Coclé: *Croat* 67262 (BM,MO); Panama: *McPherson* 7438 (BM,MO).

The epiphytic habit of this species is unusual in *Piper*. *Piper thomasi* can also be identified by its reddish, glandular, long-pubescent stems, glandular coriaceous leaves, and glandular petioles with clustered yellowish hairs at the base. It is a species of high forest, endemic to Panama.

66. ***Piper terrabanum*** C.DC. in *Bull. Soc. r. Bot. Belg.* 30 (1): 217 (1892). Type: Costa Rica, *Pittier* 3604 (G!-holotype).

Fig. 5A,a,b.

P. dilatatum var. *acutifolium* C.DC. in *Bull. Soc. r. Bot. Belg.*

30(1): 217 (1892). Type: Costa Rica, *Pittier* 3385 (G!-holotype).

P. cyclophyllum C.DC. in *An. Inst. fis.-geogr. C. Rica* 9: 167 (1897). Type: Costa Rica, *Pittier* s.n. (G!-holotype).

P. laevifolium C.DC. in *An. Inst. fis.-geogr. C. Rica* 9: 169 (1897), non Blume (Art. 50c). Type: Costa Rica, *Pittier* 8586 (G!-holotype).

P. falcigerum Trel. in *Contr. U.S. natn. Herb.* 26: 147 (1929). Type: Costa Rica, El Silencio, near Tilarán, *Standley & Valerio* 44747 (US-holotype).

P. sinuatifolium Trel. in *Contr. U.S. natn. Herb.* 26: 147 (1929). Type: Costa Rica, *Standley & Valerio* 45537 (US-holotype; ILL!-isotype).

P. sublaevifolium Trel. in *Contr. U.S. natn. Herb.* 26: 147 (1929). Type: Costa Rica, Boca de Zhorquin, *Tonduz* 8586 (US-holotype).

P. auriculiferum Trel. in *Contr. U.S. natn. Herb.* 26: 156 (1929). Type: Costa Rica, El Silencio, near Tilarán, *Standley & Valerio* 44648 (US-holotype).

P. celatipetiolum Trel. in *Contr. U.S. natn. Herb.* 26: 156 (1929). Type: Costa Rica, Capulín, Alajuela, *Standley* 40178 (US-holotype).

P. disparifolium Trel. in *Contr. U.S. natn. Herb.* 26: 156 (1929). Type: Costa Rica, Pejivalle, *Standley & Valerio* 47082 (US-holotype).

P. anisophyllum Trel. in *Contr. U.S. natn. Herb.* 26: 157 (1929). Type: Costa Rica, El General, *Pittier* 3385 (US!-holotype).

P. celatipetiolum var. *brenesii* Trel. in *Cufod., Arch. bot. Sist. Fitogeogr. Genet.* 10: 26 (1934). Type: Costa Rica, Pacífica, *Brenes* 80 (ILL!-holotype).

P. anisophyllum var. *granulatum* Trel. ex Standl. in *Publ. Field Mus. nat. Hist. (Bot.)* 18: 331 (1937). Type: Costa Rica, El General, *Skutch* 2740 (US-holotype; NY!-isotype).

P. verruculaepetiolum Trel. ex Standl. in *Publ. Field Mus. nat. Hist. (Bot.)* 18: 368 (1937). Type: Panama, Changuinola Valley, Bocas del Toro, *Dunlap* 494 (F!-holotype).

P. wedelii Yunck. in *Ann. Mo. bot. Gdn* 37: 56 (1950). Type: Panama, near Chiriquí Lagoon, *Wedel* 1021 (MO-holotype).

Shrubs 1.5–2 (–2.5) m high, glabrous or minutely puberulent. Leaves 15–24 (–30) cm long, 6–10 cm wide, ovate-elliptic to obovate, minutely puberulent on veins below, apex acuminate, base unequal, with one side slightly lobed. Venation with 3–6 pairs of secondary veins arcuate-ascending to apex. Petioles 5–12 mm long, glabrous or minutely puberulent, with minute ligule-like structure 0.5 mm long. Prophylls 20–30 mm long, minutely puberulent. Inflorescences erect, 6–12 cm long; peduncles 5–15 mm long, glabrous or minutely puberulent. Anthers 0.2–0.3 mm long. Floral bracts 0.3–0.8 mm wide, triangular, white-ciliate. Fruits 0.5–1 mm wide, obovoid, round-trigonous, glabrous, glandular; stigmas 3, in slight depression.

Shaded sites in forest, edges of roads or streams; 0–1000 m.

DISTRIBUTION. Nicaragua to Panama. **Nicaragua**, Zelaya: *Shank & Molina* 4866 (F). **Costa Rica**, Alajuela: *Croat* 46940 (MO); Cartago: *Skutch* 4593 (NY); Heredia: *Opler* 1595 (MO); Puntarenas: *Croat* 35102 (MO); San José: *Skutch* 2740 (NY). **Panama**, Bocas del Toro: *Kirkbride & Duke* 630

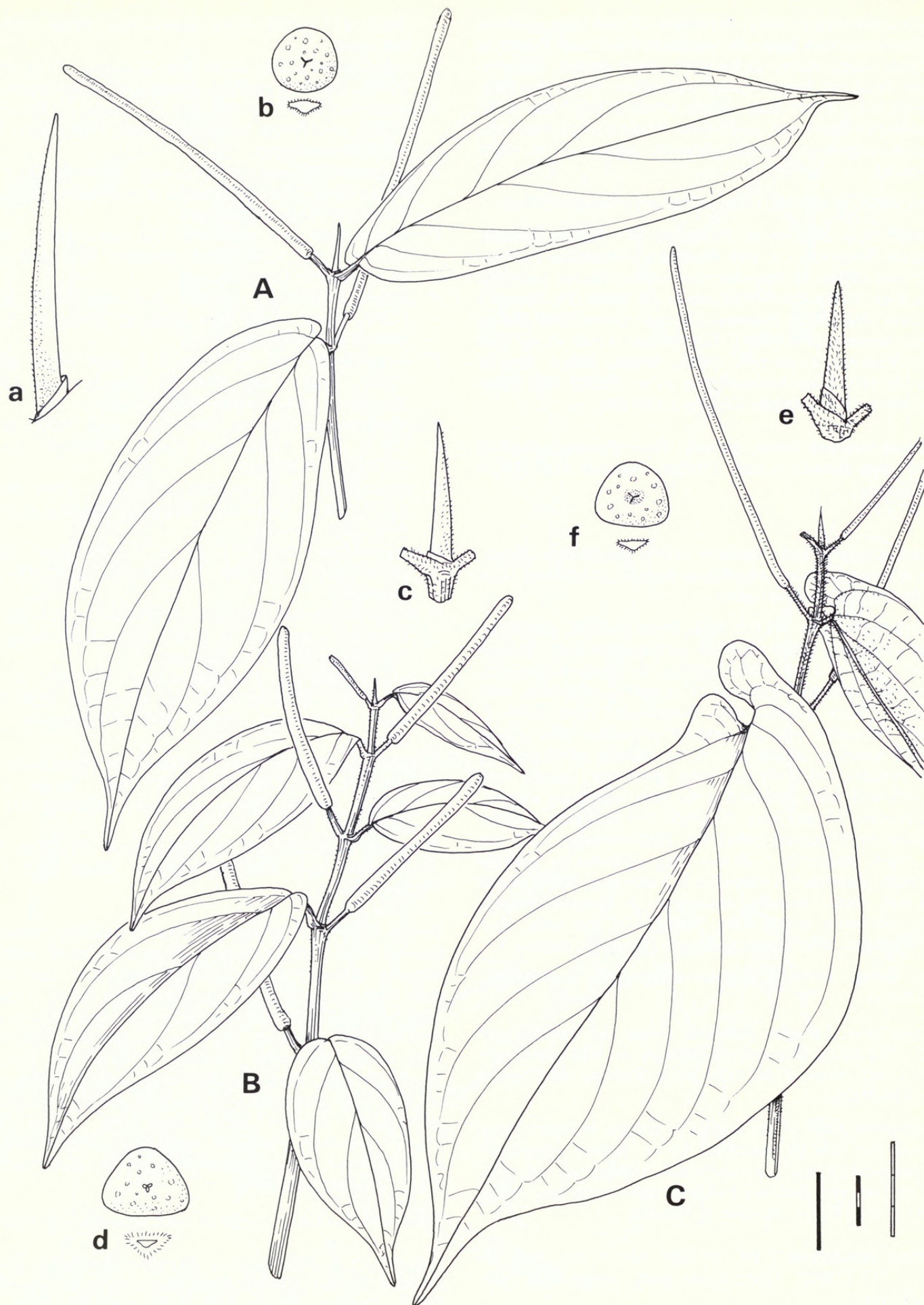


Fig. 5 A: *P. terrabanum*, habit; a: prophyll; b: fruit and bract. B: *P. littorale*, habit; c: prophyll; d: fruit and bract. C: *P. otophorum*, habit; e: prophyll; f: fruit and bract.

(MO); Chiriquí: *Croat* 21947 (MO); Panama: *Croat* 27058 (MO); San Blas: *Croat* 16950 (MO); Veraguas: *Mori & Kallunki* 4738 (MO).

Piper terrabanum is similar to *P. dilatatum* Rich., but can be distinguished by its larger leaves and prophylls, floral bracts that are triangular, rather than semi-lunar as in *P. dilatatum*, and glandular fruits.

67. **Piper littorale** C.DC. in Pittier, *Fl. Costaricensis* 2: 252 (1898). Type: Costa Rica, bord de la mer, Porto Viejo, Talamanca, *Tonduz* 8736 (NY!-isotype). Fig. 5B,c,d.

P. maternale Trel. in *Publ. Field Must. nat. Hist. (Bot.)* 18: 349 (1937). Type: Panama, Bocas del Toro, *Cooper* 210 (F-holotype).

Shrubs 1–2 m high, stems sparsely to moderately pubescent, sometimes green or purple-maculate. Leaves 5–15 cm long, 2–6 cm wide, ovate to ovate-elliptic, slightly succulent, subcoriaceous when dry, upper surface glabrous, lustrous, underside minutely puberulent, apex acuminate, base unequal, obtuse to slightly cordulate. Venation with 3–4 pairs of secondary veins arising from the lower to middle part of the midrib, curving to the apex. Petioles 3–7 mm long, puberulent, with ligule-like structure 0.5–1 mm long. Prophylls 5–10 mm long, puberulent along midrib, drying dark brown. Inflorescences 4–8 cm long, erect; peduncles 6–12 mm long, glabrous or minutely pubescent. Anthers 0.2 mm long. Floral bracts 0.5–0.7 mm wide, triangular, densely yellow-ciliate. Fruits 0.7–1 mm wide, trigonous from above, glabrous, glandular; stigmas 3.

Near seashores, in shady places such as edges of woods or under palms; sea-level.

DISTRIBUTION. Nicaragua to Panama. **Nicaragua**, Rio San Juan: *Nelson* 5270 (F). **Costa Rica**, Limón: *Burger* et al. 10358 (F,MO). **Panama**, Bocas del Toro: *Wedel* 2047 (MO); Colón: *Croat* 10038 (MO).

Piper littorale can be found growing on the strand, often in the shade of palm trees. It can be distinguished by its often maculate stems, subcoriaceous, slightly succulent leaves, and glabrous, glandular fruits.

68. **Piper otophorum** C.DC. in *Bull. Soc. r. Bot. Belg.* 30(1): 220 (1892). Type: Costa Rica, bois de Siguirres, *Pittier* 3183 (G!-holotype). Fig. 5C,e,f.

P. sperdinum C.DC. in *Smithson. misc. Collns* 71(6): 1 (1920). Type: Panama, San Blas, *Pittier* 4348 (US-holotype; G!-isotype).

P. milciadesii Trel. & Yunck., *Piperac. N. South Amer.* 1: 314 (1950). Type: Colombia, El Valle, *Killip & Dussan* 34732 (US-holotype, photograph!).

Shrubs (0.5) 1–2 m high, stems densely yellowish white pubescent. Leaves 14–24 cm long, 6–10 cm wide, asymmetrically elliptic to ovate, upper surface smooth or slightly scabrous, glandular, underside puberulent on veins, apex long-acuminate, base unequal, with one lobe distinctly auriculate, 1–2 cm across, covering the petiole. Venation with 3–5 pairs of secondary veins arising from the lower part of the

midrib, arcuate-ascending to apex. Petioles 3–12 mm long, densely puberulent, with ligule-like structure 0.5 mm long. Prophylls 9–15 (–20) mm long, densely pale-pubescent. Inflorescences 6–12 cm long, erect, maroon or brown; peduncles 10–25 mm long, densely puberulent. Anthers 0.2–0.3 mm long. Floral bracts 0.3–0.8 mm wide, triangular, minutely ciliate. Fruits 0.5–0.8 mm wide, obovoid, obpyramidal-trigonous, glabrous, glandular, with a minute depression on upper surface; stigmas 2–3.

Shade of moist forest, stream sides; 0–1200 m.

DISTRIBUTION. Costa Rica to Colombia. **Costa Rica**, Limón: *Grayum* et al. 8665 (BM,CR); San José: *Greig* 446 (BM). **Panama**, Bocas del Toro: *Antonio* 3126 (MO); Colón: *Knapp & Sytsma* 2394 (BM,MO); Darien: *McDonagh* et al. 617 (BM); Panama: *Gentry & Nee* 8648 (MO); San Blas: *Nevers & Gonzalez* 3682 (BM,MO); Veraguas: *Antonio* 3544 (BM,MO). **Colombia**, Antioquia: *Haught* 4630 (ILL).

Piper otophorum can be recognized by its asymmetric leaves, which have one distinctive auriculate basal lobe, overlapping the petiole. The inflorescences are often brown or maroon.

69. **Piper malpasoensis** Tebbs, *sp. nov.* Type: Mexico, Ocozacoatlán de Espinosa, Chiapas, 550 m, *Breedlove & Thorne* 20762 (MO!-holotype). Fig. 6A,a,b.

Frutex 1–2 m altus, caulibus albo-pilosis. Folia elliptico-ovata pilosa, basin auriculata, petiolo albo-piloso. Bacca trigona glabra.

Shrubs 1–2 m high, stems white-puberulent. Leaves 8–12 cm long, 3.5–6 cm wide, elliptic-ovate, upper surface glabrous, underside with soft white hairs on veins, apex acute-acuminate, base narrowly unequally lobed, the lobes curved around and concealing the petiole. Venation with 3–5 secondary veins arising steeply from the lower to middle part of the midrib, curving towards the apex. Petioles 1–4 mm long, white-pubescent, with glabrous ligule-like structure 0.5 mm long. Prophylls 8–10 mm long, narrow, acute, with narrow central strip of white hairs. Inflorescences 4–6 cm long, erect; peduncles 7–10 mm long, white-pubescent. Anthers 0.2–0.4 mm long. Floral bracts 0.3–0.6 mm wide, triangular, with pale centres, shortly white-ciliate. Fruit 0.8–1 mm wide, obovoid, trigonous to round from above, glabrous; stigmas 3.

Steep moist ravines in lower montane rain forest; (50–) 100–1200 m.

DISTRIBUTION. Southern Mexico. **Mexico**, Chiapas: *Breedlove* 34894 (MO); Tabasco: *Conrad & Gallegos* 2872 (MO, BM).

P. malpasoensis can be recognized by its white-puberulent stems and leaves, short erect inflorescences on puberulent peduncles, and glabrous fruits. It is closely related to *Piper enganyanum*, but that species can be distinguished by its very narrow leaves with dark glands on the undersides, and different venation. The distribution for *P. malpasoensis* is limited to southern Mexico, whereas *P. enganyanum* is found in Panama and Colombia.

70. **Piper enganyanum** Trel. & Yunck. in *Piperac. N. South Amer.* 1: 292 (1950). Type: Colombia, along Río Engaña, El Valle, *Killip* 34750 (US-holotype; BM!-isotype).



Fig. 6 A: *P. malpasoensis*, habit; a: prophyll; b: fruit and bract. B: *P. enganyanum*, habit; c: prophyll; d: fruit and bract.

Fig. 6B,c,d.

Slender, spindly shrubs 1–2.5 (–3) m high; stems shortly pubescent. Leaves 6–10 cm long, 1–3 cm wide, lanceolate, upper surface glabrous, slightly scabrous, underside with minute dark glands and short hairs on veins, apex narrowly long-acuminate, base unequal, slightly to strongly auriculate, concealing the petioles. Venation with 3–4 pairs of secondary veins mostly arising from along the length of the midrib, loop-connecting to the apex. Petioles 1–3 mm long, pubescent, with a minute ligule-like structure 0.5 mm long, mostly obscured by short pale hairs. Prophylls 5–7 mm long, narrow, acute, pubescent along the midrib. Inflorescences 3–5 cm long, erect; peduncles 3–5 mm long, puberulent. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.7 mm wide, densely white-ciliate with pale, glabrous centres. Fruit 0.8–1 mm wide, obovoid, trigonous from above, glabrous, glandular; stigmas 3, recurved.

Rich, moist forest; 200–700 m.

DISTRIBUTION. Panama to Colombia. **Panama**, Chiriquí: Croat 22473 (F,NY).

Piper enganyanum is easily recognized by its narrow, lanceolate leaves with unequal, auriculate bases, concealing the short petioles.

71. **Piper lanceifolium** Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* 1: 49 (1816). Type: Peru, Jaen de Bracamoros, *Humboldt & Bonpland* s.n. (B-holotype).

Fig. 7A,a,b.

Artanthe lanceaefolia (Kunth) Miq., *Syst. piperac.*: 433 (1844).

Piper lanceifolium var. *acutiusculum* C.DC. in DC., *Prodr.* 16(1): 317 (1869). Type: Ecuador, *Jameson* 380 (K!-holotype; BM!-isotype).

P. friedrichsthali C.DC. in DC., *Prodr.* 16(1):327 (1869). Type: Guatemala, *Friedrichsthal* 1424, (V-holotype; ILL!, K!-isotypes).

P. linearifolium C.DC. in *Linnaea* 37: 355 (1872). Type: Costa Rica, Hacienda Santa Rosa, *Oersted* s.n. (G-holotype).

P. pseudolanceaefolium Trel. in *Contr. U.S. natn. Herb.* 26: 170 (1929). Type: Costa Rica, *Tonduz* 12665 (US-holotype; G!-isotype).

P. excultum Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* 13: 164 (1936). Type: Peru, San Martin, *Llewelyn Williams* 7461 (F-holotype; ILL!-isotype).

P. lineatum var. *leucolepidum* Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* 13: 184 (1936). Type: Peru, *Killip & Smith* 22495 (US-holotype; ILL!-isotype).

P. goergeri Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* 18: 344 (1937). Type: Costa Rica, Finca Castillo, Río Reventazón, *Dodge & Goerger* 9421 (MO-holotype; ILL!-isotype).

P. liratinerve Trel. in *Ann. Mo. bot. Gdn* 24: 186 (1937). Type: Panama, Chiriquí, *Seibert* 158 (MO!-holotype; ILL, NY!-isotypes).

P. alveatum Trel. in *Ann. Mo. bot. Gdn* 27: 287 (1940). Type: Panama, Bocos del Toro, *Woodson et al.* 1837 (ILL!-holotype; NY!-isotype).

P. arctilimum Trel. in *Ann. Mo. bot. Gdn* 27: 288 (1940).

Type: Panama, Coclé, *Miller* 1813 (US-holotype; ILL!-isotype).

Shrub or small tree 1–4 (–6) m high, stems sparsely to densely pubescent. Leaves 10–20 (–22) cm long, 2–8 cm wide, lanceolate to elliptic-lanceolate, greenish brown, upper surface softly pubescent, smooth to the touch, underside pubescent, apex acuminate, base narrow, slightly unequal. Venation with 4–7 pairs of sharply ascending secondary veins, prominent on underside. Petioles 4–9 (–12) mm long, with a ligule-like structure 1–2 mm. Prophylls 1–4 cm long, acute, sparsely to densely dull-white pubescent, glandular. Inflorescences 5–16 (–18) cm long, arching; peduncles 0.5–3 (–5) cm long, pubescent. Floral bracts 0.8–1 mm wide, crescent-shaped, densely white-ciliate. Fruit 0.7–1 mm wide, obovoid, trigonous, glabrous; stigmas 3, linear.

Moist forest, damp pastures, roadsides; 0–2800 m.

DISTRIBUTION. Costa Rica to Peru. **Costa Rica**, Alajuela: *Lent* 1817 (NY); Cartago: *Skutch* 4620 (MO); Heredia: *Godrey* 66152a (MO); Limón: *Burger & Liesner* 6888 (NY); Puntarenas: *Semple* 81 (MO); San José: *Skutch* 3104 (MO). **Panama**, Chiriquí: *Stern et al.* 1063 (MO); Coclé: *Allen* 2003 (NY); Panama: *Wilbur et al.* 11892 (MO). **Colombia**, El Chocó: *Killip & Garcia* 33579 (BM); Cundinamarca: *Killip* 33984 (BM); Narino: *Ewan* 16639 (BM); Valle: *Killip* 34904 (BM). **Ecuador**, Napo: *Davis* 346 (S); Pichincha: *Balslev & Boom* 2490 (B). **Peru**, Ayacucho: *Killip & Smith* 22451 (ILL); Loreto: *Klug* 3177 (B).

P. lanceifolium can be distinguished from *P. aduncum*, which also has arching inflorescences, by its crescent-shaped bracts, trigonous fruits, and the smooth upper surfaces of its leaves. *P. aduncum* has extremely rough upper leaf surfaces, triangular bracts, and round fruits.

P. friedrichsthali C.DC. has been reduced to synonymy under *P. lanceifolium* as it is considered merely to be a narrow-leaved form of this species. The specimens examined for this study show a wide variation in leaf width. The wide-leaved forms sometimes have a prominent stipular structure at the petioles, but this has also been found in plants with narrow leaves. The same type of pubescence is found on the leaves and the prophylls are glandular-pubescent. The inflorescence characters are identical, with crescent-shaped, white-fringed bracts and trigonous, glabrous fruits.

72. **Piper aduncum** L., *Sp. pl.* 1: 29 (1753). Type: Jamaica, *Houston* s.n. (BM!-lectotype).

Fig. 7B,c,d.

P. angustifolium Ruiz & Pav., *Fl. peruv.* 1: 38 (1798). Type: Peru, Ruiz López & Pavón s.n. (Madrid-holotype, photograph!).

P. elongatum Vahl, *Enum. pl.* 1: 312 (1805). Type: Peru, *Herb. Willd.* 659 (B-holotype).

P. celtidifolium Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* 1: 50 (1816).

Artanthe adunca (L.) Miq., *Comm. phytogr.*: 49 (1838).

Artanthe elongatum (Vahl) Miq., *Syst. piperac.*: 434 (1844).

A. galleoti Miq., *Syst. piperac.*: 451 (1844). Type: Mexico, Jalapa, *Galleotti* s.n. (G-holotype; K!-isotype).

Steffensia adunca (L.) Kunth in *Linnaea* 13: 633 (1839).

A. celtidifolia (Kunth) Miq., *Syst. piperac.*: 452 (1844).

Piper pseudo-velutinum var. *flavescens* C.DC. in *Bull. Soc. r.*



Fig. 7 A: *P. lanceifolium*, habit; a: prophyll; b: fruit and bract. B: *P. aduncum*, habit; c: prophyll; d: fruit and bract. C: *P. mollicomum*, habit; e: prophyll; f: fruit and bract.

- Bot. Belg.* **30**(1): 203 (1891). Type: Costa Rica, Río Tilerí, near San José, *Pittier* 3175 (G-holotype).
- P. kuntzei* C.DC. in Kuntze, *Revis. gen.* **3** (2): 274 (1898). Type: Bolivia, Velasco, *Kuntze* s.n. (S-holotype; G!-isotype).
- P. fatioanum* C.DC. in *Smithson. misc. Collns* **71**(6): 7 (1920). Type: Panama, Colón, *Pittier* 3935 (US-holotype).
- P. aduncum* var. *laevifolium* C.DC. in *Smithson. misc. Collns* **71**(6): 8 (1920). Type: Panama, Porto Bello, Colón, *Pittier* 2438 (US-holotype).
- P. elongatum* var. *brachyarthrum* Trel. in *Contr. U.S. natn. Herb.* **26**: 37 (1927). Type: Panama, Chiriquí, *Maxon* 5139 (US-holotype).
- P. disparispicum* Trel. in *Contr. U.S. natn. Herb.* **26**: 170 (1929). Type: Costa Rica, Escasí, San José, *Standley* 32319 (US-holotype).
- P. aduncifolium* Trel. in *Contr. U.S. natn. Herb.* **26**: 171 (1929). Type: Costa Rica, Carrillo, *Pittier* 1196 (US-holotype).
- P. anguillispicum* Trel. in *Contr. U.S. natn. Herb.* **26**: 175 (1929). Type: Costa Rica, near San Ramon, *Brenes* 14197 (US-holotype).
- P. oblanceolatum* var. *fragilicaule* Trel. in *Contr. U.S. natn. Herb.* **26**: 175 (1929). Type: Costa Rica, El Arenal, Guanacaste, *Standley & Valerio* 45228 (US-holotype).
- P. submolle* Trel. in *Contr. U.S. natn. Herb.* **26**: 178 (1929). Type: Costa Rica, Carmen, Limón, *Standley & Valerio* 48363 (US-holotype).
- P. flavescens* (C.DC.) Trel. in *Contr. U.S. natn. Herb.* **26**: 184 (1929). Type: Costa Rica, Río Tilerí near San José, *Tondus* 3175 (US-holotype).
- P. elongatifolium* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **13**: 161 (1936). Type: Peru, Junin, *Macbride* 5287 (F!-holotype; ILL!-isotype).
- P. elongatum* var. *pampayacusum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **13**: 162 (1936). Type: Peru, *Macbride* 5047 (F-holotype; ILL!-isotype).
- P. lineatum* var. *hirtipetiolatum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **13**: 184 (1936). Type: Peru, *Macbride* 4182 (F-holotype; ILL!-isotype).
- P. cuatrecasasii* Trel. in *Trab. Mus. Cienc. Nat., Madrid, Ser. Bot.* **33**: 48 (1936). Type: Colombia, Tolima, *Cuatrecasas* 2426 (ILL!-holotype).
- P. cumbricola* Trel. in *Trab. Mus. Cienc. Nat., Madrid, Ser. Bot.* **33**: 48 (1936). Type: Colombia, La Cumbre, *Cuatrecasas* 2012, 2427 (ILL-syntypes).
- P. illudens* Trel. in *Trab. Mus. Cienc. Nat., Madrid, Ser. Bot.* **33**: 50 (1936). Type: Colombia, Ibagué, *Cuatrecasas* 2424 (ILL!-holotype).
- P. intersitum* Trel. in *Caldasia* **1**: 86 (1940). Type: Colombia, Antioquia, *Daniel* 890 (US-holotype).
- P. aduncum* var. *brachyarthrum* (Trel.) Yunck. in *Ann. Mo. bot. Gdn* **37**: 32 (1950).

Shrub or small tree 2–5 (–8) m high, stems sparsely to densely pubescent. Leaves 12–20 cm long, (3–) 5–9 cm wide, oblong-elliptic to lanceolate, yellow-green, upper surface of leaf scabrous, sometimes rugose or bullate, underside pubescent, apex acuminate, base unequally rounded to obtuse, occasionally narrowly lobed. Venation with 4–7 pairs of steeply ascending secondary veins. Petioles 2–5 (–8) mm long, pubescent, vaginate at base, with a small ligule-like structure 0.5–1 mm long, sometimes reduced to a rim of hairs. Prophylls 20–25 mm long, acute, pubescent. Inflorescences

5–17 cm long, arching; peduncles 8–15 mm long, sparsely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.4–0.7 mm wide, triangular-round, densely yellow-white ciliate. Fruits 0.8–1 mm wide, obovoid, round from above, glabrous; stigmas 3.

Open or disturbed areas, roadsides and edges of woods and streams; 0–1500 m.

DISTRIBUTION. Mexico to Brazil, West Indies. **Mexico**, Chiapas: *Croat* 40344 (MO); Oaxaca: *Martínez* 883 (B); Veracruz: *Rosas* 716 (K); Yucatan: *Gentle* 1533 (K). **Belize**, Cayo: *Croat* 23652 (CAS). **Guatemala**, Alta Verapaz: *Croat* 41713 (MO); Izabal: *LeDoux* et al. 2108 (NY); Petén: *Contreras* 9904 (K); Santa Rosa: *Standley* 60467 (F). **Honduras**, Colón: *Bados* 105 (BM); Cortés: *Croat* 42712 (MO); Comayagua: *Yuncker* et al. 5698 (MO); Morazan: *Williams* 23286 (CAS); Ocotepeque: *House* 031 (BM); Olancho: *Corat & Hannon* 64179 (MO). **El Salvador**, San Salvador: *Standley* 22451 (NY); Sonsonate: *Standley* 23476 (NY). **Nicaragua**, Volcan Mombachó: *Baker* 175 (CAS). **Costa Rica**, Alajuela: *Liesner* et al. 3467 (MO); Puntarenas: *Raven* 21726 (DS); San José: *Brenes* 21351 (NY). **Panama**, Panama: *Miller* et al. 855 (MO). **Colombia**, Bogotá: *Triana* 1820 (BM); Chocó: *Croat* 56619 (BM,MO); El Meta: *Killip* 34357 (BM); Santa Marta: *Smith* 1229 (BM); Valle: *Alston* 7967 (BM). **Venezuela**, Aragua: *Alston* 5342 (BM); Carabobo: *Alston* 5738 (BM). **Guyana**, Mazaruni: *Jenman* 5290 (BM). **Ecuador**, Chimborazo: *Camp* 3244 (BM,NY); Esmeraldas: *Játiva & Epling* 891 (S); Los Ríos: *Holm-Nielsen* et al. 2887 (S); Napo-Pastaza: *Mexia* 7137 (BM). **Peru**, Chachapoyas: *Wurdack* 1792 (S); Cuzco: *Mexia* 8025 (BM); Huanuco: *Mexia* 8121 (BM); Lima: *Mexia* 8094 (BM). **Bolivia**, Nor Yungas: *Mexia* 7793 (BM). **Brazil**, Minas Gerais: *Mexia* 4973 (B); Montenegro: *Sehnem* 5042 (B); Río de Janeiro: *Bailey* 65 (BM).

Piper aduncum is a widespread species which can be found from Mexico to Brazil. It is easily recognizable by its arching inflorescences, extremely rough upper surfaces of the leaves, triangular bracts, and round, glabrous fruits. *P. lanceifolium* also has arching inflorescences, but has smooth upper leaf surfaces, semi-lunar bracts, and trigonous fruits. *P. marginatum*, with arching, and *P. cinereum* with slightly curving inflorescences, have very different leaf venation and fruits.

73. *Piper mollicomum* Kunth in *Linnaea* **13**: 648 (1839). Type: Brazil, *Sellow* s.n. (BM!-holotype). Fig. 7C,e,f.

Artanthe mollicoma (Kunth) Miq., *Syst. piperac.*: 438 (1844). *Piper pisoense* C.DC. in DC., *Prodr.* **16**(1): 278 (1869). Type: Brazil, *Riedel* 2 (LE-holotype).

P. pseudovelutinum C.DC. in DC., *Prodr.* **16**(1): 282 (1869). Type: Brazil, *Lhotzky* s.n. (G!-holotype).

P. olivaceum C.DC. in *Linnaea* **37**: 344 (1872). Type: Brazil, Corcovado, *Warming* s.n. (C!-holotype).

Shrubs 1–2 (–3) m high, stems moderately to densely puberulent. Leaves 10–20 cm long, 4–8 (–10) cm wide, lanceolate-elliptic to ovate-elliptic, often rugose, upper surface puberulent, sometimes scabrous, underside dark glandular, densely pubescent, especially on veins, apex acute-acuminate, base unequally obtuse to cordulate. Venation with 4–6 pairs of secondary veins arising from the lower to middle part of the midrib, ascending steeply to the apex.

Petioles 5–10 mm long, pale-puberulent. Prophylls 5–8 mm long, pale-puberulent. Inflorescences 7–15 cm long, erect or curved; peduncles (10–) 15–30 mm long, puberulent. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.8 mm wide, triangular-round, sparsely to densely pale-ciliate. Fruits 0.8–1 mm long, round from above, glabrous, sometimes glandular; stigmas 3.

Wooded slopes, banks and track-sides, in partial shade; 0–1500 m.

DISTRIBUTION. Colombia, Venezuela, Brazil. **Colombia**, Bogotá: *Miguel* 1 (ILL); Santander: *Killip & Smith* 16406 (ILL); Valle: *Killip & Hazen* 8352 (ILL). **Venezuela**, Bolívar: *Killip* 37255 (ILL). **Brazil**, Ceará: *Gardner* 1848 (BM); Minas Gerais: *Mexia* 4617 (BM); Rio de Janeiro: *Peckolt* 1934 (ILL).

Piper mollicomum can at first be mistaken for *P. aduncum*, with similarly shaped leaves, sometimes curving inflorescences, and round, glabrous fruits. The inflorescences, however, do not have the distinctive arch of those of *P. aduncum*. *Piper mollicomum* can also be distinguished by its generally smaller habit, much more puberulent leaves, without the extremely rough texture of those of *P. aduncum*, much shorter prophylls, longer peduncles, and often glandular fruits.

74. **Piper achoteanum** Trel. in *J. Wash. Acad. Sci.* **19**: 328 (1929). Type: Honduras, El Achote near Siguatepeque, *Standley* 56125 (F!-holotype).

Fig. 8A,a,b.

P. pictamentum Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* **17**: 352 (1938). Type: Honduras, vicinity of Siguatepeque, *Yuncker, Dawson & Youse* 5902 (ILL!-holotype; MO!-isotype).

P. pictamentum var. *fluminis* Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* **17**: 352 (1938). Type: Honduras, river bank near Siguatepeque. *Yuncker, Dawson & Youse* 5718 (ILL!-holotype; MO!-isotype).

Shrubs 1–2 (–3) m high, stems pinkish especially at nodes, densely pubescent with yellowish white hairs. Leaves 5–12 cm long, 3–6 cm wide, narrowly ovate-cordate, scabrous above, pubescent on underside, yellowish green, apex blunt, base unequally attached to petiole, lower part slightly lobed or cordate. Venation with 3–5 secondary nerves arising from the lower to middle part of midrib, arising fairly steeply to apex. Petioles 0–3 mm long, pubescent, concealed by lower leaf-base, with ligule-like structure 0.5–1 mm long. Prophylls 6–12 mm long, pale green, pubescent. Inflorescences 5–10 cm long, erect or slightly curved; peduncles 6–10 mm long, pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.8 mm wide, centres pale, yellowish white ciliate. Fruits 0.8–1 mm wide, obovoid, round from above, glabrous or minutely granular; stigmas 3, sessile.

Rocky hillsides, river banks, subalpine bogs, moist areas in pine forest; 800–1500 m.

DISTRIBUTION. Mexico to Honduras. **Mexico**, Chiapas: *Matuda* 4474 (NY). **Guatemala**, Amatitlán: *Morales* 1165 (F). **Honduras**, Comayagua: *Yuncker* et al. 5902 (F); El Paraiso: *Standley* 25692 (F); Morazán: *Rodriguez* 499 (F).

This species is similar in some ways to *P. aduncum*, with yellow-green leaves with surfaces that are extremely rough to

the touch, pale-ciliate bracts, and round, mostly glabrous fruits. *P. achoteanum* differs mainly by its smaller, ovate-lanceolate leaves with small basal lobes concealing the short petioles, 6–12 mm long prophyll, and erect or only slightly curving spikes. It also grows mainly above 800 m, while *P. aduncum* can be found in lowland areas.

75. **Piper fuligineum** Kunth in *Linnaea* **13**: 655 (1939). Type: Brazil, *Sellow* s.n. (B?-holotype).

Fig. 8B,c,d.

Steffensia fuliginea (Kunth) Kunth in *Linnaea* **13**: 655 (1839). *Artanthe amplexans* Miq. in *Linnaea* **20**: 155 (1847). Type: Brazil, Minas Gerais, *Martius* s.n. (M-holotype).

Piper palustre C.DC. in DC., *Prodr.* **16**(1): 293 (1869). Type: Brazil, *Riedel* 125 (K!-isotype).

P. amplexans (Miq.) C.DC. in DC., *Prodr.* **16**(1): 293 (1869).

Stout herbs or slender shrubs 0.7–1 (–2) m high; stems ridged, pale-pubescent. Leaves 5–15 cm long, 3–7.5 cm wide, broadly to narrowly unequally ovate-cordate, yellowish green, upper surface extremely scabrous, underside crisply puberulent on veins, apex obtuse to moderately acuminate, base unequally cordate. Venation with 3–5 prominent secondary veins mostly arising from the lower part of the midrib, curving steeply to the apex. Petioles 0–4 mm long, with a ligule-like structure 0.5–1 mm long, mostly hidden by hairs. Prophylls 5–8 mm long, pale pubescent, with glabrous margins. Inflorescences 3–7 cm long, erect; peduncles stout, 20–60 mm long, sparsely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.7–1 mm wide, densely yellow-ciliate, with yellowish brown, glabrous centres. Fruits 0.8–1 mm wide, round to trigonous from above, glabrous; stigmas 3.

Damp ground, edges of streams and creeks, damp places in savanna; 700–1600 m.

DISTRIBUTION. Surinam to Paraguay. **Surinam**, R. Palaime: *Wessels Boer* 843 (K). **Brazil**, Goiás: *Hunt & Ramos* 6197 (K); Mato Grosso: *Ratter* et al. 1535 (K); Minas Gerais: *Irwin* et al. 26278 (K); Paraná: *Callejas* et al. 1839 (K); São Paulo: *Mattos* 8215 (K). **Paraguay**, Sierra de Amambay: *Hassler* 10035 (K).

Piper fuligineum is similar to *P. achoteanum*, with yellowish green leaves, pale yellow-ciliate floral bracts, and round fruits. It can be separated from that species by its much rougher leaf surfaces and shorter inflorescences on peduncles up to 6 cm long.

76. **Piper flavidum** C.DC. ex Donn.Sm. in *Bot. Gaz.* **19**: 258 (1894). Type: Guatemala, Alta Verapaz, *Smith* 1744 (G!-holotype).

Fig. 8C,e,f,g.

Shrubs 0.5–1.5 m high, glabrous, nodes close together. Leaves 7–13 cm long, 0.7–3 cm wide, linear-lanceolate, sometimes falcate, both surfaces glabrous, apex acuminate, base acute to cuneate. Venation with 1–2 pairs of prominent veins arising from lower part of midrib and running parallel to apex, with prominent cross venation. Petioles 2–5 mm long, glabrous, with ligule-like structure 1 mm long. Prophylls 7–10 mm long, glabrous. Inflorescences 2–3 cm long, erect; peduncles 2–6 (–10) mm long. Anthers 0.2 mm long. Floral



Fig. 8 A: *P. achoteanum*, habit; a: prophyll; b: fruit and bract. B: *P. fuligineum*, habit; c: prophyll; d: fruit and bract. C: *P. flavidum*, habit; e: narrow leaf; f: prophyll; g: fruit and bract.

bracts 0.6–0.8 mm wide, triangular, with densely ciliate margins. Fruits 0.8–1 mm wide, obovoid, round from above, densely pale-puberulent; stigmas 3, linear.

Slopes and stream sides in moist forest; 250–1300 m.

DISTRIBUTION. Mexico, Guatemala. **Mexico**, Chiapas: *Breedlove* 26545 (MO); Tabasco: *Rosario & Cowan* 2962 (CAS). **Guatemala**, Alta Verapaz: *Tuerckheim* 8564 (NY); Izabal: *Matuda* 3697 (F); Quiché: *Skutch* 1819 (F).

This species is sometimes confused with the narrow-leaved forms of *P. lanceifolium*. However, the leaves of *P. flavidum* are often falcate, and have only 1–2 pairs of secondary veins with prominent cross-veining. The round, pale-puberulent fruits and triangular floral bracts further distinguish it from *P. lanceifolium*, which has trigonous, glabrous fruits and semi-lunar floral bracts.

77. **Piper silvivagum** C.DC. in *An. Inst. fis.-geogr. C. Rica* 9: 162 (1897). Type: Costa Rica: forêts sur les bords du R. Zhorquin, *Tonduz* 8595 (US!-holotype; G!-isotype).

Fig. 9C,e,f.

P. vitibundum Trel. in *Contr. U.S. natn. Herb.* 26: 38 (1927). Type: Panama, Bocas del Toro, *Dunlap* 338 (US-holotype, photograph!).

P. pseudo-albuginiferum Trel. in *Contr. U.S. natn. Herb.* 26: 165 (1927). Type: Costa Rica, Cartago, *Standley & Valerio* 50948 (US-holotype, photograph!).

Scandent or climbing to 2 m high, stems slender, glabrous or shortly pale-pubescent on younger growth. Leaves 8–15 cm long, 2.5–6 cm wide, elliptic-lanceolate, upper surface glabrous to slightly scabrous, underside puberulent on veins, apex acuminate, base unequally narrowly obtuse. Venation with 3–4 secondary veins arising from the lower to middle part of the midrib, ascending steeply to apex. Petioles 3–12 mm long, sparsely to densely pubescent, with a ciliate, ligule-like structure 1–2 mm long. Prophylls 5–15 mm long, minutely puberulent. Inflorescences 6–14 cm long, erect; peduncles 5–15 mm long, glabrous. Anthers 0.1–0.2 mm long. Floral bracts 0.3–0.7 mm wide, triangular to round, white-ciliate, with dark, glabrous centre. Fruits 0.7–1 mm wide, obovoid, minutely pale-puberulent; stigmas 3, sessile.

Forest shade; 0–1400 m.

DISTRIBUTION. Mexico, Costa Rica to Peru. **Mexico**, Morelos: *Croat & Hannon* 65771 (MO). **Costa Rica**, Cartago: *Lent* 861 (NY); Heredia: *Opler* 1642 (MO); Limón: *Burger* 8489 (NY). **Panama**, Chiriquí: *Hammel* 2240 (BM). **Ecuador**, Esmeraldas: *Mexia* 7792 (B,BM). **Bolivia**, Nor Yungas: *Mexia* 7792 (BM). **Peru**, Cuzco: *Mexia* 8063 (BM,K); Mariscal Caceres: *Schunke* 3725 (F,NY); Loreto: *Mexia* 6382 (B).

Piper silvivagum is one of a small group of species in *Piper* with a scandent or climbing habit. In section *Radula* there is only one other species with this habit, *P. multiplinervium*, which can be distinguished from *P. silvivagum* by its extremely vigorous growth, glabrous, ovate to cordate leaves with sheathing petioles, and yellow, scented inflorescences. *P. silvivagum* mostly occurs from Costa Rica southwards and only one specimen from Mexico has been positively identified as this species.

78. **Piper pseudoasperifolium** C.DC. in DC., *Prodr.* 16 (1): 318 (1869). Type: Mexico, Oaxaca, *Boissier* s.n. (G!-holotype).

Fig. 9B,c,d.

P. cartagoanum C.DC. in *Linnaea* 37: 350 (1872). Type: Costa Rica, Cartago, *Oersted* s.n. (S-holotype; C!-isotype).

P. vestitifolium C.DC. in *Bot. Gaz.* 70: 183 (1920). Type: Guatemala, near Cajabón, Alta Verapaz, *Cook & Griggs* 651 (F-holotype; G!-isotype).

P. indignum Trel. in *J. Wash. Acad. Sci.* 19: 333 (1929). Type: Honduras, Siguatepeque, *Standley* 55990 (F!-holotype).

P. micoense Trel. in *J. Wash. Acad. Sci.* 19: 334 (1929). Type: Guatemala, Sierra del Mico, Izabal, *Kellerman* 6715 (F!-holotype).

P. sibunense Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* 12: 408 (1936). Type: Belize, Gracie Rock, *Gentle* 1562 (MICH-holotype; MO!-isotype).

Shrubs 1–3 m high, stems densely white- or yellow-pubescent. Leaves 8–22 cm long, 3–8 cm wide, ovate-lanceolate to elliptic-lanceolate, bullate, glandular, upper surface scabrous, shortly hispid, underside densely pubescent on veins, apex narrowly acuminate, base unequally rounded to obtuse. Venation with 4–5 pairs of secondary veins arising from the lower two-thirds of the midrib, curving to the apex. Petioles 4–10 mm long, densely pubescent, with hispid ligule-like structure 1–3 mm long. Prophylls 12–15 mm long, pubescent along midrib. Inflorescences 7–9 cm long, erect; peduncles 3–8 mm long, pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.7–0.9 mm wide, densely yellow- to white-ciliate. Fruits 0.8–1 mm wide, round from above, glabrous; stigmas 3.

Moist forest, thickets, pine woods; 0–1500 m.

DISTRIBUTION. Mexico to Costa Rica. **Guatemala**, Alta Verapaz: *Standley* 69370 (F); Huehuetenango: *Standley* 82813 (F); Petén: *Steyermark* 46195 (F).

79. **Piper villiramulum** C.DC. in *Smithson. misc. Collns* 71: 11 (1920). Type: Panama, Loma de la Gloria near Fató, Colón, *Pittier* 4083 (US-holotype; NY!-isotype).

Fig. 9A,a,b.

P. talamancanum Trel. in *Contr. U.S. natn. Herb.* 26: 173 (1929). Type: Costa Rica, Shirores, Talamanca. *Tonduz* 9274 (US-holotype; F-isotype).

P. laevius (C. DC). Trel. in *Contr. U.S. natn. Herb.* 26: 174 (1929).

P. comatum Trel. in *Contr. U.S. natn. Herb.* 26: 175 (1929). Type: Costa Rica, Río Corazal, *Tonduz* 9932 (US-holotype).

P. granulatum Trel. in *Contr. U.S. natn. Herb.* 26: 175 (1929). Type: Costa Rica, Buenas Aires, *Pittier* 3593 (US-holotype).

P. leucophlebium Trel. in *Contr. U.S. natn. Herb.* 26: 176 (1929). Type: Costa Rica, Tilarán, *Standley & Valerio* 44277 (US-holotype; ILL!-isotype!).

P. capacibracteum Trel. in *Contr. U.S. natn. Herb.* 26: 183 (1929). Type: Costa Rica, between Aserri and Tarbaca, *Standley* 41397 (US-holotype; F!,ILL-isotypes).

P. cayoense Trel. ex Standl. in *Publs Field Mus. nat. Hist.*

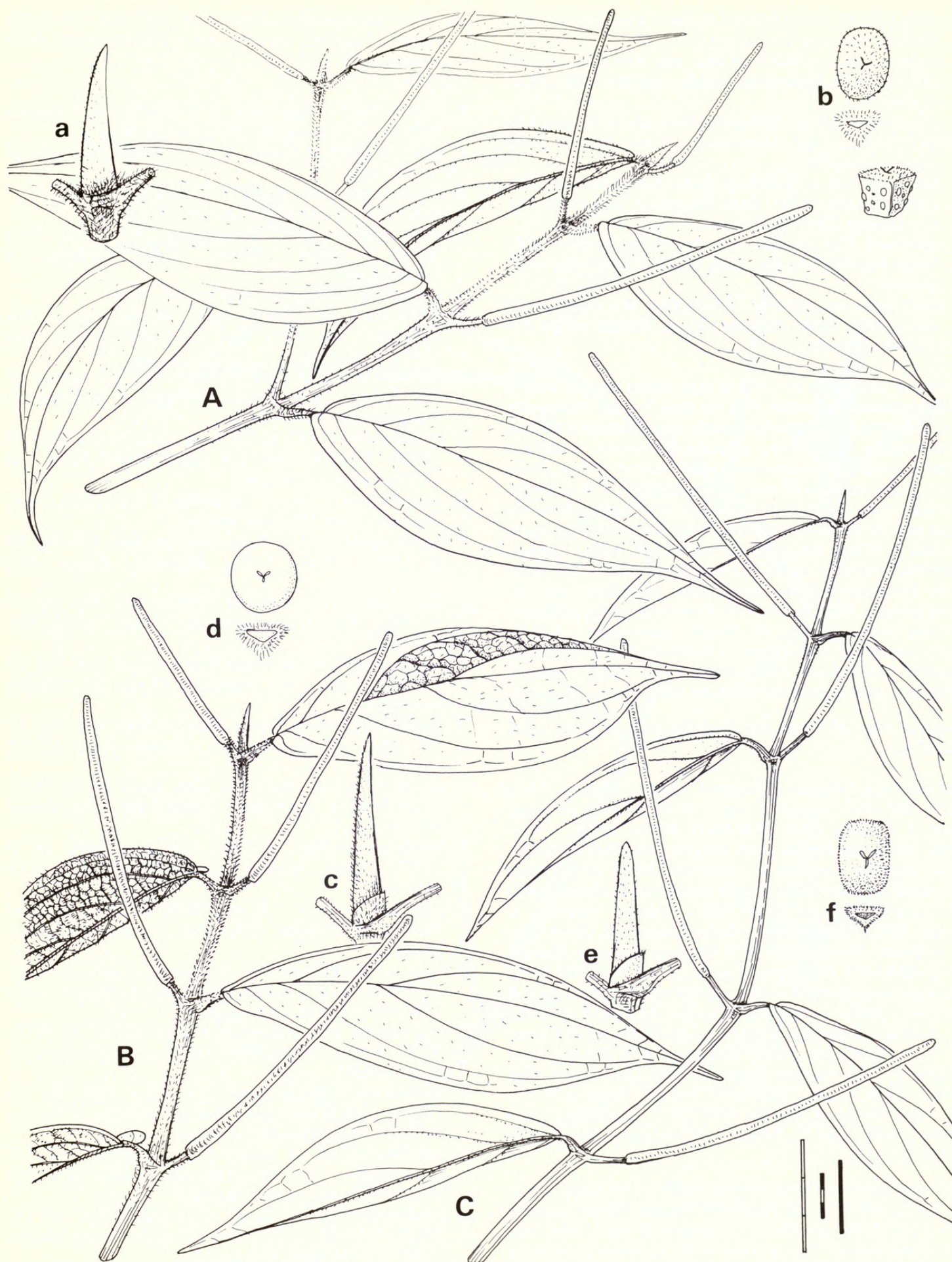


Fig. 9 A: *P. villiramulum*, habit; a: prophyll; b: fruit and bract. B: *P. pseudoasperifolium*, habit; c: prophyll; d: fruit and bract. C: *P. silvivagum*, habit; e: prophyll; f: fruit and bract.

- (Bot.) 12: 407 (1936). Type: Belize, Cayo, Bartlett 13070 (MICH-holotype; K!-isotype).
- P. tikalense* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* 17: 234 (1937). Type: Guatemala, Petén, Bartlett 12595 (ILL!-holotype).
- P. yalochanum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* 17: 234 (1937). Type: Guatemala, Petén, Bartlett 12849 (ILL!-holotype).
- P. bocasense* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* 18: 333 (1937). Type: Panama, Changuinola Valley, Dunlap 234 (F!-holotype).
- P. yapeanum* Trel. in *Ann. Mo. bot. Gdn* 25: 827 (1938). Type: Panama, Darien, Allen 351 (ILL!-holotype; MO!-isotype).
- P. gamboanum* var. *yapense* Trel. in *Ann. Mo. bot. Gdn* 27: 291 (1940). Type: Panama, Yape, Darien, Allen 854 (ILL!-holotype).

Shrubs or small trees (1–) 2–3 m high, stems usually densely whitish-pubescent. Leaves 7–24 cm long, 2–9 cm wide, ovate to elliptic-ovate or elliptic-lanceolate, upper surface scabrous, often rugose or bullate, sparsely pubescent, underside densely pubescent, with minute dark red or brown glands visible, apex acuminate, base unequally obtuse or rounded. Venation with 3–5 pairs of secondary veins arising from the lower part of the midrib and ascending fairly steeply to apex. Petioles 3–10 mm long, densely pubescent, with a minute, ligule-like structure up to 0.5 mm long, hidden by dense hairs. Prophylls 8–20 mm long, acute, pubescent with glabrous margins. Inflorescences 6–11 cm long, erect; peduncles 4–8 mm long, sparsely to densely puberulent. Anthers 0.1–0.2 mm long. Floral bracts 0.3–0.6 mm wide, triangular, densely white-ciliate. Fruits 0.6–0.8 mm wide, obovoid, pubescent, with prominent glands on sides; stigmas 3, sessile.

Shade at edge of forest and thickets, road or track sides; 0–1000 m.

DISTRIBUTION. Mexico to Ecuador. **Mexico**, Chiapas: Croat 47174 (BM,MO); Nayarit: Croat 45346 (BM,MO); Veracruz: Croat & Hannon 63089 (BM,MO). **Belize**, Belize: Dwyer 12684 (MO). **Guatemala**, Alta Verapaz: Standley 70240 (F); Baja Verapaz: Lundell & Contreras 19653 (F); Izabal: Stevens et al. 25488 (BM); Petén: Lundell & Contreras 20535 (F); Quiché: Proctor 25209 (MO); Zacapa: Harmon & Fuentes 1862 (F). **Honduras**, Colón: Guerra 128 (BM); Islas de la Bahía: Molina 20737 (F); Olancho: Croat & Hannon 64143 (BM,MO). **Nicaragua**, Boaco: Stevens 5918 (BM,MO); Jinotega: Araquistain & Castro 1856 (F); Zelaya: Marshall & Neill 6473 (MO). **Costa Rica**, Alajuela: Molina et al. 17414 (F); Cartago: Rodriguez 426 (MU); Limón: Burger & Liesner 6873 (F); Puntarenas: Burger & Liesner 6575 (F); San José: Whitmore 54 (F). **Panama**, Bocas del Toro: Correa et al. 4004 (MO); Colón: Croat 67321 (BM); Panama: Atencio 24 (F); San Blas: Nevers & Herrera 4523 (MO). **Colombia**, Santa Marta: Smith 1228 (S). **Ecuador**, Esmeraldas: Fagerlind & Wibom s.n. (S).

Piper villiramulum is often confused with *P. hispidum*. It can be distinguished by its rugose or bullate leaves, densely pubescent stems, petioles, and prophylls, and fruits with prominent glands. The petioles of *P. hispidum* have more prominent ligule-like structures than those of *P. villiramulum*, which are difficult to see amongst the dense pubescence.

80. *Piper hispidum* Sw., *Prodr. Veg. Ind. Occ.*: 15 (1788). Type: Jamaica, Swartz s.n. (M!-holotype; BM!-photograph). Fig. 10A,a,b.
- P. scabrum* Sw., *Fl. Ind. occid.* 1: 59 (1797). Type: Jamaica, Wiles s.n. (B?-holotype; BM!-photograph).
- P. hispidum* Kunth in Humb., Bonpl. & Kunth, *Nov. gen. sp.* 1: 50 (1816).
- Steffensia hirsuta* (Sw.) Kunth in *Linnaea* 13: 640 (1839).
- S. scabra* (Sw.) Kunth in *Linnaea* 13: 640 (1839).
- Artanthe olfersiana* Miq., *Syst. piperac.*: 445 (1844). Type: Brazil, Campos Vittoria, Bahia, Sellow s.n. (B-holotype).
- A. scabra* (Sw.) Miq., *Syst. piperac.*: 446 (1844).
- Piper hirsutum* var. *tonduzii* C.DC. in *Bull. Soc. r. Bot. Belg.* 30(1): 203 (1892). Type: Costa Rica, Asseri, Pittier 1270 (G!-holotype).
- P. alluvicola* C.DC. in *Annu. Conserv. Jard. bot. Genève* 21: 313 (1920). Type: Mexico, Michoacan & Guerrero, Langlasse 664 (G!-holotype).
- P. erectamentum* C.DC. in *Smithson. misc. Collns* 71(6): 10 (1920). Type: Panama, Los Siguas Camp, Pittier 3191 (US-holotype; G!-isotype).
- P. scabrilimbus* C.DC. in *Candollea* 1: 121 (1923). Type: Panama, Pittier 5584 (not located).
- P. bayamonanum* Trel. in *Feddes Reprium Spec. nov. veg.* 23: 9 (1926). Type: Cuba, Bayamon, Eggers 4689 (B-holotype).
- P. sabanillanum* Trel. in *Feddes Reprium Spec. nov. veg.* 23: 9 (1926). Type: Cuba, Sabanilla, Ekman 10659 (EHH-holotype).
- P. sumideranum* Trel. in *Feddes Reprium Spec. nov. veg.* 23: 9 (1926). Type: Cuba, Sumidero, Ekman 18211 (EHH-holotype).
- P. maestranum* Trel. in *Feddes Reprium Spec. nov. veg.* 23: 10 (1926). Type: Oriente, Ekman 14347 (EHH-holotype).
- P. williamsii* Trel. in *Contr. U.S. natn. Herb.* 26: 32 (1927). Type: Panama, Marragantí, Williams 986 (US-holotype; NY!-isotype).
- P. trachydermum* Trel. in *Contr. U.S. natn. Herb.* 26: 33 (1927). Type: Panama, Sutton Hayes 791 (NY!-holotype).
- P. killipi* Trel. in *Contr. U.S. natn. Herb.* 26: 33 (1927). Type: Panama, El Boquete, Killip 3549 (US-holotype, photograph!).
- P. killipi* var. *calderanum* Trel. in *Contr. U.S. natn. Herb.* 26: 33 (1927). Type: Panama, Rio Caldera, Chiriquí, Killip 3544 (US-holotype, photograph!).
- P. cataractarum* Trel. in *Mem. N.Y. bot. Gdn* 7: 224 (1927). Type: Bolivia, Bopi river, Rusby 672 (NY-holotype; ILL!-isotype).
- P. gonagricum* Trel. in *Contr. U.S. natn. Herb.* 26: 171 (1929). Type: Costa Rica, Heredia, Standley & Valerio 49082 (US-holotype; ILL!-isotype).
- P. pejivallense* Trel. in *Contr. U.S. natn. Herb.* 26: 171 (1929). Type: Costa Rica, Pejivalle, Standley & Valerio 46727 (US-holotype, photograph!).
- P. genuflexum* Trel. in *Contr. U.S. natn. Herb.* 26: 172 (1929). Type: Costa Rica, Santa Rosa del Copey, Tonduz 11687 (US-holotype; NY!-isotype).
- P. pergeniculatum* Trel. in *Contr. U.S. natn. Herb.* 26: 172 (1929). Type: Costa Rica, Cañas Gordas, Pittier 11033



Fig. 10 A: *P. hispidum*, habit; a: prophyll; b: fruit and bract. B: *P. sancti-felicis*, habit; c: prophyll; d: bract and fruit.

- (US-holotype, photograph!).
- P. pavasense* Trel. in *Contr. U.S. natn. Herb.* **26**: 173 (1929). Type: Costa Rica, Las Pavas, San José, Pittier 3188 (US-holotype, photograph!).
- P. scalpens* Trel. in *Contr. U.S. natn. Herb.* **26**: 176 (1929). Type: Costa Rica, San José, Tonduz 10154 (US-isotype, photograph!).
- P. caudatifolium* Trel. in *Contr. U.S. natn. Herb.* **26**: 177 (1929). Type: Costa Rica, Las Pavas, Pittier 3191 (US-holotype).
- P. inhorrescens* Trel. in *Contr. U.S. natn. Herb.* **26**: 177 (1929). Type: Costa Rica, Las Pavas, Standley 36083 (US-holotype).
- P. torresanum* Trel. in *Contr. U.S. natn. Herb.* **26**: 177 (1929). Type: Costa Rica, Río Torres, San Francisco de Guadalupe, Tonduz & Pittier 8971 (US-holotype).
- P. trichophlebium* Trel. in *Contr. U.S. natn. Herb.* **26**: 177 (1929). Type: Costa Rica, Asserí, Tonduz 1270 (G!-holotype).
- P. valetudinari* Trel. in *Contr. U.S. natn. Herb.* **26**: 178 (1929). Type: Costa Rica, San José, Tonduz 7235 (NY!-isotype).
- P. carminis* Trel. in *Contr. U.S. natn. Herb.* **26**: 179 (1929). Type: Costa Rica, Carmen, Limón, Standley & Valerio 48383 (US-holotype).
- P. coronatibracteum* Trel. in *Contr. U.S. natn. Herb.* **26**: 179 (1929). Type: Costa Rica, Hamburg Finca, Limón, Standley & Valerio 48844 (US-holotype).
- P. baculiferum* Trel. in *Contr. U.S. natn. Herb.* **26**: 180 (1929). Type: Costa Rica, El Arenal, Standley & Valerio 45052 (US-holotype).
- P. punctiunculatum* Trel. in *Contr. U.S. natn. Herb.* **26**: 180 (1929). Type: Costa Rica, Tilarán, Standley & Valerio 45712 (US-holotype, photograph!).
- P. abuginiferum* Trel. in *Contr. U.S. natn. Herb.* **26**: 181 (1929). Type: Costa Rica, El Muñeco, Cartago, Standley & Torres 51102 (US-holotype).
- P. injucundum* var. *praecalvinervium* Trel. in *Contr. U.S. natn. Herb.* **26**: 181 (1929). Type: Costa Rica, El Muñeco, Cartago, Standley & Torres 51101 (US-holotype, photograph!).
- P. injucundum* var. *praepubinervium* Trel. in *Contr. U.S. natn. Herb.* **26**: 181 (1929). Type: Costa Rica, El Muñeco, Cartago, Standley & Valerio 51067 (US-holotype, photograph!).
- P. lanatibracteum* Trel. in *Contr. U.S. natn. Herb.* **26**: 182 (1929). Type: Costa Rica, El Muñeco, Cartago, Standley 33419 (US-holotype, photograph!).
- P. lanosibracteum* Trel. in *Contr. U.S. natn. Herb.* **26**: 182 (1929). Type: Costa Rica, Río Reventado, Standley & Valerio 49457 (US-holotype, photograph!).
- P. phanorolepidum* Trel. in *Contr. U.S. natn. Herb.* **26**: 182 (1929). Type: Costa Rica, El Muñeco, Cartago, Standley 33570 (US-holotype, photograph!).
- P. pullibracteatum* Trel. in *Contr. U.S. natn. Herb.* **26**: 182 (1929). Type: Costa Rica, La Estrella, Cartago, Standley 39236 (US-holotype, photograph!).
- P. curridabatanum* Trel. in *Contr. U.S. natn. Herb.* **26**: 183 (1929). Type: Costa Rica, between San Pedro Montes de Oca & Curridabat, San José, Standley 32787 (US-isotype).
- P. fusco-bracteatum* Trel. in *Contr. U.S. natn. Herb.* **26**: 183 (1929). Type: Costa Rica, Escasú, San José, Standley 32631 (US-holotype).
- P. rivi-vetusti* Trel. in *Ann. Mo. bot. Gdn.* **24**: 186 (1937). Type: Panama, Chiriquí, Seibert 192 (MO!-holotype).
- P. aquacalientis* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 330 (1937). Type: Costa Rica, SW. of Agua Caliente, Stork 1317 (F-holotype).
- P. articulatum* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 332 (1937). Type: Costa Rica, San Ramon to La Paz, Brenes 6060 (F!-holotype).
- P. humoense* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 346 (1937). Type: Costa Rica, Pejivalle Farm, Cartago, Dodge & Thomas 4371 (GH-holotype; MO!-isotype).
- P. subasperatum* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 362 (1937). Type: Costa Rica, San José, Skutch 2157 (US-holotype; NY!-isotype).
- P. meritum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **9**: 279 (1940). Type: Honduras, Atlántida, Yuncker, Koepper & Wagner 8363 (ILL!-holotype; MO!-isotype).
- P. barbirostre* Trel. in *Ann. Mo. bot. Gdn* **27**: 288 (1940). Type: Panama, Chiriquí, Allen 1365 (ILL!-holotype; MO!-isotype).
- P. casitense* Trel. in *Ann. Mo. bot. Gdn* **27**: 289 (1940). Type: Panama, Casita Alta, Chiriquí, Woodson, Allen & Seibert 978 (ILL!-holotype; NY!-isotype).
- P. cerro-puntoense* Trel. in *Ann. Mo. bot. Gdn* **27**: 289 (1940). Type: Panama, Chiriquí, White 52 (ILL!-holotype; MO!-isotype).
- P. konkintoense* Trel. in *Ann. Mo. bot. Gdn* **27**: 293 (1940). Type: Panama, Bocas del Toro, Woodson, Allen & Seibert 1894 (ILL!-holotype; NY!-isotype).
- P. margaretae* Trel. in *Ann. Mo. bot. Gdn* **27**: 293 (1940). Type: Panama, Chiriquí, White 158 (ILL!-holotype; MO!-isotype).
- P. pervicax* Trel. in *Ann. Mo. bot. Gdn* **27**: 296 (1940). Type: Panama, near Volcan de Chiriquí, Woodson, Allen & Seibert 843 (ILL!-holotype).
- P. argentamentum* Trel. & Yunck. in *Piperac. N. South Amer.* **1**: 256 (1950). Type: Colombia, Istmina, Chocó, Killip 35452 (US-holotype; BM!-isotype).
- P. rivialbi* Trel. & Yunck. in *Piperac. N. South Amer.* **1**: 265 (1950). Type: Colombia, Tio Digua Valley, El Valle, Killip 34723 (US-holotype; BM!-isotype).
- P. phaeophyllum* Trel. in *Fieldiana Bot.* **24**: 316 (1952). Type: Guatemala, above Tamahu, Alta Verapaz, Standley 70911 (F!-holotype).

Shrubs to 4 m high, stems sparsely to densely white-pubescent. Leaves 7–18 (–21) cm long, 3–10 cm wide, ovate to elliptic-oblong, yellowish green, scabrous above, sometimes with short whitish hairs, underside sparsely to densely pubescent, especially on veins, apex acuminate, base unequally obtuse or rounded. Venation with 3–5 pairs of secondary veins curving to apex. Petioles 4–18 mm long, sparsely to densely pubescent, with a glandular, sometimes ciliate ligule-like structure 1–3 mm long. Prophylls 6–20 mm long, acute, sparsely to densely pubescent. Inflorescences 6–12 cm long, slender, erect or slightly curving; peduncles 4–20 mm long. Anthers 0.2 mm long. Floral bracts 0.3–0.6 mm wide, triangular to round, densely white-ciliate. Fruits 0.8–1 mm wide, obovoid, oblong to round from above, pubescent; stigmas 3, sessile.

Disturbed areas, moist thickets, edges of woods and tracksides; 0–2000 m.

DISTRIBUTION. Throughout tropical America. **Mexico**, Chiapas: *Breedlove* 6194 (F); Nayarit: *Miller & Tellez* 3239 (MO). **Belize**, Toledo: *Gentle* 7291 (F). **Guatemala**, Baja Verapaz: *Contreras* 11269 (K); Huehuetenango: *Standley* 81395 (F); Izabal: *Lundell & Contreras* 19346 (K); Petén: *Contreras* 9835 (K); Retalhuleu: *Standley* 66691 (F). **Honduras**, Comayagua: *Molina* 7111 (F); Copán: *Molina* 11749 (F); Morazan: *Molina* 6125 (F); Paraíso: 11315 (F). **Nicaragua**, Managua: *Garnier* 1669 (F). **Costa Rica**, Alajuela: *Molina et al.* 17123 (F); Cartago: *Utley* 801 (CR); Guanacaste: *Chacon* 2170 (MO); Heredia: *Croat* 68396 (MO); Limón: *Burger* 8444 (F); Puntarenas: *Liesner* 3068 (MO); San José: *Greig* 442 (BM). **Panama**, Coclé: *Croat* 67464 (BM); Darien: *Garwood et al.* 2056a; Panama: *Greig* 214 (BM). **Colombia**, Chocó: *Killip* 35034 (BM); El Meta: *Killip* 34463 (BM); El Valle: *Killip* 35564 (BM). **Venezuela**, Bolívar: *Croat* 53979 (MO), Carabobo: *Alston* 5753 (BM); Caracas: *Linden* 121 (BM); Lara: *Davidse & González* 21058 (BM); Orinoco basin: *Rusby* 58 (BM). **Ecuador**, Esmeraldas: *Mexia* 8415 (B); Leon: *Mexia* 6726 (BM); Los Ríos: *Mexia* 6631 (BM); Napo-Pastaza: *Mexia* 7157 (BM). **Peru**: *Mathews* 1706 (BM). **Bolivia**, Yungas: *Buchtien* 753 (BM). **Brazil**, Matogrosso: *Moore* 123 (BM); Pará: *Huber* 1348 (BM).

Probably the most confused and confusing of the taxa in this section and often difficult to identify, especially without mature inflorescences. The vegetative plasticity of *P. hispidum* has given rise to the description of numerous taxa. Many of these have now been reduced to synonymy, mainly by Trelease & Yuncker (1950). The main characters of this species are scabrous, ovate-elliptic leaves (often pale or yellowish green in colour especially when dry), petioles with distinct, often ciliate ligule-like structures, acute prophylls, slender, erect or slightly curving inflorescences, and small, obovoid, pubescent, often green fruits. *Piper villiramlum* and *P. sancti-felicitis* are probably the most closely related species to *P. hispidum*, but can be separated by the densely pubescent stems, rugose, glandular leaves and fruits of *P. villiramlum*, and the long prophylls and ligule-like structures drying dark brown of *P. sancti-felicitis*.

81. ***Piper sancti-felicitis*** Trel. in *Contr. U.S. natn. Herb.* **26**: 35 (1927). Type: Panama, Chiriquí, *Pittier* 5124 (US-holotype, photograph!).

Fig. 10B,c,d.

- P. spicilongum* Trel. in *Contr. U.S. natn. Herb.* **26**: 177 (1929). Type: Costa Rica, Santo Domingo de Golfo Dulce, *Tonduz* 9962 (US-holotype; F!-isotype).

- P. rectamentum* Trel. in *Contr. U.S. natn. Herb.* **26**: 180 (1929). Type: Costa Rica, Guanacaste, *Standley & Valerio* 45237 (US-holotype, photograph!).

- P. fragranum* Trel. in *J. Wash. Acad. Sci.* **19**: 332 (1929). Type: Honduras, La Fragua, *Standley* 55730 (F!-holotype).

- P. tentatum* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 365 (1937). Type: Costa Rica, Alajuela, *Brenes* 15032 (F-holotype; NY!-isotype).

- P. pseudo-viridicaule* var. *nievecitanum* Trel. in *Ann. Mo. bot. Gdn* **27**: 296 (1940). Type: Panama, Bocas del Toro, *Woodson, Allen & Seibert* 1829 (ILL!-holotype; NY!-isotype).

- P. variitrichum* Yunck. in *Ann. Mo. bot. Gdn* **37**: 37 (1950).

Type: Panama, Darien, *Terry & Terry* 1428 (MO!-holotype).

Shrubs 1.5–4 m high, stems densely pale-puberulent. Leaves 12–20 cm long, 5–10 cm wide, widely elliptic to obovate, upper surface scabrous, underside with hairs on veins, and minute dark glands, apex acute-acuminate, base unequally rounded to obtuse. Venation with 4–5 pairs of secondary veins arising steeply from the upper to middle part of the midrib, curving to apex. Petioles 6–15 mm long, pubescent, with ligule-like structure 6–18 mm long, glabrous or with scattered hairs, drying dark brown. Prophylls 12–22 mm long, drying dark brown, prominently veined, midrib pubescent. Inflorescences 8–15 cm long, erect; peduncles 5–10 mm long, pubescent. Anthers 0.1–0.2 mm long. Floral bracts 0.2–0.5 mm wide, triangular, pale-ciliate, with dark centres. Fruits 0.5–0.8 mm wide, obovoid, sides with prominent glands, oblong or square from above, with white or yellowish hairs; stigmas 3, minute.

Forest, edges of streams, damp thickets, and roadsides; 0–1000 m.

DISTRIBUTION. Mexico to Venezuela, West Indies. **Mexico**, Chiapas: *Purpus* 7301 (BM); Veracruz: *Williams* 8821 (F). **Belize**, Toledo: *Schipp* 504 (BM). **Guatemala**, Izabal: *Standley* 72887 (F); Petén: *Ortiz* 1129 (F); Quetzaltenango: *Standley* 84609 (F); Suchitepequez: *Standley* 66888 (F). **Honduras**, Atlántida: *Mitchell* 11 (F); Comayagua: *Molina* 8141 (BM); Olanchito: *Standley* 18439 (F). **Nicaragua**: Bluefields: *Proctor et al.* 27293 (F); Chontales: *Narvaez* 3358 (BM); Nueva Segovia: *Atwood et al.* 6831a (F); Zelaya: *Shank & Molina* 4934 (F). **Costa Rica**, Alajuela: *Burger & Stolze* 4962 (F); Cartago: *Croat* 36526 (MO); Heredia: *Greig* 612 (BM); Limón: *Robles* 2143 (CR); Puntarenas: *Raven* 21482B; San José: *Greig* 445 (BM). **Panama**, Bocas del Toro: *Cooper* 165 (F); Chiriquí: *Nee* 10665 (MO); Coclé: *Gracia* 49 (F); Darien: *Garwood* 2766A (BM); Herrera: *Sytsma & Darcy* 3261 (MO); Panama: *Saiz* 33 (F); Veraguas: *Mori et al.* 7531 (MO).

This species can be distinguished from *P. hispidum* by its large, leaf-like prophylls, and ligule-like structures almost equalling the length of the prophylls, both drying to dark brown. The leaves of *Piper sancti-felicitis* are dark green, drying to brown, while those of *P. hispidum* are a pale yellowish green, even when dry.

82. ***Piper poasanum*** C.DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 206 (1892). Type: Costa Rica, vallee du Río Poas, *Pittier* 2386 (G!-holotype).

Fig. 11A,a,b.

- P. palmasanum* C.DC. in *Smithson. misc. Collns* **71**(6): 3 (1920). Type: Panama, Cuesta de las Palmas, Chiriquí, *Pittier* 3225 (US-holotype, photograph!).

- P. pexum* Trel. in *Contr. U.S. natn. Herb.* **26**: 140 (1929). Type: Costa Rica, Rio Blanco, San José, *Standley* 41887 (US-holotype, photograph!).

- P. silvanorum* Trel. in *Contr. U.S. natn. Herb.* **26**: 169 (1929). Type: Costa Rica, Las Nubes, San José, *Standley* 38500 (US-holotype, photograph!).

- P. crispatimargine* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 339 (1937). Type: Costa Rica, Palmira del Naranjo, *Brenes* 3499 (F-holotype).



Fig. 11 A: *P. poasanum*, habit; a: prophyll; b: fruit and bract. B: *P. bisasperatum*, habit; c: prophyll; d: fruit and bract. C: *P. umbricola*, habit; e: prophyll; f: fruit and bract.

Shrubs or small trees 1–3 (–4) m high, stems sparsely to densely yellow-pubescent. Leaves 8–18 cm long, 4–9 cm wide, elliptic to ovate, coriaceous, upper surface glabrous, underside with hairs on veins, apex acuminate, base slightly unequal, rounded to subcordate. Venation with 3–4 pairs of deeply impressed secondary veins mostly arising from the lower part of the midrib, arcuate ascending to apex. Petioles 10–20 mm long, with ligule-like structure 10–15 mm long, usually caducous. Prophylls 15–20 (–30) mm long, pale, pubescent along midrib. Inflorescences 3–12 cm long, erect, with short sterile tip; peduncles 6–18 (–22) mm long, glabrous or pubescent. Anthers 0.3–0.4 mm long. Floral bracts (0.5–) 1–1.2 mm wide, deeply triangular, pale whitish or yellowish ciliate with a dark, glabrous centre. Fruits 1–1.5 mm wide, obovoid, round from above, glabrous or minutely white-pubescent or granular; stigmas 3.

Partial shade in moist or wet forest; 1500–2600 m.

DISTRIBUTION. Costa Rica, Panama. **Costa Rica**, Alajuela: *Lent* 1661 (BM); San José: *Burger & Stolze* 5203 (F). **Panama**, Chiriquí: *Davidson* 368 (F).

Piper poasanum is a plant of high altitudes. It can be recognized by its rather coarse leaves with deeply impressed venation, and ciliate floral bracts with dark glabrous centres. When crushed, the leaves have a spicy aromatic odour.

83. ***Piper bisasperatum*** Trel. in *Contr. U.S. natn. Herb.* **26**: 173 (1929). Type: Costa Rica, Cerro de la Carpintera, Cartago, *Standley* 35723 (US-holotype).

Fig. 11B,c,d.

P. blepharilepidum Trel. in *Contr. U.S. natn. Herb.* **26**: 160 (1929). Type: Costa Rica, Tilarán, *Standley & Valerio* 46217 (US-holotype).

P. coactoris Trel. in *Contr. U.S. natn. Herb.* **26**: 161 (1929). Type: Costa Rica, Alajuela, *Standley & Torres* 47935 (US-holotype).

P. pubens Trel. in *Contr. U.S. natn. Herb.* **26**: 163 (1929). Type: Costa Rica, La Estrella, Cartago, *Standley* 39329 (US-holotype, photograph!).

P. emollitum Trel. in *Contr. U.S. natn. Herb.* **26**: 181 (1929). Type: Costa Rica, El Silencio, Guanacaste, *Standley & Valerio* 44650 (US-holotype).

P. ventoleranum Trel. in *Contr. U.S. natn. Herb.* **26**: 184 (1929). Type: Costa Rica, Volcán Poas, *Standley* 34712 (US-holotype).

P. austinii Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 1546 (1938). Type: Costa Rica, Tapesco de Zarcero, *Smith* H435 (F!-holotype).

P. austinii var. *aequilaterum* Trel. in *Publs Field Mus. nat. Hist. Bot.* **18**: 1546 (1938). Type: Costa Rica, Zaote de San Carlos, *Smith* H860 (F!-holotype).

Shrubs, rarely small trees, 1.5–5 (–5) m high, stems glandular, glabrous or pubescent, with whitish multicellular hairs up to 1.5 mm long. Leaves 10–24 cm long, 4–11 cm wide, elliptic to ovate-lanceolate, upper surface scabrous, glabrous to sparsely pubescent, sometimes bullate, underside sparsely to densely pubescent, especially on veins, both surfaces with orange glands visible, apex narrowly acuminate, apiculate, base unequally obtuse or slightly rounded. Venation with 3–5 pairs of secondary veins mostly arising from the lower to middle part of the midrib, ascending fairly steeply to apex.

Petioles 5–12 (–16) mm long, glandular, glabrous or pubescent, with ligule-like structure 4–10 mm long, with prominent orange glands and sparse hairs on margin. Prophylls 15–30 mm long, acute, pale, glabrous or sparsely pubescent, with prominent orange glands. Inflorescences 6–12 cm long, erect, with pubescent tip 2–4 mm long; peduncles 5–12 (–20) mm long, glandular, glabrous or pubescent. Anthers 0.1–0.2 mm long. Floral bracts 0.4–0.6 mm wide, triangular, white-ciliate with dark glabrous centre. Fruits 1–1.2 mm wide, obovoid, oblong from above, pale puberulent; stigmas 3, in slight depression, sessile.

Shady, moist places in open forest, forested slopes near streams, shaded road and track sides; 800–2000 m.

DISTRIBUTION. Mexico to Venezuela. **Mexico**, Chiapas: *Breedlove* 35413 (F); Tabasco: *Cowan & Nino* 3381 (MO); Veracruz: *Barnett et al.* 92 (BM,MO). **Costa Rica**, Cartago: *Burger & Gentry* 9200 (F); Guanacaste: *Burger & Pohl* 7824 (F); Heredia: *Antonio* 755 (F,BM); Puntarenas: *Burger & Gentry* 8549 (F,MO); San José: *Burger & Stolze* 5356 (F). **Panama**, Chiriquí: *Croat* 26834 (MO). **Colombia**, Amazonas: *Plowman & Martin* 130 (S). **Venezuela**, Táchira: *Berti & Pena* 552–779 (G).

Piper bisasperatum can be distinguished by its scabrous leaves with long, sharp apices, large prophylls and ligule-like structures at the petioles, all with prominent orange glands, and its occurrence at altitudes above 800 m. It is closely related to *P. chrysostachyum* which has similarly shaped leaves, prophylls and ligule-like structures. However, *P. chrysostachyum* has pale coloured bracts with whitish gibbous bases, whereas those of *P. bisasperatum* are densely pale-ciliate, with dark, glabrous centres. *Piper chrysostachyum* also tends to grow in dryer areas and at lower altitudes.

84. ***Piper umbricola*** C.DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 215 (1891). Type: Costa Rica, Rodeo de Pacaca, *Pittier* 3238 (G!-holotype).

Fig. 11C,e,f.

P. brachistopodium C.DC. in *Bot. Gaz.* **70**: 182 (1920). Type: Costa Rica, Tucurrique, *Tonduz* 13143 (US).

P. nodosum C.DC. in *Bot. Gaz.* **70**: 185 (1920). Type: Costa Rica, Canas Gordas, *Pittier* 11072 (F!-isotype).

P. disparipes Trel. in *Contr. U.S. natn. Herb.* **26**: 162 (1929). Type: Costa Rica, El Silencio, Tilarán, *Standley & Valerio* 44766 (US-holotype).

P. imparipes Trel. in *Contr. U.S. natn. Herb.* **26**: 163 (1929). Type: Costa Rica, La Verbena, *Standley & Valerio* 32244 (US-holotype).

P. papulatum Trel. in *Contr. U.S. natn. Herb.* **26**: 163 (1929). Type: Costa Rica, Capulin, Alajuela, *Standley* 40181 (US-holotype).

P. injucundum Trel. in *Contr. U.S. natn. Herb.* **26**: 181 (1929). Type: Costa Rica, El Muneco, *Standley & Valerio* 51351 (US-holotype).

P. captum Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 335 (1937). Type: Costa Rica, El General, *Skutch* 2158 (US-holotype; K!,MO!-isotypes).

P. pustulicaule Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 357 (1937). Type: Costa Rica, El General, *Skutch* 2938 (US-holotype; MO!-isotype).

Shrubs 1–3 m high, stems glabrous or minutely puberulent.

Leaves 11–24 cm long, 4–9 cm wide, elliptic to ovate or rhombic, upper surface dark, glossy, glabrous, underside minutely pubescent on veins, apex acuminate, base unequally obtuse or rounded. Venation with 3–4 pairs of secondary veins arising steeply towards apex. Petioles 4–15 mm long, glabrous or minutely puberulent, with ciliate ligule-like structure 1–2 mm long. Prophylls 12–25 mm long, acute, glabrous, drying dark brown or black. Inflorescences 5–11 cm long, erect; peduncles 2–8 (–12) mm long, glabrous. Anthers 0.1–0.3 mm long. Floral bracts 0.4–0.6 mm wide, triangular, minutely ciliate, with glabrous centres. Fruits 0.6–0.9 mm wide, obovoid, round to oblong from above, glabrous; stigmas 3, in central depression.

Moist forest; 500–1500 m.

DISTRIBUTION. Mexico to Costa Rica. **Mexico**, Chiapas: *Spellman* et al. 181 (BM); Nayarit: *Croat* 45325 (BM,MO); Oaxaca: *Croat & Hannon* 65585 (MO); Veracruz: *Gentry* et al. 32551 (BM,MO). **Honduras**, Comayagua: *Molina* 25468 (F); Cortez: *Yuncker* 4874 (F). **Nicaragua**, Granada: *Stevens* 10849 (F). **Costa Rica**, Guanacaste: *Standley & Valerio* 44228 (F); Puntarenas: *Grayum & Sleeper* 5898 (BM,MO).

85. ***Piper chrysostachyum*** C.DC. in *Bull. Soc. r. Bot. Belg.* **30**(1): 207 (1892). Type: Costa Rica, near San Mateo, *Pittier* 4073 (G!-holotype).

Fig. 12A,a,b.

- P. stenocladum* C.DC. in *An. Inst. fis-geogr. C. Rica* **9**: 162 (1897). Type: Costa Rica, forests of Boruca, *Tonduz* 6747, pro parte (G!-holotype).

- P. davidianum* C.DC. in *Smithson. misc. Collns* **71**(6): 9 (1920). Type: Panama, Dos Bocas, Colón, *Pittier* 4210 (US-holotype).

- P. callibracteum* C.DC. in *Smithson. misc. Collns* **71**(6): 13 (1920). Type: Panama, Chiriquí, *Pittier* 2940 (US!-holotype).

- P. chamissonis* var. *rubellibracteum* C.DC. in *Smithson. misc. Collns* **71**(6): 13 (1920). Type: Panama, El Boquete, Chiriquí, *Pittier* 2899 (US-holotype).

- P. nitidifolium* C.DC. in *Smithson. misc. Collns* **71**(6): 14 (1920). Type: Panama, El Boquete, Chiriquí, *Maxon* 4943 (US-holotype; G!-isotype).

- P. diquisanum* C.DC. in *Bot. Gaz.* **70**: 185 (1920). Type: Costa Rica, Diquís, *Pittier* 10567 (US-holotype; G!-isotype).

- P. surubresanum* Trel. in *Contr. U.S. natn. Herb.* **26**: 148 (1929). Type: Costa Rica, Río Surubres, San Mateo, *Biolley* 17353 (US-holotype).

- P. vicinum* Trel. in *Contr. U.S. natn. Herb.* **26**: 157 (1929). Type: Costa Rica, *Tonduz* 6635 (US-holotype).

- P. alajuelanum* Trel. in *Contr. U.S. natn. Herb.* **26**: 158 (1929). Type: Costa Rica, Nuestro Amo, Alajuela, *Jimenez* 988 (US-holotype).

- P. verruculigerum* Trel. in *Contr. U.S. natn. Herb.* **26**: 165 (1929). Type: Costa Rica, Quebrada Serena, Guanacaste, *Standley & Valerio* 46239 (US-holotype; ILL!-isotype).

- P. hanckeli* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 345 (1937). Type: Costa Rica, Guanacaste, *Dodge, Hanckel & Thomas* 6384 (GH-holotype; MO!-isotype).

- P. luridispicum* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 348 (1937). Type: Costa Rica, El Rodeo,

Lankester 1322 (F-holotype).

- P. papulaeacale* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 352 (1937). Type: Costa Rica, Guanacaste, *Dodge & Thomas* 6286 (GH-holotype; MO!-isotype).

- P. rubripes* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 358 (1937). Type: Costa Rica, Guanacaste, *Dodge, Hanckel & Thomas* 6382 (GH-holotype; MO!-isotype).

- P. tacaresense* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 364 (1937). Type: Costa Rica, Tacares, *Valerio* 302 (F!-holotype).

Shrubs 1–3 m high, stems glabrous or minutely puberulent. Leaves 10–22 cm long, 4–9 cm wide, elliptic to ovate-lanceolate, upper surface glabrous, slightly scabrous, underside glabrous or minutely pubescent, both sides glandular, apex acute-acuminate, base unequally obtuse to rounded. Venation with 3–5 pairs of secondary veins arising from the lower to middle part of the midrib, curving to apex. Petioles 5–15 mm long, with a ligule-like structure 1–2 mm long, glandular, sparsely ciliate. Prophylls 8–15 (–18) mm long, acute, glabrous or minutely pubescent, glandular, drying to dark brown or black. Inflorescences 5–12 cm long, erect, yellow or white, sometimes with short sterile tips; peduncles 6–14 (–18) mm long, glabrous. Anthers 0.1–0.2 mm long. Floral bracts 0.2–0.4 mm wide, triangular, glabrous or minutely ciliate, with a yellowish or white bulge at the base. Fruits 0.5–0.8 mm wide, obovoid, oblong or round from above, minutely yellow-puberulent; stigmas 3, sessile, in slight depression.

Seasonally dry evergreen forest mostly on Pacific side; 0–1300 (–1500) m.

DISTRIBUTION. Nicaragua to Panama. **Nicaragua**, Granada: *Williams & Molina* 20003 (F); Jinotega: *Hawkes* et al. 2175 (F); Rivas: *Neill & Vincelli* 3212 (F); Zelaya: *Pipoly* 4684 (MO). **Costa Rica**, Alajuela: *Haber* 1487 (MO); Guanacaste: *Valerio* 1145 (F); Puntarenas: *Burger* et al. 10634 (F); San José: *Burger & Liesner* 7153 (F). **Panama**, Chiriquí: *Croat* 13560 (MO); Coclé: *Gentry* 7420 (F, MO); Veraguas: *Mori & Kallunki* 6141 (MO).

The inflorescences with minute floral bracts bulging basally and the yellow-puberulent fruits distinguish *Piper chrysostachyum* from other species.

86. ***Piper epigynium*** C.DC. in *Linnaea* **37**: 346 (1872). Type: Costa Rica, Turrialba, *Oersted* 858 (C!-holotype).

Fig. 12B,c,d.

- P. villosisquamulum* Trel. in *Contr. U.S. natn. Herb.* **26**: 158 (1929). Type: Costa Rica, La Hondura, *Standley* 37799 (US-holotype).

- P. villistipulum* Trel. in *Contr. U.S. natn. Herb.* **26**: 162 (1929). Type: Costa Rica, El Muñeco, S. of Navarra, Cartago, *Standley* 33438 (US-holotype).

- P. subdivaricatum* Trel. in *Contr. U.S. natn. Herb.* **26**: 163 (1929). Type: Costa Rica, La Hondura, San José, *Standley* 36489 (US-holotype).

Shrubs or small trees, 1.5–6 m high, stems glabrous. Leaves 12–26 cm long, 4–9 cm wide, elliptic to narrowly ovate, glandular, upper surface glabrous, sometimes slightly scabrous, dark green, underside with pale hairs on the veins,



Fig. 12 A: *P. chrysostachyum*, habit; a: prophyll; b: fruit and bract. B: *P. epigynium*, habit; c: prophyll; d: fruit and bract. C: *P. dotanum*, habit; e: prophyll; f: fruit and bract.

apex acuminate, base unequally obtuse or rounded. Venation with 3–4 pairs of secondary veins arising mostly from the lower to middle part of the midrib. Petioles 4–14 (–20) mm long, with glandular ligule-like structure 1–3 mm long. Prophylls 14–30 (–40) mm long, glandular, sparsely puberulent along midrib. Inflorescences 6–15 cm long, erect, sometimes pinkish to purple in early stages; peduncles 8–16 mm long, glabrous. Anthers 0.1–0.2 mm long. Floral bracts 0.2–0.3 mm wide, triangular, with pale bulge at base, glabrous or with minute hairs. Fruits 0.4–0.6 mm wide, obovoid, minutely puberulent, glandular; stigmas 3, sessile.

Cloud forest, ravines, open areas, stream and trail sides in moist forest; 600–2000 m.

DISTRIBUTION. Guatemala to Panama. **Guatemala**, San Marcos: Williams et al. 26970 (F). **Nicaragua**, Granada: Croat 39087 (MO). **Costa Rica**, Alajuela: Liesner 4761 (MO); Heredia: Nee 14007 (F); Puntarenas: Dinerstein 3; San José: Burger & Gentry 9082 (F). **Panama**, Chiriquí: van der Werff 6751 (MO); Veraguas: Croat & Folsom 34270 (MO).

Piper epigynium can be recognized by its often showy brick-red inflorescences and large, glabrous, glandular prophylls. It is only found at altitudes above 600 m.

87. **Piper dotanum** Trel. in *Contr. U.S. natn. Herb.* **26**: 165 (1929). Type: Costa Rica, Santa María de Dota, San Jose, Standley 41739 (US-holotype; ILL!-isotype).

Fig. 12C,e,f.

Shrubs 1–4 m high, stems glabrous, slender, spreading. Leaves 5–13 cm long, 1.5–4 cm wide, elliptic-lanceolate to ovate-lanceolate, glabrous, upper surface glossy, slightly scabrous, underside with prominent dark glands, apex acuminate, base unequally rounded. Venation with 3 pairs of secondary veins arising from the lower to middle part of the midrib, loop-connecting to apex. Petioles 2–7 mm long, glabrous, with a sparsely ciliate, ligule-like structure 1–2 mm long. Prophylls 6–14 mm long, glabrous, drying to dark brown or black. Inflorescences 4–6 cm long, cream-coloured, erect, with short sterile tips; peduncles 4–12 mm long, glabrous. Anthers 0.1–0.2 mm long. Floral bracts 0.2–0.4 mm wide, triangular, densely puberulent. Fruits 0.5–0.7 mm wide, obovoid, oblong to round from above, glabrous to minutely puberulent; stigmas 3, sessile.

Deep shade in forest; 500–1800 m.

DISTRIBUTION. Costa Rica. **Costa Rica**, Alajuela: Brenes 20417 (NY); Guanacaste: Garwood et al. 797 (BM); Puntarenas: Haber 4042 (MO).

Piper dotanum is a slender, rather spindly plant growing in forest shade in the drier regions of Costa Rica. It can be identified by its small, glossy, glabrous leaves, glabrous prophylls, prominent ligule-like structure, and slender, cream-coloured inflorescences.

88. **Piper polytrichum** C.DC. ex A. Schroed. in *Candollea* **3**: 138 (1926). Type: Costa Rica, Canas Gordas, Pittier 11070 (G!-holotype).

Fig. 13A,a,b.

Shrubs 1–3 m high, stems covered with thin yellowish multicellular hairs up to 2 mm long. Leaves 6–17 cm long, 2–7 cm

wide, narrowly elliptic to ovate or ovate-lanceolate, upper surface dark green, slightly scabrous with scattered whitish hairs, underside densely pubescent on the veins, apex acuminate, base unequally obtuse or rounded. Venation with 3–5 pairs of secondary veins arising from the lower to middle part of the midrib, ascending fairly steeply to apex. Petioles 4–7 mm long, densely pubescent, ligule-like structure 0.5 mm long, hidden by hairs. Prophylls 10–20 mm long, acute, hirsute along the midrib, drying dark brown. Inflorescences 5–9 cm long, erect; peduncles 5–7 mm long, densely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.2–0.5 mm wide, triangular to round, mostly glabrous with a few minute pale hairs at the base. Fruits 0.6–1 mm wide, obovoid, oblong from above, glabrous or sparsely pubescent; stigmas 3.

Shade of moist forest; 600–1200 m.

DISTRIBUTION. Costa Rica to Panama. **Costa Rica**, Cartago: Skutch 4657 (NY); Puntarenas: Davidson 7158 (NY); San José: Burger & Liesner 7113A (F). **Panama**, Colón: Dressler 3854 (F); Darien: Gentry Mori 13905 (F); Panama: Maas & Dressler 712 (F).

Piper polytrichum can be confused with *P. biauratum* because of similar indumentum and leaf-shape. However, *P. biauratum* has red or purple inflorescences and pale, glandular prophylls, whereas *P. polytrichum* has green or whitish inflorescences and smaller prophylls drying to a dark brown.

89. **Piper peracuminatum** C.DC. in *Smithson. misc. Collns* **71**(6): 9 (1920). Type: Panama, Dos Bocas, Río Fató valley, Pittier 4210 (US-holotype; G!-isotype).

Fig. 13B,c,d.

P. fusco-granulatum Trel. in *Contr. U.S. natn. Herb.* **26**: 180 (1929). Type: Costa Rica, Hacienda de Zent, United Fruit Co. 269 (US-holotype).

Shrubs or small trees 2–3 m high, stems hirsute with yellowish hairs 0.2–1.5 mm long. Leaves 15–27 cm long, 8–13 cm wide, elliptic-obovate to ovate, upper surface glossy, slightly scabrous, sparsely and minutely puberulent, underside pubescent on veins, apex acuminate, base unequally obtuse or slightly lobed on one side. Venation with 4–5 pairs of secondary veins arising from the lower to middle part of the midrib, ascending fairly steeply to apex. Petioles 7–16 mm long, pubescent, ligule-like structure minute or absent. Prophylls 10–14 mm long, acute, hirsute along midrib, drying dark brown. Inflorescences 10–16 cm long, erect; peduncles 10–22 mm long, pubescent. Anthers 0.3–0.4 mm long. Floral bracts 0.4–0.7 mm wide, yellow-ciliate with glabrous centres. Fruits 0.5–0.8 mm wide, obovoid, oblong or round from above, minutely puberulent; stigmas 3, recurved.

Lowland moist forest; 0–500 m.

DISTRIBUTION. Costa Rica to Panama. **Panama**, Coclé: Lewis et al. 5526 (MO); Panama: Kennedy & Dressler 2966 (MO).

90. **Piper zacatense** C.DC. in *An. Inst. fis-geogr. C. Rica* **9**: 161 (1897). Type: Costa Rica, Boca Zacate, Pittier 6828 (W-holotype; G!-isotype).

Fig. 13C,e,f.

P. zacatense var. *percaudatum* C.DC. in *An. Inst. fis-geogr.*

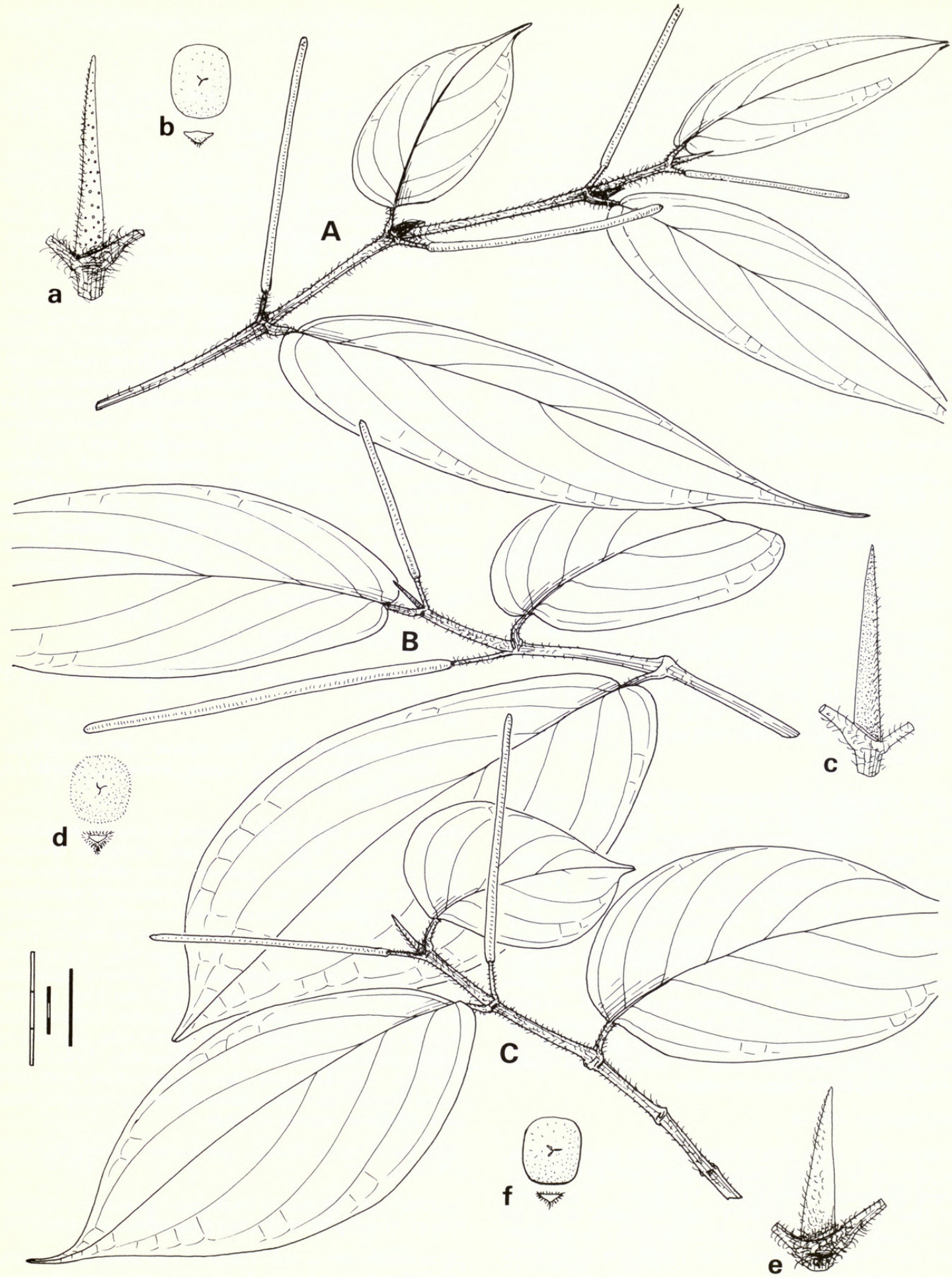


Fig. 13 A: *P. polytrichum*, habit; a: prophyll; b: fruit and bract. B: *P. peracuminatum*, habit; c: prophyll; d: fruit and bract. C: *P. zacatense*, habit; e: prophyll; f: fruit and bract.

C. Rica 9: 161 (1897). Type: Costa Rica, Golfo Dulce, Pittier 9914 (G!-holotype).

Shrubs or slender trees; stems densely pubescent with yellow-brown hairs 0.5–2 mm long. Leaves 16–28 cm long, 7–12 cm wide, elliptic to rhombic, upper surface dark, smooth or slightly scabrous, minutely puberulent, underside pubescent on veins, apex long-acuminate, base unequally obtuse or rounded. Venation with 4–5 pairs of secondary veins arising from the lower to middle part of the midrib, curving steeply to apex. Petioles 6–12 mm long, densely pubescent, with a minute ligule-like structure 0.5 mm long. Prophylls 12–15 mm long, acute, densely puberulent. Inflorescences 3–9 cm long, erect; peduncles 8–14 mm long, minutely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.3–0.6 mm wide, yellow-ciliate with glabrous centres. Fruits 0.7–1 mm wide, obovoid, oblong from above, sparsely puberulent; stigmas 3, in central depression.

Lowland moist forest; 0–500 m.

DISTRIBUTION. Costa Rica.

P. zacatense is very rare, and not well represented in herbaria. Only type material has been seen for this study.

91. **Piper biauratum** C.DC. in *An. Inst. fis-geogr. C. Rica* 9: 161 (1897). Type: Costa Rica, forest of Xirores, Talamanca, Tonduz 9270 (G!-holotype).

Fig. 14A,a,b.

- P. tortuosipilum* Trel. in *Contr. U.S. natn. Herb.* 26: 148 (1929). Type: Costa Rica, El Muñeco, Cartago, Standley & Valerio 51026 (US-holotype).

- P. insolens* Trel. in *Contr. U.S. natn. Herb.* 26: 156 (1929). Type: Costa Rica, Santa María de Dota, San José, Standley & Valerio 43306 (US-holotype, photograph!; ILL-isotype).

Shrubs 1–2 m high, stems pubescent with long, pale, multicellular hairs. Leaves 11–25 cm long, 5–12 cm wide, elliptic to ovate, both surfaces sparsely to densely covered with long white hairs, especially on veins beneath, apex acute-acuminate, base unequally obtuse to cordulate. Venation with 4–5 pairs of secondary veins arising from the lower to middle part of the midrib. Petioles 4–10 (–20) mm long, pubescent, ligule-like structure minute or absent. Prophylls 15–20 (–25) mm long, acute, pale, glandular, with long pale hairs. Inflorescences 7–12 cm long, reddish or purple, erect; peduncles 8–22 mm long, glabrous or pubescent. Anthers 0.1–0.2 mm long. Floral bracts 0.4 mm wide, triangular, with pale bulge and pale hairs at the base, or glabrous. Fruits 0.8–1 mm wide, obovoid, round or oblong from above, minutely puberulent; stigmas 3, sessile.

Moist slopes; 0–1600 m.

DISTRIBUTION. Costa Rica to Panama. **Costa Rica**, Alajuela: Burger et al. 107724 (F); Cartago: Greig 380 (BM); Limón: Burger & Antonio 10999 (CAS); Puntarenas: Skutch 5268; San José: Davidse et al. 23179 (MO). **Panama**, Bocas del Toro: Croat & Grayum 60136 (MO); Chiriquí: Churchill 5381 (BM, MO); Darien: Hammel et al. 16173 (BM,MO); Veraguas: Nee 9903 (MO).

92. **Piper perhispidum** C.DC. in *Bot. Gaz.* 70: 183 (1920).

Type: Costa Rica, near San Juan de San Ramon, Tonduz 17771 (G!-holotype).

Fig. 14C,e,f.

- P. pileatum* Trel. in *Contr. U.S. natn. Herb.* 26: 184 (1929). Type: Costa Rica, forests of Copey, Tonduz 11895 (NY-holotype; F!,MO!-isotypes).

- P. pileatum* var. *obliquum* Trel. in *Contr. U.S. natn. Herb.* 26: 184 (1929). Type: Costa Rica, El Copey, Tonduz 11675 (US-holotype, photograph!).

- P. rugosifolium* Trel. in *Contr. U.S. natn. Herb.* 26: 185 (1929). Type: Costa Rica, Finca Las Cónnavas, Cartago, Standley 41533 (US-holotype, photograph!).

Shrubs 1–3 m high, stems covered with yellow-brown multicellular hairs up to 2.5 mm long. Leaves 10–24 cm long, 2.5–9 cm wide, elliptic-ovate to lanceolate, bullate, scabrous above, both surfaces covered with long hairs, apex acuminate, base unequally obtuse or rounded. Venation with 3–5 pairs of secondary veins arising from the lower to middle part of the midrib. Petioles 3–10 (–20) mm long, densely pubescent, with pubescent ligule-like structure 1 mm long. Prophylls 10–20 mm long, acute, puberulent with glabrous margins. Inflorescences 6–11 cm long, erect; peduncles 8–14 mm long, densely villous. Anthers 0.2–0.3 mm long. Floral bracts 0.4–0.6 mm wide, triangular, densely pale-pubescent. Fruits 0.5–1 mm wide, obovoid, minutely puberulent, sides glandular; stigmas 3, sessile, in slight depression.

Moist forest; 1000–2000 m.

DISTRIBUTION. Costa Rica.

93. **Piper chamissonis** (Miq.) Steud., *Nomencl. bot.* ed.2, 2: 340 (1841).

Fig. 14D,g,h.

- Artanthe chamissonis* Miq., *Syst. piperac.*: 457 (1844). Type: Mexico, Hacienda de la Laguna, Veracruz, Schiede s.n. (B-holotype; G!-drawing).

Shrubs 1–2.5 m high, stems glabrous or sparsely pubescent. Leaves 13–21 cm long, 5–9 cm wide, elliptic to obovate, upper surface dark green, glabrous, lower surface pale with yellowish white hairs on veins, apex narrowly acuminate, base slightly unequal, cuneate. Venation with 3–5 secondary veins arising from lower to middle part of midrib, loop-connecting to apex. Petioles 8–15 mm long, glabrous to sparsely pubescent, with pale-glandular, glabrous ligule-like structure 2–3 mm long. Prophylls 10–20 mm long, narrow, glabrous or minutely puberulent, drying dark. Inflorescences 6–10 cm long, erect; peduncles 8–12 mm long, glabrous or sparsely pubescent. Anthers 0.4–0.5 mm long. Floral bracts 0.8–1 mm wide, triangular, densely pale-ciliate, with dark centre. Fruits 1 mm wide, obovoid, oblong-trigonus from above, glabrous; stigmas 3, sessile.

Moist forest, damp thickets, and wooded ravines; 900–2000 (–3000) m.

DISTRIBUTION. Mexico to Guatemala. **Guatemala**, Quezaltenango: Standley 68161 (F); San Marcos: Standley 68946 (F).

Piper chamissonis is only found at high altitudes in moist, wooded or thicketed areas. It can be recognized by its elliptic to obovate leaves with yellowish white hairs on the veins of the undersides, prominent prophylls, pale-ciliate bracts, and



Fig. 14 A: *P. biauratum*, habit; a: prophyll; b: fruit and bract. B: *P. colonense*, habit; c: prophyll; d: fruit & bract. C: *P. perhispidum* C. DC., habit; e: prophyll; f: fruit and bract. D: *P. chamissonis*, habit; g: prophyll; h: fruit and bract.

glabrous fruits. *Piper chrysostachyum* has similar leaves but very different floral bracts.

94. ***Piper colonense*** C.DC. in *Smithson. misc. Collns* 71(6): 11 (1920). Type: Panama, Río Fato valley, Colón, *Pittier* 4221 (US!-holotype; BM!-isotype).

Fig. 14B,c,d.

- P. culebratum* C.DC. ex A. Schroed. in *Candollea* 3: 136 (1926). Type: Panama, Río Culebra, *Pittier* 4154 (G!-holotype).

- P. varablancanum* Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* 18: 1547 (1938). Type: Costa Rica, Vara Blanca de Sarapiquí, *Skutch* 3205 (US-holotype; MO!, NY!-isotypes).

Shrubs or spindly tree 1.5–6 (–7) m high, stems sparsely to densely pubescent. Leaves 12–25 cm long, 4–10 cm wide, oblong-elliptic to oblanceolate, upper surface glaucous, glabrous or with sparse hairs, underside usually with conspicuous red or orange glands, and long hairs on veins, apex acute-acuminate, tapering abruptly, base slightly unequal, round to obtuse. Venation with 3–4 pairs of secondary veins ascending steeply to apex. Petioles 5–10 mm long, pubescent, with ligule-like structure to 1 mm long. Prophylls 6–20 mm long, sparsely pubescent, glandular, drying dark brown or black. Inflorescences 6–12 cm long, erect; peduncles 5–12 mm long, glabrous or sparsely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.7–1 mm wide, triangular, yellowish-ciliate, with glabrous centre. Fruits 1–1.2 mm wide, obovoid, round or oblong from above, fleshy, glabrous; stigmas 3, sessile.

Disturbed or cleared areas of forest, along trails and roadsides; 0–1600 m.

DISTRIBUTION. Nicaragua to Panama. **Nicaragua**, Zelaya: *Bunting & Licht* 1252 (F). **Costa Rica**, Alajuela: *Utley* 2235 (F); Cartago: *Holm & Iltis* 76 (F); Heredia: *Burger & Stolze* 5758 (F); Limón: *Burger & Liesner* 7006 (F); San José: *Skutch* 4931 (NY). **Panama**, Chiriquí: *Croat* 22343 (MO); Colón: *Hammel* 4492 (BM, MO); Panama: *Mori* 7744 (BM, MO).

95. ***Piper oblanceolatum*** Trel. in *Contr. U.S. natn. Herb.* 26: 175 (1929). Type: Costa Rica, Los Ayotes, Tilarán, *Standley & Valerio* 45558 (US-holotype, photograph!).

Fig. 15A,a,b.

Shrubs or small trees 2–8 (–10) m high, stems glabrous to sparsely pubescent, with yellowish hairs 0.5–1 mm long. Leaves 10–18 cm long, 3–6 cm wide, narrowly elliptic to oblanceolate, upper surface dark green, slightly scabrous, glabrous or minutely pubescent, underside with whitish hairs on veins, apex long-acuminate, base unequally obtuse or cuneate. Venation with 3–5 pairs of secondary veins arising from the lower part of the midrib, arcuate ascending to apex. Petioles 2–8 mm long, glabrous or sparsely pubescent, with a ciliate ligule-like structure 0.5 mm long. Prophylls 10–22 mm long, acute, puberulent along midrib, glandular, drying dark brown or black. Inflorescences 5–10 cm long, erect; peduncles 14–25 mm long, glabrous to sparsely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.4–0.6 mm wide, narrowly triangular, upper part glabrous, glandular, lower sparsely ciliate. Fruits 0.5–0.8 mm wide, obovoid, oblong from above;

stigmas 3, in slight depression.

Shade of moist forest; 600–2000 m.

DISTRIBUTION. Nicaragua to Costa Rica. **Nicaragua**, Jinotega: *Standley* 10697 (F). **Costa Rica**, Alajuela: *Lent* 1673 (MO); Monteverde: *Feinsinger* s.n. 'Y' (F).

96. ***Piper hirtellipetiolum*** C.DC. in *Smithson. misc. Collns* 71(6): 3 (1920). Type: Panama, vicinity of David, Chiriquí, *Pittier* 2932 (US-holotype; G!, NY!-isotypes).

Fig. 15B,c,d.

- P. tapianum* Trel. in *Contr. U.S. natn. Herb.* 26: 30 (1927). Type: Panama, near Tapia River, *Maxon & Harvey* 6709 (US-holotype; ILL!-isotype).

Shrubs 1–2 m high, stems glabrous or sparsely covered with white multicellular hairs. Leaves 8–14 cm long, 2.5–5 cm wide, lanceolate, glabrous, glandular, upper surface glossy, underside dull, apex acuminate, base acute to obtuse. Venation with 2–4 pairs of secondary veins arising from lower to middle part of midrib, loop-connecting to apex. Petioles 3–5 mm long, villous, with a sparsely ciliate, ligule-like structure 0.5–2 mm long. Prophylls 6–12 mm long, acute, glabrous. Inflorescences 3–6 cm long, erect; peduncles 3–10 mm long, puberulent. Anthers 0.2–0.3 mm long. Floral bracts 0.8–1 mm wide, triangular, densely yellow-ciliate. Fruits 1 mm wide, obovoid, round from above, glabrous; stigmas 3, sessile.

Moist remnant forest, edges of streams, roadsides; 0–1000 (–2000) m.

DISTRIBUTION. Panama. **Panama**, Canal Zone: *Miller* 1790 (MO); Chiriquí: *Him & Gordon* 270 (MO); Coclé: *Miller* 1814 (MO); Herrera: *Stern et al.* 33618 (MO); Panama: *Duke* 12565 (MO); Perlas Is.: *Johnston* 754 (MO); Taboga Is.: *Pittier* 3618 (NY).

97. ***Piper decurrens*** C.DC. in *J. Bot., Lond.* 4: 215 (1866). Type: Costa Rica, monte Candelaria, *Hoffmann* 853 (B-holotype, photograph!).

Fig. 15C,e,f.

- P. leptoneuron* C.DC. in *Bot. Gaz.* 70: 184 (1920). Type: Costa Rica, Santa Clara, *Pittier* 10675 (G!-holotype).

- P. gracilipedunculum* Trel. in *Contr. U.S. natn. Herb.* 26: 148 (1929). Type: Costa Rica, Fraijanes, Alajuela, *Standley & Torres* 47519 (US-holotype).

Shrubs 1–3 (–5) m high, stems glabrous. Leaves 6–12 (–16) cm long, 2.5–7 cm wide, elliptic to obovate, glossy, glabrous, apex acute-acuminate, base cuneate. Venation with 2–3 pairs of secondary veins arising from lower to middle part of midrib, with prominent cross-veins. Petioles 3–12 mm long, glabrous, with ligule-like structure 1 mm long. Prophylls 6–20 mm long, glabrous. Inflorescences 2–5 (–6) cm long, with sterile tip 1–2 mm long; peduncles 6–25 mm long. Floral bracts 0.5–1 mm wide, triangular, white-ciliate, with pale centres. Anthers 0.5 mm long. Fruits 1–2 mm wide, obovoid, round from above, glabrous; stigmas 2–3.

Moist, shady places in cloud forest and lower rain forest; 700–2000 m.

DISTRIBUTION. Mexico, Costa Rica. **Mexico**, Chiapas:

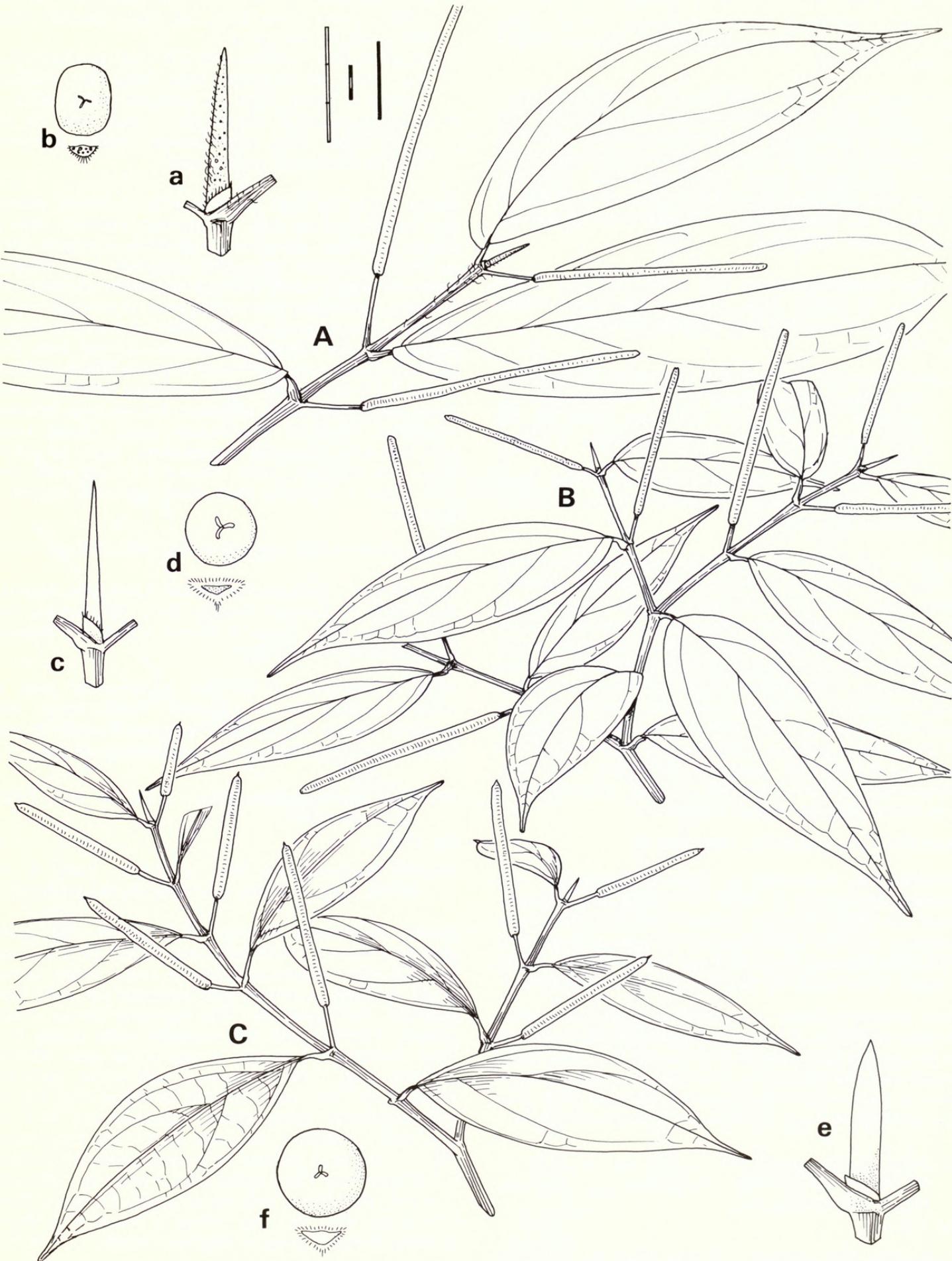


Fig. 15 A: *P. oblanceolatum*, habit; a: prophyll; b: fruit and bract. B: *P. hirtellipetiolum*, habit; c: prophyll; d: fruit and bract. C: *P. decurrens*, habit; e: prophyll; f: fruit and bract.

Breedlove & Raven 13022 (CAS). **Costa Rica**, Alajuela: *Lent* 2371 (F); Guanacaste: *Burger & Gentry* 9108 (F, BM); Heredia & San José: *Antonio* 777 (MO); Puntarenas: *Burger & Gentry* 8581 (MO).

Piper decurrens can be recognized by its small, glabrous, glossy leaves and short inflorescences with sterile tips. It is very similar in appearance to *P. tenuimucronatum*, but can be distinguished by its much shorter ligule-like structure on the petiole, pale-centred bracts, and larger fruits. Only one specimen has been seen from Mexico, growing at 1700 m. It displays all the characteristics of *P. decurrens*, although the leaves are larger than usual.

98. ***Piper tenuimucronatum*** C.DC. in *Smithson. misc. Collns* 71(6): 12 (1920). Type: Panama, Los Sigüas Camp, Chiriquí, *Maxon* 5421 (US-holotype; G!-isotype).

Fig. 16A,a,b.

P. infraleucum Trel. in *Contr. U.S. natn. Herb.* 26: 33 (1927). Type: Panama, *Sutton Hayes* 793 (NY!-holotype).

P. tractifolium Trel. in *Contr. U.S. natn. Herb.* 26: 166 (1929). Type: Costa Rica, Heredia, *Standley & Valerio* 52052 (US-holotype).

P. perfugii Trel. in *Ann. Mo. bot. Gdn* 27: 295 (1940). Type: Panama, Chiriquí, *Woodson, Allen & Seibert* 928 (ILL!-holotype; MO!-isotype).

Shrubs 1–3 m high, stems glabrous. Leaves 6–12 cm long, 2–5 cm wide, elliptic to narrowly ovate, glandular, glabrous, upper surface dark green, lustrous, underside whitish green, apex acuminate, sometimes apiculate, base unequally obtuse or acute. Venation with 2–13 pairs of secondary veins mostly arising from the lower half of the midrib. Petioles 5–11 mm long, glabrous, with a glabrous, ligule-like structure 2–10 mm long. Prophylls 8–20 (–25) mm long, pale, glabrous. Inflorescences 2.5–8 cm long, erect, with short sterile tips; peduncles 10–20 mm long, glabrous. Anthers 0.4–0.5 mm long. Floral bracts 0.6–0.8 mm wide, triangular, pale-ciliate, with a dark, glabrous centre. Fruits 1 mm wide, obovoid, round to oblong from above, glabrous; stigmas 3, sessile.

Moist forest, wooded slopes; 1000–2000 m.

DISTRIBUTION. Guatemala to Panama. **Guatemala**, Alta Verapaz: *Williams et al.* 40468 (F). **Costa Rica**, Alajuela: *Smith* 434 (MO); Cartago: *Burger* 7600 (F); Guanacaste: *Davidse et al.* 23355 (MO); San José: *Grayum & Sleeper* 6113 (BM, MO). **Panama**, Bocas del Toro: *McPherson* 9591 (MO); Chiriquí: *Dwyer et al.* 523 (K); Panama: *Tyson* 4035 (MO).

Piper tenuimucronatum is confined to moist forest above altitudes of 1000 m. It has much larger ligule-like structures on the petioles than those of *P. decurrens* and darker floral bracts; otherwise there is very little difference between them. However, unless more specimens are collected which show intermediates, they are best maintained as separate species.

99. ***Piper carpinteranum*** C.DC. in *An. Inst. fís.-geogr. C. Rica* 9: 165 (1897). Type: Costa Rica, La Carpintera, *Pittier* 4348 (G!-holotype).

Fig. 16B,c,d.

P. ejuncidum Trel. in *Contr. U.S. natn. Herb.* 26: 164 (1929). Type: Costa Rica, Heredia, *Standley & Valerio* 52220 (US-holotype).

P. rotundibaccum Trel. in *Contr. U.S. natn. Herb.* 26: 164 (1929). Type: Costa Rica, San José, *Standley* 42902 (US-holotype, photograph!).

P. rotundibaccum var. *fraijanesanum* Trel. in *Contr. U.S. natn. Herb.* 26: 164 (1929). Type: Costa Rica, Alajuela, *Standley & Torres* 47669 (US-holotype, photograph!).

P. zonulatispicum Trel. in *Contr. U.S. natn. Herb.* 26: 164 (1929). Type: Costa Rica, Cartago, *Standley & Valerio* 51116 (US-holotype, photograph!).

Shrubs 1–2 (–3) m high, stems sparsely to densely puberulent. Leaves 8–15 cm long, 3–7 cm wide, narrowly ovate to elliptic, glandular, upper surface glabrous, underside paler, puberulent on veins, apex long-acuminate, base unequal, lower side slightly lobed, overlapping petiole. Venation with 3–4 pairs of secondary veins arising from the lower part of the midrib, curving towards apex. Petioles 2–8 mm long, densely puberulent, with a ligule-like structure 1–5 mm long. Prophylls 10–20 mm long, puberulent along the midrib. Inflorescences 2–5 (–8) cm long, erect, becoming pendulous, with sterile tip 1–3 mm long; peduncles 1–3 cm long, minutely puberulent. Anthers 0.3–0.4 mm long. Floral bracts 0.6–1 mm wide, triangular to semi-lunar, white- to yellow-ciliate with glabrous centres. Fruits 0.8–1.2 mm wide, obovoid, round to trigonous from above, glabrous; stigmas 3, recurved.

Shade in moist forest, edges of woods; 1000–2500 m.

DISTRIBUTION. Costa Rica to Panama. **Costa Rica**, Alajuela: *Smith* 1040 (F); Cartago: *Standley* 39812 (F); Heredia: *Lent* 223 (F); San José: *Burger & Liesner* 6205A (F). **Panama**, Chiriquí: *Kirkbride* 122 (MO).

Piper carpinteranum C.DC. can be separated from *P. tenuimucronatum* by its pubescent stems, leaves with unequal, slightly lobed bases, puberulent petioles with shorter ligule-like structures, and pubescent prophylls.

100. ***Piper hostmannianum*** (Miq.) C.DC. in DC., *Prodr.* 16(1): 287 (1869).

Fig. 16D,g,h.

Artanthe hostmannianum Miq. in *J. Bot., Lond.* 4: 465 (1845). Type: Surinam, *Hostmann* 116 (K!-holotype).

Shrubs, occasionally scandent, 1–3 (–5) m high, stems sparsely to densely yellow-pubescent. Leaves 13–24 cm long, 6–12 cm wide, elliptic-lanceolate to ovate, upper surface glossy, glabrous, underside pale-pubescent on veins, pale-glandular, apex acuminate, base unequally obtuse or subcordate. Venation with 4–6 secondary veins arising from lower two-thirds of midrib, curving to the apex. Petioles 5–10 mm long, yellow-pubescent, with ciliate ligule-like structures 2–5 mm long. Prophylls 6–12 mm long, densely yellow-pubescent along midrib. Inflorescences 10–12 cm long, erect, sometimes with sterile tips 1–2 mm long; peduncles 8–15 mm long, glabrous to sparsely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.5–0.8 mm wide, triangular or round, pale-ciliate, with darker glabrous centres. Fruits 0.8–1.2 mm wide, obovoid, oblong or round from above, glabrous or slightly granular; stigmas 3, sessile.

Upland forest, disturbed areas along roads and railways; 0–1000 m.

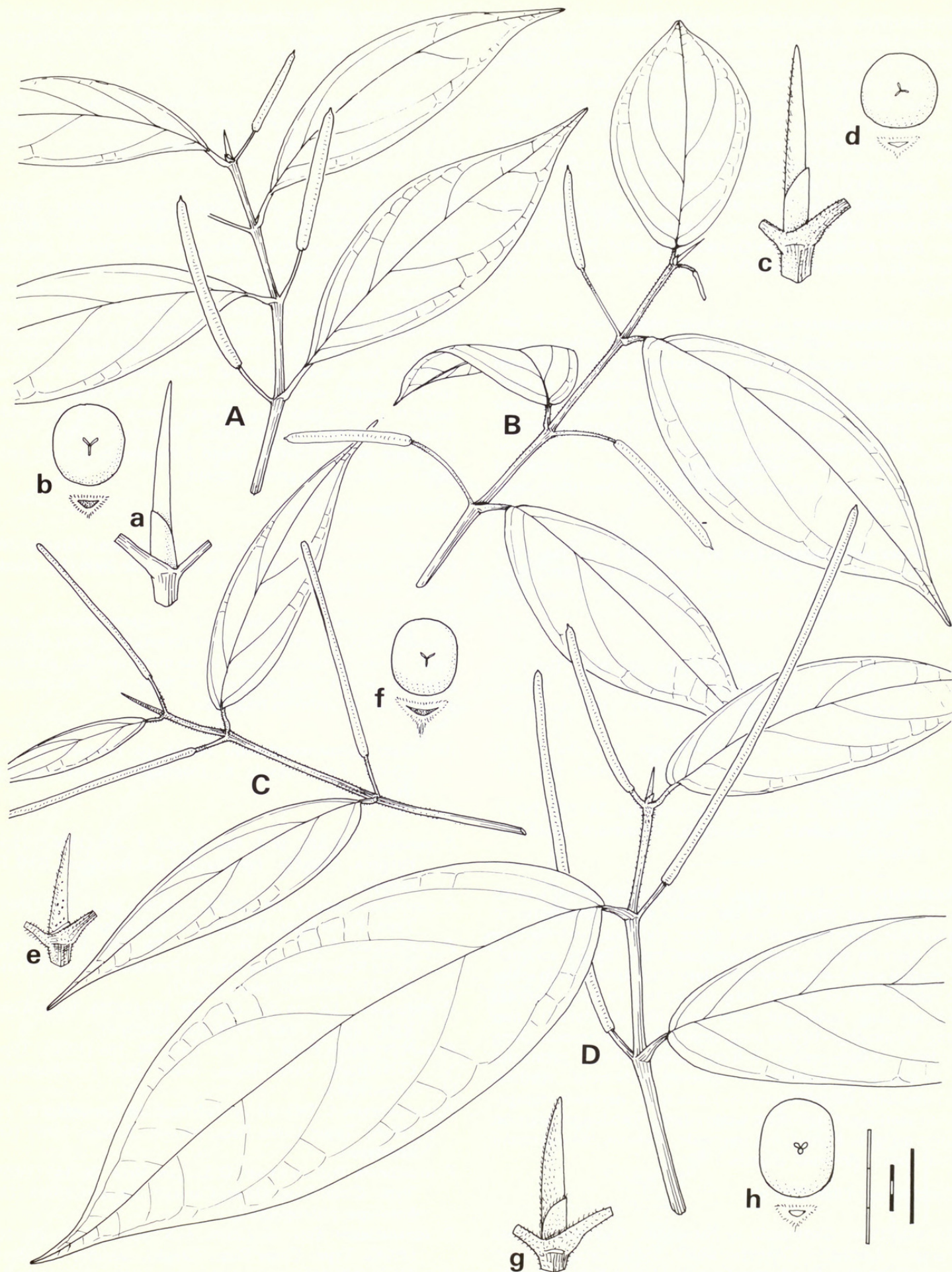


Fig. 16 A: *P. tenuimucronatum*, habit; a: prophyll; b: fruit and bract. B: *P. carpinteranum*, habit; c: prophyll; d: fruit and bract. C: *P. scalarispicum*, habit; e: prophyll; f: fruit and bract. D: *P. hostmannianum*, habit; g: prophyll; h: fruit and bract.

DISTRIBUTION. Venezuela to Brazil. **Venezuela**, Atabapo: *Liesner* 17872 (MO); Atures: *Steyermark* et al. 122312 (NY); Bolívar: *Liesner & González* 5850 (NY). **Guyana**, Kaieteur Plateau: *Cowan & Soderstrom* 2250A (NY); Mazaruni R.: *De la Cruz* 2279 (NY); Pomeroon: *De la Cruz* 1827 (MO); Tumatumari: *Gleason* 307 (NY). **Surinam**, Lely mts.: *Lindeman* et al. 675 (NY). **French Guiana**, Cayenne: *Lescure* 107 (NY); Pompidou-Papaichton: *Sastre* 4051 (NY); Saul: *Mori & Boom* 14906 (MO). **Peru**, Loreto: *Lleras* et al. P17112 (MO). **Bolivia**, Beni: *Boom* 4074 (MO); Pando: *Prance* et al. 5870 (MO). **Brazil**, Amazonas: *Nascimento* 551 (NY); Manaus: *Lowe* 4233 (E); Mato Grosso: *Berg* et al. P18395 (US); Pará: *Cid & Ramos* 1156 (NY); Rondonia: *Prance* et al. 5955 (MO).

Piper hostmannianum is very similar vegetatively to *P. jacquemontianum*, with large, glossy leaves and yellow pubescence. These species can be distinguished by their different inflorescences. Those of *P. jacquemontianum* are shorter, with semi-lunar, densely yellow-ciliate floral bracts and larger round fruits covered with a distinctive, felty brown indumentum. Although usually found growing as a shrub, *P. hostmannianum* often has spreading stems that are capable of climbing upwards, presumably by means of adventitious roots at the nodes.

101. **Piper scalarispicum** Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* 17: 353 (1938). Type: Honduras, El Achote, SW. of Siguatepeque, *Yuncker, Dawson & Youse* 6156 (ILL!-holotype; F!, MO!-isotypes).

Fig. 16C,e,f.

- P. nubigaudens* Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* 17: 351 (1938). Type: Honduras, range above El Achote, *Yuncker, Dawson & Youse* 5991 (ILL!-holotype; F!-isotype).

- P. segoviarum* Standl. & L.O. Williams in *Ceiba* 1: 142 (1950). Type: Nicaragua, Jinotega, *Standley* 9912 (F!-holotype).

- P. brujoense* Trel. & Standl. in *Fieldiana Bot.* 24: 290 (1952). Type: Guatemala, Chiquimula, *Steyermark* 31049 (F!-holotype).

Weak shrubs 1–2 (–4) m high, with pubescent stems. Leaves 5–12 (–15) cm long, 1.5–4 cm wide, elliptic-lanceolate to lanceolate, upper surface dark green, glabrous, undersurface with hairs on veins, apex acuminate, base slightly unequal. Venation with 2–4 pairs of secondary veins arising from lower to middle part of midrib, loop-connecting to apex. Petioles 3–6 mm long, pubescent, with ligule-like structure 0.5 mm long. Prophylls 7–10 mm long, drying dark, pubescent along midrib. Inflorescences 3–8 cm long, erect; peduncles 7–10 mm long, glabrous or sparsely pubescent. Anthers 0.3 mm long. Floral bracts 0.8–1 mm wide, narrowly triangular to semi-lunar, yellowish white ciliate, with longer hairs on lower margins. Fruits 0.8–1 mm wide, obovoid, oblong-round from above, glabrous; stigmas 3.

Cloud forest; 1300–2500 m.

DISTRIBUTION. Guatemala to Nicaragua. **Guatemala**, Baja Verapaz: *Lundell & Contreras* 18965 (MO); Zacapa: *Steyermark* 29884 (F). **Honduras**, Cortés: *Molina* 8211 (F); Intibuca: *Molina* 6408 (F); La Páz: *Molina* 14078 (F); Morazán: *Molina* 8525 (F); Ocotepeque: *Molina* 31403a; Paraíso:

Molina 26148 (F). **El Salvador**, Santa Ana: *Molina* 12642 (F). **Nicaragua**, Jinotega: *Standley* 10672 (F); Matagalpa: *Williams* et al. 23527 (F).

102. **Piper curvatipes** Trel. in *Publ. Field Mus. nat. Hist. (Bot.)* 17: 231 (1937). Type: Guatemala, Petén, *Lundell* 3122 (ILL!-holotype; F!-isotype).

Fig. 17A,a,b.

Shrubs 1–2.5 m high, stems slender, pale-glandular, slightly granular. Leaves 8–12 cm long, 2–4.5 cm wide, oblong-lanceolate, pale-glandular, glabrous, upper surface lustrous, underside with prominent veins, apex acute-acuminate, base unequally obtuse. Venation with 2–3 pairs of prominent secondary veins arising from the lower part of the midrib, ascending steeply to the apex. Petioles 3–8 mm long, glabrous, with ligule-like structures 1–2 mm long. Prophylls 5–12 mm long, acute, glabrous. Inflorescences 2–4 cm long, erect or slightly curved; peduncles 4–9 mm long, glabrous. Anthers 0.2–0.3 mm long. Floral bracts 0.6–1 mm wide, triangular, densely yellow-ciliate, with dark centres. Fruits 1–1.2 mm wide, obovoid, round from above, densely pale-yellow pubescent; stigmas 3, sessile.

Moist forest; 0–200 m.

DISTRIBUTION. Mexico to Guatemala. **Mexico**, Chiapas: *Shilom Ton* 2604 (CAS). **Belize**, Cayo: *Gentle* 2606 (F). **Guatemala**, Petén: *Molina* 15586 (F).

Piper curvatipes is similar to *P. jacquemontianum*, with densely pubescent fruits and ciliate bracts on a stout inflorescence. It can be distinguished by its much smaller, glabrous, glandular leaves, not as glossy as those of *P. jacquemontianum*, and its glabrous prophylls.

103. **Piper jacquemontianum** Kunth in *Linnaea* 13: 631 (1839). Type: Insula S. Domingo, *Jacquemont* s.n. (B-holotype).

Fig. 17B,c,d.

- P. panamense* C.DC. in *J. Bot., Lond.* 4: 216 (1866). Type: Panama, Chagres, *Fendler* 270 (K!-holotype; BM!, F!-isotypes).

- P. citrifolium* sensu C.DC. in DC., *Prodr.* 16(1): 270 (1869). Type: Porto Rico, *Blaumer* s.n. (G!-holotype).

- P. pilibaccum* C.DC. in *Bot. Gaz.* 70: 179 (1920). Type: Costa Rica, Matamba, Nicoya Peninsula, *Cook & Doyle* 702 (US-holotype, photograph!).

- P. uvitanum* C.DC. in *Bot. Gaz.* 70: 182 (1920). Type: Costa Rica, Limón, *Pittier* 12690 (G!-holotype).

- P. subcitrifolium* C.DC. in *Bot. Gaz.* 70: 186 (1920). Type: Guatemala, Santa Rosa, *Smith* 3827 (US-holotype; G!-isotype).

- P. barbulatum* C.DC. ex A. Schroed. in *Candollea* 3: 135 (1926). Type: Costa Rica, Nicoya, *Tonduz* 13697 (G!-holotype).

- P. orosianum* Trel. in *Contr. U.S. natn. Herb.* 26: 143 (1929). Type: Costa Rica, Orosi, Cartago, *Standley* 39764 (US-holotype, photograph!).

- P. tabanicidum* Trel. in *Contr. U.S. natn. Herb.* 26: 162 (1929). Type: Costa Rica, Tilarán, *Standley & Valerio* 45676 (US-holotype).

- P. aeruginosibaccum* Trel. in *J. Wash. Acad. Sci.* 19: 336 (1929). Type: Honduras, near La Ceiba, Atlántida,

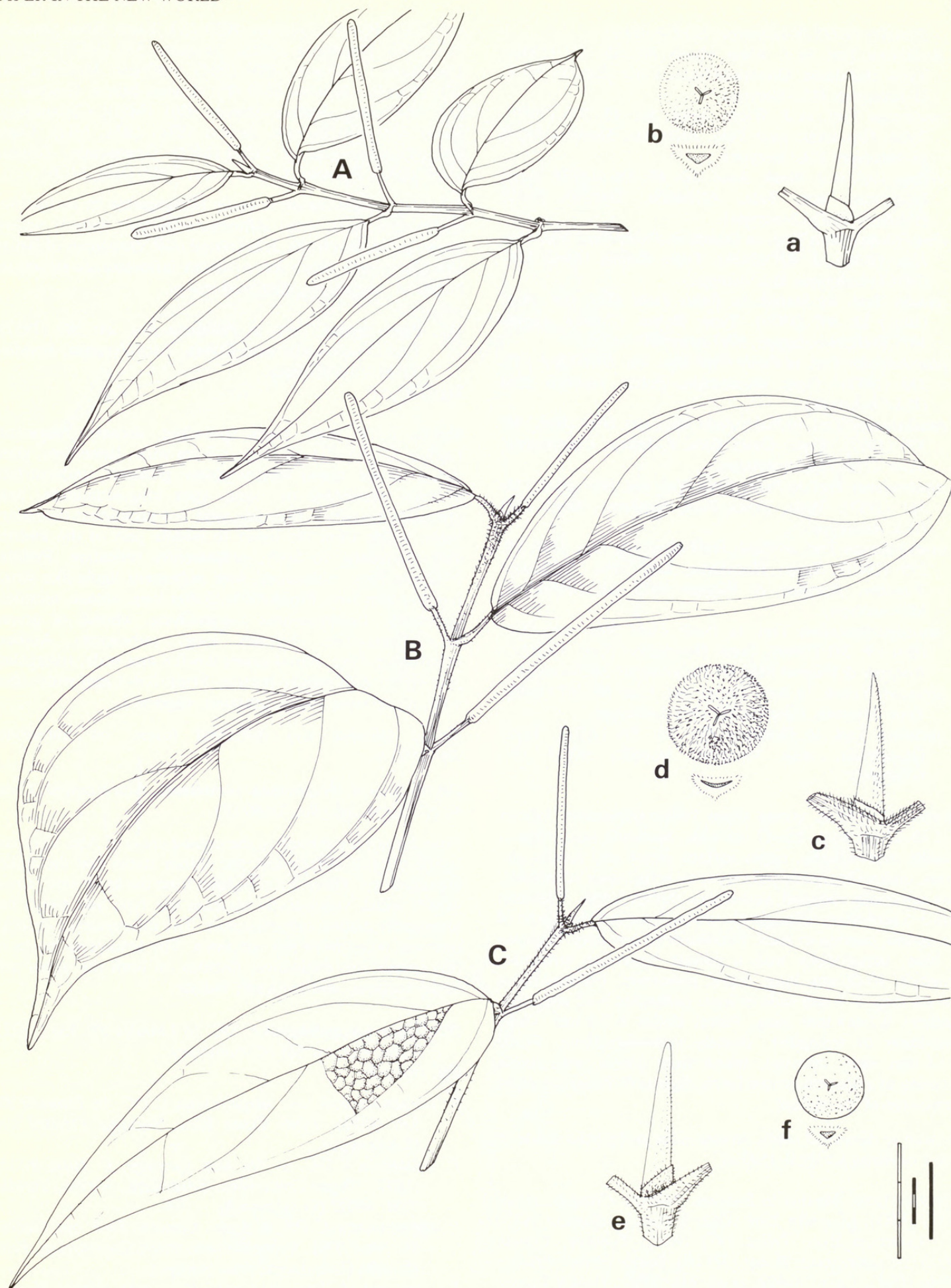


Fig. 17 A: *P. curvipes*, habit; a: prophyll; b: fruit and bract. B: *P. jacquemontianum*, habit; c: prophyll; d: fruit and bract. C: *P. biritak*, habit; e: prophyll; f: fruit and bract.

- Standley* 56735 (F-holotype; ILL!-isotype).
- P. dedittium* Trel. in *J. Wash. Acad. Sci.* **19**: 331 (1929). Type: Honduras, Quebrada Seca, Yoro, *Standley* 53937 (F-holotype; ILL!-isotype).
- P. onerosum* Trel. in *J. Wash. Acad. Sci.* **19**: 335 (1929). Type: Honduras, near Tela, Atlántida, *Standley* 53696 (F-holotype; ILL!-isotype).
- P. vexans* Trel. in *J. Wash. Acad. Sci.* **19**: 336 (1929). Type: Honduras, near Tela, Atlántida, *Standley* 54742 (F-holotype; ILL!-isotype).
- P. dimorphophyllum* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **12**: 407 (1936). Type: Belize, *Gentle* 1387 (MICH-holotype; ILL!-isotype).
- P. gentlei* Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **12**: 407 (1936). Type: Belize, Corazal, *Gentle* 1077 (MICH-holotype; NY!-isotype).
- P. plumbeicolor* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **17**: 233 (1937). Type: Guatemala, Petén, *Lundell* 2554 (ILL!-holotype).
- P. catalinianum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 335 (1937). Type: Costa Rica, Catalina, Guanacaste, *Stork* 2779 (ILL!-holotype).
- P. siquirresense* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 361 (1937). Type: Costa Rica, Siquirres, *Stork* 2251 (ILL!-holotype).
- P. evulsipilosum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **9**: 279 (1940). Type: Honduras, La Ceiba, Atlántida, *Yuncker, Koepfer & Wagner* 8015 (ILL!-holotype; MO!-isotype).
- P. tumidipedunculatum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **9**: 281 (1940). Type: Honduras, Yoro, *Yuncker, Koepfer & Wagner* 8151 (ILL!-holotype; MO!-isotype).
- P. gleasonii* Yunck. in *Bull. Torrey bot. Club* **75**: 287 (1948). Type: Guyana, *Gleason* 857 (NY-holotype).
- P. jactatum* Trel. in *Fieldiana Bot.* **24**: 305 (1952). Type: Guatemala, Alta Verapaz. *Standley* 90614 (F!-holotype).

Shrubs 2–3 (–4) m, young stems brown-pubescent. Leaves (3–) 10–22 cm long, 2.5–11 cm wide, narrowly lanceolate to broadly ovate-elliptic, upper surface glossy and mostly glabrous, underside shortly pubescent on veins, apex acuminate, base unequally rounded, sometimes slightly lobed. Venation with 3–5 secondary veins mostly arising from the lower part of the midrib, curving to apex. Petioles 6–16 mm long, vaginate at base, occasionally with a minute ligule-like structure. Prophylls 10–20 mm long, acute, pubescent. Inflorescences 4–8 cm long, 2–4 mm wide in fruit; peduncles 3–12 mm long. Anthers 0.2–0.4 mm long. Floral bracts 0.7–1 mm wide, semi-lunar or triangular, densely yellowish-ciliate. Fruits 1–1.5 mm wide, obovoid, round from above, with dense covering of yellowish brown hairs; stigmas 3, linear, in slight depression at top of fruit.

Cleared or disturbed areas, stream sides and partial shade in forest or dense scrub; 0–1500 m.

DISTRIBUTION. Mexico to Panama. **Mexico**, Chiapas: *Croat* 40307 (MO); *Laughlin* 2566 (DS); Escuintla: *Matuda* 16720 (F); Quintana Roo: *Tellez* 1951 (BM); Tabasco: *Cowan* 29925 (DS); Veracruz: *Rosas* 1371 (F). **Belize**, Belize: *Proctor* 29546 (BM); Cayo: *Sutton et al.* 314 (BM); Honey Camp: *Lundell* 556 (DS). **Guatemala**, Alta Verapaz: *Tuerckheim* 1904 (NY); Escuintla: *Standley* 89278 (F); Izabal: *Contreras*

9973 (K); Petén: *Contreras* 8999 (K); Santa Rosa *Standley* 78378 (F). **Honduras**, Colón: *Saunders* 518 (MO); Cortés: *Blackmore & Chorley* 4003 (BM); Intibucá: *Molina* 13942 (F); Olancho: *Molina*: 8318 (F); Ruatan Island: *Gaumer* 47 (K). **Nicaragua**, Boaco: *Stevens* 9261 (MO); Chinandega: *Baker* 26 (DS); Zelaya: *Stevens* 18714 (BM, MO). **Costa Rica**, Cartago: *Liesner* 14389 (MO); Guanacaste: *Tonduz* 13697 (BM). **Panama**, Colón: *Croat* 36890 (BM, MO).

Piper jacquemontianum is easily recognizable by its lustrous leaves and short, stout inflorescences with densely yellow brown pubescent fruits. It is related to *P. curvatipes* of Belize and Guatemala which has a similar inflorescence structure, but short, lanceolate, glandular leaves.

104. *Piper biritak* Trel. in *Fieldiana Bot.* **24**: 289 (1952). Type: Guatemala, near Cobán, Alta Verapaz, *Standley* 69345 (F!-holotype).

Fig. 17C,e,f.

Shrubs 1–2 m high, stems spreading, densely pubescent. Leaves 12–16 (–21) cm long, 2–5 cm wide, lanceolate, glandular, bullate, upper surface glossy, glabrous, undersurface lustrous, pubescent on veins, apex long-acuminate, base unequally rounded. Venation with 3–4 prominent secondary veins arising from the lower to middle part of the midrib, loop-connecting to apex, prominently reticulate. Petioles 3–10 mm long, pubescent, with pubescent ligule-like structure 1–3 mm long. Prophylls 7–15 mm long, obtuse, minutely pubescent. Inflorescences 5–6 cm long, whitish or green, erect; peduncles 4–6 mm long, pubescent. Anthers 0.3–0.4 mm long. Floral bracts 0.6–0.8 mm wide, triangular, pale-ciliate with darker centres. Fruits 0.8–1 mm wide, obovoid, round from above, granular; stigmas 3.

Rocky hillsides and disturbed forest, on limestone; 900–1500 m.

DISTRIBUTION. Guatemala. **Guatemala**, Alta Verapaz: *Croat* 41387 (MO), *Standley* 91690 (F).

Piper biritak is confined to the upland areas of Alta Verapaz. In the original description, the author states that the spikes are unknown. There is a collection from the same area (*Croat* 41387) which vegetatively matches the type and which has reasonably mature inflorescences. The inflorescence description was taken from this specimen. The lanceolate leaves of this species are distinctive, lustrous on both the upper and under surfaces, and markedly bullate.

105. *Piper pseudolindenii* C.DC. in *Linnaea* **37**: 336 (1872). Type: *Oersted* 888 (C!-holotype).

Fig. 18A,a,b.

P. pseudo-lindenii var. *magnifolium* C.DC. in *Linnaea* **37**: 336 (1872). Type: Costa Rica, Naranjo, *Oersted* s.n. (S-holotype).

P. virillanum C.DC. in *An. Inst. fis-geogr. C. Rica.* **9**: 158 (1897). Type: Costa Rica, bord du R. Virilla, *Tonduz* 9831, 10127 (G-syntypes).

P. udimontanum C.DC. in *Annu. Conserv. Jard. bot. Genève* **21**: 306 (1920). Type: Mexico, above Cuernavaca, *Pringle* 6828 (G-holotype; cm!-isotype).

P. pertractatum Trel. in *Contr. U.S. natn. Herb.* **26**: 130 (1929). Type: Costa Rica, Nuestro Amo, Alajuela, *Jimenez* s.n. (US-holotype, photograph!).



Fig. 18 A: *P. pseudolindenii*, habit; a: large leaf; b: prophyll; c: fruit and bract. B: *P. sanctum*, habit; d: prophyll; e: fruit and bract.

- P. magnifolium* (C.DC.) Trel. in *Contr. U.S. natn. Herb.* **26**: 131 (1929). Type: Costa Rica, Naranjo, *Oersted* s.n. (US-holotype).
- P. colaphitolerans* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **17**: 231 (1937). Type: Guatemala, Lake Petén, *Lundell* 3827 (ILL!-holotype).
- P. humorigaudens* Trel. in *Ann. Mo. bot. Gdn* **27**: 293 (1940). Type: Panama, north rim of El Valle de Anton, Coclé, *Allen* 1833 (ILL!-holotype).
- P. oblique-ovatum* Trel. in *Publs Field Mus. nat. Hist. (Bot.)* **22**: 10 (1940). Type: Guatemala, Concepcion, Chimaltenango, *Johnston* 557 (F!-holotype).
- P. stillans* Trel. & Standl. in *Fieldiana Bot.* **24**: 325 (1952). Type: Guatemala, Quiche, *Skutch* 1822 (F!-holotype).

Shrubs 1–4 m high, stems glabrous or minutely puberulent. Leaves 6–17 (–22) cm long, 2–7 (–9) cm wide, oblong-lanceolate to elliptic, slightly asymmetric, apex acuminate, base obtuse to slightly lobed and overlapping the petiole. Venation palmate, with 3–5 secondary veins arising from the base and ascending steeply to apex. Petioles 1–10 (–15) mm long, glabrous or minutely pubescent, with minute ligule-like structure. Prophylls 3–6 mm long, apex acute, glabrous. Inflorescences 4–10 cm long, minutely pubescent; peduncles 6–12 (–15) mm long, minutely pubescent. Anthers 0.2–0.3 mm long. Floral bracts 0.4–0.6 mm wide, triangular or round with ciliate margins. Fruits 1–2 mm wide, obovoid, round or rhomboid from above, glabrous; stigmas 3–4, sessile.

Montane, deciduous and evergreen forest, damp ravines, edges of forest tracks and river banks; 0–2200 m.

DISTRIBUTION. Mexico to Panama. **Mexico**, Chiapas: *Croat* 47402 (BM,MO); Jalisco: *Breedlove & Almeda* 45635 (CAS); Michoacan: *Arsene* 8445 (BM); Morelos: 6828 (BM); Oaxaca: *Calderón* 525 (BM); Veracruz: *Calderón* 1734 (CAS). **Belize**, Cayo: *Lundell* 6483 (DS). **Guatemala**, El Quiché: *Proctor* 25254 (MO); Izabal: *Croat* 41842 (MO); Petén: *Contreras* 5841 (DS). **Honduras**, Atlántida: *Izaguirre* 1 (MO); Comayagua: *Molina* 23334 (BM); El Paraíso: *Molina* 11916 (BM); Intibucá: *Bonilla* 100 (BM); Olanchito: *Nelson & Romero* 4642 (BM); Santa Barbara: *Cruz* G-088 (MO). **El Salvador**, Santa Ana: *Croat* 42400 (MO); Sonsonate: *Croat* 42211 (MO). **Nicaragua**, Boaco: *Stevens* 9260 (BM,MO). **Costa Rica**, Cartago: *Grayum & Sleeper* 3274 (BM,MO); Puntarenas: *Davidse* 24468 (BM,MO); San José: *Tonduz* 7145 (BM). **Panama**, Chiriquí: *Proctor* 31822 (MO); Coclé: *Alston* 8721 (BM); Los Santos: *Croat* 34531 (BM,MO); Panama: *Croat* s.n. (BM,MO).

Piper pseudo-lindenii can be distinguished by its slightly asymmetric, palmately veined leaves and the rather lumpy appearance of its infructescence. It is a fairly common species of disturbed forest, often growing at high altitudes.

The original description of *Piper oblique-ovatum* Trel. was based on a sterile specimen collected by Johnston in Guatemala. This plant has a shrubby, glabrous habit, with lanceolate-ovate leaves and the base slightly lobed, overlapping the petioles. In the Latin diagnosis of *P. oblique-ovatum*, the leaves are described as follows: 'folia lanceolato-ovata vel saepius late ovata-acuta, basi gibboso-cordata, lobo majore petiolum occultante.' This is very similar to that of *P. pseudolindenii* C.DC.: 'foliis breviter petiolatis lanceolato-oblongis apice acuminatis, acumine acuto, basi inaequalis

gibbosis, latere majore rotundato minore acute.' The type material shows that both species have the same sort of leaf venation and inflorescence structure. Examination of a wide range of specimens has shown that plants with larger basal lobes tend to occur at lower altitudes.

106. *Piper sanctum* (Miq.) Schltdl. in DC., *Prodr.* **16**(1): 330 (1869). Type: Mexico, Atlacomulco, *Schiede* 105 (?B-holotype).

Fig. 18B,c,d.

Artanthe sancta Miq., *Syst. piperac.*: 339 (1844).

Piper papantlense C. DC. in DC., *Prodr.* **16**(1): 338 (1869). Type: In sylvis Papantlae, *Fischer* 74 (?B-holotype).

P. diandrum C.DC. in *Linnaea* **37**: 364 (1872). Type: Mexico, Pital, *Liebmann* 55 (C!-holotype).

P. venulosum Trel. in *Contr. U.S. natn. Herb.* **26**: 132 (1929). Type: Costa Rica, San Ramón, *Brenes* 14192 (US-holotype, photograph!).

P. dissimulans Trel. in *Contr. U.S. natn. Herb.* **26**: 133 (1929). Type: Costa Rica, Tucurrique, *Tonduz* 12773 (US-holotype, photograph!).

P. heterophlebium Trel. ex Standl. in *Publs Field Mus. nat. Hist. (Bot.)* **18**: 345 (1937). Type: Costa Rica, San José, *Skutch* 2293 (US-holotype).

Shrubs or small tree 1.5–4 (–5) m high, stems glabrous. Leaves 10–20 cm long, 7–16 cm wide, broadly ovate to elliptic, pale green, glabrous, apex acute-acuminate, base round to shallowly cordate on older, lower leaves. Venation palmate, with 3–7 prominent secondary veins arising from the leaf-base and ascending fairly steeply to apex. Prophylls 5–15 (–20) mm long, slender, apex acute, glabrous. Petioles 10–20 mm long. Inflorescences 7–22 cm long, erect, becoming pendulous in fruit; peduncles 12–25 mm long. Anthers 0.1–0.2 mm. Floral bracts 0.3–0.5 mm wide, triangular to round, margins ciliate. Fruits 1 mm wide, obovoid, round from above, glabrous; stigmas 3–4.

Wet forest, river banks, disturbed ground; 0–2500 m.

DISTRIBUTION. Mexico to Costa Rica. **Mexico**, Chiapas: *Breedlove* 34522 (DS); Hidalgo: *Croat & Hannon* 66004 (BM,MO); Morelos: *Croat & Hannon* 65774 (BM,MO); Veracruz: *Calderon* 2232 (CAS). **Belize**, Toledo: *Proctor* 36075 (BM). **Guatemala**, Baja Verapaz: *Tuerckheim* 111704 (BM). **Honduras**, Colón: *Ramos* 193 (BM); Morazán: *Molina* 826 (BM). **Nicaragua**, Chontales: *Grijalva & Ríos* 3451 (BM); Granada: *Sandino* 2941 (BM); Managua: *Stevens* 5409 (BM); Rivas: *Sandino* 4289 (BM); Zelaya: *Stevens* 6931 (BM). **El Salvador**, Ahuachapán: *Berendsohn & Villacorta* 1112 (BM); La Libertad: *Berendsohn et al.* 1044 (BM). **Costa Rica**, Guanacaste: *Garwood et al.* 682 (BM); San José: *Tonduz* 12773 (BM).

Excluded species

Piper gaudichaudianum Kunth in *Linnaea* **13**: 638 (1839)–(as *Steffensia gaudichaudiana*). The original description indicates that vegetatively this taxon is very like *P. aduncum* L. Specimens at the BM, named by Yuncker (1972) as *P. gaudichaudianum*, are actually *P. aduncum* L., with scabrous upper leaf surfaces, arching inflorescences, and round glabrous fruits. As the holotype (*Gaudicaud & Luschnath* s.n.) was not available for this study, and judging from the original

description, presumably has immature inflorescences, *P. gaudichaudianum* has been excluded from this study.

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P. elongatum var. *pampayacusum* Trel., 21
P. emollitum Trel., 31
P. enganyanum Trel. & Yunck., 17
P. epigynium C.DC., 32
P. erectamentum C.DC., 26
P. evulsipilosum Trel., 44
P. excultum Trel., 19
P. falcigerum Trel., 15
P. fatoanum C.DC., 21
P. flavescens (C.DC.) Trel., 21
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P. fraguanum Trel., 29
P. friedrichsthalii C.DC., 19
P. fuligineum Kunth, 22
P. fusco-bracteatum Trel., 28
P. fusco-granulatum Trel., 34
P. gamboanum var. *yapense* Trel., 26
P. gaudichaudianum Kunth, 46
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P. genuflexum Trel., 26
P. gleasonii Yunck., 44
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P. gonagricum Trel., 26
P. gracilipedunculum Trel., 38
P. granulatum Trel., 24
P. griseo-pubens Trel., 12
P. griseo-pubens var. *revocabile* Trel., 12
P. hanckeli Trel. ex Standl., 32
P. heterophlebium Trel. ex Standl., 46
P. hirsutum var. *tonduzii* C.DC., 26
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P. hispidum Kunth, 26
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P. indignum Trel., 24
P. infraleucum Trel., 40
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P. injucundum var. *praecalvinervium* Trel., 28
P. injucundum var. *praepubinervium* Trel., 28
P. insolens Trel., 36
P. intersitum Trel., 21
P. jacquemontianum Kunth, 42
P. jactatum Trel., 44
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P. killipi var. *calderanum* Trel., 26
P. konkintoense Trel., 28
P. kuntzei C.DC., 21
P. laevifolium C.DC., 15
P. laevius (C. DC.) Trel., 24
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P. lanceifolium Kunth, 19
P. lanceifolium var. *acutiusculum* C.DC., 19
P. lanosibracteum Trel., 28
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P. lineatum var. *leucolepidum* Trel., 19
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P. luridispicum Trel. ex Standl., 32
P. maestranum Trel., 26
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P. malpasoensis Tebbs, 17
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P. marginatum var. *marginatum* forma *catalpaefolium* (Kunth) Steyer., 9
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P. maternale Trel., 17
P. meritum Trel., 28
P. micoense Trel., 24
P. milciadesii Trel. & Yunck., 17
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P. multiplinervium C.DC., 10
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P. nodosum C.DC., 31
P. nubigaudens Trel., 42
P. obiter-sericeum Trel. ex Standl., 13
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P. oblanceolatum var. *fragilicaule* Trel., 21
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P. onerosum Trel., 44
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