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Source: Systematic Botany, 39(1) : 10-16

Published By: The American Society of Plant Taxonomists

URL: https://doi.org/10.1600/036364414X678206

Systematic Botany (2014), 39(1): pp. 10–16

DOI 10.1600/036364414X678206
Date of publication 02/05/2014

Two New Species of *Piper* from the Greater Antilles

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Communicating Editor: Daniel Potter

Abstract*—**Two new Antillean endemic species, ***Piper abajoense from Puerto Rico, and ***Piper claseanum*** from the Dominican Republic, are described and illustrated. The former species resembles the widely distributed *Piper hispidum*, including the somewhat scabrous leaf surfaces, typically asymmetric leaf bases, and the bracts, flowers, and fruits forming distinct bands around the spike, but is distinguished by the combination of glabrous and stylose fruits (vs. densely puberulent and estylose), laterally (vs. apically) dehiscent anthers, and shorter spikes. The latter species resembles *Piper samanense,* another endemic species from the Dominican Republic, in vegetative morphology, including the leathery leaves with pellucid dots visible below when dry, but differs in its long-pedicellate flowers and fruits (vs. sessile or pseudo-pedicellate), puberulent rachis and pedicels (vs. densely white-pubescent), and puberulent vs. pubescent fruits. A phylogeny based on the nuclear ribosomal Internal Transcribed Spacer (ITS) and chloroplast intron *psbJ-petA* indicates proper placement of these two new species within clades *Radula* and *Enckea*, respectively. Two keys are provided, one to all species of *Piper* from Puerto Rico, the other to the palmate-veined species from the Dominican Republic.

Resumen*—**Se describen e ilustran aquí dos especies nuevas de *Piper* endémicas a las Antillas, ***Piper abajoense de Puerto Rico y ***Piper claseanum*** de la República Dominicana. La primera especie es similar a la especie de amplia distribución, *P. hispidum*, incluyendo las hojas algo híspidas, las bases asimétricas de las hojas, y las brácteas, flores, y frutos que forman bandas distintas alrededor de la espiga, pero se distingue por la combinación de los frutos glabros y con estilos (vs. densamente puberulentos y sin estilos), anteras con dehiscencia lateral (vs. apical), y espigas más cortas. La segunda especie se asemeja a *P. samanense*, otra especie endémica a la República Dominicana, en su morfología vegetativa, incluso las hojas correosas con puntos translúcidos visibles en el envés en hojas secas, pero se diferencia de esta por los frutos con los pedicelos largos (vs. sésiles o con pedicelos falsos), el raquis y pedicelo puberulentos (vs. densamente blanco pubescentes), y los frutos puberulentos (vs. pubescentes). Una filogenia, basada en el espaciador transcribible interno del ADN ribosómico nuclear (ITS) y el intrón del cloroplasto *psbJ-petA* indica que las dos especies pertenecen a los clados *Radula* y *Enckea* respectivamente. Se proporcionan dos claves, una para todas las especies de *Piper* en Puerto Rico, y la otra para las especies de la República Dominicana con las hojas con venación palmada.

***Keywords*—**clade *Enckea,* clade *Radula,* Dominican Republic, Piperaceae, Puerto Rico.

The Piperaceae are a pantropical family in which five genera, organized into three subfamilies (Samain et al. 2008), are currently recognized based on recent molecular (Wanke et al. 2007) and morphological analyses (Samain et al. 2010). The vast majority (>99%) of species in the family are classified in the two "giant" genera *Piper* L. and *Peperomia* Ruíz and Pav., each with an estimated minimum of 1,600 species (Quijano-Abril et al. 2006; Wanke et al. 2007; Samain et al. 2008; Samain et al. 2009; Samain et al. 2010). The other three genera include *Manekia* Trel. with three species (Schubert et al. 2012), *Verhuellia* Miq. with three species (Wanke et al. 2007; Samain et al. 2008; Samain et al. 2010), and the monotypic *Zippelia* Blume.

The genus *Piper* in the Neotropics consists mostly of medium-sized shrubs or small trees (ca. two to eight m tall), occasional vines, or relatively uncommon sub-shrubs under one meter in height (Jaramillo and Callejas 2004; Isnard et al. 2012). The leaves are always alternate and simple with either palmate or pinnate venation, many of which have readily visible pellucid dots (especially when dry) due to the presence of ethereal oil cells. Moreover, pipers are generally easy to identify in the field based on their swollen nodes, spicate inflorescences with perianth-less flowers, and aromatic properties. Flowers in the Neotropical species are bisexual and typically consist of two to six stamens with three or four fused carpels; the fruit is a small, one-seeded berry (usually reported erroneously as a drupe).

Piper species in the New World occur naturally from Mexico, Central America, and the Antilles, southward to Brazil and Argentina, with high levels of diversity in the Andes region. They grow most abundantly in moist conditions of the forest understory, including stream banks, trails, and forest edges. Several species (e.g. *Piper aduncum* L.) are known to be rather weedy (Weber 2003), occurring commonly in disturbed areas. In the Greater Antilles, 10 species are reported from Puerto Rico, none endemic (Liogier 1985; Axelrod 2011), 27 species from Hispaniola, including 16 endemics (Liogier 1996), ca. 10 species from Jamaica, including two to three endemics (Yuncker 1960; Adams 1972), and 19 species from Cuba, including 10 endemics (Saralegui-Boza 2004).

As a result of collecting trips to Puerto Rico (in 2011 and 2013) and the Dominican Republic (in 2012), two new species have been discovered, which are described in detail below. In addition, the phylogenetic placement of these new species in their respective clades is provided within the framework created by Jaramillo et al. (2008), based on DNA sequence analysis of the nuclear ribosomal ITS and the *psbJ-petA* chloroplast regions. A key to all species in Puerto Rico is provided, along with a key to palmate-veined species from the Dominican Republic for comparative purposes.

Materials and Methods

Fieldwork in January 2011, 2012, and 2013 provided materials for subsequent analysis, including dried herbarium specimens, preserved flowers and fruits in FAA (formaldehyde, acetic acid, alcohol), and DNA samples from leaves that were field-dried and stored in silica gel. Measurements of plant parts were made from herbarium specimens and preserved materials using an Olympus SZ61TR stereomicroscope and

reported in the descriptions as a range, mean, median, and number of observations (N). Descriptive terminology concerning leaf features follows Ellis et al. (2009). Additional specimens of *Piper abajoense* were obtained on loan from UPRRP, along with gift specimens of *Piper claseanum* from JBSD to SEMO (Holmgren et al. 1990).

DNA of both species was extracted using Qiagen DNeasy plant mini kits (Qiagen, Valencia, California). Amplification of the nuclear ribosomal ITS and cpDNA *psbJ-petA* regions followed the methods of Jaramillo et al. (2008). The sequences were placed into the aligned matrix of Jaramillo et al. (2008) and analyzed with maximum parsimony using PRAP2 (Müller 2004) in conjunction with PAUP* (Swofford 2002). Support for placement of the two new species was evaluated using the bootstrap (Felsenstein 1985) with 1,000 replicates.

Results

Sequences for both *psbJ-petA* and ITS were obtained for three accessions of the new species, including the type specimens (*Bornstein et al. 1250, Bornstein & Schubert 1267*, and *Bornstein et al. 1283*). GenBank numbers are provided in Table 1. The new sequences were included in the alignment used in Jaramillo et al. (2008; see Fig. 1) and the maximum parsimony analysis resulted in 213 trees of 4,336 steps each. The consistency index (Kluge and Farris 1969) was 0.3536, the retention index and rescaled consistency index (Farris 1989) were 0.7550 and 0.3195, respectively.

Taxonomic Treatment

Piper abajoense Bornst., sp. nov.—TYPE: PUERTO RICO. Municipality of Utuado: Río Abajo Forest Reserve, near electric power station along road (Hwy 621) beyond the ranger station, 18°20′N, 66°43′W, 315 m, 10 January 2011, *A. Bornstein, H. Schubert, and F. Axelrod 1250* (holotype: UPRRP; isotypes: MO, SEMO).

Medium-sized, multi-branched shrub, ca. 1.5–3.0 m tall, stems with thickened nodes and diam up to 4–5 cm on well-developed specimens; leafy internodes 1.5–5.3 cm long (mean = 3.15 cm, median = 3.20 cm; N = 54), pubescent with multicellular hairs up to 0.75 mm long. Prophylls 0.90–2.45 cm long (mean = 1.84 cm, median = 2.00 cm; N = 8), apex angle acute, apex shape straight, glabrous except for pubescent along midvein region abaxially with multicellular hairs up to 0.75 mm long, caducous and usually drying dark brown to black. Leaves with petioles 0.20–1.20 cm long (mean = 0.49 cm, median = 0.45 cm; N = 41), pubescent with multicellular hairs up to 0.75 mm long, vaginate near the base and with a stipule-like structure present at flowering nodes, 1.0–2.5 mm long, densely ciliate; lamina 10.8–19.2 cm long (mean = 15.52 cm, median = 15.60 cm; N = 35) and 3.5–7.3 cm wide (mean = 5.78 cm, median = 5.95 cm; N = 38), elliptic to oblong-elliptic, medially symmetrical, apex angle acute, apex shape straight to often acuminate, base symmetrical to most commonly slightly asymmetrical, the two sides inserted 0.0–0.6 mm apart (mean = 0.32 mm, median = 0.35 mm; N = 41), base angle acute, base shape convex to rounded, venation pinnate with 4–5 pairs of secondary veins arising along lower ⅔ of midvein, the central vein and two uppermost secondary veins extending to tip of apex, drying thin-chartaceous and with numerous pellucid dots visible below (at least upon drying), smooth to slightly scabrous adaxially, but moderately pubescent along midvein and secondaries with multicellular hairs, pubescent abaxially, especially along the primary and secondary veins, with multicellular hairs up to 0.75 mm long. Spikes erect at all stages and free of the leaf base, yellowish at anthesis, becoming green in fruit, sometimes with sterile tip to 2.5 mm long; peduncles 0.9–2.0 cm long (mean = 1.31 mm, median = 1.30 mm; N = 22), pubescent with multicellular hairs 0.5–0.6 mm long; rachis 4.35–6.60 cm long (mean = 5.71 cm, median = 5.78 cm; N = 22) and 3.0–6.0 mm wide (mean = 4.21 mm, median = 4.0 mm; N = 21) in fruit, glabrous; floral bracts 0.3–0.8 mm wide (mean = 0.51 mm, median = 0.50 mm; N = 55), rounded-triangular in general outline, glabrous centrally but densely fimbriate along entire margin; flowers densely grouped along rachis, forming distinct bands around the spike, sessile; stamens 3, anthers 0.250–0.425 mm long (mean = 0.30 mm, median = 0.30 mm; N = 50), with lateral dehiscence. Fruits narrowly obovoid, round to somewhat angular in apical view, flattened laterally, 1.2–1.7 mm long (mean = 1.594 mm, median = 1.60 mm; N = 20) and 0.65–1.10 mm wide (mean = 0.892 mm, median = 0.90 mm; N = 25), glabrous or sparsely pubescent near apex, stigmas 2 or 3, elongate, recurved, borne on a style ca. 0.5 mm long within a central depression. Figure 2.

Additional Specimens Examined—PUERTO RICO. Arecibo: Bosque Río Arriba, along 1 km stretch at S end of pilot road for Rt. 10, 18°20.33′N, 66°40.67′W, 250–275 m, 1 June 1994, *F. Axelrod & B. Waide 7816* (UPRRP); Bosque Río Arriba, in sinkhole 1 km along S end of pilot road for Rt. 10, 18°20.33′N, 66°40.67′W, ca. 225 m, 1 June 1994, *F. Axelrod & B. Waide 7818* (UPRRP); Bosque Río Arriba, Río Abajo Forest Reserve, on slopes of sinkhole about 2 km N of S end of pilot road for proposed Rt. 10, 18°20.86′N, 66°41.00′W, 275 m, 22 July 1994, *F. Axelrod & L. Pérez 8062* (UPRRP); Bosque Sabana Hoyos, Finca Las Abras, forested abra between mogotes, 18°20.19′N, 66°33.13′W, ca. 300 m, 21 September 2002, *J. C. Trejo-Torres et al. 1788* (UPRRP). Isabela: Bosque Arenales Altos, sinkhole near and W of road 112 at km 9, ca. 18°25.129′N, 67°02.093′W, 150 m, 19 July 2006, *J. C. Trejo et al. 3065* (UPRRP). Utuado: Bosque Santa Rosa, Río Abajo Forest Reserve, along Las Perdices Trail, ca. 350 m, 11 August 1993, *F. Axelrod 6807* (UPRRP); Río Abajo Forest Reserve, ca. 100 m past electric power station along old logging road S of road 621, ca. 2.5 km beyond the María Soto campground, 18°20′N, 66°43′W, 315 m, 10 January 2013, *A. Bornstein, C. Wisniewski, and D. Wood 1288* (MO, NY, SEMO, UPRRP); Río Abajo Forest Reserve, S of road 621, fourth mogote if coming from reserve office, June 1999, *J. C. Trejo-Torres & A. Alicea 1394* (UPRRP); Orcovis: Hwy 143 at Verada La Torre, Toro Negro Recreation Area, growing along stream below pool area, 18°10′N, 66°29′W, 890 m, 14 January 2011, *A. Bornstein & H. Schubert 1267* (MO, NY, SEMO, UPRRP).

Notes—*Piper abajoense* occurs in the northern limestone hills (mogotes) and central mountains of Puerto Rico. It grows in partially shaded sites along forest edges or in cleared, disturbed areas between 200–900 m elevation. Plants were in both flower and fruit in January, and late flower into full fruit from June to September; they are likely to flower and fruit throughout the year. The epithet *abajoense* is in reference to the main location where it has been collected (Río Abajo Forest Reserve), a wonderful nature preserve where all of the *Piper* species in Puerto Rico are known to co-occur.

Piper abajoense belongs to clade *Radula* (see Fig. 1), which is a monophyletic group of species distinguished by the presence of pinnately veined leaves, typically erect inflorescences with the flowers, fruits, and bracts forming distinct bands

Table 1. Genbank accession information for *Piper abajoense* and *Piper claseanum*.

Taxon	Collection	ITS	*psbJ-petA*
Piper abajoense	*Bornstein et al. 1250*	KF207822	KF207825
	Bornstein & Schubert 1267	KF207823	KF207826
Piper claseanum	*Bornstein et al. 1283*	KF207824	KF207827

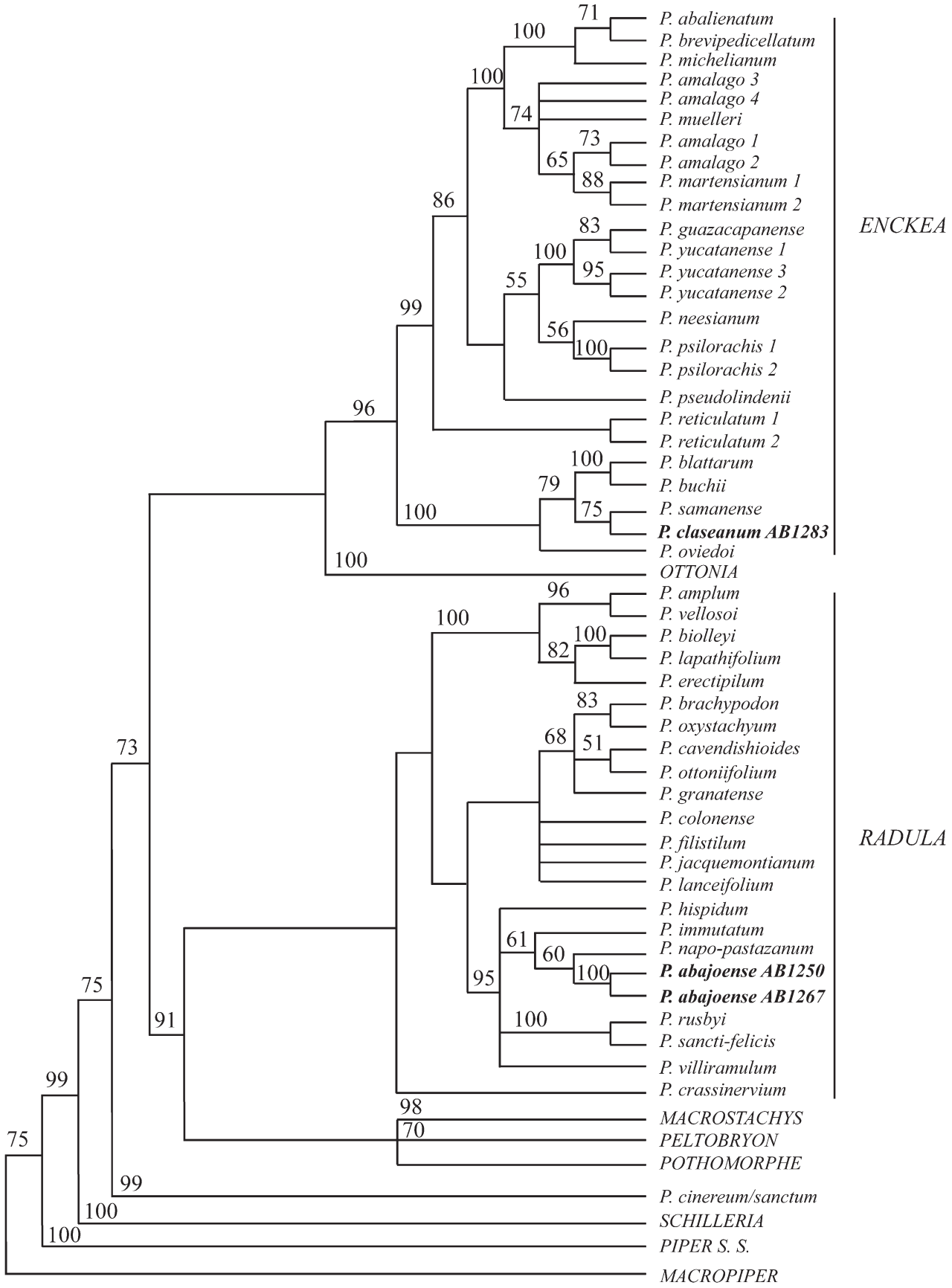

FIG. 1. A 50% majority rule tree of the genus *Piper* from the bootstrap analysis using maximum parsimony (213 trees of 4,336 steps each, consistency index = 0.3536, retention index = 0.7550, rescaled consistency index = 0.3195), with emphasis on clades *Radula* and *Enckea* to demonstrate placement of the two new species, *Piper abajoense* and *Piper claseanum*. Note that other major clades of *Piper* (indicated in italicized capital letters) have been collapsed, but contain the same species as Jaramillo et al. (2008).

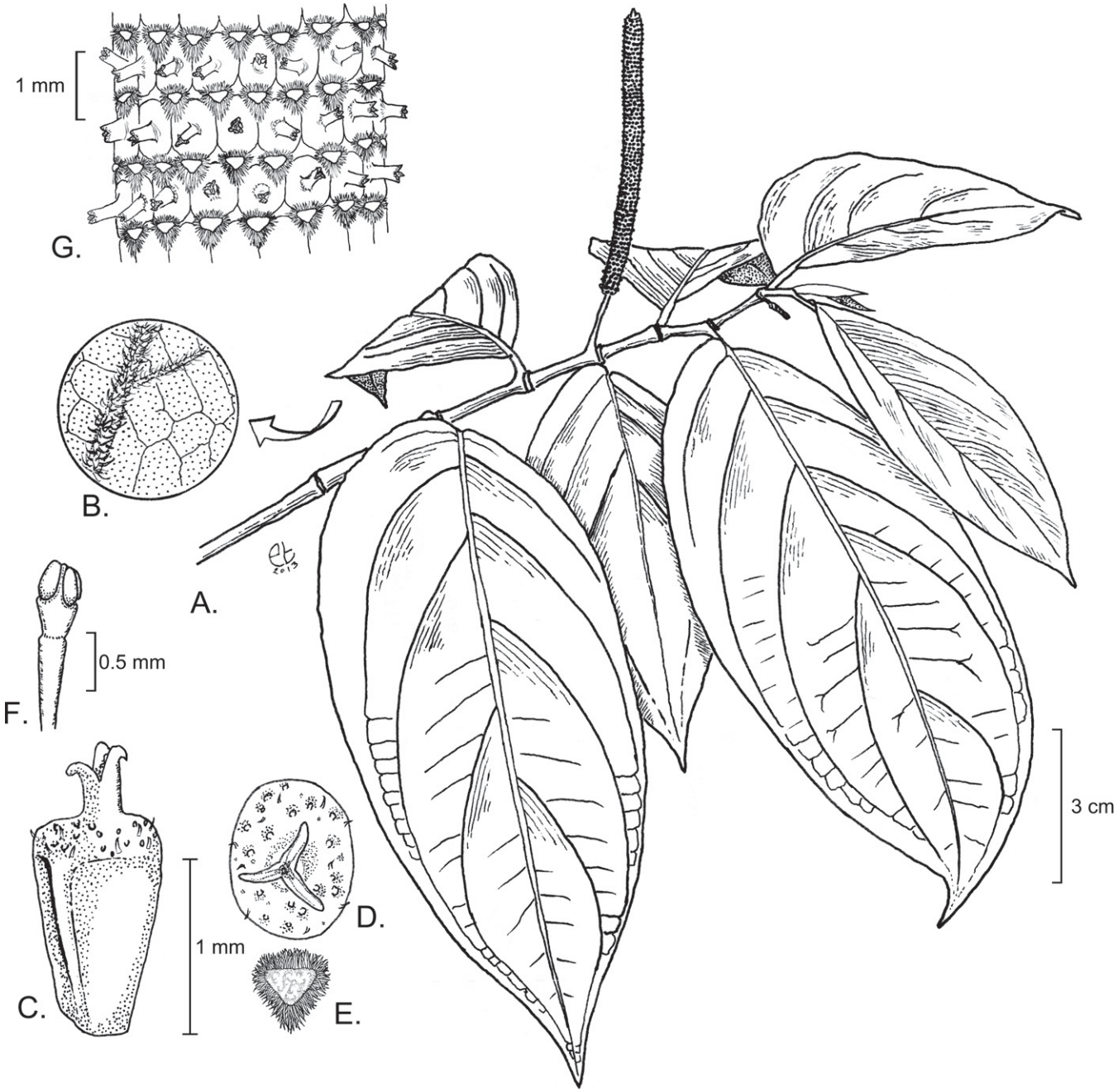

Fig. 2. *Piper abajoense* Bornstein. A. Branch with leaves and inflorescence. B. Abaxial leaf surface to indicate pubescent veins and minute pellucid dots. C. Fruit in lateral view. D. Fruit and associated bract in apical view. E. Floral bract. F. Stamen with laterally dehiscent anther. G. Portion of inflorescence with banded fruits and bracts. Drawn from pressed and liquid-preserved material from *Bornstein & Schubert 1267*.

around the spikes, bracts often fimbriate-margined and lacking an umbo, lack of basal callosities at the junction of the lamina and petiole, and fruits triangular or rounded. In Puerto Rico this species most closely resembles *Piper hispidum* Sw., but can be distinguished by the ± glabrous fruits (vs. apically densely puberulent), stylose (vs. estylose) ovary and young fruits, laterally (vs. apically) dehiscent anthers, and shorter inflorescences (< 8 cm vs. 10 + cm).

The following key can be used to identify *P. abajoense* and the other 10 species of *Piper* known from Puerto Rico.

Key to Puerto Rican Species of *Piper*

1. Spikes arranged in umbellate or paniculiform clusters (3–13 spikes per group), appearing axillary; stamens 2 per flower; plants subshrubs, scarcely woody 2
   2. Leaves rounded with peltate petiole attachment; stems, petioles, and main veins along abaxial leaf surface glabrous ..... *P. peltatum*
   2. Leaves cordiform at base with marginal petiole attachment; stems, petioles, and main veins along abaxial leaf surface puberulent ..... *P. umbellatum*
1. Spikes solitary, leaf-opposed; stamens 3–6 per flower; plants distinctly woody 3

3. Leaves palmately veined 4
4. Leaves ciliate marginally; spikes distally curved; flowers, fruits and floral bracts forming bands around the spike; plants with anise-like odor when crushed; stems, petioles, and peduncles glabrous; petioles vaginate ca. ¾ of length; floral bracts triangular or rounded when viewed from above; stamens 4 . . . . *P. marginatum*
4. Leaves glabrous marginally; spikes erect at all stages; flowers, fruits, and floral bracts not forming bands around the spike; plants lacking anise-like odor when crushed; stems, petioles, and peduncles pubescent; petioles vaginate only at very base; floral bracts cucullate; stamens 5–6 . . . . *P. amalago*
3. Leaves pinnately veined 5
5. Flowers loosely organized along the rachis, not forming bands around the spike; fruits globose, orange to red; leaves with two pairs of major secondaries, one at very base, the other at mid-region of lamina . . . . *P. blattarum*
5. Flowers densely organized along rachis, forming distinct bands around the spike; fruits rounded, triangular, or rectangular, green to brown; leaves with 3 + pairs of veins 6
6. Leaf lamina with 10–12 pairs of secondary veins that diverge along entire length of midvein; fruits rectangular (tetragonous) due to lateral compression . . . . *P. swartzianum*
6. Leaf lamina with 3–6 pairs of secondary veins that diverge along lower ½ - ⅔ length of midvein; fruits rounded to triangular 7
7. Leaves smooth and completely glabrous on adaxial surface 8
8. Petiole vaginate-winged entire length (to base of blade), the margins caducous and leaving linear scars on adaxial surface of petiole; fruits glabrous; bracts shallowly W-shaped, glabrous; prophylls 4–5 cm long . . . . *P. glabrescens*
8. Petiole vaginate at very base, lacking scar tissue; fruits apically densely pubescent; bracts triangular, short-fimbriate; prophylls 1–2 cm long . . . . *P. jacquemontianum*
7. Leaves scabrous and/or pubescent adaxially (at least along the midvein) 9
9. Spikes curved distally . . . . *P. aduncum*
9. Spikes straight throughout 10
10. Fruits apically densely puberulent; ovary and fruit lacking a style (stigmas sessile); anthers apically dehiscent; spikes (peduncle + rachis) 10 + cm long . . . . *P. hispidum*
10. Fruits essentially glabrous; ovary and young fruit with style ca. 0.5 mm long; anthers laterally dehiscent; spikes less than 8 cm long . . . . *P. abajoense*

Piper claseanum Bornst., sp. nov.—TYPE: DOMINICAN REPUBLIC. Province of Azua: Sierra Martín García, 11.2 km from Hwy. 44, ca. 8 km W of El Cruce de Quince, S of Tábara Abajo, Los Manantiales, 18°23′01″N, 70°59′09″W, 810 m, 10 January 2012, *A. Bornstein, E. Tepe, and T. Clase 1283* (holotype: JBSD; isotypes: MO, MU, SEMO).

Medium-sized, multi-branched shrub, ca. 1.7–3.0 m tall, stems with thickened nodes; leafy internodes 0.8–4.6 cm long (mean = 1.82 cm, median = 1.75 cm; N = 40), smooth, dark brown to black, and glabrous to puberulent when young, becoming striate to canaliculate, pale gray-brown, and bearing numerous warty lenticels with age. Immature prophylls 0.90–1.50 mm long (mean = 1.26 mm, median = 1.35 mm; N = 9), apex angle acute, apex shape convex, rounded, glabrous, drying dark brown to black. Leaves with petioles 1.30–4.50 mm long (mean = 2.47 mm, median = 2.40 mm; N = 40), glabrous to puberulent, vaginate at the base and lacking a stipule-like structure at all nodes; lamina 3.5–5.9 cm long (mean = 4.75 cm, median = 4.90 cm; N = 39) and 1.9–4.4 cm wide (mean = 2.74 cm, median = 2.60 cm; N = 39), elliptic, broadly elliptic, or oblong-elliptic, occasionally obovate, medially symmetrical, apex angle acute to obtuse, apex shape straight, rounded, or acuminate, base symmetrical with two black, gland-like callosities present, one on each side of the petiole, base angle acute, base shape convex to rounded, venation palmate with 3 major veins organized in basal, acrodromous pattern, coriaceous and with numerous pellucid dots visible abaxially upon drying, smooth on both surfaces, glabrous, dark green adaxially, pale green abaxially. Racemes erect at all stages and free of the leaf base, white at anthesis and in fruit; peduncles 0.30–0.95 cm long (mean = 0.55 cm, median = 0.55 cm; N = 40), glabrous to sparsely puberulent; rachis 1.20–4.85 cm long (mean = 2.87 cm, median = 2.75 cm; N = 40) and 0.4–0.8 (1.2) mm wide (mean = 0.60 mm, median = 0.60 mm; N = 40) when dry, puberulent; floral bracts 0.200–0.475 mm wide (mean = 0.31 mm, median = 0.30 mm; N = 40), cucullate in general outline, glabrous; flowers loosely organized (widely spaced) along rachis, not forming distinct bands around the axis, pedicellate, the pedicels gradually broadening to the apex, 1.3–4.2 mm long (mean = 2.66 mm, median = 2.60 mm; N = 40), puberulent; stamens 5–7, borne at top of pedicel immediately below ovary, anthers laterally dehiscent (measurements not available due to very limited material). Fruits white at maturity, ovoid to globose, 2.0–3.2 mm long (mean = 2.68 mm, median = 2.70 mm; N = 20) and 2.1–3.8 mm wide (mean = 3.14 mm, median = 3.20 mm; N = 20), glabrous to sparsely puberulent, stigmas 2–4, broad, sessile. Figure 3.

Additional Specimens Examined—DOMINICAN REPUBLIC. Azua: Sierra Martín Garciá, Distrito municipal Tábara Abajo, en un lugar denominado Los Manantiales, 203866 N, 290281 E, 760 m, 19 Feb 2008, *B. Peguero & T. Clase 4267 and 4268* (JBSD, SEMO).

Notes—*Piper claseanum* is apparently endemic to the south-central mountain range known as Sierra Martín García in the province of Azua in the Dominican Republic. It grows in shaded sites on steep, rocky hillsides from 700–850 m elevation. Plants were in late flower or mature fruit in January, so it is likely to be in full flower in November and December, with fruits persisting into February or March; additional collecting at these times would be necessary for confirmation, and similar efforts in other months would be helpful to determine if year-round flowering and fruiting occurs. The epithet *claseanum* is in honor of Teodoro Clase, long-time student of the flora of the Dominican Republic and one of the initial individuals to recognize this new species.

Piper claseanum belongs to clade *Enckea*, which includes a group of species with palmately veined leaves and the usual presence of two basal callosities at the petiole/lamina junction, erect inflorescences with the flowers, fruits, and associated bracts usually loosely organized around the inflorescence and not forming distinct bands, bracts sessile or short-pedicellate, cucullate in overall shape, and the fruits globose, ovoid, or flask-shaped. This species is most closely related to *Piper samanense* Urban based on molecular data (Fig. 1), and in

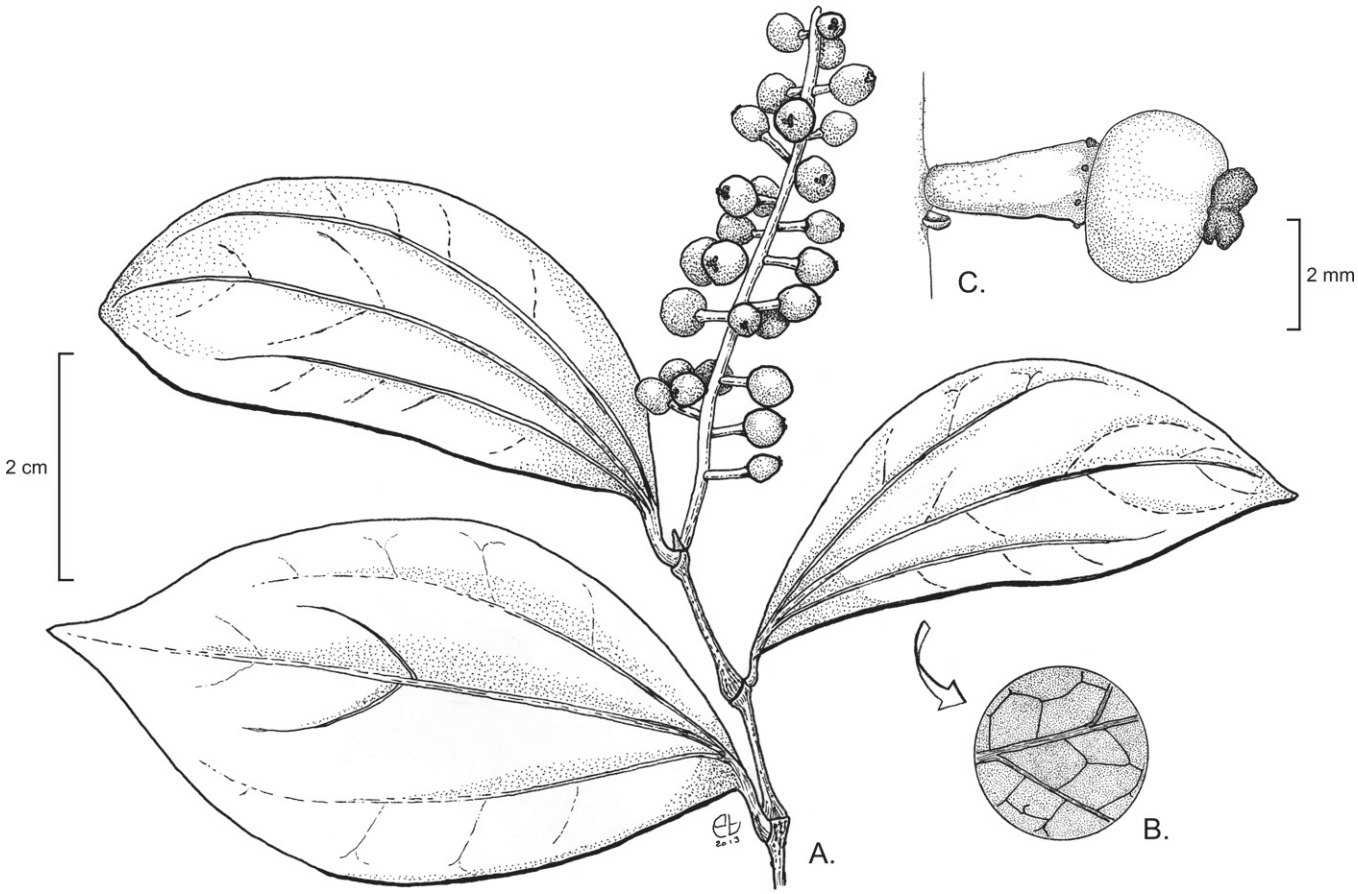

Fig. 3. *Piper claseanum* Bornstein. A. Branch with leaves and inflorescence. B. Abaxial leaf surface to indicate lack of pubescence and minute pellucid dots. C. Fruit with pedicel and associated bract. Drawn from field observations, pressed and liquid-preserved material from *Bornstein et al. 1283*.

vegetative condition appears similar due to the relatively small, leathery leaves with three primary veins and the numerous pellucid dots evident upon drying. They also share the unusual white fruit color, which appears to be a synapomorphy for these taxa. The two species can be easily distinguished because *P. samanense* has more densely packed flowers along the densely white-pubescent (vs. puberulent) rachis, the pedicels are shorter and broader, and only develop if the fruit matures (= pseudo-pedicellate), the fruits are more densely puberulent to pubescent, and the stigma lobes are quite narrow.

It is also interesting to note that the endemic species of *Enckea* from the Greater Antilles form a clade that is sister to the largely continental taxa (only the widespread *Piper amalago* L. and *P. reticulatum* L. occur in the Antilles). Further sampling of the enckeoid species endemic to Cuba [e.g. *Piper lindenianum* C. DC., *P. mananthum* C. Wright, *P. perditum* Trel., and *P. sphaerocarpum* (Griseb.) C. DC. ex C. Wright] and Haiti (*P. sinuatispicum* Trel. and *P. perpallidum* Ekman, Urb. & Trel.) would be necessary to confirm if this pattern holds.

The following key can be used to identify *P. claseanum* and other palmate-veined species from the Dominican Republic.

Key to Species of *Piper* with palmate leaf venation from the Dominican Republic

1. Spikes arranged in umbellate or paniculiform clusters (3–13 spikes per group), appearing axillary; stamens 2; plants subshrubs, scarcely woody ..... *P. peltatum*
1. Spikes solitary, leaf-opposed; stamens 3–6; plants distinctly woody 2
   2. Petiole vaginate at least ½ of entire length, with caducous wing tissue 3
      3. Stems, petioles, leaf lamina, bracts, and fruits densely reddish glandular (with pellucid dots) upon drying; inflorescence rachis densely white-pubescent; fruits oblong-elliptic with distinct style; flowers, fruits, and bracts not forming bands around the spike ..... *P. oviedoi*
      3. Stems, petioles, leaf blades, bracts, and fruits lacking glands (pellucid dots) upon drying, or if present, translucent, not reddish; inflorescence rachis glabrous; fruits round or tetragonous; flowers, fruits, and bracts forming bands around the spike 4
         4. Leaves ciliate marginally; spikes distally curved; plants with anise-like odor when crushed; stems, petioles, and peduncles glabrous; floral bracts densely fimbriate; fruits rounded ..... *P. marginatum*
         4. Leaves glabrous marginally; spikes straight at all stages; plants lacking anise-like odor when crushed; stems, petioles, and peduncles tomentose; floral bracts hirsute; fruits tetragonous ..... *P. picardae*
   2. Petiole vaginate only at very base, lacking wing tissue 5
      5. Leaves membranous to chartaceous with 5–7 primary veins; fruits brown to black 6

6. Leaves hirsutulous along main veins below; inflorescences with flowering segment 0.5–1.5 cm long, borne on filiform peduncle; fruits depressed globose, lacking a style . . . . . *P. buchii*
6. Leaves glabrous or puberulent below; inflorescences with flowering segment 3 + cm long, borne on stout peduncle; fruits ovoid, evidently stylose . . . . . *P. amalago*

5. Leaves coriaceous with 3 primary veins; fruits white 7
7. Flowers closely spaced along inflorescence axis; rachis densely white-pubescent; flowers sessile, but fruits with pseudo-pedicel (developing upon fruit maturation); pseudo-pedicel 1.5–2 mm long, 2.5–3.5 mm wide, densely white-pubescent; fruits > 5 mm wide, densely white-pubescent; stigma lobes narrow, < 0.25 mm wide . . . . . *P. samanense*
7. Flowers widely spaced along inflorescence axis; rachis puberulent; flowers and fruits with true pedicels; pedicels 1.3–4.2 mm long (μ = 2.66), 0.5–1.2 mm wide, puberulent; fruits < 4 mm wide, glabrous to puberulent; stigma lobes broad, 0.4–0.75 mm wide. . . . . *P. claseanum*

Acknowledgments. We are grateful for logistic and field assistance during our travels to James Ackerman and Frank Axelrod at the University of Puerto Rico-Río Piedras (UPRRP), Francisco Peréz at El Verde Field Station in Puerto Rico, and Alberto Veloz and Theodoro Clase at the Jardín Botánico Nacional Dr. Rafael M. Moscoso in the Dominican Republic. Heather Schubert also provided valuable field assistance to AJB during the 2011 collecting trip. We appreciate the useful comments and suggestions of one anonymous reviewer and Stefan Wanke to improve the manuscript. Travel expenses to AJB for all three field sessions were provided by the Grants and Research Funding Committee at Southeast Missouri State University and to EJT for the 2012 collecting trip by the National Science Foundation PBI: *Solanum* grant (DEB-0316614).

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