



A revision of the genus *Ruagea* (Meliaceae: Melioideae)

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Summary. The neotropical genus *Ruagea* H.Karst. is revised. Fifteen species are recognised, including three *R. obovata* T.D.Penn., *R. beckii* T.D.Penn. and *R. parvifructa* T.D.Penn. which are described as new to science. A key to the species is presented, along with information on the morphology, distribution, ecology, conservation assessments, local names, uses and field characters. All species are mapped and illustrated with line drawings and all specimens seen are cited in a list of exsiccatae.

Key Words. Andes, conservation, distribution, montane forest, morphology, trees.

Introduction

Ruagea is a small genus of trees comprising 15 species in Guatemala, Costa Rica, Panama and throughout Andean South America from Venezuela to Bolivia. Surprisingly it has not yet been recorded in Honduras or Nicaragua, but it is to be expected there. With only two exceptions all species of *Ruagea* are confined to montane rain forest or cloud forest, mostly between 1000 m and 3500 m altitude. The two exceptions are *R. insignis* and *R. glabra*, both of which do occur at high altitude (up to 3500 m), but are also present in lowland rain forest down to 200 m altitude.

Ruagea forms a monophyletic group within the subfamily Melioideae, with both morphological and molecular data indicating a close relationship with *Guarea* F.Allam. ex L. (C. de Candolle 1878) (69 species in tropical America), Pennington (1975, 1981), Muellner *et al.* (2006), Koenen *et al.* (2015)). Both genera share the staminal tube of completely united filaments with anthers inserted within the throat, stipitate nectary-disk below the ovary, ovary locules with 1 – 2 superposed ovules and loculicidal capsular fruit with fleshy seeds. The two diagnostic morphological characters that separate *Ruagea* from *Guarea* are the imbricate (quincuncial) sepals (calyx with an entire margin or with open aestivation in *Guarea*), and the seed with a strongly swollen basal sarcotesta (sarcotesta in *Guarea* not swollen at base). Other supporting characters separating *Ruagea* from *Guarea* are the pinnate leaves lacking a dormant terminal bud, whereas most *Guarea* species have pinnate leaves with a dormant terminal bud (pseudogemma) exhibiting periodic growth increments, 5-merous flowers (mostly 4-merous in *Guarea*), 3-valved capsule (2 – 10-valved in *Guarea*), embryo

with collateral cotyledons (embryo usually with superposed cotyledons in *Guarea*).

Ruagea also has a close morphological similarity to *Cabrlea* A.Juss. (*C. canjerana* (Vell.) Mart., a single widespread species in tropical America (Harms 1940; Pennington 1981) and specimens of the two genera are often confused (Harms 1940; Pennington 1975). They share the pinnate leaf without a dormant terminal bud, 5-merous flowers with imbricate sepals, complete staminal tube with anthers inserted within the throat and embryo with collateral cotyledons. *Ruagea* differs from *Cabrlea* in generally lacking the transparent lines and dots in the leaves (which are abundant in *Cabrlea*), in the stipitate nectary-disk (cyathiform in *Cabrlea*), in the 3-locular ovary (5-locular in *Cabrlea*) and in the 3-valved capsule (5-valved in *Cabrlea*). The presence of the cyathiform nectary in *Cabrlea*, which is unique in tropical American Meliaceae, is indicative of a relationship with the South East Asian and Pacific genus *Dysoxylum* Blume (Roemer 1846; Harms 1940; Pennington 1975). This relationship is confirmed by recent molecular analyses (Muellner *et al.* 2006; Koenen *et al.* 2015), with the most recent study placing *Cabrlea* as sister to a clade of South Pacific *Dysoxylum* species, including *D. spectabile* Hook.f. (New Zealand), *D. rufescens* Vieill. ex Sebert & Pancher (New Caledonia) and *D. bijugum* (Labill.) Seem. (Fiji) (Koenen *et al.* 2015).

In the most recent monographic account of *Ruagea* (Pennington 1981), five poorly defined species were recognised, plus four species of doubtful status based on inadequate material. Since then two new species (*R. membranacea*, *R. microphylla*) have been described by Palacios (1994) and a full account published for the *Flora of Ecuador* (Palacios 2007).

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The present study, which recognises 15 species, including three new species, is based on a morphological analysis of 580 collections, with 120 of these providing supplementary molecular data for an ongoing phylogenetic study (Rojas-Andres *et al.* [submitted](#)). As in 1981, it is still the case that most species are morphologically poorly defined and often based mainly on very variable quantitative leaf characters. Molecular data appears to provide good support for some species such as *Ruagea membranacea*, *R. insignis*, *R. ovalis* and *R. beckii*, but a group of species surrounding *R. glabra* containing *R. tomentosa*, *R. trisperma*, *R. pubescens* is still unresolved (Rojas-Andres *et al.* [submitted](#)).

Three of the four species classed as ‘doubtful’ in the previous account (Pennington 1981) can now be placed with some certainty: *Ruagea subviridiflora* is recognised as a species distinct from *R. glabra* on the basis of copious new Bolivian collections, *R. smithii* is confirmed as a synonym of *R. pubescens* and *R. tomentosa* is recognised as a distinct species, confirming the decision of Palacios (2007). We also agree with Palacios (2007) in recognising *R. trisperma* as a distinct species. *Ruagea floribunda*, formerly regarded as a synonym of *R. glabra* (Pennington 1981), is provisionally recognised here as a doubtfully distinct species.

NOTE ON SPECIMEN CITATION. All cited specimens have been seen by the first author. ‘Representative Collections’ indicates that one specimen from each major political division (Department) is cited. ‘Collections Examined’ indicates that all specimens studied are cited. All specimens used in this study are in the List of Exsiccatae at the end.

Morphology

HABIT. All *Ruagea* species are treelets or medium to large trees up to 35 m high and 130 cm dbh. The very limited information on bark characteristics indicates that both smooth bark (*R. insignis*) and fissured bark (*R. pubescens*) occur in the genus. The bark slash is usually coloured pinkish and is fragrant. All species except *R. insignis* are evergreen.

YOUNG GROWTH. The twigs are frequently stout, up to 1.5 cm diam. and in the majority of species hollow. The hollow twigs may be inhabited by ants, as in *R. insignis*. The buds are usually naked and the young twigs generally smooth, pale-coloured and generally with some raised lenticels. *Ruagea insignis* is unusual in having a ring of small coriaceous bud scales surrounding the apex of the fertile shoots. This species is sometimes briefly deciduous and the bud scales subtend the new inflorescences which develop before or at the same time as the new foliage. The bud scales are caducous, leaving a ring of small persistent scars

and the distance between each ring of scars indicates each growth increment.

LEAVES. The leaves of all *Ruagea* species are clustered at the shoot apex and pinnate. *Ruagea insignis* is always paripinnate, lacking the terminal leaflet which is present in all other species. In most species all the leaflets develop at the same time, but in *R. glabra* and in *R. floribunda* there is a distinct tendency for the lower pair or lower several pairs to develop first, with the upper leaflets developing later. In this characteristic it closely resembles *Cabralea* and sterile material of these species is often confused. This unequal development of the leaflets can be seen as a progression towards the condition found in the closely related *Guarea*, which has pinnate leaves with an apical bud (pseudogemma) showing one or more increments of growth over the lifetime of the leaf. The number of leaflets varies from 2 – 20 pairs, and is sometimes an important specific character, but elsewhere it is extremely variable, so must be used with caution. The indumentum is of simple, multicellular, unbranched hairs, mostly easily visible with a × 10 hand lens, but a much higher magnification is required to see the closely appressed indumentum of *R. trisperma*. Venation is generally eucamptodromous or brochidodromous or a combination of both, in which case it is eucamptodromous in the lower half and brochidodromous towards the apex. Higher order venation is generally reticulate, but occasionally oblique and parallel as in *R. tomentosa*.

FLOWERS. Inflorescences are generally clustered near the shoot apex in the axils of recently opened leaves, or as in *Ruagea insignis* slightly before leaf development in the axils of small bud scales. The inflorescence varies from a slender, little-branched panicle a few cm long to a large much-branched panicle to 50 cm long. The flowers are functionally unisexual (plant dioecious), but the male and female flowers are morphologically similar with both bearing well-developed rudiments of the opposite sex. Male flowers have well-developed, fully functional dehiscent anthers with pollen and a pistillode containing rudimentary ovules with style and discoid style-head. Female flowers have a slightly larger ovary with larger better-developed ovules and well-developed stamens, but the anthers are somewhat shrunken, indehiscent and do not contain pollen. Flower size in the genus *Ruagea* varies from c. 0.3 – 1.2 cm long and all species have 5 sepals, 5 petals, 10 stamens fused into a complete staminal tube and a 3-locular ovary. The 5 sepals are minute, generally only 1 – 2 mm long, but clearly imbricate at least at the base. The corolla consists of 5 free, imbricate (quincuncial) petals, usually glabrous and often with a ciliate margin. The androecium comprises usually 10 stamens completely fused into a staminal tube with a crenulate or shallowly lobed margin, the lobes alternating with the anthers which

are inserted in the throat of the tube. The anthers may be completely included or partially exerted from the apex of the tube. Both staminal tube and anthers may bear varying amounts of indumentum or are completely glabrous. Sometimes, as in *R. hirsuta*, the anthers are distinctly barbate, with a few long hairs protruding from the base. A nectary-disk, in the form of a small swelling or collar below the ovary, is usually present. The ovary is 3-locular, with each locule containing 1–2 superposed ovules and the short style bears a large discoid style-head just above the anthers and completely filling the space at the apex of the staminal tube.

FRUIT AND SEED. The fruit of *Ruagea* is a leathery 3-valved loculicidal capsule, usually with conspicuous pale lenticels, with a thin cartilaginous endocarp and dehiscing from the apex to the base. The number of seeds varies from 2 superposed in each of the 3 valves by progressive abortion to a solitary seed filling the entire fruit. The seeds are fleshy, with a thin membranous coat and covered by a sarcotesta which is much swollen at the base. The report of a free arillode partially surrounding the seed of *R. insignis* (Pennington 1981) has not been reconfirmed. The embryo has thick plano-convex collateral cotyledons with a small apical radicle extending to the surface and it lacks endosperm. No information is available on the germination or seedling characteristics.

Taxonomic Treatment

Ruagea *H.Karst.* (Karsten 1863: 51, t.126); Triana & Planchon (1872: 367); Harms (1940: 137, t. 31, fig. Z); Pennington (1975: 492, fig. 11c; 1981: 242); Palacios (2007: 47).

Guarea sect. *Ruagea* C.DC. (de Candolle 1878: 577).
Type Species. *Ruagea pubescens* H.Karst.

Evergreen or rarely deciduous *trees or treelets* with pinnate leaves, usually imparipinnate (paripinnate in *Ruagea insignis*), leaves sometimes with limited apical growth. Young shoots usually naked, but in *R. insignis* protected by a cluster of small bud scales. *Leaves* not glandular-punctate or -striate. *Flowers* unisexual (plants dioecious), in axillary panicles or clustered at the shoot apex in the axils of fallen bud scales. *Sepals* (4–) 5 (– 6), free, quincuncial. *Petals* 5, free, quincuncial. *Staminal tube* cylindrical, campanulate or urceolate, margin undulate, crenulate or shortly lobed, lobes sometimes emarginate. *Anthers* (8–) 10 (– 11), inserted in the throat of the staminal tube, included or partly exerted and alternating with the lobes of the staminal tube. *Nectary* short, broad and stipitate, sometimes expanded into a disk below the ovary, sometimes absent. *Ovary* 3-locular, locules with 1–2 superposed ovules, often glabrous, style-head discoid. *Fruit* a leathery usually lenticellate 3-valved loculicidal capsule, valves containing 1–2 superposed seeds or fewer by abortion and fruit sometimes 1-seeded; endocarp thin, cartilaginous. *Seed* with a thick fleshy basal sarcotesta. Seed coat membranous. Embryo with thick, plano-convex, collateral cotyledons, radicle apical, extending to the surface; endosperm absent.

DISTRIBUTION. Fifteen species confined largely to montane rain forest or cloud forest, from Guatemala, Costa Rica and Panama and Andean South America from Venezuela to Bolivia.

Key to the species of *Ruagea*

1. Leaves paripinnate, bud scales present on new growth subtending the inflorescences 2. **R. insignis**
1. Leaves imparipinnate, bud scales absent 2
2. Leaves essentially glabrous 3
2. Leaves with obvious indumentum (lens required to see fine appressed indumentum of *R. trisperma*) 9
3. Leaflets 8–12 pairs, uppermost lateral leaflets 3–4 times as long as broad, petals c. 4 mm long. 7. **R. beckii**
3. Leaflets mostly 2–7 pairs, uppermost lateral leaflets 2–3 times as long as broad, petals 4.5–10.5 mm long 4
4. Uppermost lateral leaflets c. 32 cm long 14. **R. floribunda**
4. Uppermost lateral leaflets <20 cm long 5
5. Uppermost lateral leaflets with obtuse to rounded or truncate apex 6
5. Uppermost lateral leaflets generally with acute, narrowly attenuate or cuneate apex 7
6. Leaflets 2–4 pairs, 11–18 cm long, obovate (central and southern Peru, Bolivia) 5. **R. obovata**
6. Leaflets 3–7 (– 9) pairs, 3.2–13.5 cm long, oblong-elliptic to oblanceolate (northern Peru and southern Ecuador) 8. **R. microphylla**
7. Leaflets membranous, panicles lax-flowered (Amazonian Ecuador) 1. **R. membranacea**
7. Leaflets chartaceous to coriaceous, panicles densely-flowered 8
8. Leaflet base asymmetric, leaflets usually coriaceous (central and southern Peru, Bolivia) 4. **R. subviridiflora**
8. Leaflet base regular, leaflets usually chartaceous (widespread) 13. **R. glabra**
9. Leaflets 8–15 (– 18) pairs 10

9. Leaflets (2–) 3–8 (–9) pairs 11
10. Petiole 5.5–8 cm long, leaf rachis 28–34.5 cm long, leaflets membranous, softly pubescent with erect hairs, petals c. 4 mm long 7. **R. beckii**
10. Petiole 1–3 cm long, leaf rachis 8–22 cm long, leaflets coriaceous, leaf indumentum of crisped hairs, petals (4.5–) 6–8 mm long 6. **R. hirsuta**
11. Uppermost lateral leaflets 17.2–37 cm long 12
11. Uppermost lateral leaflets 3–17 cm long 15
12. Petals mostly 8–14 mm long 13
12. Petals mostly 5.5–7 mm long 14
13. Leaflets coriaceous, leaflet apex and base obtuse to rounded or truncate, secondary veins 10–17 pairs, lower lamina with crisped pubescence, tertiary and higher order venation obscure 10. **R. pubescens**
13. Leaflets chartaceous, leaflet apex and base narrowly attenuate, acuminate, acute or obtuse, secondary veins 15–22 pairs, lower lamina softly pubescent with erect hairs, tertiary and higher order venation prominent 11. **R. tomentosa**
14. Fruit 1–1.1 cm long, lower lamina softly pubescent with erect hairs 9. **R. parvifructa**
14. Fruit 3.5–4.5 cm long, indumentum of lower lamina of minute appressed hairs (lens needed) 12. **R. trisperma**
15. Petals (7–) 10–14 mm long, fruit 3.2–5 cm long 10. **R. pubescens**
15. Petals 3–9 mm long, fruit 1–2.5 cm long 16
16. Lower lamina softly pubescent with erect hairs, leaflet apex mostly acute, acuminate or cuspidate 13. **R. glabra**
16. Lower lamina with indumentum of short crisped hairs, leaflet apex mostly obtuse, rounded or truncate 17
17. Petals 4.5–6 mm long, staminal tube 4–5 mm long, mostly glabrous (southern Ecuador, northern Peru) 8. **R. microphylla**
17. Petals 3–5 mm long, staminal tube 2–3 mm long, often coarsely hairy inside (southern Peru and Bolivia) 3. **R. ovalis**

1. **Ruagea membranacea** W.Palacios (1994: 162), (2007: 52). Type. Ecuador, Napo, El Chaco, right bank of R. Quijos (Coca), La Ave Brava, 0.36S, 77.31W, Sept. 1990, fl., Palacios 5445 (holotype QCNE, n.v.; isotypes K n.v., MO n.v., NY, QCA n.v.).

Bud scales absent. Young shoots 3–5 mm diam., smooth, finely appressed puberulous, soon glabrous, lenticels few or absent. *Leaves* imparipinnate, petiole 1.4–3.5 (–5) cm long, semiterete or slightly channelled above, sparsely appressed puberulous to glabrous; rachis 3–13.5 cm long, semiterete and slightly marginate below the leaves, sparsely appressed puberulous to subglabrous; petiolule of lateral leaflets 1–2 mm long, petiolule of terminal leaflet 4–8 mm long. *Leaflets* opposite or subopposite, 2–5 pairs, uppermost lateral 5.2–13.7 cm long, 1.9–3.8 cm broad, oblong-elliptic or elliptic, apex narrowly acuminate, base narrowly attenuate, sometimes slightly asymmetric, membranous, glabrous; basal leaflets 1.8–6.8 cm long, 1.1–3.5 cm broad, elliptic or elliptic-lanceolate, apex acuminate, base narrowly attenuate, often slightly asymmetric; terminal leaflet 5.5–15 cm long, 2.1–5 cm broad, oblong or elliptic, apex narrowly acuminate, base narrowly attenuate to acute; venation usually eucamptodromous in the lower half, brochidodromous in the upper half, midrib flat or slightly sunken on the upper surface, secondaries 10–16 pairs, ascending, slightly arcuate and convergent; intersecondaries short to moderate; tertiaries reticu-

late. *Inflorescence* axillary, 10–26 cm long, a lax-flowered panicle, the lower lateral branches to 6 cm long, subglabrous, pedicel 2–3 mm long above the articulation. *Flowers* unisexual (plant dioecious), male flowers only seen. *Sepals* 5, c. 1 mm long, ovate to suborbicular, apex obtuse to rounded, with scattered short hairs outside, glabrous inside, margin sparsely ciliate. *Petals* 5, 6–8 mm long, 2–3 mm broad, oblong to broadly spatulate, apex rounded, glabrous, margin not ciliate. *Staminal tube* 5–6 mm long, 2–3 mm broad, tubular or tubular-campanulate, margin crenulate, glabrous, anthers 10, c. 1 mm long, glabrous. *Nectary* a slightly swollen stipe below the ovary, c. 1 mm long, glabrous. *Ovary* in female flower not seen. *Pistillode* of male flower c. 1.5 mm long, ovoid, glabrous, 3 (–4)-locular, locules with 2 superposed ovules, style 2.5–3 mm long, glabrous, style-head discoid. *Capsule* c. 2 cm long, 2–3 cm broad, globose to obovoid, apex rounded, base obtuse to rounded, smooth, brown with pale lenticels, 3 (–4)-valved, valves with 1–2 superposed seeds, pericarp c. 0.5 mm thick. *Seed* c. 1.2 × 1 cm, with a thick basal sarcotesta, seed coat membranous; embryo with thick plano-convex, collateral cotyledons, radical apical, included. Fig. 1.

FIELD CHARACTERS. Evergreen treelet to 7 m high and 7 cm diam. with hard, pinkish wood. The foliage is membranous and almost transparent when young (Palacios 1994). Flowers with pale green or greenish-

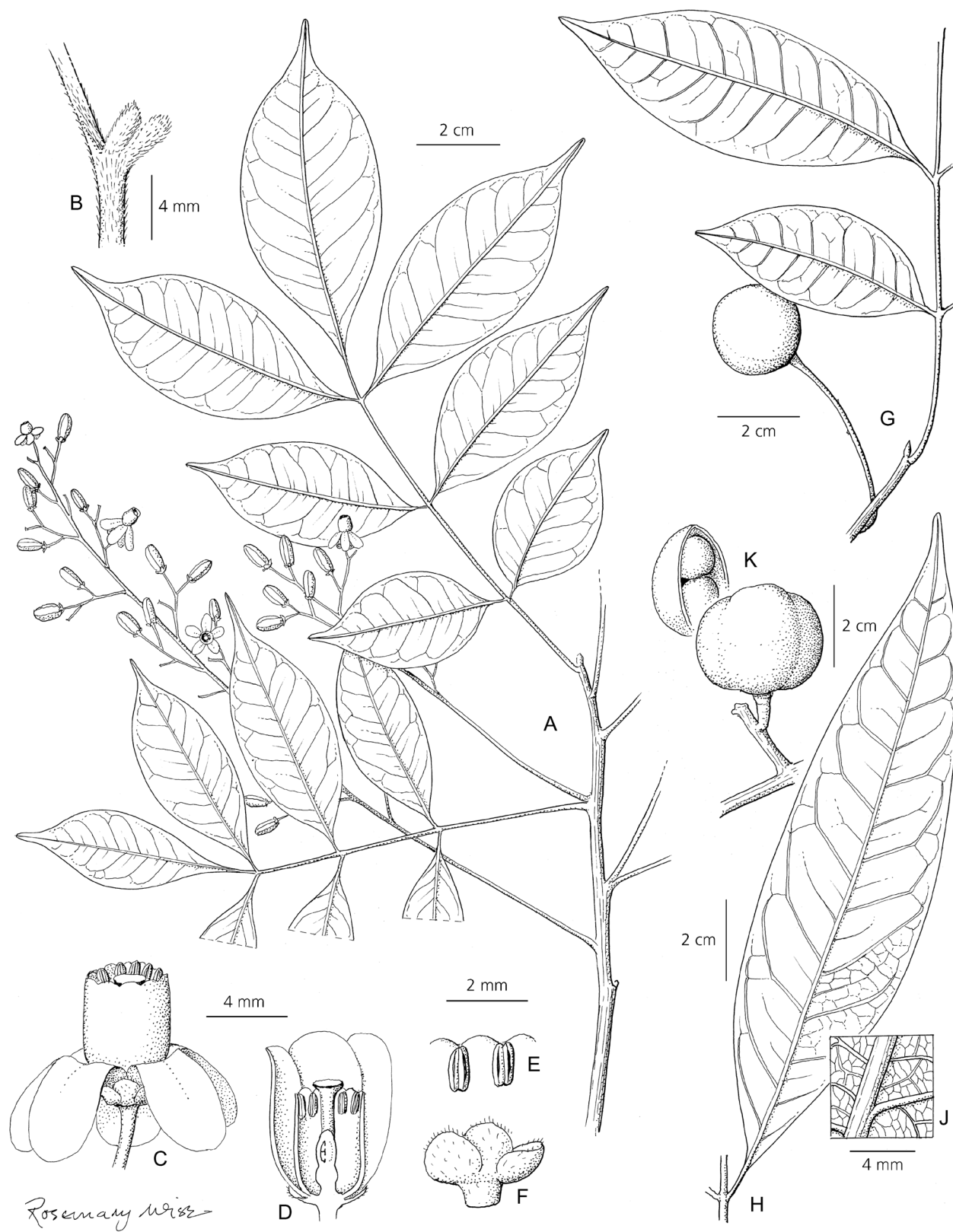


Fig. 1. *Ruagea membranacea*. A habit with inflorescence; B shoot apex; C flower; D half flower; E anthers; F calyx; G leaf and fruit; H leaflet; J enlargement of leaflet underside; K fruit. A, B Palacios & Neill 4714; C – F Homeier & Chinchero 1783; G J. L. Clark 2278; H – K Palacios 5333. DRAWN BY ROSEMARY WISE.

cream petals. Fruit maturing yellowish or orange with pale lenticels, and the seeds have a red sarcotesta. Flowering recorded from Sept. to Nov. and mature fruit have been collected in Sept. and March.

DISTRIBUTION AND ECOLOGY. Known only from two small populations on the slopes of the Volcán Sumaco and surrounding areas on the eastern slopes of the Ecuadorean Andes. On volcanic soils in very wet montane forest (rainfall in excess of 4500 mm per annum) between 1700 m and 2000 m alt. (Map 1).

COLLECTIONS EXAMINED. ECUADOR. Napo: Sumaco-Galeras National Park, south slope of Sumaco, 0.36S, 77.35W, *Homeier & Chinchero* 1783 (K); Cantón Archidona, Volcán Sumaco, between crater lake and Pacto, 0.36S, 77.38W, *J. L. Clark* 2278 (K, MO, US); Cantón El Chaco, R. Quijos, Finca La Ave Brava, 0.12S, 77.39W, *Palacios* 5309 (K, MO), 5333 (K, MO), 5445 (NY); Cantón Archidona, southern flank of Volcán Sumaco, 0.36S, 77.35W, *Palacios & Neill* 4714 (MO).

CONSERVATION STATUS. This species was assessed by Valenzuela & Pitman (2004) as Vulnerable B1ab(iii). It has a very small extent of occurrence (EOO) of 45 km² and is known from only two subpopulations, which are threatened by habitat destruction.

RELATIONSHIPS. A distinctive species on account of the few, slender, membraneous, glabrous leaflets, lax-flowered inflorescence and glabrous flowers. DNA

data indicates that *Ruagea membranacea* (plus 1 unidentified Colombian collection, (*Huertas & Camargo* 6510)) is a strongly supported basal clade, sister to the rest of the genus (*Rojas-Andres et al. submitted*).

2. *Ruagea insignis* (C.DC.) T.D.Penn. (Pennington 1981: 249); *Palacios* (2007: 51).

Cabralea insignis C.DC. (in J. D. Smith 1894: 1). Type.

Guatemala, Dept. Zacatepequez, Acatepeque, fr., *J. D. Smith* 2570 (holotype G; isotypes G, K (fr. only), NY, US).

Guarea caoba C.DC. (de Candolle 1905: 421). Type.

Costa Rica, Cartago, Tucurrique, fl., fr., *Tonduz & Pittier* 13113 (holotype G; isotypes BM, CR, G, GH, K, M, MICH, W).

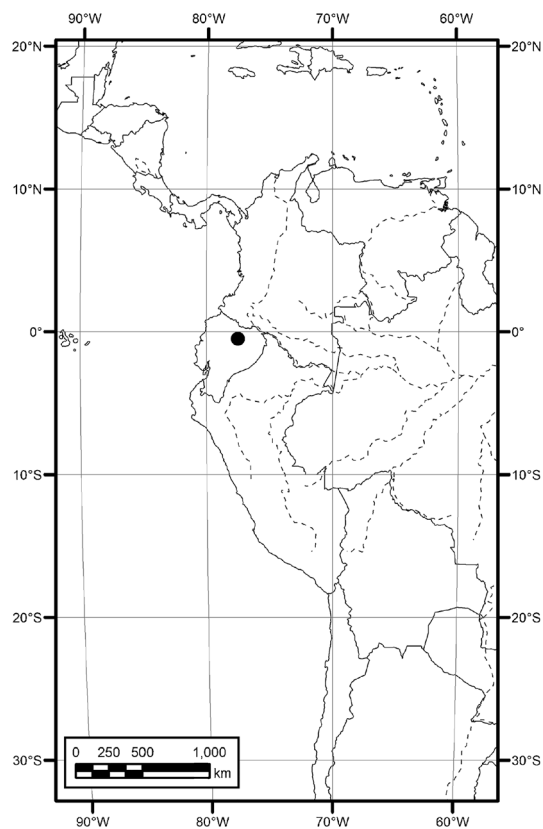
Ruagea caoba (C.DC.) Harms (1925: 428).

Ruagea tessmannii Harms (1928: 241). Type. Peru, upper Amazon, mouth of Santiago R., fl., *Tessmann* 4029 (isosyntype G).

Ruagea surutuensis Harms (1928: 347). Type. Bolivia, Prov. Sara, Dept. Santa Cruz, Rio Surutu, fl., *Steinbach* 7283 bis (holotype B destroyed; isotypes A, BM, F, G, GH, GOET, K, MO, NY, PH, S, U).

Guarea tessmannii (Harms) J.F. Macbr. (Macbride 1949: 773).

Young fertile shoots terminated by a congested cluster of broadly lanceolate bud scales which subtend the inflorescences; twigs usually hollow, 0.6 – 2 cm diam., sparsely puberulous at first, soon glabrous, pale greyish-brown, smooth, lenticellate. *Leaves* paripinnate, petiole 4.5 – 12 cm long, terete or semiterete, sometimes striate, subglabrous or sparsely puberulous; rachis 14 – 52 cm long, terete or semiterete, sometimes striate, sparsely puberulous to glabrous; petiolule 0 – 1.5 mm long. *Leaflets* opposite, 5 – 20 pairs, uppermost 8 – 21 cm long, 2 – 7.3 cm broad, narrowly oblong, oblong-elliptic or oblong-lanceolate, apex obtuse, acute or narrowly attenuate, base usually asymmetric, acute one side, obtuse to rounded or cordate on the other, or occasionally base symmetrical and rounded, chartaceous, sparse pale yellowish pubescence on undersurface or glabrous; basal leaflets (often caducous) 2.3 – 3.5 cm long, 1.3 – 2.8 cm broad, ovate, apex acute or obtuse, base truncate or cordate; venation usually eucamptodromous, sometimes brochidodromous in the upper half, occasionally entirely brochidodromous, midrib flat or slightly sunken on the upper surface; secondaries 12 – 20 pairs, ascending, straight or arcuate, parallel or slightly convergent; intersecondaries few to numerous, short to moderately long; tertiaries reticulate. *Inflorescences* clustered in the axils of fallen bud scales or axillary, 6.5 – 18 cm long, a slender panicle with a few short branches near the base to 2 cm long, subglabrous, pedicel 0.75 – 1 mm long above the articulation. *Flowers* unisexual (plant dioecious). *Sepals* 5, 0.5 – 2 mm long, ovate to orbicular, apex acute to rounded, pubescent outside, glabrous inside, margin ciliate. *Petals* 5, 5 – 6 mm



Map 1. Distribution of *Ruagea membranacea*.

long, 1.5 – 2 mm broad, oblong to spatulate, sparsely puberulous to glabrous outside, glabrous inside, margin slightly ciliate or not. *Staminal tube* 4 – 5 mm long, 2 – 3 mm broad, shortly tubular or campanulate, shortly crenulate or with 10 small lobes, glabrous, anthers 8 – 11, 0.5 – 0.75 mm long, glabrous, antherodes in female slender, without pollen, not dehiscent. *Nectary* a small swollen stipe below the ovary, c. 0.5 mm long, glabrous, sometimes absent. *Ovary* 1 – 1.5 mm long, ovoid, glabrous, 3-locular, locules with 2 superposed ovules, style 1.5 – 2.5 mm long, glabrous, style-head discoid, pistillode similar, with well-developed non-functional ovules. *Capsule* 3.7 – 4.5 cm diam., +/-globose, with rounded apex and base, with or without a short stout stipe, rather rough, brown (when dry) with numerous large pale lenticels, glabrous, 3-valved, valves with 1 – 2 superposed seeds, pericarp 1 – 1.5 mm thick, endocarp usually differentiated as a cartilaginous layer surrounding each seed. *Seed* (when solitary in valve) c. 1.8 – 2 × 1.6 × 1.2 cm, with large ventral hilum 1.2 – 1.6 × 0.9 – 1.3 cm, and with thickened basal sarcotesta, when valves 2-seeded then upper seed truncate at base and lower seed truncate at apex, seed coat membranous; embryo with thick, plano-convex, collateral cotyledons, radical apical included or extending to the surface. Fig. 2.

FIELD CHARACTERS. A large briefly deciduous or evergreen tree to 35 m high and 130 m diam., with smooth lenticellate bark. The twigs are often massive and hollow and frequently inhabited by ants. Leaves on sterile shoots can reach more than 1 m long. The bud scales which subtend new growth bearing the inflorescences are unique to this species of *Ruagea*, but they do not occur on sterile shoots, so are absent from many herbarium specimens. The ring of scars left by the fallen bud scales remain visible on old shoots, clearly indicating the growth increments. Flowers with sweet scent and pale green or occasionally reddish petals. Mature fruit orange-brown with orange or red seeds. Flowering recorded Sept. and Feb. (Costa Rica), May and Oct. (Ecuador), Sept. to Jan. (Peru), Oct. (Bolivia). Mature fruit in March (Guatemala), Feb., March, June (Costa Rica and Panama), Jan., April and June (Ecuador).

DISTRIBUTION AND ECOLOGY. Guatemala, Costa Rica, Panama, Pacific and Amazonian Ecuador, Amazonian Peru and Bolivia, not yet recorded from Colombia but almost certainly present. This species has a wide altitudinal range in lowland and montane rain forest from 200 m to 2500 m altitude (Map 2).

REPRESENTATIVE COLLECTIONS. GUATEMALA. Chimaltenango: Volcán Fuego, Finca Montevideo, *Steyermark* 52068 (US). **Solola:** Volcán Atitlan, *Steyermark* 48030 (F). Zacatepequez: Aguacatepec, 14.00N, 90.00W, *J. D. Smith* 2570 (G, K). **COSTA RICA. Cartago:** Cantón Turrialba, Tuis, Calle Rivel, 9.49N, 83.34W, *Rodríguez et al.* 1936 (F, K). **Limón:** Parque Nacional Talamanca, La Amistad, sector Laguna

Dabagri, 9.37N, 83.16W, *Bridgewater* 4146 (MO). **Puntarenas:** Las Cruces, Jardín Botánico Wilson, 8.47N, 82.58W, *Vargas et al.* 1367 (K). **San José:** Tarazu, Naranjillo, Cuenca Río Naranjo, 9.33N, 84.01W, *Estrada et al.* 2246 (F, K). **PANAMA. Chiriquí:** near Paso Canoas, 8.00N, 82.00W, *Liesner* 224 (MO). **ECUADOR. Esmeraldas:** Río Hoja Blanca, 0.00N, 79.00W, *Little & Dixon* 21072 (NY). **Loja:** Cantón Macara, Achima, junction to Papayal, 4.18S, 79.49W, *Palacios* 3346 (K). **Napo:** Yasuní National Park, Pozo Daimi, 1.02S, 76.10W, *Neill et al.* 8452 (G, K). **Orellana:** Yasuní National Park, via Repsol, NPF-Tivacuno km 9, 0.40S, 76.20W, *Perez et al.* 2925 (MO). **Pichincha:** Santo Domingo, 0.00S, 79.00W, *Benoist* 3014 (S). **Sucumbios:** 3 km NW of Añangu, Sacha Lodge, 0.39S, 76.26W, *J. L. Clark et al.* 1142 (K, US). **PERU. Amazonas:** Bagua Distr., Aramango, Cerros de Nueva Esperanza, 5.28S, 78.23W, *Vásquez et al.* 27498 (K, MO). **Huánuco:** Prov. Puerto Inca, Dto Yuyapichis, Dantas, 9.40S, 75.02W, *Flores & Tello* 1210 (MOL). **Junin:** Prov. Jauja, Satipo, Granja Reserva Forestal, 11.00S, 74.00W, *B. Vasquez* 40 (MOL). **BOLIVIA. La Paz:** Franz Tamayo, ANMI, Apolobamba, between Pelechuco and Apolobamba, 14.46S, 69.01W, *Fuentes et al.* 10334 (K). **Santa Cruz:** Prov. Sara, R. Surutu, 17.00S, 63.00W, *J. Steinbach* 7283 (F, G, K, NY).

CONSERVATION STATUS. This species has a large extent of occurrence of over 2.3 million km² and an area of occupancy of 92 km². However, considering the wide range of this species, the area of occupancy is thought to be highly underestimated and a consequence of low surveying effort. Although information on its population size is unknown, given its widespread distribution and relatively high number of herbarium collections, it is likely to have a large population. There are no known direct threats, although deforestation for agriculture and mining is an ongoing cause of habitat loss throughout its range.

LOCAL NAMES AND USES. Cedro blanco (Bolivia), caoba (Costa Rica).

RELATIONSHIPS. *Ruagea insignis* is distinguished from all other species of the genus by the stout hollow twigs with a characteristic ring of small bud scales subtending the new fertile growth. Other characteristic features are the paripinnate leaves, numerous glabrous chartaceous leaflets which dry pale green, conspicuous venation and the large fruit. The molecular data confirms its monophyly (*Rojas-Andres et al.* [submitted](#)).

3. *Ruagea ovalis* (Rusby) Harms (1925: 428); Pennington (1981: 252).

Trichilia ovalis Rusby (1893: 14). Type. Bolivia, La Paz, Songo, Nov. 1890, fl., *Bang* 848 (holotype NY; isotypes BM, E, F, G, GH, K, M, MO, PH, W).

Guarea ovalis (Rusby) Rusby (1895: 205).

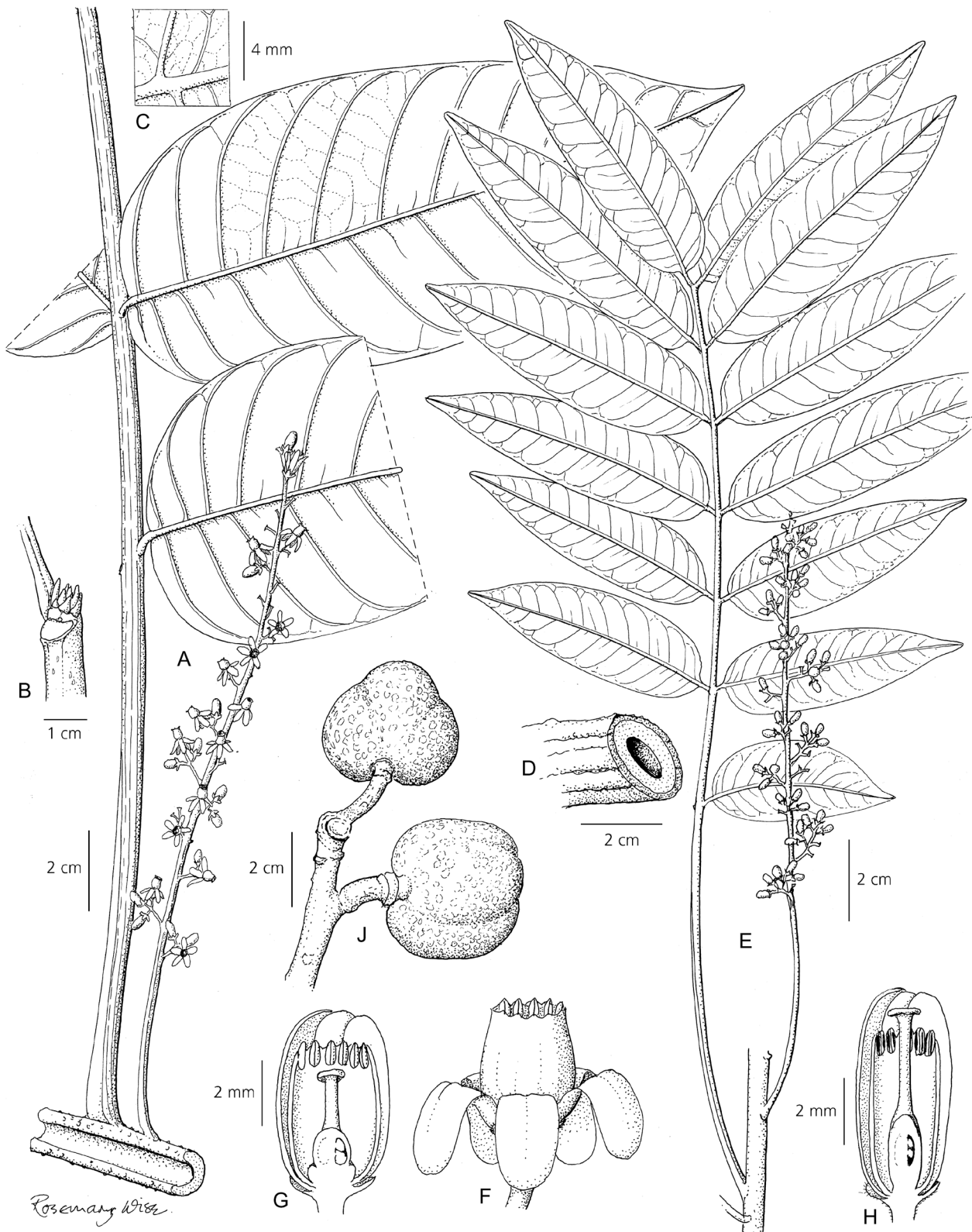
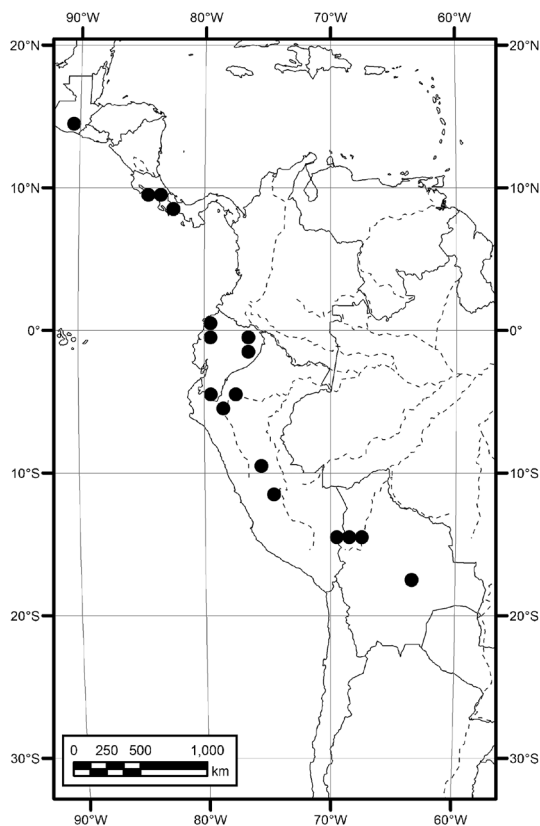


Fig. 2. *Rugea insignis*. A habit with inflorescence; B shoot apex with bud scales; C enlargement of lower leaflet surface; D hollow twig; E habit with inflorescence; F female flower; G half flower female; H half flower male; J fruit. A, C *Tonduz* 13113; B, D *Rodriguez et al.* 4218; E, H *Tessmann* 5010; F, G *Webster* 21870; J *Estrada* 2081. DRAWN BY ROSEMARY WISE.



Map 2. Distribution of *Ruagea insignis*.

Bud scales absent. *Young shoots* 6 – 10 mm diam., terete, densely golden-tomentose, indumentum sparser with age, usually lenticellate. *Leaves* imparipinnate, petiole 1 – 7 cm long, terete, tomentose to pubescent; rachis 4.5 – 30 cm long, semiterete or terete, tomentose to softly pubescent; petiolule of lateral leaflets 0.5 – 2 mm long, petiolule of terminal leaflet 0.5 – 3 mm long. *Leaflets* opposite to subopposite, 4 – 8 pairs, uppermost lateral 4 – 15 cm long, 1.6 – 7 cm broad, broadly elliptic, elliptic-lanceolate or obovate, apex shortly and narrowly attenuate, acute, obtuse or rounded, base usually asymmetric, one side acute or obtuse, the other rounded or truncate, coriaceous, upper surface with pubescent midrib and secondary veins, lower surface uniformly crisped pale-pubescent, minute red papillae dense on lower surface, sparser above; basal leaflets 1.5 – 6 cm long, 1 – 5 cm broad, broadly elliptic to suborbicular, apex obtuse or rounded, base asymmetric, obtuse to rounded; terminal leaflet 4.7 – 18 cm long, 2.3 – 5.8 cm broad, broadly elliptic or oblanceolate, apex acute, obtuse or rounded, base acute or narrowly attenuate; venation eucamptodromous to brochidodromous in the upper half, midrib flat or slightly sunken on the upper surface; secondaries 8 – 15 pairs, ascending, straight or arcuate, parallel or slightly convergent; intersecondaries few, short to long; tertiaries oblique

and parallel to reticulate, often obscure. *Inflorescence* axillary, 3.5 – 36.5 cm long, a slender to broad, densely-flowered panicle, with lateral branches branches 1 – 10 cm long, pubescent to tomentose, pedicel 0.5 – 1.5 mm long above the articulation. *Flowers* unisexual (plant dioecious). *Sepals* 5, 0.75 – 1 mm long, ovate, apex acute to obtuse, pubescent outside, glabrous inside, margin ciliate. *Petals* 5, 3 – 5 mm long, 1 – 2 mm broad, oblong, oblanceolate or broadly spatulate, apex rounded, glabrous, margin not ciliate. *Staminal tube* 2 – 3 mm long, 1 – 1.5 mm broad, shortly tubular or campanulate, margin crenulate or lobed, lobes alternating with the anthers, lobes sometimes emarginate, outside with scattered hairs or glabrous, inside coarsely hairy or less frequently glabrous, anthers 7 – 10, 0.5 – 0.75 mm long, indumentum of scattered coarse hairs or glabrous, antherodes in female narrower, without pollen, not dehiscing. *Nectary* a small swollen disk below the ovary, 0.3 – 0.5 mm long, glabrous. *Ovary* 0.75 – 1.5 mm long, ovoid, densely strigose to pubescent or glabrous, 3-locular, locules with 2 superposed ovules, style 0.5 – 1.5 mm long, glabrous, style-head discoid, pistillode in male similar but with less developed ovules. *Infructescence* to 30 cm long, many-fruited. *Capsule* (immature) c. 1 cm diam., globose, apex and base rounded, smooth, brown with pale lenticels, glabrous, pericarp c. 1 mm thick. *Seed* not seen. Fig. 3.

FIELD CHARACTERS. Evergreen tree to 20 m high and 25 cm diam., with smooth brown bark. Flowers greenish-white to yellowish-cream. Mature fruit not seen. Flowering mostly June to Nov., young fruit Feb. to April, and June – July and Sept.

DISTRIBUTION AND ECOLOGY. Andean Peru and northern and central Bolivia, in wet montane rain forest with associated genera *Hedyosmum*, *Cyathea*, *Clethra*, *Weinmannia*, *Podocarpus* (Bolivia: La Paz). Altitudinal range generally 1900 m to 2600 m, with a single record from Oxapampa, Peru at 1200 m (Map 3).

REPRESENTATIVE COLLECTIONS. **PERU.** **Cuzco:** Distr. Lacco, Yabero. 12.28S, 72.29W, *Valenzuela et al.* 3904 (MO). **Pasco:** Oxapampa, Distr. Huancabamba, Parque Nacional Yanachaga-Chemillen, La Colmena, 10.26S, 75.26W, *Valenzuela et al.* 11758 (K). **Piura:** Prov. Moropon, Distr. Chalaco, Caserio Vista Alegre, 5.00S, 79.00W, *Soto* 111 (MOL). **BOLIVIA.** **Cochabamba:** Carrasco, Sehuencas to Pajcha, 17.42S, 65.16W, *Altamirano & Alcazar* 3006 (MO). **La Paz:** Larecaja, Ancoma to Tipuani, Lambrmani, 15.39S, 68.22W, *Arellano et al.* 3123 (K).

CONSERVATION STATUS. This species was assessed by the World Conservation Monitoring Centre (1998) as Vulnerable D2. The addition of further records from Bolivia and Peru significantly extend the range of this species, with the extent of occurrence now calculated as 119,781 km² which exceeds thresholds for a threatened category under Criterion B. The

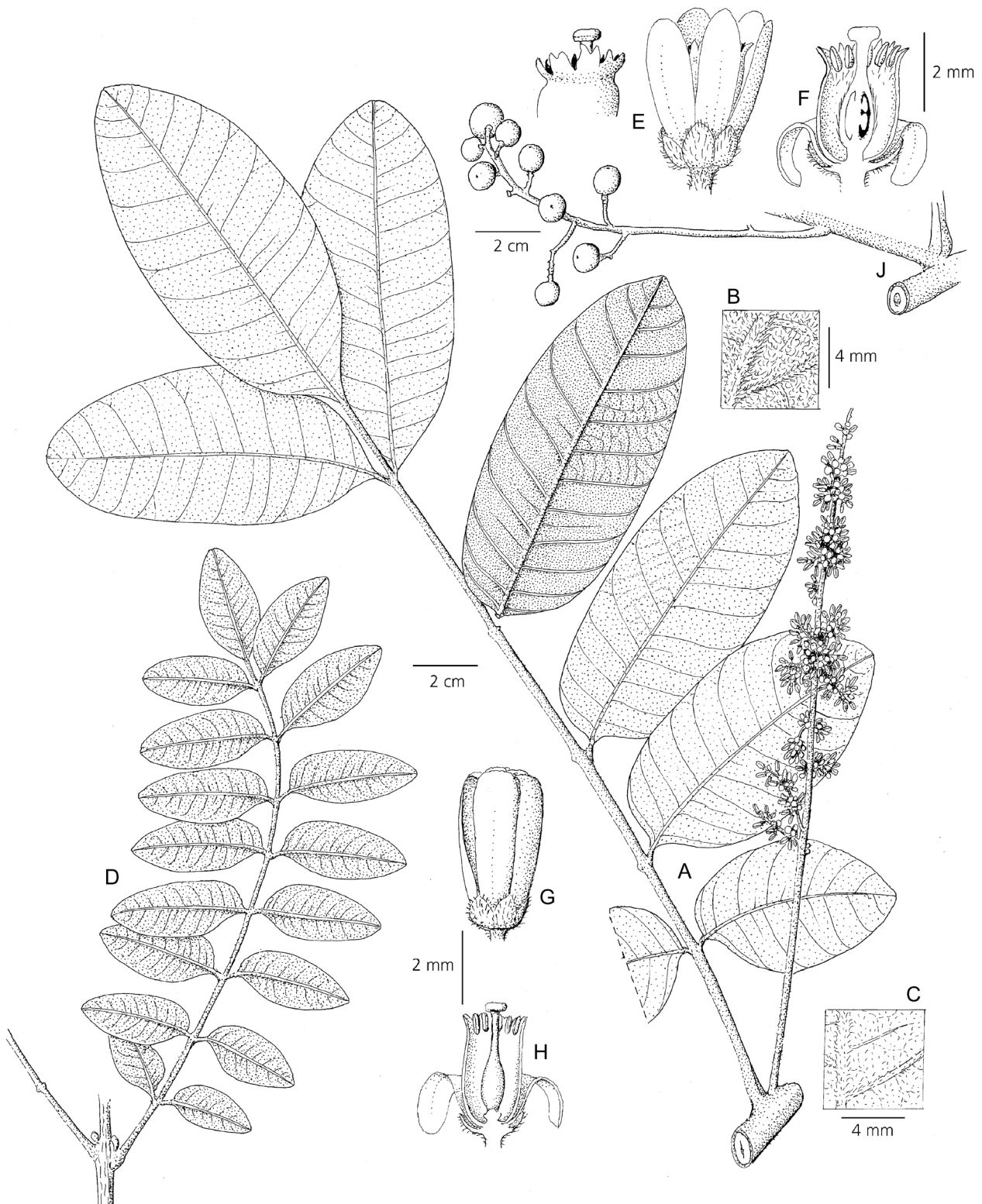
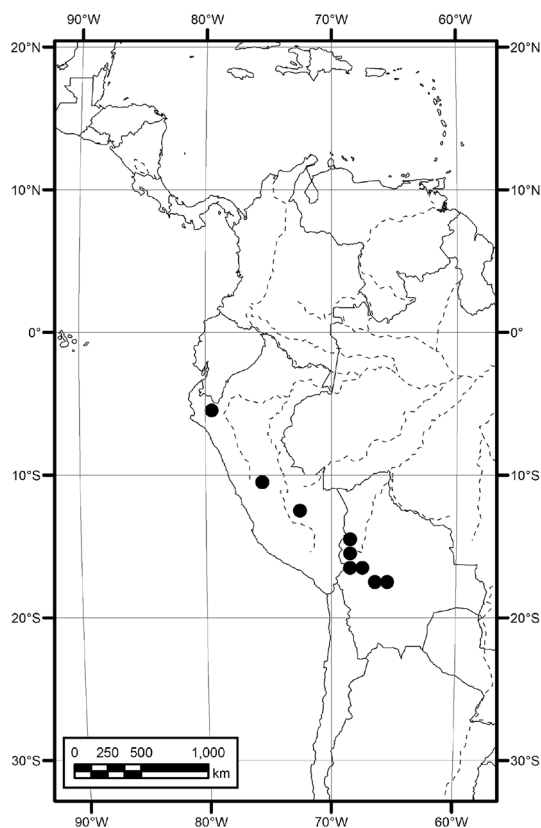


Fig. 3. *Ruagea ovalis*. A habit with inflorescence; B enlargement of leaflet undersurface; C enlargement of leaflet upper surface; D leaf; E female flower; F half flower female; G male flower; H half flower male; J infructescence. (A – C, G, H Castillo *et al.* 255; D Gentry & Solomon 52065; E, F Valenzuela *et al.* 7834; J Vasquez *et al.* 31100. DRAWN BY ROSEMARY WISE.



Map 3. Distribution of *Ruagea ovalis*.

area of occupancy is thought to exceed thresholds for a threatened category. This species is therefore reassessed as Least Concern (LC). There are no known direct threats, although deforestation for agriculture and mining are ongoing causes of habitat loss across its range.

LOCAL NAME. Cedrillo (Peru: Oxapampa).

RELATIONSHIPS. *Ruagea ovalis* is recognised by the 4–8 pairs of leaflets which are persistently and uniformly crisped-pubescent on the lower leaf surface, and the large many-flowered inflorescence with very small flowers (petals 3–5 mm long), staminal tube 2–3 mm long). Some specimens might be confused with *R. hirsuta*, but that species has more numerous, often overlapping leaflets, frequently with a cordate base, and larger flowers (petals usually 6–8 mm long).

4. *Ruagea subviridiflora* (C.DC.) Harms (1925: 428); Pennington (1981: 255).

Guarea subviridiflora C.DC. ex Harms (1922: 448).

Type. Peru, Cuzco, above Lucumayo, between Cuzco and Santa Ana, fl., *Weberbauer* 4984 (holotype, B destroyed; isotype frag. G).

Bud scales absent. *Young shoots* 5–10 mm diam., often hollow, terete, minutely and closely appressed puberulous at first, soon glabrous, usually with

numerous raised lenticels. *Leaves* imparipinnate; petiole 1.5–9.3 cm long, semiterete and usually marginate below the nodes, minutely appressed puberulous at first, soon glabrous; rachis 8–21.8 cm long, semiterete and slightly broadened below the nodes, appressed puberulous at first, soon glabrous; petiolule of lateral leaflets 1–3 (–6) mm long, petiolule of terminal leaflet 0.5–1.2 (–1.8) cm long. *Leaflets* opposite or subopposite, 4–7 pairs, uppermost lateral 5.5–16 cm long, 2–6.8 cm broad, usually oblanceolate or elliptic, apex usually acute or narrowly acuminate, occasionally obtuse, base asymmetric, narrowly attenuate or often one side acute and the other obtuse to truncate, margin sometimes slightly revolute, usually coriaceous, glabrous or sometimes with some appressed indumentum on the upper midrib, minute red papillae present on both surfaces; basal leaflets 2.3–9 cm long, 1.2–5.2 cm broad, elliptic, ovate or obovate, apex obtuse, acute or acuminate, base asymmetric, narrowly attenuate to truncate; terminal leaflet 5–18 cm long, 1.9–7.2 cm broad, usually oblanceolate or elliptic, apex acute, obtuse or acuminate, rarely rounded, base narrowly attenuate; venation eucamptodromous in the lower half, brochidodromous above, midrib flat or slightly sunken on the upper surface, secondaries 10–13 pairs, ascending, slightly arcuate, parallel or slightly convergent; intersecondaries short to long; tertiaries reticulate, sometimes obscure. *Inflorescence* axillary, 9.5–18 cm long, a slender to broadly pyramidal panicle, lower lateral branches 1–10 cm long, often many-flowered, minutely appressed puberulous, pedicel 0.75–2 mm long above the articulation. *Flowers* unisexual (plant dioecious) (only mature male flowers seen). *Sepals* 5, 0.75–1.5 mm long, ovate to suborbicular, apex rounded to obtuse, glabrous or with a few scattered hairs outside, margin ciliate. *Petals* 5, 6–10.5 mm long, 1.5–3 mm broad, broadly oblong or spatulate, apex rounded and often hooded, glabrous, margin usually not ciliate. *Staminal tube* 4–8 mm long, 1.5–3 mm broad, broadly tubular to campanulate, margin crenulate or lobed, lobes alternating with the anthers, glabrous or with scattered hairs inside, anthers 7–10, 1–2 mm long, glabrous. *Nectary* a short swollen stipe below the ovary, 0.3–0.5 mm long, glabrous. *Pistillode* 2–4 mm long, ovoid, glabrous or occasionally with a few short hairs, 3-locular, locules with 2 superposed ovules, style 1–3 mm long, glabrous, style-head discoid. *Infructescence* 8–15 cm long, with few branches. *Capsule* 2–3 cm long, globose to broadly pyriform, apex rounded to truncate, base rounded, smooth, brown, lenticellate, glabrous, pericarp 1–3 mm thick, endocarp cartilaginous, 3-valved, valves 1-seeded. *Seed* 0.8–1.3 cm long, plano-convex, with thick basal sarcotesta, seed coat membranous;

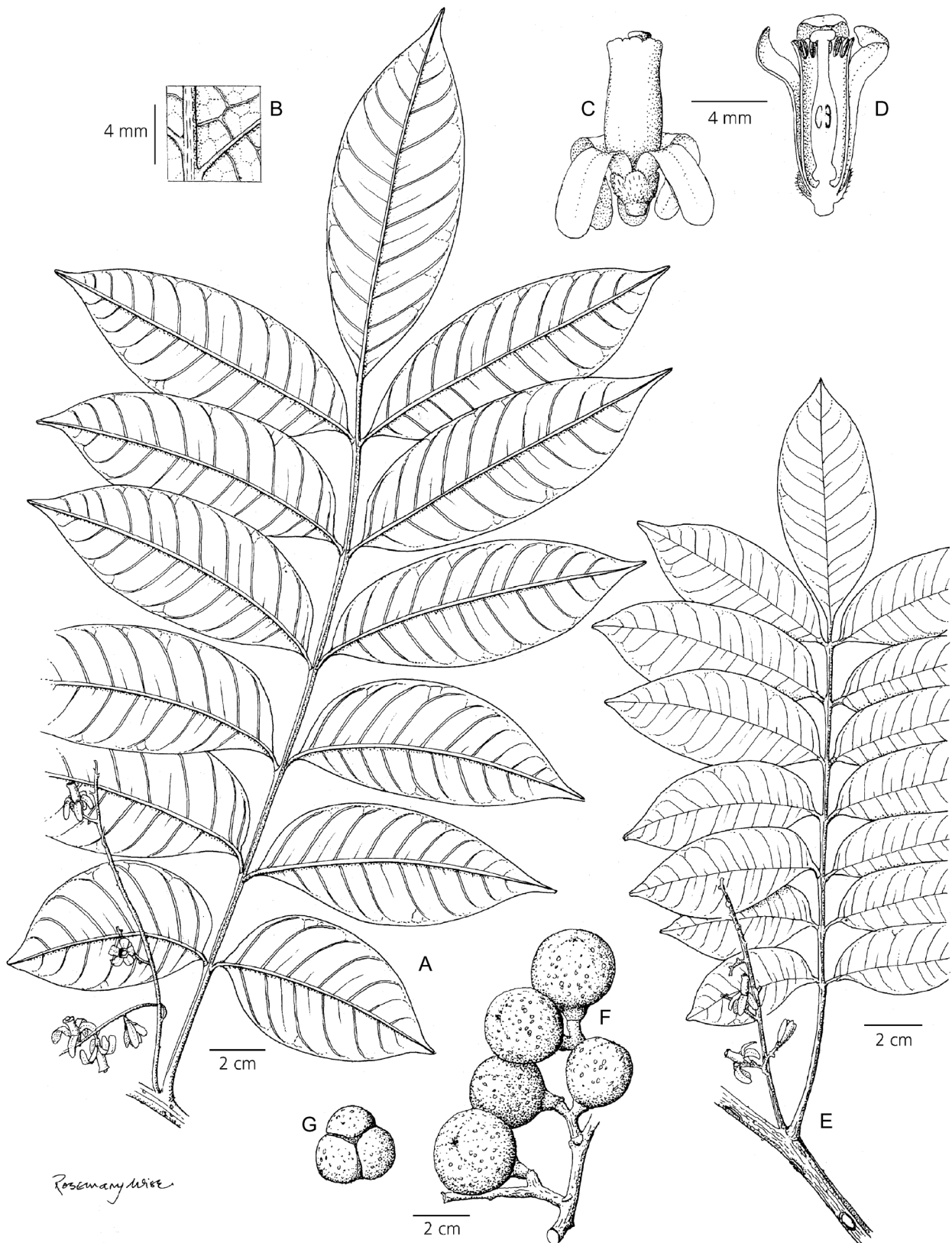


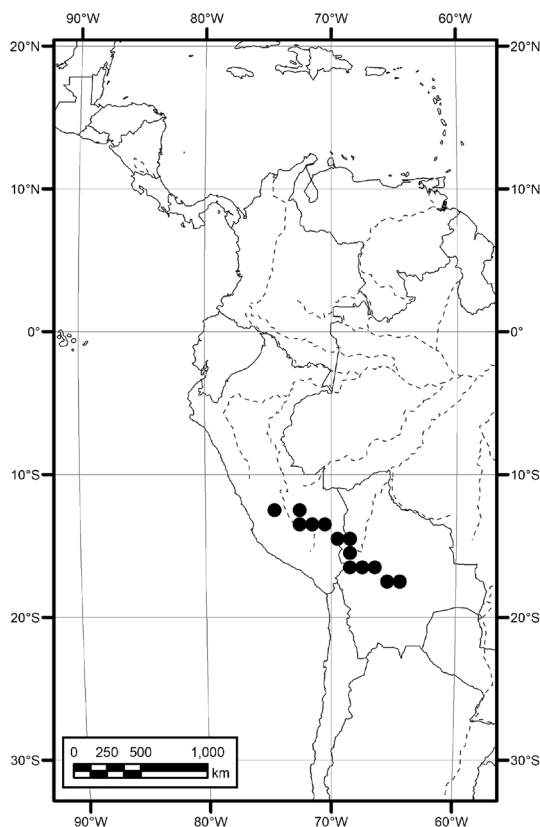
Fig. 4. *Ruagea subviridiflora*. A habit; B enlargement of leaflet undersurface; C male flower; D half flower male; E habit with inflorescence; F infructescence; G fruit. A – D Farfan *et al.* 965; E Valenzuela *et al.* 3481; F, G Valenzuela 5440. DRAWN BY ROSEMARY WISE.

embryo with plano-convex, collateral cotyledons, radical included or extending to the surface. Fig. 4.

FIELD CHARACTERS. Evergreen tree to 20 m high and 35 cm diam., with smooth brown bark. Flowers sweetly scented, with pale green or yellowish-green petals and staminal tube. Fruit maturing orange-green or yellowish, with conspicuous lenticels. Flowering recorded mostly between Feb. and July, with fruit maturing during the same period.

DISTRIBUTION AND ECOLOGY. Central and southern Andean Peru and Bolivia, in wet montane forest and cloud forest between 1700 m and 3400 m altitude. Associated genera include *Hedyosmum*, *Weinmannia*, *Podocarpus*, *Crinodendron*, *Chusquea*, *Alnus*. (Map 4).

REPRESENTATIVE COLLECTIONS. PERU. Cuzco: Distr. Santa Ana, Tunquimayo, 12.54S, 72.48W, *Valenzuela et al.* 732 (K, MO). **Huancavelica:** Prov. Tayacapa, Ampurco, between Salcabamba and Surcaba, 12.08S, 74.45W, *Tovar* 3777 (US). **BOLIVIA. Cochabamba:** Chaparé, 23.8 km N of Colomi, upper R. Cayami, 17.10S, 65.53W, *Solomon* 14366 (G, MO). **La Paz:** Bautista Saavedra, Apolobamba, Chulina, 15.07S, 68.52W, *Fuentes & Rodas* 16082 (K). **Santa Cruz:** Caballero Prov., Amboro National Park, Cerro Bravo, 17.64S, 64.32W, *Abbott & Jardim* 17056 (K, MO).



Map 4. Distribution of *Ruagea subviridiflora*.

CONSERVATION STATUS. This species has a large extent of occurrence of over 118,000 km² which falls outside of thresholds for a threatened category under Criterion B. It also has an area of occupancy of 136 km², although this is thought to be highly underestimated as a result of low surveying effort within this species' range. It is therefore assessed as Least Concern (LC). Deforestation driven by conversion of land for agriculture is an ongoing threat to this species' habitat and the presence of mineral and fossil fuel concessions in the Peruvian part of its range are likely to contribute to further habitat loss in the future.

LOCAL NAME. Cedrillo (Peru: Huancavelica).

RELATIONSHIPS. Morphologically and phylogenetically *Ruagea subviridiflora* is closely related to *R. obovata* and specimens of both species were formerly identified as *R. glabra*. *Ruagea subviridiflora* differs from *R. obovata* in the more numerous elliptic or oblanceolate leaflets with a narrowly attenuate apex. The coriaceous leaflet texture and leaflet shape distinguish it from *R. glabra*, and molecular data confirms the wide separation of these two species (Rojas-Andres *et al.* submitted).

5. *Ruagea obovata* T.D.Penn. sp. nov. Type. Peru, Pasco, Oxapampa, parte alta de la Quebrada San Luis, 10.34S, 75.21W, May 2007, fl., yfr., A. Monteagudo, J. Arteaga, J. Mateo & N. Arteaga 14133 (holotype, K).

<http://www.ipni.org/urn:lsid:ipni.org:names:77217897-1>

Bud scales absent. *Young shoots* 0.5 – 1 cm diam., often hollow, terete, finely appressed puberulous at first, soon glabrous, with numerous raised lenticels. *Leaves* imparipinnate; petiole 4.5 – 9 cm long, terete, glabrous; rachis 6 – 10 cm long, semiterete and slightly broadened below the nodes, glabrous; petiolule of lateral leaflets 1 – 6 mm long; petiolule of terminal leaflet 4 – 8 mm long. *Leaflets* opposite or subopposite, 2 – 4 pairs, uppermost lateral 11 – 18 cm long, 4.8 – 7.9 cm broad, obovate, apex obtuse or rounded, base slightly asymmetric, acute to narrowly attenuate, margin usually slightly to strongly revolute, coriaceous, glabrous, minute red papillae present on both surfaces; basal leaflets 6.2 – 8 cm long, 3.6 – 5.2 cm broad, broadly elliptic, apex rounded, base asymmetric, narrowly cuneate to acute; terminal leaflet 9 – 18 cm long, 4.7 – 9 cm broad, obovate, apex obtuse to rounded, base acute to narrowly attenuate; venation eucamptodromous in the lower half, brochidodromous in the upper half, midrib slightly sunken on the upper surface, secondaries 9 – 12 pairs, ascending, arcuate, parallel or slightly convergent; intersecondaries short to moderately long; tertiaries reticulate. *Inflorescence* axillary, 4 – 35 cm long, a narrow to broadly pyramidal panicle, lower lateral branches to 12 cm long, many-flowered, glabrous, pedicel 1 – 2 mm long above the articulation. *Flowers* unisexual (plant dioecious) (only mature male flowers seen). *Sepals* 5, c. 1 mm long, broadly ovate to orbicular, apex rounded, with few

scattered hairs outside, glabrous within, margin ciliate. *Petals* 5, 5–6.5 mm long, 2–2.5 mm broad, broadly oblong or spatulate, apex rounded, glabrous, margin usually slightly ciliate. *Staminal tube* 3–4.5 mm long, 2–3 mm broad, broadly tubular or tubular-campanulate, margin crenulate, glabrous, anthers 8–10, 0.9–1.1 mm long, glabrous; antherodes in female narrower, not dehiscing, without pollen. *Nectary* a short swollen stipe below the ovary, 0.5–0.75 mm long, glabrous, or absent. *Ovary* c. 2 mm long, ovoid, with some sparse appressed hairs or glabrous, 3-locular, locules with 2 superposed ovules, style 1–1.5 mm long, glabrous, style-head discoid; pistillode in male flower similar but with less-developed ovules. *Infructescence* to 25 cm long. *Capsule* (immature only seen) to 1.5 cm diam, globose, apex rounded, smooth, brown, lenticellate. Fig. 5.

FIELD CHARACTERS. Evergreen tree to 25 m high and 25 cm diam., with greenish-yellow flowers, immature fruit greenish-brown. Flowering recorded in May, June, Aug. and Sept., young fruit collected in May, Aug. and Oct.

RECOGNITION. Distinguished from other species by the 2–4-jugate, coriaceous leaves, with broadly oblanceolate or obovate leaflets with rounded apex, and few secondary veins.

DISTRIBUTION AND ECOLOGY. At present known only from the eastern slopes of the Andes in San Martín, Pasco and Cuzco, Peru and from northern Bolivia. In wet montane forest with a seasonal climate, altitudinal range from 1400 m to 2750 m. Associated genera in Bolivia are *Guadua*, *Weinmannia*, *Miconia* and *Cyathea*. (Map 5).

COLLECTIONS EXAMINED. **PERU.** **Cuzco:** La Convención, Distr. Quellouno, Abra de Yavero, 12.28S, 72.29W, *Calatayud et al.* 4646 (K); La Convención, Distr. Quellouno, Lacco, 12.36S, 72.14W, *Valenzuela et al.* 6850 (K, MO), 6859 (K), 6860 (K, MO), 10064 (K, MO); La Convención, above Quellouno, 12.26S, 72.30W, *van der Werff et al.* 21059 (K, MO). **Pasco:** Distr. Oxapampa, Parque Nacional Yanachaga-Chemillén, Refugio del Cedro, 10.32S, 75.21W, *Monteagudo et al.* 3798 (K); Distr. Huancabamba, Parque Nacional Yanachaga-Chemillén, near Laguna San Daniel, 10.15S, 75.16W, *Monteagudo et al.* 9281 (K); Distr. Oxapampa, Quebrada San Luis, 10.33S, 75.20W, *Monteagudo et al.* 14133 (K); Oxapampa, Distr. Chontabamba, El Ripio, track to Pusagno, 10.38S, 75.25W, *Rojas et al.* 2285 (K); Oxapampa, Parque Nacional Yanachaga-Chemillén, Quebrada Yanachaga, 10.23S, 75.28W, *Vásquez et al.* 28332 (K). **San Martín,** Mariscal Cáceres, San Abiseo National Park, E of Pajeten ruins, 7.00S, 77.00W, *Young* 4099 (MOL), same loc. W of Pajeten camp, *Young* 4247 (K, MOL). **BOLIVIA.** **La Paz:** Franz Tamayo, Apolobamba, Pelechuco, Coronara 11, 14.46S, 68.59W, *Villalobos et al.* 85 (K).

CONSERVATION STATUS. This species has an extent of occurrence of 92,918 km², and an area of occupancy of 92 km². Given the wide range of this species, the area of

occupancy is thought to be highly underestimated and a consequence of low surveying effort. There are no known direct threats and it has been recorded from protected areas. It is therefore currently assessed as Least Concern. However, low levels of deforestation have been taking place across its range and the presence of oil, gas and mining concessions mean future deforestation is likely.

RELATIONSHIPS. Material of this species has previously been placed in *Ruagea glabra*. *Ruagea obovata* shares the glabrous habit and similar-sized flowers with *R. glabra*, but differs in the combination of leaflet shape (obovate with rounded to obtuse apex and tapering base), coriaceous leaflet texture (usually chartaceous in *R. glabra*), and glabrous flowers (usually some indumentum inside the staminal tube of *R. glabra*). Molecular data also shows *R. obovata* to be widely separated from *R. glabra*, but closer to *R. hirsuta* (Rojas-Andres *et al.* submitted). *Ruagea obovata* is also closely related to *R. subviridiflora* and their relationships are discussed under that species.

Two Colombian collections (*Huertas & Camargo* 6510, *Galeano et al.* 521) are morphologically very close to *Ruagea obovata*, but their molecular data places them with *R. membranacea* at the foot of the tree, in a group which is sister to the rest of the genus (Rojas-Andres *et al.* submitted). They may represent a distinct species.

6. *Ruagea hirsuta* (C.DC.) Harms (1925: 428); Pennington (1981: 247); Palacios (2007: 50).

Guarea hirsuta C.DC. (de Candolle 1878: 578). Type.

Peru 'Nueva Hispania', fr., *Pavon* s.n. (holotype G).

Guarea pilanthera C.DC. ex Harms (1924: 55). Type.

Peru, Dept. Ayacucho, Prov. Huanta, fl., *Weberbauer* 5656 (holotype B, destroyed; lectotype G (Pennington 1981: 247).

Ruagea pilanthera (C.DC.) Harms (1925: 428).

Guarea yungasana Briq. (Briquet 1935: 20). Type.

Bolivia, La Paz, Nor Yungas, Coroico, fr., *Bang* 2428 (holotype G; isotypes BM, C, E, F, G, GH, K, M, MO, PH, US).

Ruagea yungasana (Briq.) Harms (1940: 138).

Ruagea silviandina Cuatrec. (Cuatrecasas 1950: 75).

Type. Colombia, Dept. Caldas, Guayabal, fl., *Cuatrecasas* 23308 (holotype F).

Bud scales absent. *Young shoots* 5–10 mm diam., rough with numerous leaf scars, densely crisped pale-pubescent to tomentose, sometimes becoming subglabrous with age, lenticels few or absent. *Leaves* imparipinnate, petiole 1–3 cm long, semiterete or sometimes channelled above, crisped pubescent to tomentose, rachis 8–22 cm long, semiterete or channelled above, crisped pubescent to tomentose, sometimes becoming subglabrous, petiolule of lateral

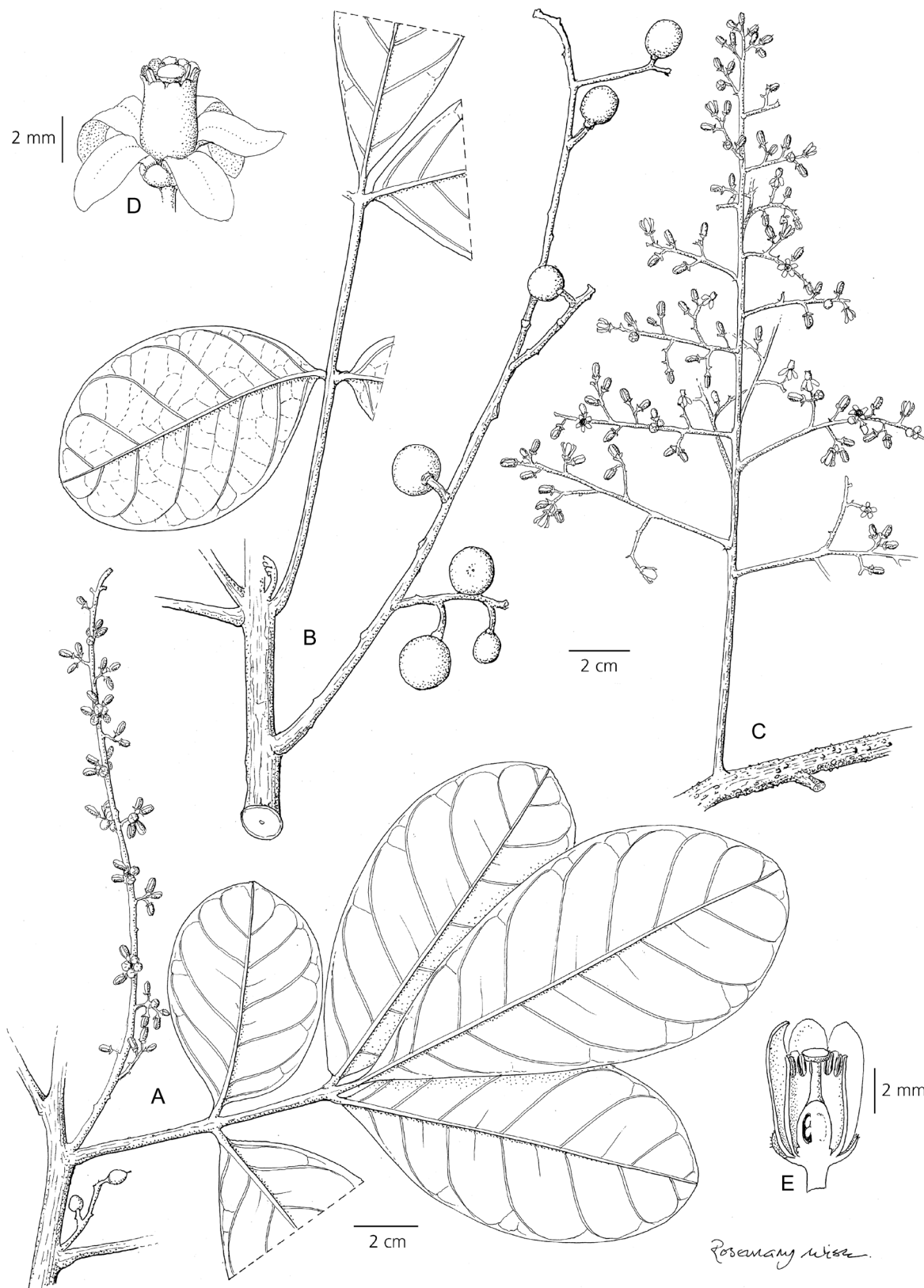
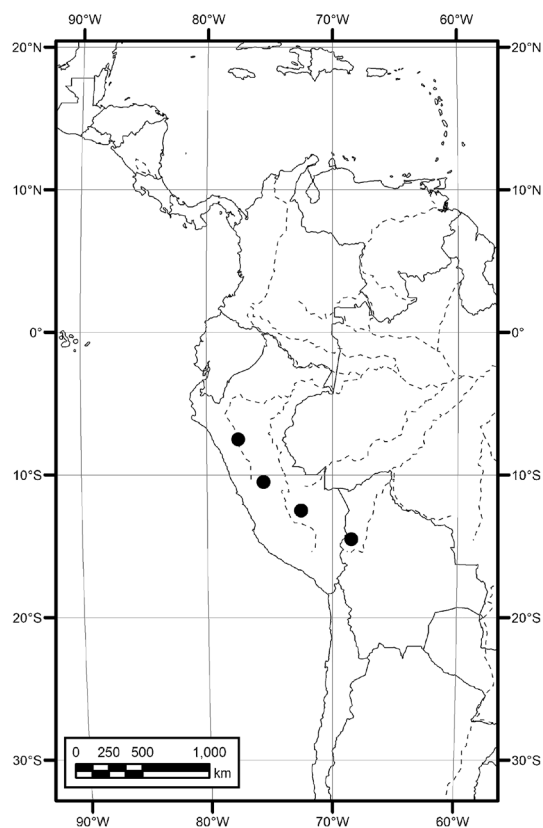


Fig. 5. *Ruagea obovata*. A habit with inflorescence; B habit with infructescence; C inflorescence; D male flower; E half flower male. A, B Monteagudo et al. 14133; C Valenzuela et al. 6850; D, E Valenzuela et al. 6859. DRAWN BY ROSEMARY WISE.



Map 5. Distribution of *Ruagea obovata*.

leaflets usually 0.5 – 1 mm long, rarely up to 4 mm long, petiolule of terminal leaflets 1 – 8 mm long. *Leaflets* opposite or subopposite, (5 –) 8 – 15 (– 18) pairs, often closely set and overlapping and sometimes conduplicate, uppermost lateral leaflets 3.4 – 10.3 cm long, 1.3 – 4.8 cm broad, elliptic to oblong or oblong-lanceolate, apex obtuse, rounded or acuminate, base usually asymmetric, acute to obtuse on one side, rounded to cordate on the other, or base cordate, coriaceous, upper surface subglabrous or pubescence confined to the midrib, lower surface tomentose along the midrib, scattered to densely crisped pubescent on the lamina, sometimes finally glabrous; basal leaflet 1.4 – 4 cm long, 0.7 – 2.8 cm broad, broadly elliptic to orbicular, apex usually obtuse or rounded, base mostly asymmetric, cordate to rounded; terminal leaflet 3.4 – 10 cm long, 2 – 5.5 cm broad, broadly elliptic, oblong or oblanceolate, apex narrowly attenuate to rounded, base usually symmetric, acute to rounded; venation eucamptodromous to brochidodromous (often both on the same leaflet), midrib flat (not raised on the upper surface), secondaries 10 – 20 pairs, shallowly ascending, straight, +/-parallel, intersecondaries short to long, sometimes only a few present, tertiaries reticulate, often visible only on the lower surface. *Inflorescence* axillary, 3 – 22 cm long, a slender panicle with flowers in dense clusters, with some lateral

branches 1 – 5 cm long, pubescent to tomentose, pedicel 0.5 – 2 mm long. *Flowers* unisexual (plant dioecious). *Sepals* 5, 0.75 – 2 mm long, broadly ovate to orbicular, apex acute to rounded, sparsely pubescent or glabrous outside, glabrous inside, margin sparsely ciliate. *Petals* 5, (4.5 –) 6 – 8 mm long, broadly oblong to spatulate, apex obtuse to rounded, margin ciliate or not, glabrous. *Staminal tube* 3 – 6.5 mm long, 1 – 2.5 mm broad, shortly tubular or tubular-campanulate, margin crenulate, outside glabrous, inside with scattered long hairs or glabrous, sometimes barbate below the anthers, anthers 10, 1 – 1.5 mm long, usually sparsely barbate at base; antherodes in female narrower, without pollen, not dehiscent. *Nectary* a stout stipe below the ovary, 0.5 – 1 mm long. *Ovary* 1 – 2 mm long, ovoid, scattered hirsute to subglabrous, 3-locular, locules with 2 superposed ovules, style 1.5 – 2.5 mm long, glabrous, style-head discoid. *Pistillode* in male similar but with less-developed ovules. *Infructescence* 10 – 32 cm long, capsule 1.4 – 2 cm long, 1.8 – 2.3 cm broad, suborbicular to 3-lobed, apex truncate, base obtuse, smooth, dark brown with pale lenticels, glabrous, 3-valved, valves 1-seeded, pericarp 1 – 2 mm thick. *Seed* 1 – 1.4 cm long, with a thick basal sarcotesta, seed coat membranous; embryo with thick plano-convex, collateral cotyledons, radical apical, extending to the surface. Fig. 6.

FIELD CHARACTERS. Evergreen tree to 20 m high and 40 cm diam., larger specimens with thick rough dark grey slightly fissured bark. The young growth has conspicuous golden brown indumentum. The flowers have pale green to yellowish-green petals and staminal tube. The fruit matures orange-yellow with conspicuous pale lenticels. Flowering recorded mostly Sept. to Jan., but with some records in March, April and June. Mature fruit recorded Feb., March, April, June and Oct.

DISTRIBUTION AND ECOLOGY. Andean Colombia, Ecuador, Peru and Bolivia in wet montane and cloud forest, with associated genera *Escallonia*, *Weinmannia*, *Podocarpus* and *Cavendishia*, altitudinal range mostly 2300 m – 3450 m, but in the extreme south of its range (16 degrees S) it occurs in *Podocarpus* forest at 1740 m (Map 6).

REPRESENTATIVE COLLECTIONS. COLOMBIA. Caldas: Cordillera Central, Río Otún, Guayabal, 4.57N, 75.44W, *Cuatrecasas* 23308 (F). **Cauca:** Cordillera Central W slope, head of Río Palo, Santo Domingo, 3.00N, 76.00W, *Cuatrecasas* 19271 (A, F, MO). **Valle del Cauca:** Municipio Tuluá, Santa Lucía, Finca las Nieves, 4.08N, 76.19W, *Devia & Prado* 1949 (MO). **ECUADOR. Carchi:** Cantón Montufar, SE of Huaca, E of Colonia Huaqueña, 0.35N, 77.42W, *Tipaz* 14 (G, US). **Cotopaxi:** E side of Illiniza, Hacienda El Pongo, Quebrada Faldiguera, 0.40S, 78.48W, *Jorgensen et al.* 92968 (NY). **Imbabura:** Cantón Otavalo, San Luis de Quichinche,

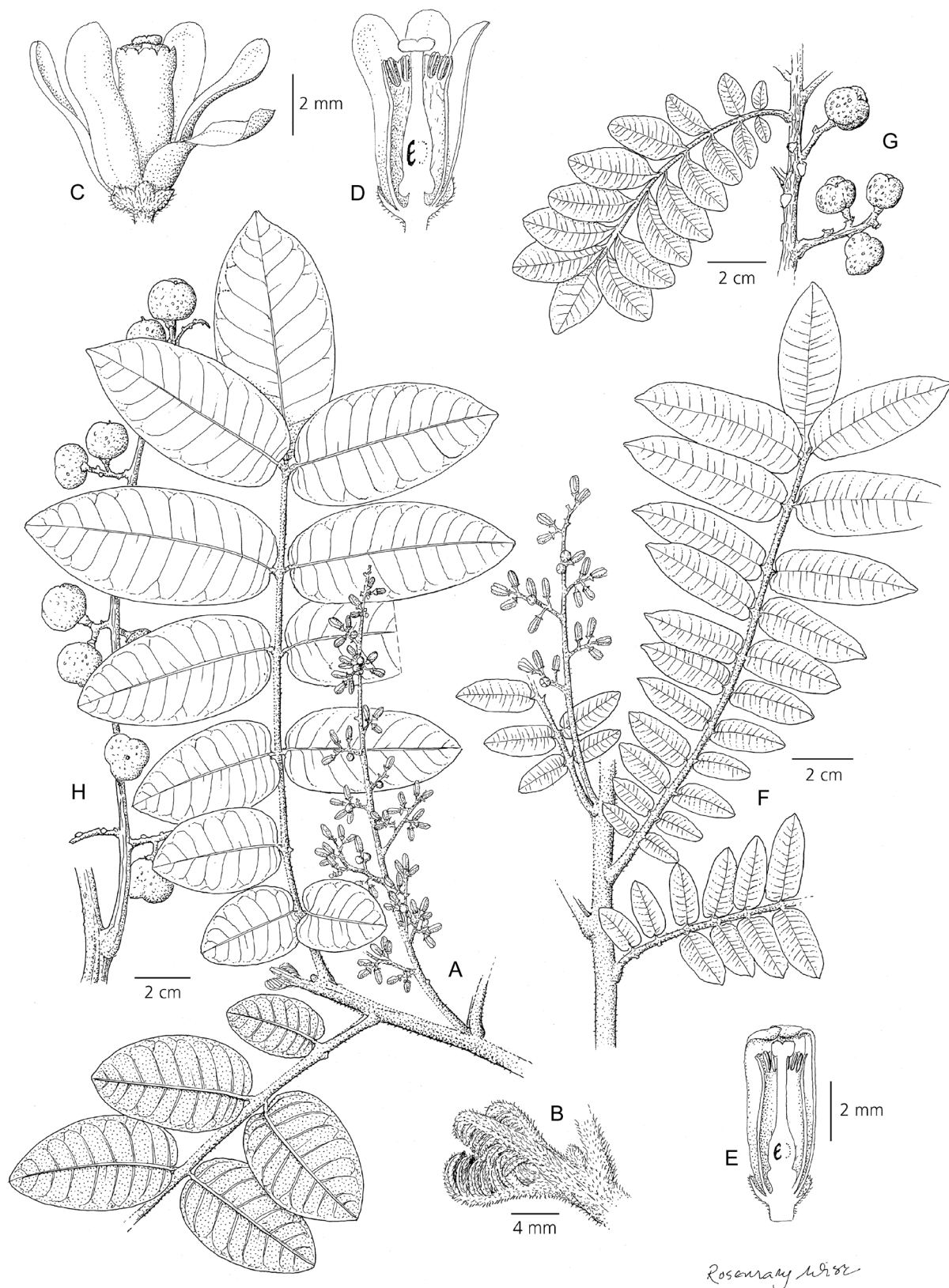


Fig. 6. *Ruagea hirsuta*. A habit with inflorescence; B shoot apex; C male flower; D half flower male; E half flower, female; F habit with inflorescence; G habit with infructescence; H infructescence. A, B, H Pennington et al. 15068; C, D Pennington et al. 15067; E Valenzuela et al. 6882; F Young 3837; G Knight 530. DRAWN BY ROSEMARY WISE.

San Alberto, 0.12S, 78.22W, *Moran et al.* 92 (G). **Loja:** Cerro Vilconaco, 10 km W of Loja, 3.11S, 79.03W, *Knight* 530 (MO). **Zamora-Chinchi:** Palanda, Tapichalaca Reserve, 4.29S, 79.07W, *Neill* 15378 (K). **PERU. Amazonas:** Leimebamba, Río El Jardín, 6.55S, 77.43W, *Gruhn et al.* 172 (K). **Cajamarca:** Prov. Chota, below Las Palmas, 24 km NE of Chota, 6.29S, 78.37W, *Dillon et al.* 6400 (F, K). **Cuzco:** Prov. La Convención, Quillabamba to Cuzco km 79, 13.05S, 72.21W, *Pennington & Daza* 15068 (K, MOL). **Junín:** Carretera Central, Carpapata, 11.15S, 75.33W, *Pennington & Daza* 18498 (K, MOL). **La Libertad:** Distr. Uchumarca, Laguna Huayllabamba, 06.59S, 77.42W, *Zambrana et al.* 8734 (K). **Pasco:** Oxapampa, Distr. Huancabamba, Yanachaga-Chemillén National Park, 10.22S, 75.28W, *Monteagudo et al.* 6784 (K). **San Martín:** Mariscal Caceres, Río Abiseo National Park, 7.45S, 77.15W, *Young* 3837 (F, K). **BOLIVIA. La Paz:** Prov. Sud Yungas, new road to Cotapata, 16.00S, 67.10W, *Navarro et al.* 1626 (LPB).

CONSERVATION STATUS. This species has a large extent of occurrence of over 1.3 million km². However, given the wide range of the species, the area of occupancy is thought to be highly underestimated and a consequence of low surveying effort. Information on its population size is unknown, but given its widespread distribution and relatively high number

of herbarium collections, it is likely to have a large population. There are no known direct threats, although deforestation for agriculture and mining is an ongoing cause of habitat loss throughout its range. This species is therefore assessed as Least Concern.

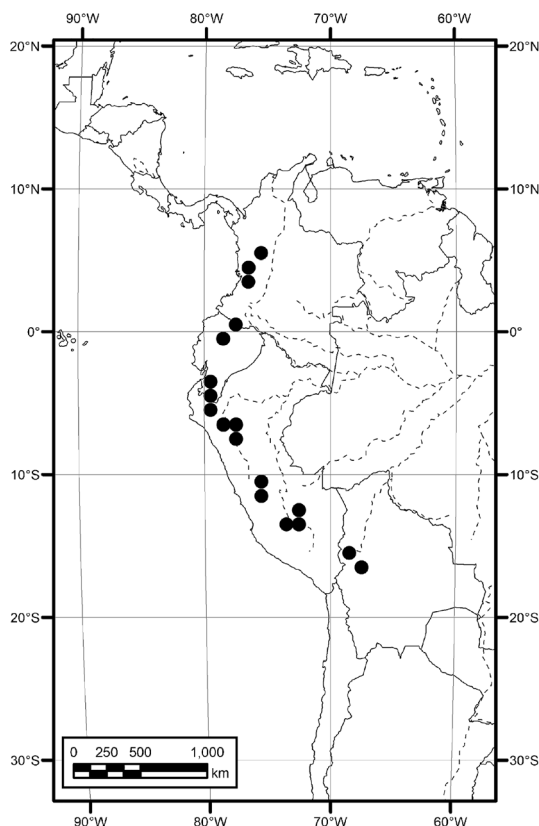
LOCAL NAMES AND USES. Cedrillo (Ecuador). The secondary xylem of *Ruagea* is similar that of the closely related *Cabrlea* (Pennington 1975), which is a large and important timber tree, but *Ruagea* rarely gets to a sufficient size to provide timber. However, *R. hirsuta* is recorded as being used for furniture-making in Ecuador.

RELATIONSHIPS. *Ruagea hirsuta* is easily recognised by its numerous small, closely set and often overlapping leaflets, which are sessile and with a strongly asymmetrical rounded to cordate base, the petals generally 6 – 8 mm long and capsule 1.4 – 2 cm long. However, like all *Ruagea* species, it shows a huge amount of vegetative variation, especially in the number of leaflets and their shape, which sometimes grade into those of *R. ovalis*. Such specimens have a longer petiolule and a tapering leaflet base (e.g. *Suclli et al.* 2222), but molecular data places them clearly within *R. hirsuta*. (Rojas-Andres *et al.* submitted.) Morphologically it is closest to *R. ovalis*, which differs in the fewer, larger leaflets and smaller flowers.

7. *Ruagea beckii* T.D.Penn. sp. nov. Type. Bolivia, Dept. Cochabamba, Prov. Chaparé, Cordillera de Mosestenez, Territorio Indígena Parque Nacional Isiboro-Securé, above Lake Carachupa, 16.13S, 66.24W, fl., *M. Macia & J. Fuertes* 7235 (holotype LPB).

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Bud scales absent. *Young shoots* 6 – 8 mm diam., hollow, terete, pubescent to densely pilose with pale straw-coloured indumentum, becoming glabrous, smooth, with leaf scars and scattered lenticels. *Leaves* imparipinnate; petiole slender, 5.5 – 8 cm long, semiterete, pilose or with scattered pubescence; rachis 24.5 – 34.5 cm long, slender, semiterete, pilose or with scattered short pubescence; petiolule of lateral leaflets 1 – 2 mm long, petiolule of terminal leaflet 2 – 2.2 cm long. *Leaflets* opposite, 6 – 12 pairs, uppermost lateral 9.5 – 13.5 cm long, 2.2 – 4.4 cm broad, oblong to oblanceolate, apex acute to shortly acuminate or obtusely cuspidate, base sometimes asymmetric, acute one side, obtuse the other, or cordate, margins not or only slightly revolute, membranous, upper surface with scattered pubescence or pilose on the midrib, otherwise glabrous, lower surface densely to sparsely pilose, or subglabrous, minute red papillae absent; basal leaflets 2.8 – 5.5 cm long, 1.8 – 4 cm broad, ovate to suborbicular, apex acute, obtuse or rounded, base slightly asymmetric, obtuse to cordate or truncate;



Map 6. Distribution of *Ruagea hirsuta*.

terminal leaflet 8 – 12 cm long, 2 – 4.9 cm broad, elliptic, apex obtuse to shortly acuminate, base acute to narrowly attenuate; venation eucamptodromous, midrib flat or slightly sunken on the upper surface, secondaries 12 – 16 pairs, ascending, straight, parallel to slightly convergent; intersecondaries short to moderate or long, tertiaries oblique and parallel or forming a lax reticulum. *Inflorescence* axillary, 15 – 22 cm long, a lax-flowered branched panicle, lower lateral branches to 8.5 cm long, sparsely pilose or pubescent to subglabrous, pedicel 0.5 – 0.75 mm long (above the articulation). *Flowers* unisexual, male flowers only seen. *Sepals* 5, c. 0.5 mm long, broadly ovate to suborbicular, apex rounded, sparse pubescence outside, glabrous inside, margin ciliate. *Petals* 5, c. 4 mm long, 1 – 1.5 mm broad, oblong to spatulate, apex rounded, glabrous, margin not ciliate. *Staminal tube* c. 3 mm long, 1 – 1.5 mm broad, tubular-campanulate, margin crenulate, sparsely and coarsely pubescent on both surfaces, anthers 9 – 10, 0.5 – 0.75 mm long, glabrous. *Nectary* a small swollen disk below the ovary, c. 0.3 mm long, glabrous. *Ovary* c. 1 mm long, ovoid, appressed pubescent, 3-locular, locules with 1 – 2 superposed ovules, style c. 0.5 mm long, glabrous, style-head discoid. Infructescence to 20 cm long, many-fruited. *Capsule* c. 0.8 × 1 cm, obovoid, apex truncate, base obtuse, smooth, glabrous, brown with pale lenticels, pericarp c. 0.5 mm thick, 3-valved, valves 1-seeded. *Seed* c. 8 mm long, c. 5 mm broad, with a thickened basal sarcotesta, embryo with thick plano-convex, obliquely collateral cotyledons, radicle apical extending to the surface. Fig. 7.

FIELD CHARACTERS. Evergreen treelet or tree to 20 m high and 26 cm diam. There is no information on the flower colour; the fruit is described as cream-coloured and lenticellate. Flowering recorded in Aug., Sept. and Nov., mature fruit in Sept.

RECOGNITION. Differing from other species in the long leaves with many oblong membraneous leaflets 3 – 4 times as long as broad, flowers with petals c. 4 mm long, pubescent androecium and ovary and small fruit.

DISTRIBUTION AND ECOLOGY. Known only from Cochabamba and La Paz, Bolivia, where it is a component of wet montane forest, between 1250 m and 2300 m altitude (Map 7).

COLLECTIONS EXAMINED. BOLIVIA. Cochabamba: Province Chaparé, Cordillera de Mosestenez, Parque Nacional Isiboro-Secure, 16.13S, 66.24W, *Macia* & *Fuertes* 7235 (LPB), 7341 (LPB). **La Paz:** Prov. Sud Yungas, Reserva Apa Apa, 16.22S, 67.28W, *Beck* MET03/71 (LPB). Prov. Nor Yungas, Coroico to Yolosa 16.00S, 67.00W, *Beck* 7534 (K, LPB). Prov. Sud Yungas, Chulumani, Cala Cala, 16.26S, 67.33W, *Lippok* & *Sonco* 799 (LPB). Prov. Sud Yungas, 7 km from Huancane, road to San Isidro, 16.21S, 67.31W, *D. N. Smith et al.* 1391 (K).

CONSERVATION STATUS. This species has a restricted range with an extent of occurrence of only 603 km² and based on the known collections, occurs at only 5 threat-defined locations. Deforestation to clear land for agriculture is an ongoing threat to this species, and satellite imagery has shown there to be recent deforestation at some of the collection localities. This species is therefore assessed as Endangered B1ab(iii).

RELATIONSHIPS. This species is distinctive on account of its long leaves with numerous membraneous, oblong leaflets, small flowers with pubescent staminal tube and ovary, and small fruit. It forms a strongly supported monophyletic group within a clade which has no other Bolivian species (Rojas-Andres *et al.* submitted.). The La Paz population of this species has much denser leaf indumentum than the specimens from Cochabamba, but is otherwise similar.

ETYMOLOGY. This species is named for Dr Stephan Beck, former Director of the Bolivian National Herbarium, author of many contributions to our knowledge of the ecology and floristics of the Bolivian flora and a great collaborator over many years.

8. *Ruagea microphylla* *W. Palacios* (1994: 164), (2007: 53). Type. Ecuador, Loja, road Loja to La Toma, Cerro Villonaco, 20 km W of Loja, 2200 – 2400 m alt., Aug. 1983, fl., fr., *J. Jaramillo* & *V. Widderskjold* 5681 (holotype AAU, isotype QCA).

Bud scales absent. *Young shoots* 6 – 10 mm diam., terete, sometimes faintly striate, pale crisped tomentose to minutely appressed puberulous or glabrous, often with raised lenticels. *Leaves* imparipinnate; petiole 1 – 7 cm long, semiterete, crisped tomentose to glabrous; rachis 4.5 – 17.7 cm long, semiterete and slightly broadened below the nodes, crisped tomentose to glabrous; petiole of lateral leaflets 0.5 – 8 mm long; petiolule of terminal leaflet 0.6 – 4 cm long. *Leaflets* opposite or subopposite, 3 – 7 (– 9) pairs, uppermost lateral 3.2 – 13.5 cm long, 1 – 6.2 cm broad, broadly oblanceolate to elliptic, apex obtuse, rounded or truncate, base acute to narrowly attenuate, sometimes slightly asymmetric, margin sometimes revolute, chartaceous to coriaceous, upper surface with tomentose midrib and veins or glabrous, lower surface crisped tomentose to glabrous, minute red papillae present on both surfaces; basal leaflets 1 – 6.5 cm long, 0.5 – 3.9 cm broad, broadly elliptic to obovate, apex obtuse, rounded or truncate; terminal leaflet 2.2 – 13 cm long, 0.9 – 7 cm broad, broadly oblanceolate or elliptic, apex obtuse to rounded, base narrowly attenuate or cuneate; venation eucamptodromous to brochidodromous, midrib flat or slightly sunken on the upper surface, secondaries 8 – 17 pairs, ascending, straight or slightly arcuate, usually +/-parallel; intersecondaries short to long, or obscure; tertiaries

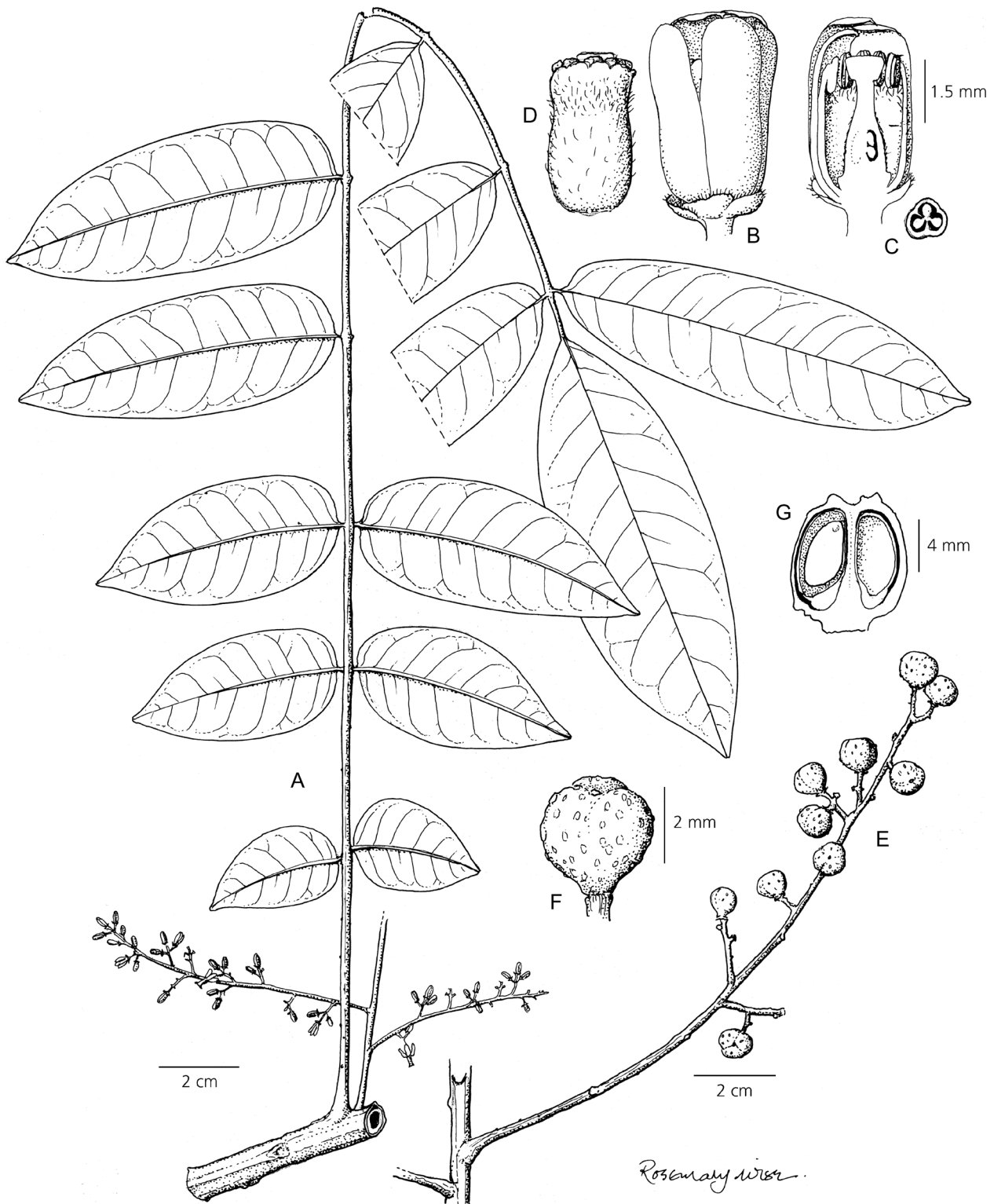
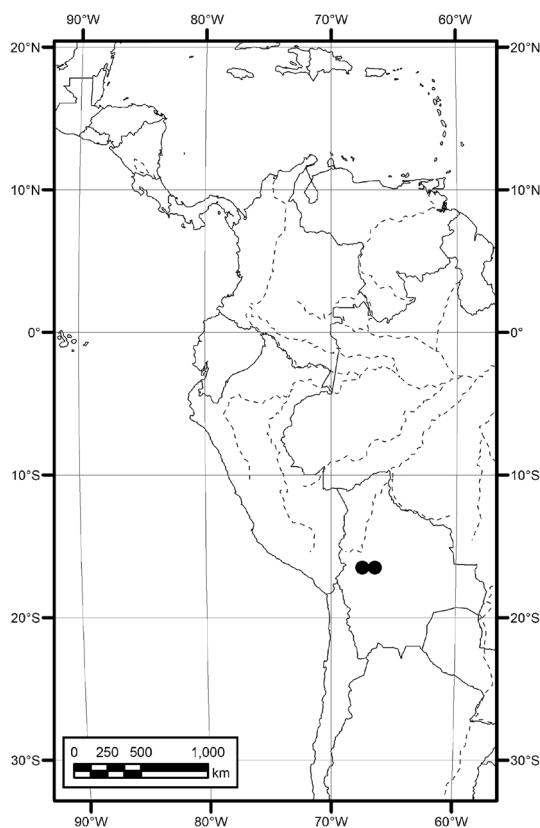


Fig. 7. *Ruagea beckii*. (glabrous form). A habit with inflorescence; B male flower; C half flower male; D staminal tube; E infructescence; F fruit; G section of fruit. A – D Macia & Fuertes 7325; E – G Macia & Fuertes 7341. DRAWN BY ROSEMARY WISE.

reticulate, obscure. *Inflorescence* axillary, 6.5–20 cm long, lateral branched 1.5–5 cm long, a pyramidal panicle,

usually many-flowered, pale-pubescent to subglabrous, pedicel 1–1.5 mm long above the articulation. *Flowers*



Map 7. Distribution of *Ruagea beckii*.

unisexual (plant dioecious) (only male flowers seen). *Sepals* 5, 1 – 1.25 mm long, broadly ovate, apex acute to rounded, sparsely pubescent to glabrous outside, glabrous inside, margin ciliate. *Petals* 5, 4.5 – 6 mm long, 1.5 – 3 mm broad, broadly oblong or spatulate, apex rounded, glabrous, margin sparsely ciliate or not. *Staminal tube* 4 – 5 mm long, 1.5 – 2 mm broad, broadly tubular, margin crenulate to subentire, glabrous or with some scattered hairs at base inside, anthers 10, 0.75 – 1 mm long, glabrous. *Nectary* a short glabrous stipe below the ovary, or absent. *Pistillode* 1 – 2 mm long, ovoid, sparsely pubescent to glabrous, 3-locular, locules with 1 – 2 superposed ovules, style 1.5 – 2 mm long, glabrous, style-head discoid. *Infructescence* 3 – 10 cm long, little-branched. *Capsule* 1.5 – 2 cm long, globose, apex and base rounded, smooth, brown, usually lenticellate, glabrous, pericarp 0.5 – 1 mm thick, 3-valved, valves with 1 – 2 superposed seeds. *Seed* c. 1.2 × 0.8 cm, plano-convex, with thick basal sarcotesta, seed coat membranous; embryo with plano-convex, collateral cotyledons, radicle included. Fig. 8.

FIELD CHARACTERS. Evergreen tree to 20 m high and 15 cm diam., flowers scented, with pale green to greenish-cream petals and staminal tube, fruit maturing light brown to pale orange, seed red. Flowering and fruiting mostly July to Dec.

DISTRIBUTION AND ECOLOGY. Southern Ecuador and northern Peru in wet montane and cloud forest between 1800 m and 3000 m altitude (Map 8).

REPRESENTATIVE COLLECTIONS. **ECUADOR.** **Loja:** Cerro Sozoranga, Cariamanga-Utuama km 29.5, 4.21S, 79.42W, *Jorgensen et al.* 651 (K). **Morona-Santiago:** 20 km SSE of Limón, 3.00S, 79.00W, *Pennington & Tenorio* 10799 (K). **Zamora-Chinchipe:** Yacuambi, Centro Shuar Kurints, 3.44S, 78.57W, *Wisum & Kajekai* 807 (K). **PERU.** **Amazonas:** Chachapoyas Province, Soloco, Olianahui, 6.00S, 77.00W, *Diaz et al.* 4285 (MO). **Cajamarca:** Jaen Province, Sallique, Lanchal to Tambillo, 5.40S, 79.16W, *Campos et al.* 5170 (F, MO). **Piura:** Prov. Ayabaca, Bosque to Huamba, above Yanchala, 4.00S, 79.00W, *Cano* 1379 (K).

CONSERVATION STATUS. This species was assessed by Vacas *et al.* (2019) as Endangered B2ab(iii,v). The addition of records from Ecuador and northern Peru, increase the extent of occurrence to 64,000 km² and the area of occupancy is also now likely to exceed thresholds for a threatened category. Although there has been deforestation within its range and it is known to be selectively harvested for timber, these are not considered to be major threats and this species should therefore be reassessed as Least Concern.

LOCAL NAMES AND USES. Cedro (Peru: Cajamarca). Larger specimens produce good quality timber (Peru: Cajamarca).

RELATIONSHIPS. Most Ecuadorean specimens of this species are distinctive on account of their 4 – 7 pairs of very small leaflets with a rounded apex, but some of the Peruvian population, especially those from the Bosque de Cachil in Cajamarca, have much larger leaflets and are consequently morphologically close to *Ruagea glabra*, but still differing from the latter in the rounded leaflet apex. The small flower size (petals 4.5 – 6 mm long) also generally distinguishes this species from *R. glabra*. *Ruagea microphylla* forms a strongly supported clade next to the Bolivian *R. beckii* (Rojas-Andres *et al.* submitted).

9. *Ruagea parvifructa* T.D.Penn. sp. nov. Type. Peru, Cajamarca, San Ignacio Province, Distr. Huarango, El Triunfo (propiedad de Edilberto Delgado), July 1996, fl., fr., *J. Campos, P. Diaz & W. Alorcan* 2945 (holotype MO).

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Bud scales absent. *Young shoots* 0.9 – 1.6 cm diam., hollow, terete, smooth, densely and softly pale-pubescent (erect hairs) eventually becoming glabrous, brown, with or without a few lenticels. *Leaves* imparipinnate; petiole 9 – 15 cm long, terete, densely and softly pubescent; rachis 16 – 31 cm long, slightly channelled above, softly pubescent; petiolule of lateral leaflets 1 – 1.5 mm long; petiolule of terminal leaflet 2

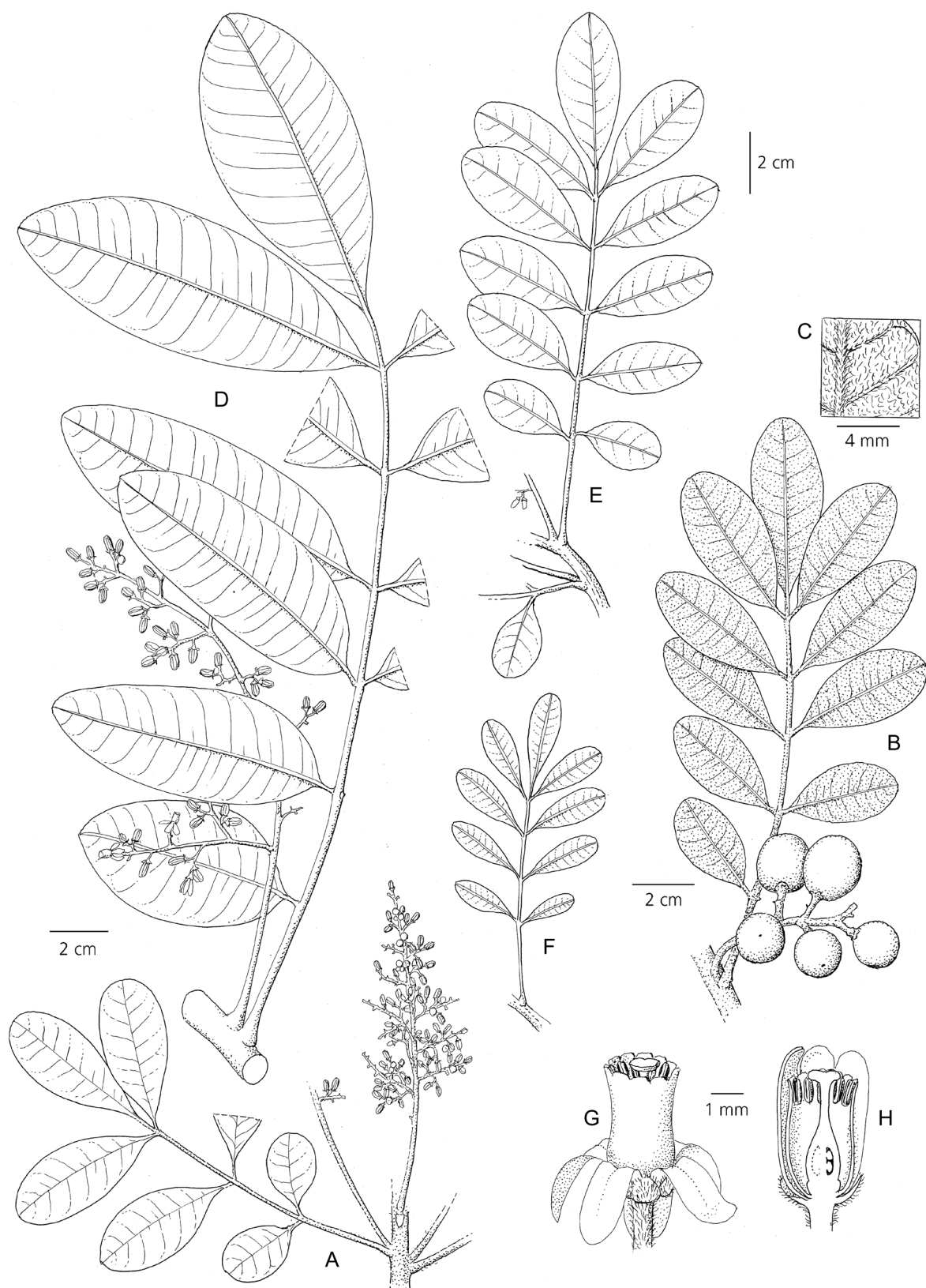
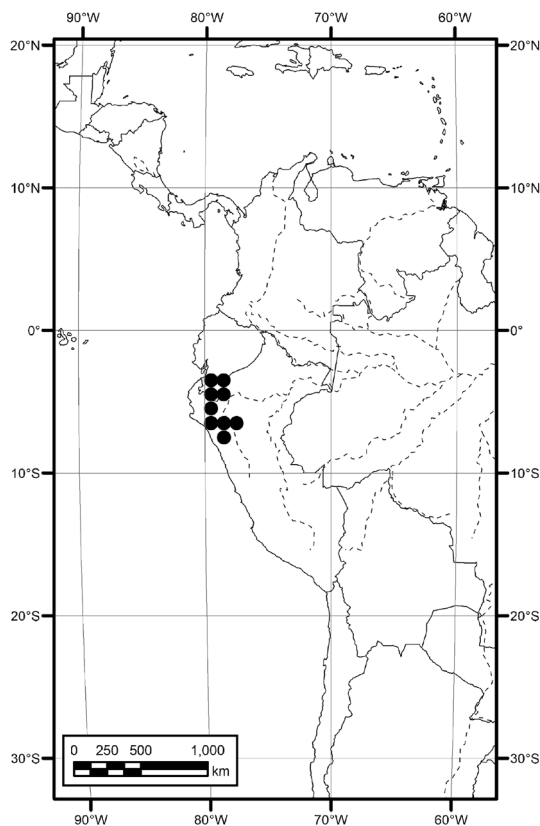


Fig. 8. *Ruagea microphylla*. A habit with inflorescence; B habit with infructescence; C enlargement of leaflet undersurface; D habit with inflorescence; E leaf; F leaf; G male flower; H half flower male. A, G, H Campos *et al.* 5154; B, C Campos *et al.* 5170; D Sagastegui & Leiva 14941; E Weigend *et al.* 98/500; F Jorgensen *et al.* 21. DRAWN BY ROSEMARY WISE.



Map 8. Distribution of *Ruagea microphylla*.

– 10 mm long. *Leaflets* opposite, 4 pairs, uppermost lateral 17.2 – 22 cm long, 8 – 9 cm broad, broadly oblanceolate, apex obtusely cuspidate, base acute or narrowly attenuate, margin slightly revolute, chartaceous, pubescent on midrib and secondary veins above, lamina glabrous, lower surface with pubescent midrib and secondary veins, lamina with scattered hairs, minute red papillae present on lower surface; basal leaflets 5.5 – 7.2 cm long, 3 – 4.1 cm broad, broadly elliptic, apex obtusely cuspidate, base obtuse, slightly asymmetric; terminal leaflet 21.5 – 30 cm long, 10 – 12 cm broad, broadly oblanceolate, apex obtusely cuspidate, base narrowly attenuate; venation eucamptodromous, midrib slightly raised on the upper surface, secondaries 15 – 16 pairs, ascending, slightly arcuate, parallel; intersecondaries short; tertiaries few oblique, obscure. *Inflorescence* axillary, male to 25 cm long, lateral branches to 15 cm long, female to 30 cm long with lateral branches to 6 cm long, a many-flowered congested panicle, pedicel to 1 mm long. *Flowers* unisexual (plant dioecious) (female flowers seen, male flowers in bud only). *Sepals* 4 – 5, 1.25 – 1.5 mm long, broadly ovate to suborbicular, apex obtuse or rounded, with scattered pubescence outside, glabrous inside, margin ciliate. *Petals* 5, 6.5 – 7 mm long, 1.5 – 2 mm broad, oblong, apex obtuse to

rounded, glabrous, margin not ciliate. *Staminal tube* c. 5.5 mm long, c. 3 mm broad, broadly tubular, margin shortly toothed, teeth rounded, glabrous, anthers 9, c. 1 mm long, glabrous, antherodes in female narrower, without pollen, not dehiscing. *Nectary* a short stipe below the ovary, c. 0.5 mm long, not swollen, glabrous. *Ovary* c. 2.5 mm long, ovoid, glabrous, 3-locular, locules with 2 superposed ovules, style c. 2.5 mm long, glabrous, style-head discoid, pistillode in male similar but with less-developed ovules. *Infructescence* to 25 cm long with lateral branches to 6 cm long, many-fruited (up to 50 fruit). *Capsule* 1 – 1.1 cm diam., globose, apex rounded and finally apiculate, base rounded, smooth, glabrous, lenticellate, pericarp c. 0.5 mm thick, 3-valved, valves 1-seeded. *Seed* c. 4 × 3 mm, obovoid, with a slightly swollen basal sarcotesta, seed coat membraneous; embryo with plano-convex, collateral cotyledons, radicle apical, extending to the surface. Fig. 9.

FIELD CHARACTERS. Evergreen treelet or small tree to 12 m high and 10 cm diam., with greenish-white flowers. Flowering recorded in July and Sept., mature fruit in March, April, June, July and Sept.

RECOGNITION. This species is close to *Ruagea tomentosa* but differs in the fewer oblanceolate leaflets, smaller flowers with a glabrous ovary and in the much smaller fruit.

DISTRIBUTION AND ECOLOGY. Known only from southern Ecuador and the adjacent region of northern Peru, in wet montane rain forest, altitudinal range 1500 m to 2300 m (Map 9).

COLLECTIONS EXAMINED. ECUADOR. Zamora-Chinchipe: Cantón Yacuambi, Centro Shuar Kurints, 3.44S, 78.57W, *Kajekai & Wisum* 761 (MO, US), 831 (K).

PERU. Amazonas: Prov. Bagua, Shillac, N by trail from Pedro Ruiz, 5.49S, 78.01W, *D. N. Smith & Vásquez* 4923 (F). **Cajamarca:** Prov. San Ignacio, Distr. Huarango, El Triunfo, 5.18S, 78.43W, *Campos et al.* 2945 (MO); Prov. San Ignacio, San José de Lourdes, Santo Tomas, 4.55S, 78.50W, *Vásquez et al.* 20161 (K); Prov. San Ignacio, San José de Lourdes, Camara, 5.00S, 78.04W, *Campos & Corrales* 3479 (F,US), *Campos et al.* 3814 (F).

CONSERVATION STATUS. This species has a relatively restricted extent of occurrence of 6,017 km² and based on the known collections, occurs at only 5 threat-defined locations. The area of occupancy is estimated as only 20 km² and although this is likely to be an underestimate due to low surveying effort, it is not expected to exceed the 2000 km² threshold for the Vulnerable category. Deforestation for agriculture and mining are the primary threats to this species' habitat, and satellite imagery has shown that several of the collection localities are in close vicinity to deforested areas. This species is therefore assessed as Vulnerable B1ab(iii) + 2ab(iii).

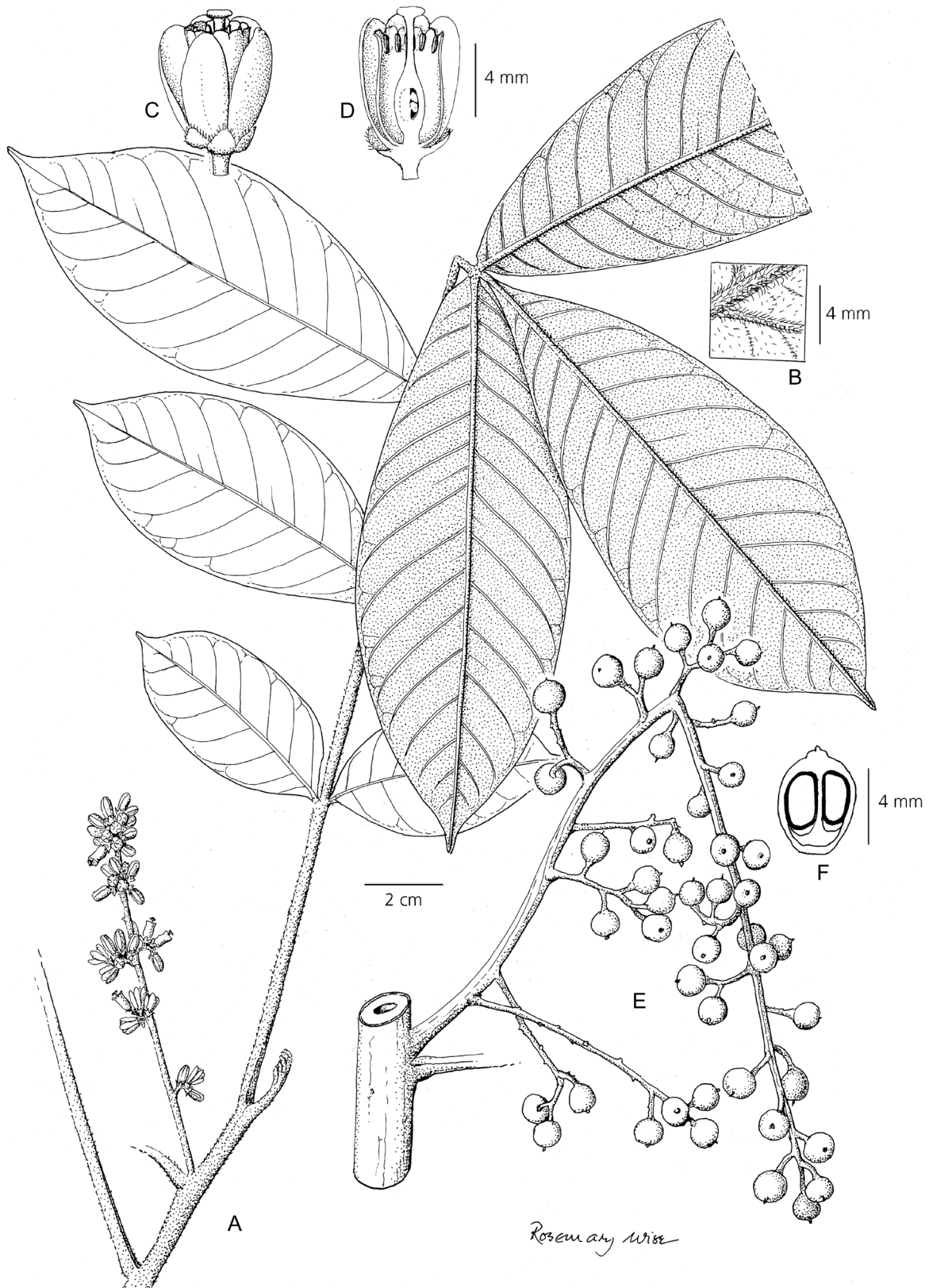
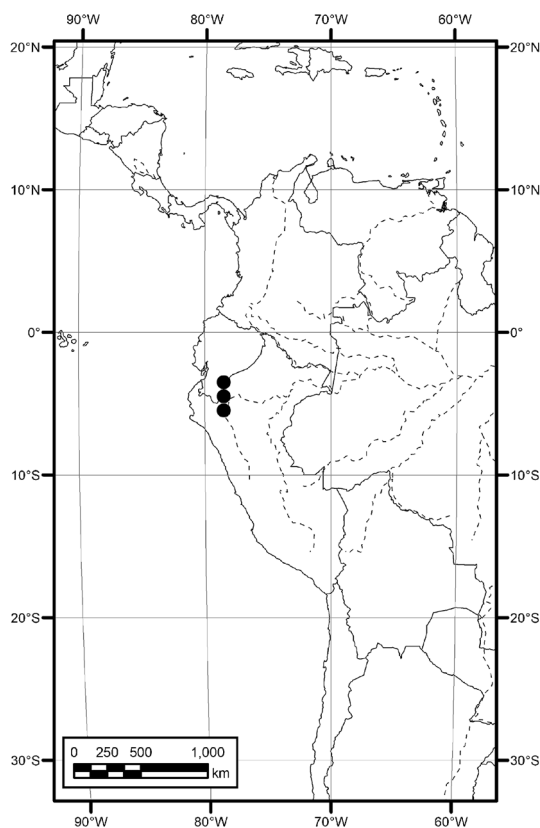


Fig. 9. *Ruagea parvifructa*. A habit with inflorescence; B enlargement of leaflet undersurface; C female flower; D half flower female; E infructescence; F section of fruit. A – D, Campos et al. 2945; E, F Campos et al. 3814. DRAWN BY ROSEMARY WISE.



Map 9. Distribution of *Ruagea parvifructa*.

RELATIONSHIPS. *Ruagea parvifructa* is morphologically closest to *R. tomentosa*, which has similar dense pubescence on the young shoots and leaves and similar leaflet size. The new species has 4 pairs of oblanceolate leaflets (4–6 pairs of broadly oblong-elliptic leaflets in *R. tomentosa*, slightly smaller flowers with a glabrous ovary (ovary pubescent in *R. tomentosa*), and a much smaller fruit 1–1.1 cm diam. (3.5–5.5 cm in *R. tomentosa*). Molecular data indicates a well-supported clade sister to that containing *R. glabra*, *R. tomentosa* and *R. trisperma* (Rojas-Andres *et al.* [submitted](#)).

10. *Ruagea pubescens* H.Karst. (Karsten 1863: 51, t. 126); Pennington (1981: 252); Palacios (2007: 53). Type. Venezuela, Aragua, Colonia Tovar, fl., fr., Karsten s.n. (holotype W; isotypes F, LE, US).

Guarea ruagea C.DC. (de Candolle 1878: 577). Name based on *Ruagea pubescens* Karst.

Guarea smithii C.DC. (de Candolle 1907: 150). Type.

Colombia, Santa Marta, fl., *H. H. Smith* 1550 (holotype G; isotypes A, BM, BR, E, F, GH, K, MO, PH, S).

Guarea mollicoma Pittier (1923: 28). Type. Venezuela, Aragua, Colonia Tovar, fl., *Pittier* 10041 (holotype VEN; isotypes GH, NY, US).

Ruagea mollicoma (Pittier) Harms (1925: 427).

Ruagea smithii (C.DC.) Harms (1925: 428).

Bud scales absent. *Young shoots* 0.5–2 cm diam., terete, shortly golden tomentose or pubescent at first, becoming sparser with age, smooth, brown, lenticels few or absent. *Leaves* imparipinnate; petiole 2.8–7 cm long, semiterete or slightly channelled above at the base, terete above, shortly tomentose at first or glabrous, becoming subglabrous; rachis 7–25.5 cm long, slightly channelled above or terete, shortly tomentose or pubescent at first; petiolule of lateral leaflets 2–5 mm long, petiolule of terminal leaflet 0.5–1.4 cm long. *Leaflets* opposite, (2–) 3–6 pairs, uppermost lateral 10.5–20 (–25) cm long, 4.5–10 (–13) cm broad, broadly elliptic to obovate, apex obtuse to rounded or truncate, base usually obtuse to rounded or truncate, occasionally acute or cuneate, margin slightly revolute, coriaceous, upper surface with shortly pubescent to tomentose midrib, otherwise glabrous, lower surface with midrib and secondary veins shortly tomentose or pubescent and shortly crisped pubescent lamina, minute red papillae abundant on both surfaces; basal leaflets 4–10 cm long, 3.3–6 cm broad, broadly ovate or elliptic, or suborbicular, apex obtuse to rounded, base acute to obtuse; terminal leaflet 11.3–20 cm long, 5–10 cm broad, broadly elliptic to obovate, apex obtuse, obtusely cuspidate or rounded, base acute or cuneate; venation eucamptodromous in the lower half, brochidodromous in the upper half, midrib flat or slightly sunken on the upper surface, secondaries 10–17 pairs, ascending, straight or slightly arcuate, parallel, intersecondaries short to moderate or absent; tertiaries oblique to reticulate, obscure. *Inflorescence* axillary, 10–50 cm long, a slender to broad many-flowered panicle, lateral branches to 12 cm long, shortly pubescent to tomentose, pedicel 0.5–1.5 mm long. *Flowers* unisexual (plant dioecious). *Sepals* 5, 1–1.5 mm long, broadly ovate to orbicular, apex obtuse or rounded, pubescent to subglabrous outside, glabrous inside, margin ciliate. *Petals* 5, (7–) 10–14 mm long, 2–4 mm broad, oblong to spatulate, apex rounded, glabrous, not ciliate. *Staminal tube* 6–9 mm long, 2.5–4 mm broad, tubular, margin crenulate or irregularly toothed, glabrous, anthers 9–10, 0.9–1.5 mm long, glabrous, antherodes in female narrower, without pollen, not dehisced. *Nectary* a short, sometimes swollen stipe below the ovary, 1–1.5 mm long, glabrous. *Ovary* 3–4 mm long, ovoid, glabrous, 3-locular, locules with 1–2 superposed ovules, style 2.5–4 mm long, glabrous, style-head discoid; pistillode in male similar but with much reduced ovules. *Inflorescence* to c. 20 cm long, several- to many-fruited. *Capsule* 3.2–5 cm long, globose or obovoid, apex rounded, base rounded or obtuse, smooth, brown with pale lenticels, glabrous, pericarp 2–3 mm thick, 3-valved, valves 1-seeded. *Seed* c. 1.3 × 1.1 cm, plano-convex, with a thick basal sarcotesta, seed coat membranous; embryo with thick, plano-convex collateral cotyledons, radicle apical, included. Fig. 10.

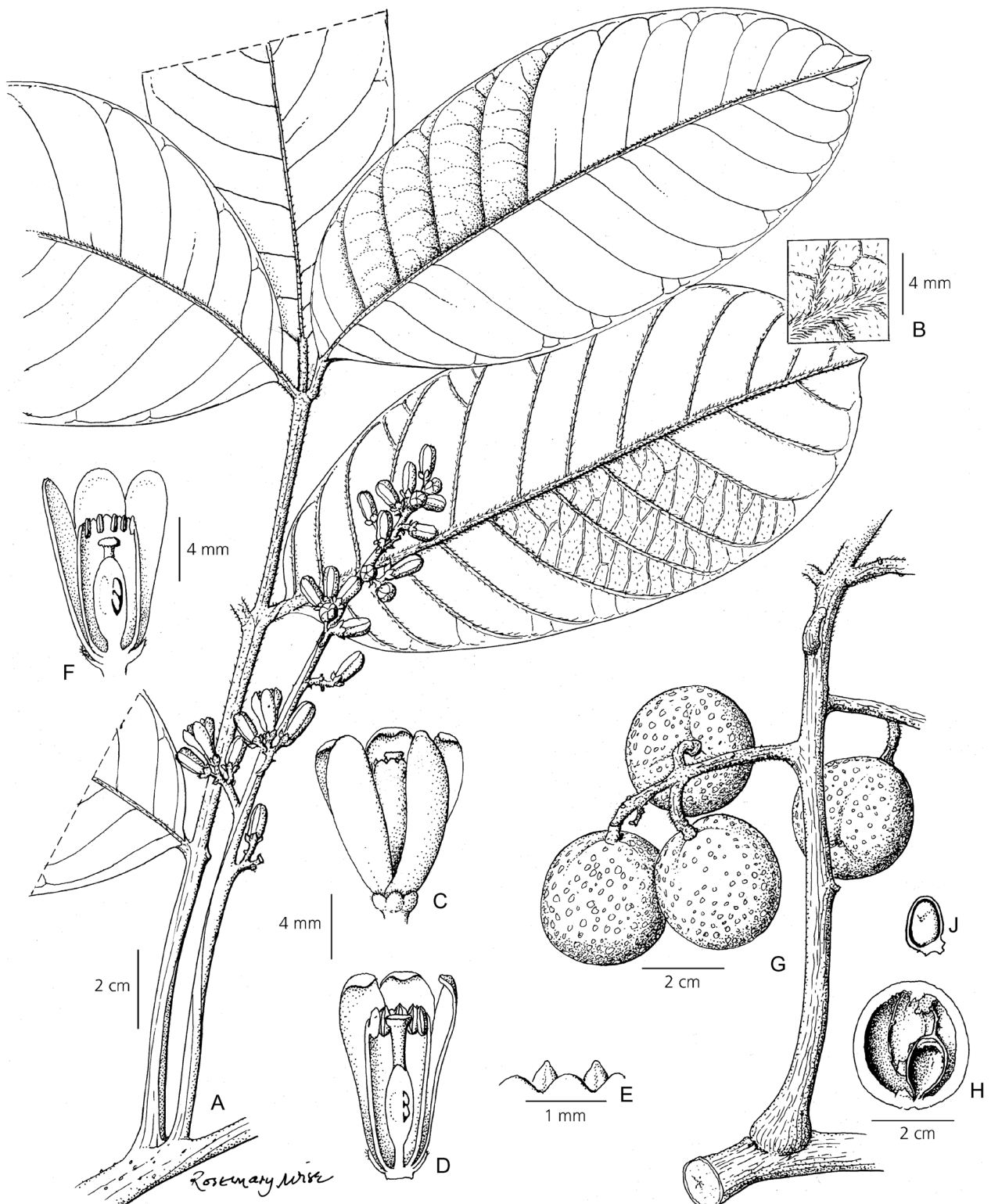


Fig. 10. *Ruagea pubescens*. A habit with inflorescence; B enlargement of leaflet undersurface; C male flower; D half flower male; E margin of staminal tube (from outside); F half flower female; G infructescence; H section of fruit; J section of seed. A – E Pennington & Tenorio 10804; F Cuello et al. 1712; G – J Liesner & Medina 13509. DRAWN BY ROSEMARY WISE.

FIELD CHARACTERS. Evergreen tree to 30 m high and 40 cm diam., with cylindrical bole and smooth to shallowly fissured brown bark and large crown; the bark slash is cream-coloured. Flowers fragrant, with dark green sepals, bright green petals and pale cream staminal tube. The fruit matures brownish-orange with conspicuous pale lenticels and the seeds (with sarcotesta) are bright red-orange. Flowering is recorded throughout the year, but most records are between Dec. and April. Mature fruit recorded throughout the year.

DISTRIBUTION AND ECOLOGY. From the coastal Cordillera in northern Venezuela, through Colombia (both eastern and western Cordilleras) to the Andes of southern Ecuador and northern Peru. In montane rain forest and cloud forest, associated with *Quercus* and *Weinmannia* in Colombia and with *Podocarpus* in Venezuela. Altitudinal range 1450 m to 3000 m (Map 10).

REPRESENTATIVE COLLECTIONS. VENEZUELA. **Aragua:** 4 km SW of Colonia Tovar, road to Capachal, 10.22N, 67.19W. *Liesner & Medina* 13509 (F, K, US). **Distrito Federal:** Monumento Natural Pico Coezy, 10.26N, 67.14W, *Meier et al.* 6432 (K). **Mérida:** La Carbonera, via La Azulita, 8.39N, 71.22W, *Marcano-Berti & Salcedo* 4979 (K). **COLOMBIA.** **Antioquia:** Municipio Frontino, road to Murri, 15 km W of Nutibara, 6.45N, 76.23W, *Brant & Martínez* 1320 (K). **Boyaca:** Villa de Leiva, Santuario Flora y Fauna Iguaque Cabaña, 5.44N, 73.28W, *Betancur et al.* 4033 (K). **Cundinamarca:** Río Subia, 4.34N, 74.42W, *Idrobo &*

Jaramillo 1682 (COL). **Magdalena:** Santa Marta, *H. H. Smith* 1550 (A, BM, BR, E, F, G, GH, MO, PH, S). **ECUADOR.** **Azuay:** Palmas to Florida, 4 km NE of Molleturo, 2.44S, 79.22W, *Cornejo et al.* 3525 (K). **Carchi:** Tulcan to Tufino to Maldonado km 42, 0.48N, 77.51W, *Jaramillo* 9109 (NY). **Cotopaxi:** road Latacunga to Quevedo, SE of Pilalo, 0.56S, 78.59W, *Pennington & Tenorio* 10804 (K). **Imbabura:** Cotocachi Cantón, Parroquia Plaza Gutierrez, road to Apuel, 0.20N, 78.26W, *Cuamacas et al.* 114 (K). **Morona-Santiago:** Gualaceo to Plan de Milagro, near Tinajillas, 3.03S, 78.33W, *Palacios & van der Werff* 3713 (MO). **Napo:** Cantón Quijos, Cosanga, Hacienda Guacamayos. 0.36S, 77.51W, *Palacios & Freire* 5045 (F). **Pichincha:** Lloa valley, Lloa to Mindo km 14, 0.10S, 78.38W, *Jorgensen* 6596 (K). **Zamora-Chinchipec:** Cordillera Nanguipa, Cerro Colorado, 4.07S, 78.46W, *Neill et al.* 13850 (K). **PERU.** **Amazonas:** Distr. Camporeddondo, Tullanya Pascana la Palma, 6.04S, 78.21W, *Vasquez et al.* 22016 (F).

CONSERVATION STATUS. This species has a large extent of occurrence of over 125,000 km² which falls outside of thresholds for a threatened category under Criterion B. It also has an area of occupancy of 124 km², although this is thought to be highly underestimated as a result of low surveying effort within this species' range. It is therefore assessed as Least Concern (LC). Deforestation driven by conversion of land for agriculture is an ongoing threat to this species' habitat and the presence of mineral and fossil fuel concessions across its range are likely to contribute to further habitat loss in the future.

LOCAL NAMES. Cedro (Ecuador: Bolívar), espermo, cedrillo de montaña (Venezuela: Mérida).

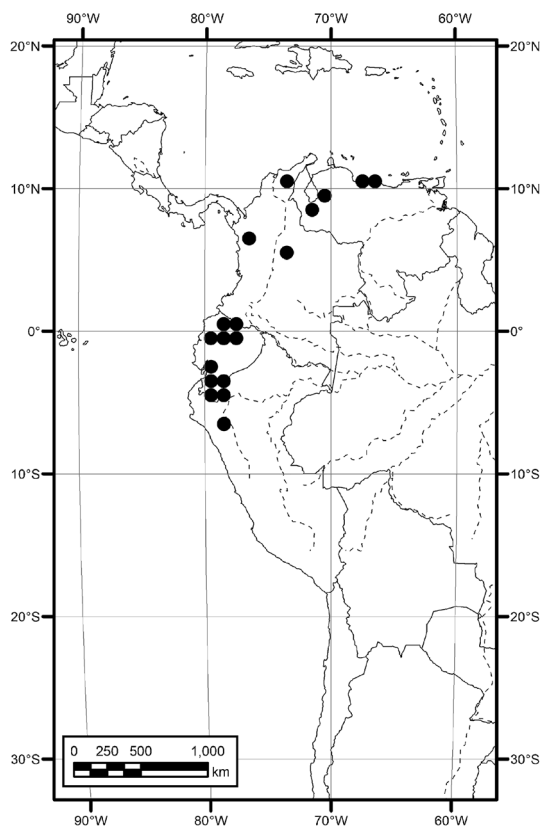
RELATIONSHIPS. This species is morphologically closest to *Ruagea tomentosa*, but differs from it on the basis of several mostly vegetative characters listed below.

Ruagea pubescens: leaflets (uppermost lateral) 10.5 – 20 cm long, apex and base usually obtuse, rounded or truncate, leaflets coriaceous, secondary veins 10 – 17 pairs, tertiary and higher order venation obscure, petals (7 –) 10 – 14 mm long, ovary glabrous.

Ruagea tomentosa: leaflets (uppermost lateral) 18 – 37 cm long, apex usually acute to acuminate, base usually obtuse, acute or narrowly attenuate, leaflets chartaceous, secondary veins 15 – 22 pairs, tertiary and higher order vein reticulum conspicuous, petals (5 –) 8 – 11 mm long, ovary with some pubescence.

11. *Ruagea tomentosa* Cuatrec. (Cuatrecasas 1950: 80); Pennington (1981: 255); Palacios (2007: 54). Type. Colombia, Dept. del Valle, Hoya del Río Cali, Río Pichinde, between Quebrada de Juntas and El Recreo, fl., fr., Aug. 1946, *Cuatrecasas* 21988 (holotype F).

Bud scales absent. *Young shoots* 0.8 – 1.8 cm diam., often hollow, terete, densely golden-brown pubescent to tomentose, becoming sparse with age, smooth,



Map 10. Distribution of *Ruagea pubescens*.

sometimes with raised lenticels. *Leaves* imparipinnate; petiole 3 – 12 cm long, terete or semiterete, pale-golden pubescent or tomentose; rachis 10 – 45 cm long, terete to slightly channelled above, tomentose to pubescent, becoming sparse with age; petiolule of lateral leaflets 2 – 6 mm long, petiolule of terminal leaflet 1.3 – 6 cm long. *Leaflets* opposite, subopposite or alternate, 4 – 6 pairs, uppermost lateral leaflets 18 – 37 cm long, 7.5 – 11.5 cm broad, broadly oblong-elliptic, apex shortly and narrowly acuminate, acute or obtuse, base obtuse, acute or narrowly attenuate, margin usually slightly revolute, chartaceous, pubescence on upper surface usually confined to midrib and secondary veins, lower surface with tomentose midrib and veins and softly pubescent lamina, minute red papillae on lower surface; basal leaflets 4 – 14 cm long, 3.2 – 8.5 cm broad, broadly elliptic or oblong-elliptic, apex acute to rounded, base rounded; terminal leaflet 21 – 30 cm long, 9 – 13.5 cm broad, broadly elliptic or obovate, apex and base narrowly acuminate; venation eucamptodromous in the lower half, brochidodromous above, midrib flat or slightly raised on the upper surface, secondaries 15 – 22 pairs, ascending, straight to slightly arcuate, parallel; intersecondaries short or absent; tertiaries oblique and parallel; higher order reticulum often visible. *Inflorescence* axillary, 7 – 36 cm long, a little-branched, few-flowered to much-branched and many-flowered panicle, lateral branches up to 10 cm long, pubescent to tomentose, pedicel c. 1 mm long. *Flowers* unisexual (plant dioecious). *Sepals* 5, 1.25 – 1.5 mm long, triangular to ovate, apex acute to rounded, pubescent or scattered hairs outside, glabrous inside, margin ciliate. *Petals* 5, (5 –) 8 – 11 mm long, oblong, apex acute to rounded, glabrous, margin not ciliate. *Staminal tube* 7 – 8 mm long, 2 – 3 mm broad, tubular, margin crenulate, glabrous, anthers 10, 1 – 1.75 mm long, glabrous; antherodes in female narrower, not dehisced, without pollen. *Nectary* a small stipe below the ovary, 1 – 1.5 mm long, glabrous. *Ovary* 2 – 3 mm long, ovoid, pubescent or with scattered hairs, 3-locular, locules with 1 – 2 superposed ovules, style 2 – 3 mm long, glabrous, style-head discoid, pistillode in male similar but with less-developed ovules. *Infructescence* to 20 cm long. *Capsule* 3.5 – 5.5 cm long, globose to obovoid, apex obtuse to rounded, base obtuse to rounded, sometimes with a short broad stipe, smooth, brown with pale lenticels, glabrous, pericarp 1 – 1.5 mm thick, 3-valved, valves with 1 – 2 superposed seeds. *Seed* c. 2 × 1.6 cm, plano-convex, with a thick basal sarcotesta, seed coat membranous; embryo with plano-convex, collateral cotyledons, radicle apical, extending to the surface. Fig. 11.

FIELD CHARACTERS. Evergreen tree to 30 m high and 40 cm diam., with smooth brown lenticellate bark, often flowering when less than 10 m high. Flowers scented,

with green sepals and petals and cream staminal tube. Mature fruit brown to yellowish-green with pale lenticels, seed surrounded by a red sarcotesta (white when immature). Flowering from Aug. to Dec., mature fruit recorded in Jan., March, May, June, Aug. and Sept.

DISTRIBUTION AND ECOLOGY. Western Cordillera of Colombia and Pacific slopes of Andean Ecuador from 7°N to 4°S, with a single record from the eastern slopes of the Ecuadorean Andes, in montane rain forest and cloud forest, altitudinal range from 1200 m to 2600 m (Map 11).

REPRESENTATIVE COLLECTIONS. **COLOMBIA.** **Antioquia:** Municipio Valdivia, Vereda San Fermin, 7.15N, 75.30W, *Callejas et al.* 6156 (NY). **Valle:** Cordillera Occidental, Río Cali, Río Pichinde, below Quebrada de Juntas and El Recreo, 3.00N, 76.00W, *Cuatrecasas* 21988 (F). **ECUADOR.** **Azuay:** Molleturo, 4 km E, 2.44S, 79.23W, *Cornejo & Bonifaz* 3250 (K). **Cañar:** Azogues, Gualleturo, 2.32S, 79.08W, *Vargas & Defas* 5910 (K). **Carchi:** Mira, El Carmen, Cerro Golondrinas, 0.50N, 78.11W, *Tirado et al.* 1335 (K, MO). **Cotopaxi:** Cantón Sigchos, Sigchos to Las Pampas km 35, Finca Sr. Galo Robalo, 0.32S, 78.58W, *Ramos et al.* 6848 (MO). **Loja:** Cantón Loja, road Loja to Zamora near the top, 3.58S, 79.04W, *Rubio et al.* 2254 (F). **Napo:** Quijos, Reserva Ecológica Antisana, Cordillera de los Guacamayos, 0.38S, 77.51W, *Vargas & Narvaez* 3344 (K). **Pichincha:** Cantón Quito, Cerro Paso Alto, 0.11N, 78.31W, *Ceron & Gallo* 37566 (MO).

CONSERVATION STATUS. This species has a large extent of occurrence of over 104,000 km² which falls outside of thresholds for a threatened category under Criterion B. It also has an area of occupancy of 60 km², although this is thought to be highly underestimated as a result of low surveying effort within this species' range. It is therefore assessed as Least Concern (LC). However, it has experienced some habitat loss, as the forests of the northwestern Andes where it occurs have experienced considerable disturbance due to deforestation for cattle grazing and agriculture.

LOCAL NAMES AND USES. Guavalon (Ecuador: Cotopaxi). Larger specimens used for timber (Ecuador: Cotopaxi).

RELATIONSHIPS. This species is similar in leaf and leaflet size to *Ruagea trisperma*, but differs from it in the spreading pubescent or tomentose indumentum, in the conspicuous tertiary and higher order venation and larger flowers (petals 8 – 11 mm long vs 5.5 – 7 mm long in *R. trisperma*). The 2 species cluster together in the molecular analysis but they are not individually resolved (Rojas-Andres *et al.* [submitted](#)).

This species was previously treated as doubtfully distinct from *Ruagea pubescens* (Pennington (1981: 255), but with the benefit of much additional material it is here treated as distinct, supporting the decision of Palacios (2007). The best morphological characters for separating the species are the leaflet shape, texture

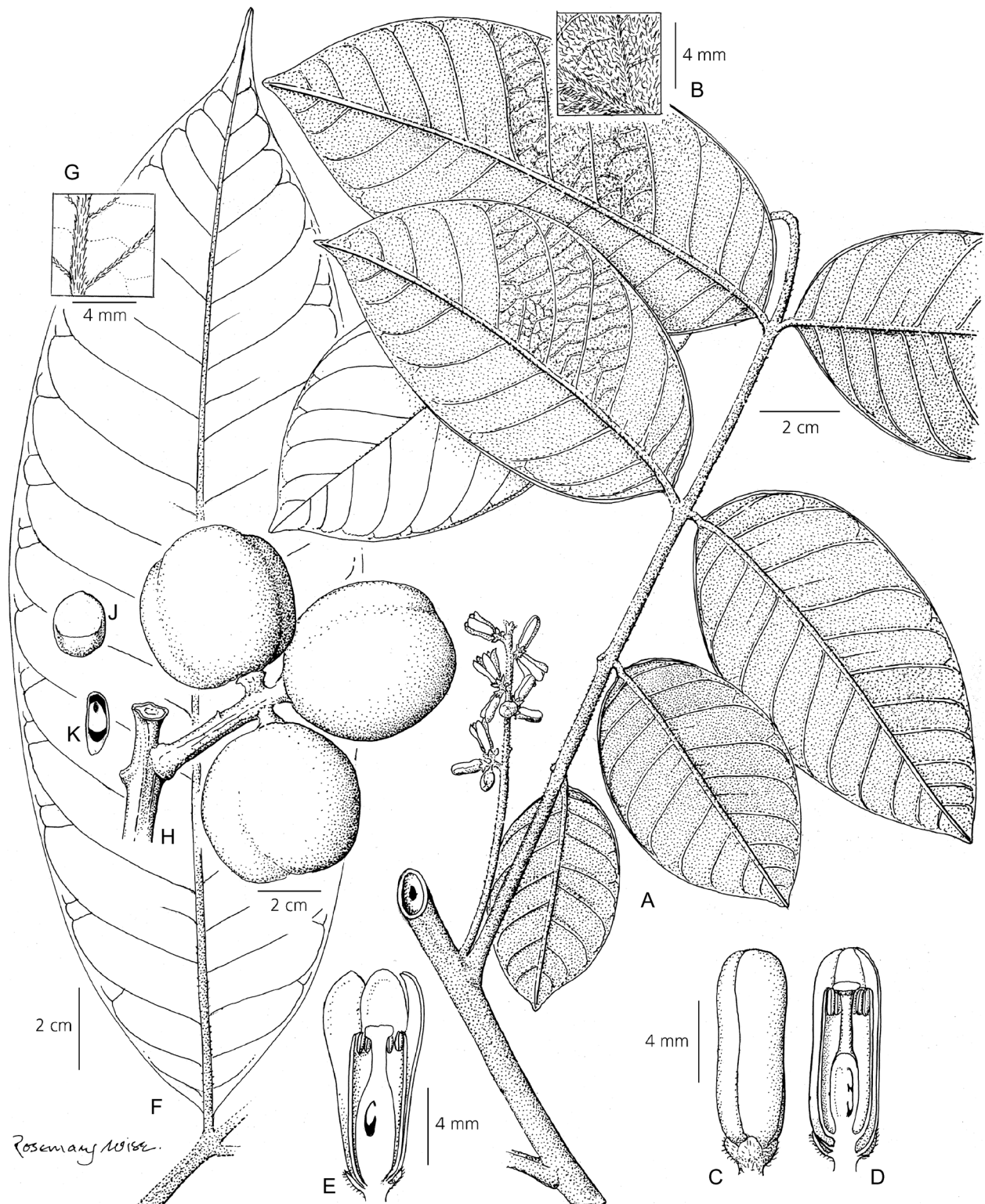
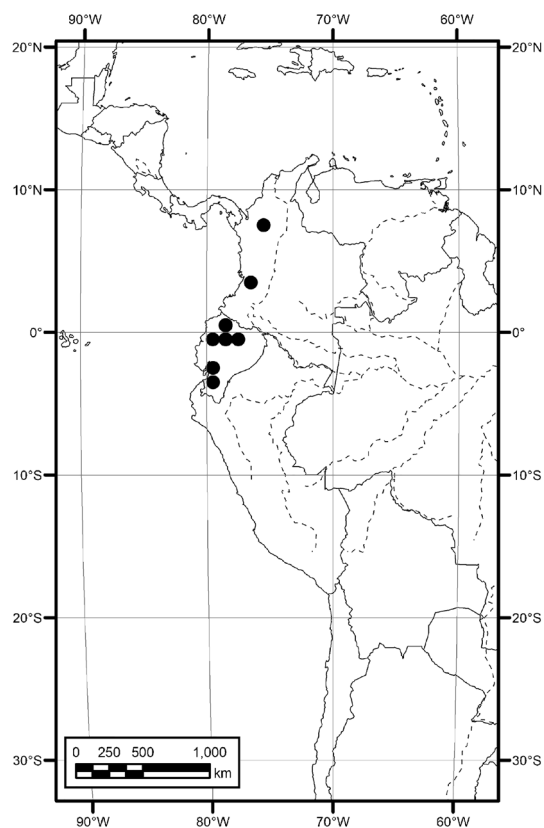


Fig. 11. *Ruagea tomentosa*. A habit with inflorescence; B enlargement of leaflet undersurface; C male flower; D half flower male; E half flower female; F leaflet; G enlargement of leaflet upper surface; H inflorescence; J seed; K section of seed. A, B, E Cuatrecasas 21988; C, D Vargas et al. 4046; F, G Tirado et al. 1335; H – K Palacios & van der Werff 3590. DRAWN BY ROSEMARY WISE.



Map 11. Distribution of *Ruagea tomentosa*.

and venation. See under *R. pubescens* for more details.

12. *Ruagea trisperma* Cuatrec. (Cuatrecasas 1950: 77); Pennington (1981: 245); Palacios (2007: 55). Type. Colombia, Dept. del Valle, Río Sanguinini, Dec. 1943, fl., fr., Cuatrecasas 15521 (holotype F).

Bud scales absent. *Young shoots* 1 – 1.5 cm diam., usually hollow, terete, closely appressed puberulous at first, soon glabrous, smooth, brown, lenticellate. *Leaves* imparipinnate; petiole 6.5 – 11 cm long, semiterete to terete, closely appressed puberulous at first, becoming glabrous; rachis 22 – 50 cm long, terete to semiterete, closely appressed puberulous to glabrous; petiolule of lateral leaflets 0.5 – 1.5 mm long, petiolule of terminal leaflet 1.5 – 2 cm long. *Leaflets* opposite to alternate, 4 – 7 pairs, uppermost lateral 22 – 34 cm long, 7 – 15 cm broad, broadly oblong to oblanceolate, apex obtusely cuspidate, obtuse or rounded, base obtuse to narrowly attenuate or rarely rounded, margin revolute, coriaceous, upper surface with closely appressed puberulous midrib or glabrous, lower surface sparsely to densely closely appressed puberulous, minute red papillae on lower surface; basal leaflets 7 – 14 cm long, 4 – 6.5 cm broad, broadly elliptic, apex obtuse to rounded, base narrowly attenuate; terminal leaflet 27 – 30 cm long, 9 –

15 cm broad, obovate to oblanceolate, apex obtuse to rounded, base narrowly attenuate; venation eucamptodromous, midrib slightly sunken on the upper surface, secondaries (15 –) 20 – 25 pairs, ascending, straight, parallel; intersecondaries short or absent; tertiaries obscure. *Inflorescence* axillary or sometimes clustered in the axils of undeveloped leaves, 15 – 41 cm long, a narrow to broad many-flowered panicle with lateral branches 5 – 15 cm long, sparsely and closely appressed puberulous, flowers subsessile. *Flowers* unisexual (plant dioecious). *Sepals* 5, c. 1 mm long, ovate, apex obtuse to rounded, sparse appressed indumentum outside, glabrous inside, margin sparsely ciliate. *Petals* 5, 5.5 – 7 mm long, oblong or narrowly elliptic, apex obtuse to rounded, with sparse closely appressed hairs outside, glabrous inside, margin not ciliate. *Staminal tube* 4 – 5 mm long, 1.5 – 3 mm broad, broadly tubular or tubular-campanulate, margin crenulate, glabrous, antherodes in female narrower, without pollen, not dehiscent. *Nectary* a small stipe below the ovary, 0.75 – 1 mm long, glabrous. *Ovary* c. 1.5 mm long, ovoid, glabrous, 3-locular, locules with 1 – 2 superposed ovules, style 1 – 1.5 mm long, glabrous, style-head discoid, pistillode in male similar but with less-developed ovules. *Infructescence* to 30 cm long, several- to many-fruited. *Capsule* 3.5 – 4.5 cm diam., apex and base rounded or obtuse, smooth, brown with pale lenticels, glabrous, pericarp c. 1 mm thick, 3-valved, valves 1-seeded. *Seed* 2 – 2.5 cm long, c. 1.5 cm broad, with a thick basal sarcotesta, seed coat membranous; embryo with thick planoconvex collateral cotyledons, radicle apical, extending to the surface. Fig. 12.

FIELD CHARACTERS. Evergreen tree to 25 m high and 60 cm diam., larger specimens buttressed to 80 cm high, but sometimes flowering as a small treelet 5 m high. Flowers with green or greenish-white petals and cream-coloured staminal tube. Mature fruit brown to orange or reddish-brown, lenticellate, containing red or orange seeds. Flowering recorded in April, May, Aug. and Dec., mature fruit in April, June, Sept. and Dec.

DISTRIBUTION AND ECOLOGY. Western Cordillera of Colombia and Pacific slopes of Andean Ecuador from 6°N to 3°S. A tree of wet montane forest and cloud forest, altitudinal range 780 m (Azuay, Ecuador) to 2500 m (Chimborazo, Ecuador) (Map 12).

REPRESENTATIVE COLLECTIONS. COLOMBIA. Antioquia: Municipio Jerico, Sitio La Leona, 5.50N, 75.45W, Callejas et al. 8418 (K). **Nariño:** Municipio Ricaurte, Reserva Natural la Planada, 1.00N, 77.00W, Beltran 20 (MO). **ECUADOR. Azuay:** 20 – 25 km E of Jesus Maria, border with Cañar, Gentry et al. 28516 (K). **Carchi:** Cantón Espejo, Cerro Golondrinas, 0.51N, 78.07W, Palacios 12771 (K). **Chimborazo:** above Maldonado, 1.00S, 78.00W, van der Werff & Gudíño 10841 (MO). **El**

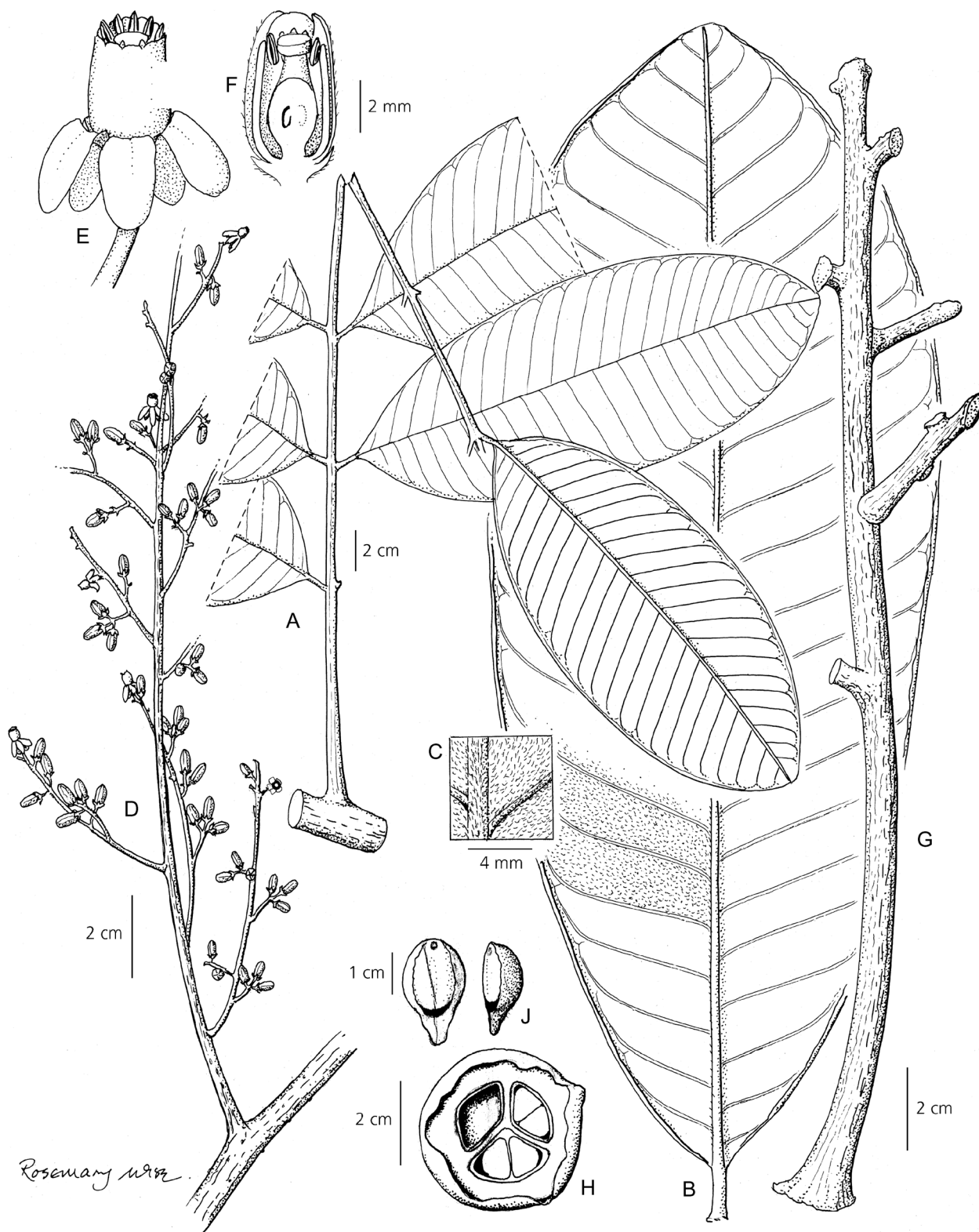
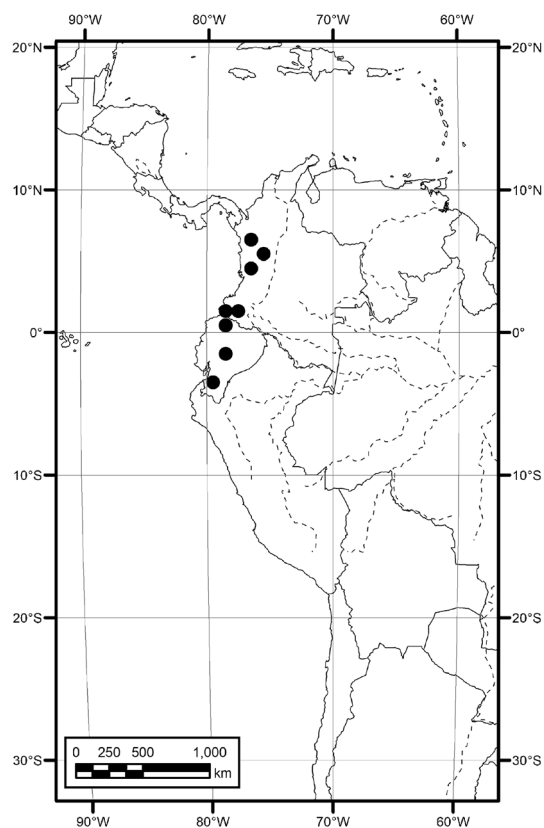


Fig. 12. *Ruagea trisperma*. A leaf; B leaflet; C enlargement of leaflet undersurface; D inflorescence; E male flower; F half flower male; G infructescence axis; H cross-section of fruit; J seed. A, E, F van der Werff & Gudino 10841; B, C, D, G – J Cuatrecasas 15521. DRAWN BY ROSEMARY WISE.



Map 12. Distribution of *Ruagea trisperma*.

Oro: Pinas, Parroquia El Placer, 3.39S, 79.44W, Vargas *et al.* 5387 (K).

CONSERVATION STATUS. This species has a large extent of occurrence of over 104,000 km² which falls outside of thresholds for a threatened category under Criterion B. It also has an area of occupancy of 60 km², although this is thought to be highly underestimated as a result of low surveying effort within this species' range. It is therefore assessed as Least Concern (LC). However, it has experienced some habitat loss, as the forests of the northwestern Andes where it occurs have experienced considerable disturbance due to deforestation for cattle grazing and agriculture.

LOCAL NAMES AND USES. Chalde (Colombia: Nariño). Larger specimens provide useful timber (Colombia: Nariño).

RELATIONSHIPS. *Ruagea trisperma* is recognised by its large leaflets lacking tertiary venation, fine, closely appressed pubescence on the young shoots, lower leaf surface and inflorescence, flowers with petals 5.5 – 7 mm long and the globose capsule 3.5 – 4.5 cm diam. The indumentum is distinctive and is not found in other species and is particularly useful in distinguishing it from large-leaved forms of *R. glabra* with which it is often confused. The indumentum and smaller flowers also distinguish it from both

R. pubescens and *R. tomentosa*. Molecular data shows *R. trisperma* clustering with *R. tomentosa* and with large-leaved specimens of *R. glabra* from the same geographical area (Colombia and Ecuador), but there is no resolution of the species within the group (Rojas-Andres *et al.* submitted).

13. *Ruagea glabra* Triana & Planch. (Triana & Planchon 1872: 368); Pennington (1981: 243); Palacios (2007: 48). Type. Colombia, Bogota, between La Mesa and Jauja, fl., fr., Triana 3362 (holotype P; isotypes BM, E, G-DC, K, US).

Guarea trianae C.DC. (de Candolle 1878: 578). Type as for *R. glabra*.

Guarea weberbaueri C.DC. (de Candolle 1907: 149).

Type. Peru, Dept. Cajamarca, Hualgayoc, fl., Weberbauer 4094 (lectotype, chosen by Pennington (1981) G; isolectotype MOL).

Cabranea weberbaueri Harms (1922: 447). Type. Peru, Dept. La Libertad, Prov. Patate, fl., Weberbauer 7069 (holotype B, destroyed; isotypes F, GH, US).

Ruagea weberbaueri (C.DC.) Harms (1925: 428).

Ruagea jelskiana Harms (1925: 426). Type. Peru, Cajamarca, Tambillo, fl., C. von Jelski 320 (holotype B destroyed; isotypes BR, F, L n.v., US).

Ruagea augusti Harms (1925: 426), based on *Cabranea weberbaueri* Harms.

Bud scales absent. *Young shoots* 5 – 9 mm diam., sometimes hollow, terete, puberulous (erect or appressed hairs) to glabrous, raised lenticels present or absent. *Leaves* imparipinnate, sometimes with slight apical growth (lower leaflets develop before upper leaflets); petiole 1.6 – 7 cm long, semiterete or terete, densely puberulous or sericeous or glabrous; rachis 5 – 27 cm long, terete or semiterete and slightly broadened below the nodes, densely puberulous to glabrous; petiolule of lateral leaflets 1 – 5 (– 9) mm long, petiolule of terminal leaflet 0.2 – 3 cm long. *Leaflets* opposite, subopposite or alternate, 3 – 5 (– 7) pairs, uppermost lateral 6 – 17 cm long, 2 – 7.5 cm broad, oblanceolate, elliptic or elliptic-oblong, apex narrowly acuminate, acute, obtuse or obtusely cuspidate, base narrowly attenuate, acute, occasionally slightly asymmetric, margin sometimes slightly revolute, usually chartaceous, rarely coriaceous, usually glabrous on the upper surface, less frequently pubescent on midrib and secondary veins, lower surface sparsely to densely puberulous, denser on veins, or glabrous, minute red papillae present, sometimes confined to the lower surface; basal leaflets 2 – 5 cm long, 1.3 – 3.5 cm broad, broadly elliptic to obovate, apex acute to obtuse or rounded, base often asymmetric, one side acute to attenuate, the other obtuse; terminal leaflet 7.5 – 19 cm long, 2.2 – 7.7 cm broad, broadly

oblanceolate, elliptic or oblong-elliptic, apex narrowly acuminate, acute or narrowly cuspidate, base usually narrowly attenuate; venation usually eucamptodromous in the lower half and brochidodromous toward the apex, occasionally completely brochidodromous, midrib flat or slightly raised on the upper surface, secondaries 7–15 pairs, ascending, straight to slightly arcuate, parallel to slightly convergent; intersecondaries few, short or absent; tertiaries obscure, oblique to reticulate. *Inflorescence* axillary, 5–32 (–50) cm long, a narrowly to broadly pyramidal panicle, or rarely a raceme, lateral branches 1–10 cm long, puberulous to sericeous or glabrous, pedicel 0.5–1 mm long. *Flowers* unisexual (plant dioecious). *Sepals* 5, c. 1 mm long, ovate, apex acute to rounded, sparsely pubescent to glabrous outside, glabrous inside, margin ciliate. *Petals* 5, 5.5–9 mm long, 1–2 mm broad, oblong, apex rounded and sometimes hooded, glabrous, margin not ciliate. *Staminal tube* 3.5–6.5 mm long, 1.5–3 mm broad, tubular to campanulate, margin crenulate or with 10 shallow truncate-emarginate teeth, outside glabrous, inside sparsely hirsute to glabrous, anthers 9–10, 0.75–1.2 mm long, sparsely hirsute especially at the point of insertion, or glabrous; antherodes in female narrower, not dehiscent, without pollen. *Nectary* a small, usually swollen, stipe below the ovary, 0.5–1.5 mm long, glabrous. *Ovary* 1.5–2.5 mm long, ovoid, with sparse appressed hairs or glabrous, 3-locular, locules with 2 superposed ovules, style 1–3 mm long, glabrous, style-head discoid, pistillode in male similar but with less-developed ovules. *Infructescence* 10–30 cm long, with a few branches or unbranched. *Capsule* 1.5–2.5 cm long, globose, apex rounded, base usually tapered to a short stout stipe, smooth, brown with pale lenticels, glabrous, pericarp 0.5–1 mm thick, 3-valved, valves with 1–2 superposed seeds. *Seed* 0.8–1.2 cm long, when superposed then truncate at base or apex, with thick basal sarcotesta, seed coat membranous; embryo with thick plano-convex collateral cotyledons, radicle apical, extending to the surface. Fig. 13.

FIELD CHARACTERS. Evergreen tree to 25 m high and 50 cm diam., with pale brown smooth or finely fissured bark and fragrant pinkish slash; flowers scented, with greenish sepals, greenish-white or yellowish-green petals and pale cream staminal tube; fruit maturing orange-brown to yellow with pale lenticels. Flowering in Costa Rica, Panama and Colombia mostly Jan. to July, in Ecuador, Peru and Venezuela mostly July to Jan. No peaks identified for fruit maturation with fruits in various stages of development recorded throughout the year.

DISTRIBUTION AND ECOLOGY. Costa Rica, western and central Panama. Not known from Nicaragua but to be expected there, Colombia, mountains of northern and

western Venezuela, Pacific coastal and Amazonian Ecuador, Amazonian Peru. *Ruagea glabra* occurs in wet montane rain forest and cloud forest. It has a wide altitudinal range from 400 m (Pacific coastal Ecuador) to 3000 m the high Andes (Map 13).

REPRESENTATIVE COLLECTIONS. **COSTA RICA.** **Alajuela:** cuenca del Sarapiquí, Hotel Posada, Volcán Posada, 10.27N, 84.10W, *Kriebel et al.* 2906 (G). **Cartago:** La Pastora de Santa Cruz to Volcán Turrialba, 9.58N, 83.48W, *Pennington & Owen* 13605 (K). **Guanacaste:** Monteverde, Sta. Elena, 4 km NE of Santa Elena, 10.21N, 84.48W, *Tanzer* 77 (F). **Heredia:** Cantón Barva, Reserva Forestal Cordillera Volcánica Central, 10.06N, 84.06W, *Rodríguez et al.* 3067 (MO). **Limón:** Cantón de Talamanca, Bratsi Amubri, 9.22N, 83.06W, *Herrera* 5505 (K). **Puntarenas:** Monteverde, San Luis R., 10.20N, 84.50W, *Haber* 3936 (K). **San José:** Dota, Cerro Lira, 9.31N, 83.51W, *Marten & Herrera* 680 (K). **PANAMA.** **Bocas del Toro:** Cerro Colorado, 12 miles from Camp Chami, 8.35N, 81.45W, *McPherson* 9539 (K). **Chiriqui:** Distr. Bugaba, Cerro Punta, 8.52N, 82.33W, *van der Werff & Herrera* 6232 (K). **Comarca de Ngobe-Bugle,** Cordillera Central, Nole Duina, Kaukiuku, 8.17N, 81.47W, *Ibañez et al.* 8130 (K). **Veraguas:** vicinity of Santa Fe, slopes of Cerro Tute-Arizona, 8.30N, 81.10W, *McPherson* 13673 (K). **VENEZUELA.** **Aragua:** Monumento Natural Pico Codazzi, 10.23N, 67.22W, *Meier et al.* 6543 (K). **Barinas:** Distr. Bolívar, between La Soledad and Santo Domingo, 8.51N, 71.35W, *van der Werff & Ortega* 6136 (K). **Mérida:** Distr. Arzobispo Chacon, Pueblos del Sur, La Veguilla, 8.18N, 71.19W, *Meier & Gutierrez* 11594 (K). **Tachira:** Mt Saisayal, Valle del Río Negro, 8.00N, 71.00W, *Bernardi* 11028 (K). **Trujillo:** Distr. Bocono, Parque Nacional Guaramacal, 9.12N, 70.09W, *Cuello et al.* 1270 (K, MO). **COLOMBIA.** **Antioquia:** Municipio Jardín Alto de Ventanas, road to Río Sucio, 5.30N, 75.50W, *Callejas et al.* 3941 (K, NY, US). **Boyaca:** NW of Bogota, region of Mount Chapon, 5.00N, 74.00W, *Lawrance* 299 (G, GH, K). **Cundinamarca:** Sasaima, Vereda San Bernardo, 4.00N, 74.00W, *García-Barriga* 11890 (US). **Risaralda:** Municipio Pereira, La Florida, SFF Otún Quimbaya, 4.44N, 75.34W, *Alzate et al.* 2030 (F). **ECUADOR.** **Carchi:** Cantón Espejo, San Isidro, Sector Chulte, 0.38N, 78.02W, *Tipaz & Palacios* 645 (MO). **El Oro:** Cerro Azul, 3.28S, 79.43W, *Cornejo & Bonifaz* 3747 (K). **Esmeraldas:** Cantón Quinde, Bilsa Biological Station, 0.22N, 79.44W, *J. L. Clark et al.* 4042 (US). **Guayas:** Cordillera Chongon, Loma Alto, Bosque Protector, 1.48S, 80.47W, *Bonifaz & Torres* 3425 (K). **Loja:** El Casine to Zaruma km 5.2, 3.16S, 79.26W, *Jorgensen et al.* 1497 (K). **Los Ríos:** Hacienda Clementina, Cerro Samana, La Torre, 1.39S, 79.20W, *Stahl et al.* 6942 (K). **Manabí:** Cantón Pedernales, Cerro Pata de Pajaro, 0.01N, 79.59W, *Neill et al.* 11355 (K). **Napo:** Baeza-Tena km 8, 0.31S, 77.50W, *Balslev & Madsen* 10425 (K, NY). **Pichincha:** Coop. Santa Maria, near Santo Domingo, 0.00S, 79.00W, *Dodson et al.* 8529 (F). **Sucumbios:** Gonzalo Pizarro, Reserva Ecológica Cayambe-Coca, 0.06S, 77.36W, *Vargas*

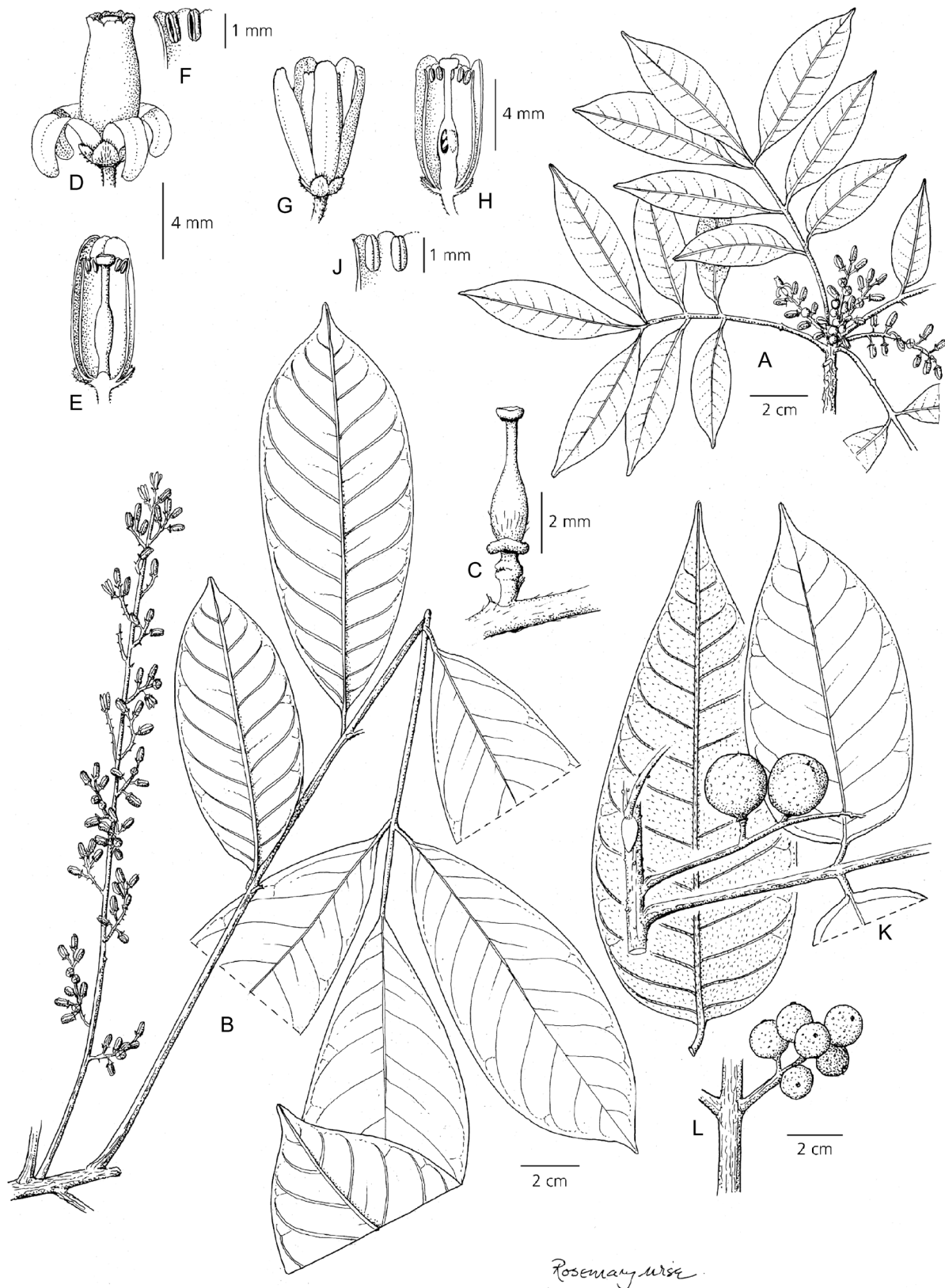
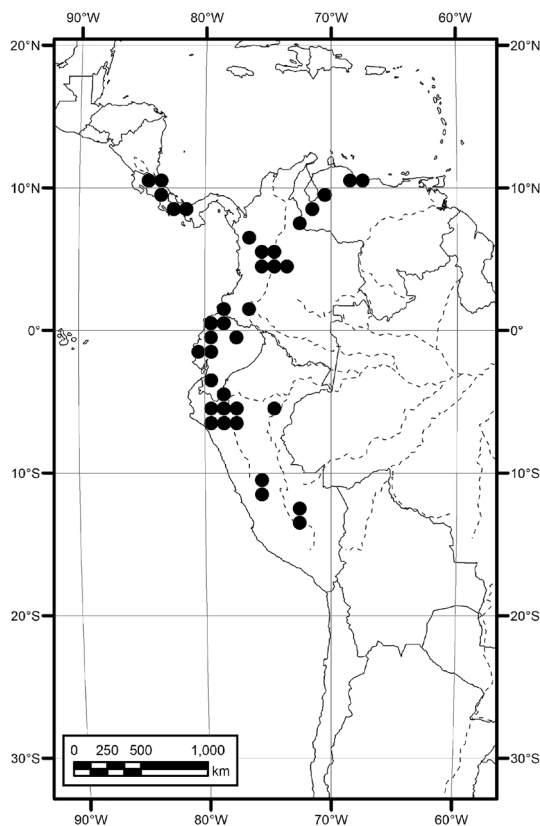


Fig. 13. *Ruagea glabra*. A habit with inflorescence; B habit with inflorescence; C ovary and nectary; D male flower; E half flower male; F anthers in male flower; G female flower; H half flower female; J antherodes in female flower; K leaflet and infructescence; L infructescence. A, G – J, *Haber* 536; B, D – F *Galdames et al.* 691; C *Hurtado* 677; K *McPherson* 8894; L *Tanzer* 77. DRAWN BY ROSEMARY WISE.



Map 13. Distribution of *Ruagea glabra*.

et al. 3901 (K). **Zamora-Chinchipe:** Palanade, Cordillera del Condor, 4.43S, 78.57W, *Quizhpe et al.* 1116 (K). **PERU. Amazonas:** Bongara, Pomacocha, turning to Zumbilla, 5.50S, 74.48W, *Pennington & Daza* 18506 (K, MOL). **Cajamarca:** San Ignacio, San José de Lourdes, Cerro las Yeguas, 5.00N, 78.54W, *Vásquez et al.* 12644 (K). **Cuzco:** La Convención, Distr. Ocobamba, Versalles, Santa Elena, 12.46S, 72.16W, *Valenzuela et al.* 10338 (K). **Junín:** Prov. Chanchamayo, Distr. San Ramón, Alto Pichita, Fundo Vista Alegre, 11.05S, 75.26W, *Daza et al.* 2675 (MOL). **La Libertad:** Prov. Pataz, *Weberbauer* 7069 (F, GH, US). **Pasco:** Oxapampa, Distr. Chontabamba, Tsachopen, 10.34S, 75.26W, *Valenzuela & Rivera* 13985 (K). **Piura:** Prov. Moropón, Distr. Chalaco, Caserio de Laguna de Mijal, A. *Cordova* 40 (MOL). **San Martín:** Venceremos, km 291 Rioja to Pomacocha, 5.45S, 77.40W, *Gentry et al.* 4529 (K).

CONSERVATION STATUS. This species was assessed as Least Concern (LC) by Condit (2019). This is due to its very widespread distribution, large population and the absence of any major threats currently affecting it or expected to affect it in the future.

LOCAL NAMES AND USES. Achote Colorado (Peru: Pasco), amargo (Ecuador: El Oro), batea caspi (Ecu-

ador: Napo), cedrillo (Ecuador: Carchi). Larger specimens are useful for sawn timber (Peru: Pasco).

RELATIONSHIPS. *Ruagea glabra* is the most commonly collected species of the genus, with a wide distribution extending from Costa Rica to southern Peru. It is distinguished by the relatively few chartaceous leaflets with a mostly attenuate acute or obtuse apex (not rounded), which are softly pubescent or glabrous and the medium-sized flowers and fruits. *Ruagea tomentosa*, *R. trisperma* and *R. floribunda* are all close to *R. glabra*, but differ from it in leaflet size and/or indumentum, and/or flower size and fruit size. They all appear in the same unresolved clade at the apex of the phylogenetic tree (Rojas-Andres *et al.* submitted).

Material of *Ruagea subviridiflora* and *R. obovata* was formerly placed in *R. glabra* where their ranges overlap in southern Peru. See under those species for further discussion.

Doubtful Species

14. *Ruagea floribunda* Cuatrec. (Cuatrecasas 1950: 79); Pennington (1981: 245). Type. Colombia, Dept. del Valle, Cordillera Occidental, vertiente occidental, Hoya del Río Digua, Quebrada del Río San Juan, above Queremal, March 1947, fl., fr., *Cuatrecasas* 23927 (holotype F (3 sheets)).

Bud scales absent. *Young shoots* c. 1 cm diam., terete, finely appressed puberulous, smooth, without lenticels. *Leaves* imparipinnate, with some apical growth (lower leaflets develop before apical leaflets); petiole c. 7.5 cm long, semiterete, finely appressed puberulous; rachis 45–50 cm long, semiterete, with sparse minute appressed hairs; petiolule of lateral leaflets 5–6 mm long, petiolule of terminal leaflet c. 1 cm long (not fully developed). *Leaflets* opposite, 5 pairs (basal pair caducous), uppermost lateral c. 32 cm long, c. 16 cm broad, elliptic, apex obtuse, base acute or narrowly acuminate, chartaceous, glabrous above, residual appressed puberulous indumentum on undersurface, some minute red papillae present on both surfaces; basal pair of leaflets not seen; terminal leaflet (immature) c. 15 cm long, c. 6 cm broad, oblanceolate, apex obtuse, base narrowly attenuate; venation eucamptodromous, secondaries 18–19 pairs, ascending, mostly straight and parallel; intersecondaries few, short; tertiaries obscure. *Inflorescences* in axils of upper leaves, 30–55 cm long, a large, laxly branched panicle, with horizontally spreading branches to 10 cm long, sparsely and finely appressed puberulous; pedicel 0–0.5 mm long. *Flowers* unisexual (plant dioecious) (female flowers only seen). *Sepals* 5, c. 1 mm long, broadly ovate, apex rounded to obtuse, with sparse appressed hairs outside, glabrous inside, not ciliate. *Petals* 5, c. 6 mm long, c. 1.5 mm broad, oblong, apex rounded, glabrous, margin not ciliate.

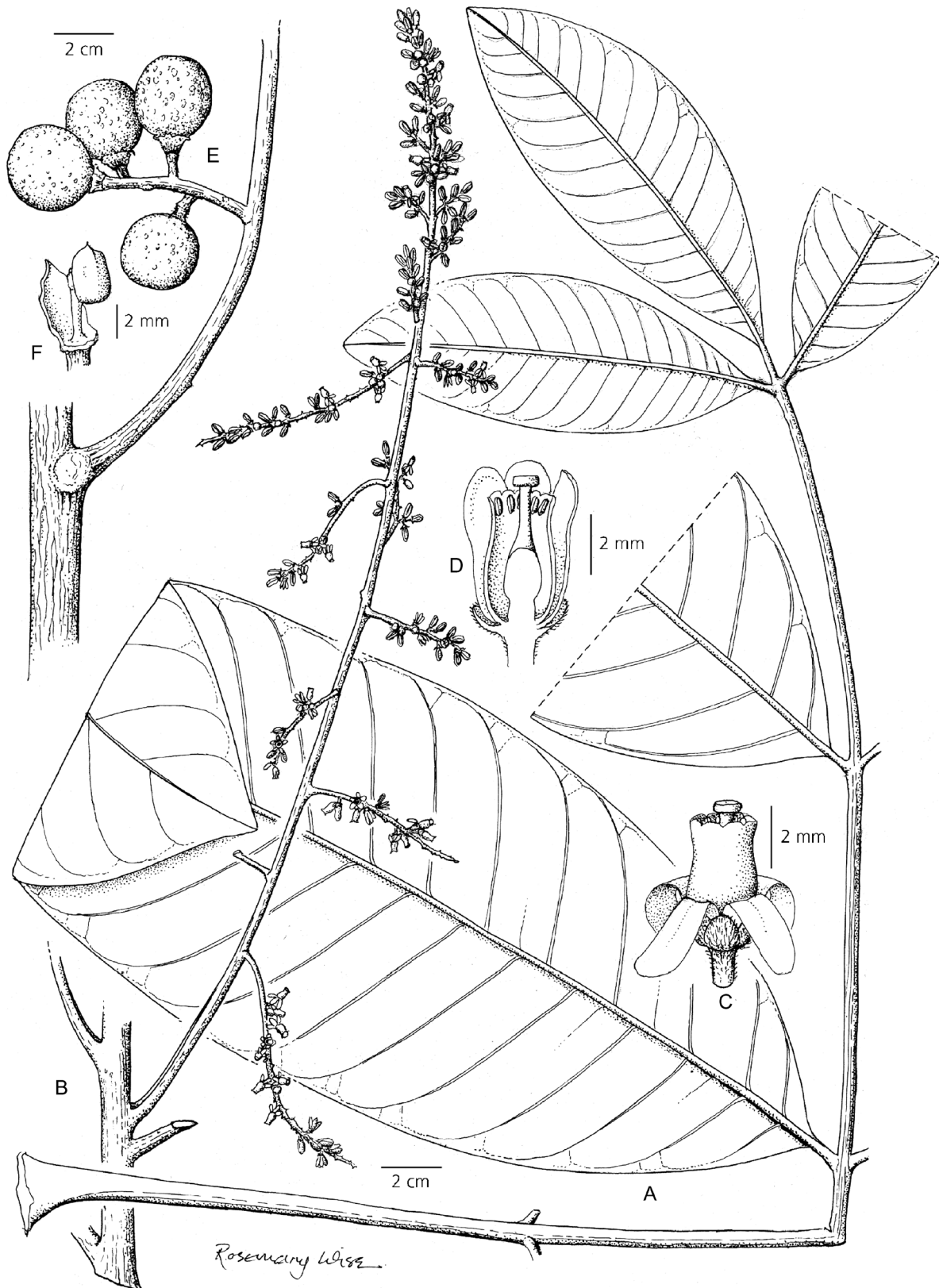


Fig. 14. *Ruagea floribunda*. A leaf; B inflorescence; C female flower; D half flower female; E infructescence; F part fruit with seed. A – F Cuatrecasas 23927. DRAWN BY ROSEMARY WISE.

Staminal tube 5 – 5.5 mm long, c. 2 mm broad, tubular-campanulate, margin crenulate, glabrous, antherodes c. 1 mm long, shrunken, not dehiscent, without pollen. *Nectary* c. 0.75 mm long, an obscure swelling below the ovary, glabrous. *Ovary* c. 1.5 mm long, ovoid, glabrous, 3-locular, locules with 1 – 2 superposed ovules, style c. 1.5 mm long, glabrous, style-head discoid. *Infructescence* to 37 cm long, lateral branches to 9 cm long, many-fruited. *Capsule* 2.5 – 3 cm diam., globose, rounded at base and apex, smooth, glabrous, brown with pale lenticels, pericarp c. 0.5 mm thick, 3-valved, valves 1-seeded (and some fruit 1-seeded). *Seed* (immature) c. 1 cm long, plano-convex with thick basal sarcotesta, seed coat membranous. Embryo not seen. Fig. 14.

FIELD CHARACTERS. Large evergreen tree. Leaves with 5 pairs of leaflets. Flowers with green sepals, pale green petals and white staminal tube. Semi-mature fruit brown.

DISTRIBUTION AND ECOLOGY. (Type only). South western Colombia, on the Pacific slopes of the Cordillera Occidental at 1950 m to 2050 m altitude, no further ecological information, but presumably in wet montane forest. The distribution of this species may extend into coastal and Amazonian Ecuador (see below under possible additional specimens).

COLLECTIONS EXAMINED. Known with certainty only from the type collection in Valle, Colombia. A few further specimens cited here are placed with some reservations in this species:

COLOMBIA. Huila: Gentry *et al.* 53927* (K); **Nariño:** Benavides 8787 (K), Gentry & Benavides 55032 (K); **Antioquia:** Brant & Martínez 1364 (K). **ECUADOR. Carchi:** Mendez *et al.* 345 (F); **Cotopaxi:** Dodson & Gentry 12810* (F), Gentry *et al.* 14422 (K), Dodson & Embree 13363 (F). **Napo:** Palacios 6079* (K), Tipaz *et al.* 383* (MO); **Morona-Santiago:** Little 647* (COL, QAME, US); **Zamora-Chinchipe:** Palacios *et al.* 8292 (K).

In the last monograph of the genus (Pennington 1981) this species was treated as a large-leaved form of *Ruagea glabra* and placed in the synonymy of that species. The flower and fruit structure are the same as in that species, and it differs only in the exceptionally large size of the leaves, leaflets and inflorescence. Unfortunately molecular data is not available for the type. The specimens listed here, which are provisionally placed in *R. floribunda*, share a similar morphology, but their molecular data (available for those specimens marked above with an asterisk) suggests that they are not closely related as they appear in widely separate parts of the phylogeny (Rojas-Andres *et al.* submitted)

15. *Ruagea raimondii* Harms (1932: 385); Pennington (1981: 254). Type. Peru, Dept. Cajamarca, Prov. Hualgayoc, Montaña del Nancho, fl., *Raimondi* 5141 (holotype B, destroyed).

No isotypes of this species have been located. In the last monograph of *Ruagea* (Pennington 1981) it was tentatively placed near *R. hirsuta* on account of the small leaflets and villosulous-pilose indumentum on the lower lamina and small corolla.

Acknowledgements

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List of Exsiccatae

(number in parentheses = species number); “sp” = ?
 Abbott & Jardim 17056 (4); Acevedo-Rodríguez *et al.* 6615 (4); Acosta Solis 5836 (5); Altamirano & Alcazar 3006 (3), 3094 (4), 3102 (4); Altamirano *et al.* 1844 (4); Alzate *et al.* 2030 (13), 2128 (sp), 2165 (sp); Araujo *et al.* 126 (3); Araujo-Murakami *et al.* 3480 (3), 3515 (3), 3636 (3), 3725 (3), 3739 (3), 3770 (3); Arellano *et al.* 3123 (3); Aymard *et al.* 5196 (13).
 Balslev & Madsen 10425 (13); Bang 848 (3), 2428 (6); Bascope *et al.* 221 (4); Beck 7304 (3), 7534 (7), 13824 (4), 25204 (4); MET03/71 (7); Bello 651 (13), 995 (13); Beltran 20 (12); Benavides 8787 (14?); Benoist 3014 (2); Bernardi 11028 (13); 18138 (13); Bernardi s.n. (13); Bernardi *et al.* 17205 (10); Betancur *et al.* 4033 (10), 15098 (12), 16657 (13); Binder *et al.* 1999/8 (8); Bonifaz & Cornejo 3840 (13); Bonifaz & Torres 3425 (13); Boyle 893 (13); Boyle *et al.* 151 (13); Brant & Martínez 1320 (10), 1364 (14?); Bridgewater 4146 (2); Buchtien 2076 (3?); Burger & Antonio 11136 (13).
 Calatayud *et al.* 1460 (13), 3392 (3), 4646 (5); Callejas *et al.* 3941 (13), 6156 (11), 8418 (12); Campos & Corrales 3479 (9); Campos *et al.* 2945 (9), 3814 (9), 5154 (8), 5170 (8), 5759 (8); Cano 1379 (8); 1380 (8); Cardozo 1292 (10); Carrasco *et al.* 259 (4); Castillo 1935 (13); Castillo *et al.* 255 (3); Cayola *et al.* 2700 (4), 3767 (4); Cerón & Gallo 37566 (11); Cerón & Hurtado 3976 (2); Cerón & Ocampo 11900 (8); Chacon & Herrera 1148 (13), 1715 (13); Chimbo & Chamba 35 (sp), 36 (13); Clark, J. L. 2278 (1); Clark, J. L. & Mora 255 (13); Clark, J. L. *et al.* 1142 (2), 2724 (13), 4042 (13); Cogollo *et al.* 7546 (10); Cordova 40 (13), 91 (6); Cornejo & Bonifaz 3250 (11), 3747 (13); Cornejo *et al.* 1074 (6?), 3525 (10); Croat 26972 (13); Cuamacas 22 (13); Cuamacas *et al.* 114 (10), 159 (10); Cuatrecasas 15521 (12), 19271 (6),

- 20415 (6), 20802 (6), 21988 (11), 23308 (6), 23927 (14), 29802 (6); *Cuello & Aymard* 2361 (10); *Cuello et al.* 1060 (13), 1270 (13), 1712 (10).
Davidse & Miller 28116 (10), 28116 (10); *Daza* 6465 (8), 6466 (8), 6467 (8); *Daza et al.* 2675 (13); *Devia & Prado* 1949 (6); *Díaz et al.* 4285 (8), 9799 (8), 9826 (8); *Dillon et al.* 6400 (6), 6492 (8); *Dodson & Embree* 13363 (14?); *Dodson & Gentry* 12810 (14?); *Dodson et al.* 8529 (13); *Dorr & Barnett* 7546 (13); *Dorr & Stergios* 8716 (13), 8774 (13); *Dorr et al.* 7278 (13); *Drew* E-367 (10); *Dumont & Idrobo* 158 (13).
Estrada 2081 (2); *Estrada et al.* 2246 (2).
Farfan et al. 554 (4), 965 (4); *Fendler* 166 (10); *Fernandez et al.* 2611 (4), 2633 (4); *Flores & Tello* 1210 (2); *Flores & Vasquez* 303 (13); *Folsom & Collins* 1780 (13); *Franco et al.* 5004 (12); *Freire et al.* 1196 (5); *Fuentes & Rodas* 16082 (4); *Fuentes et al.* 1029 (3), 6879 (4), 8778 (3), 10334 (2), 10431 (4), 10812 (4), 11403 (sp), 11599 (4), 14847 (3), 17539 (4), 17542 (4), 17637 (4).
Galdames et al. 687 (13), 691 (13); *Galeano et al.* 521 (sp); *Galiano et al.* 4277 (13); *Garcia H.* 11890 (13); *Garcia-Barriga* 11890 (13), 12557 (13); *Gentry & Benavides* 55032 (14?); *Gentry & Smith* 45242 (13); *Gentry & Solomon* 44737 (4), 52065 (3); *Gentry et al.* 14422 (14?), 28516 (12), 35050 (13), 45290 (13), 45515 (13), 48849 (13), 53927 (14?), 71751 (13), 74648 (8), 75090 (8); *Gomez et al.* 21098 (13), 23307 (13); *Gomez-Laurito* 9848 (13), 11836 (13); *Grayum et al.* 6181 (13), (13); *Gruhn et al.* 172 (6); *Gudino & Tipaz* 159 (10); *Gustaffson & Cornejo* 608 (13).
Haber 536 (13), 776 (13), 855 (13), 1287 (13), 3936 (13), 5026 (13); *Haber & Bello* 2278 (13), 2708 (13); *Haber ex Bello* 6413 (13); *Hammel* 2156 (13); *Herrera* 680 (13), 5505 (13); *Herrera et al.* 4919 (13); *Hodge & Evinger* 487 (6); *Homeier* 80 (13); *Homeier & Chinchero* 1783 (1), 1838 (13); *Homeier et al.* 1037 (8), 1755 (13); *Huamantupa* 9641 (60); *Huamantupa et al.* 10146 (4); *Huertas & Camargo* 6510 (sp); *Hurtado* 677 (13).
Ibanez et al. 8130 (13); *Idrobo* 158 (13).
Jaramillo 8628 (10), 9109 (1); *Jaramillo & Widderskjold* 5681 (8); *Jaramillo & Zak* 8090 (11); *Jaramillo et al.* 12285 (13); *Jardim* 2838 (4); *Jardim et al.* 2818 (4); *Jelski* 320 (13); *Jimenez et al.* 631 (13); *Jorgensen* 65965 (10); *Jorgensen et al.* 21 (8), 390 (8), 651 (8), 958 (8), 1122 (8), 1376 (8), 1497 (13), 92968 (6).
Kajekai & Wisum 761 (9), 831 (9); *Karsten* s.n. (10); *Killeen* 3822 (2), 3840 (2); *Killeen & Vargas* 4080A (4); *Knapp et al.* 4146 (13); *Knight* 530 (6); *Kriebel* 2906 (13).
Lawrance 299 (13); *Leiva et al.* 1547 (8); *Lent* 994 (13); *Lewis et al.* 2939 (6); *Liesner* 224 (2); *Liesner & Medina* 13502 (10), 13509 (10); *Liesner et al.* 12988 (13); *Linden* 213 (10); *Lippok & Sonco* 799 (7); *Little* 647 (14?), 6546 (11), 6643 (13); *Little & Dixon* 21072 (2); *Loza et al.* 1217 (4), 1934 (4?).
Macia & Fuertes 7235 (7), 7341 (7); *Madrinan & Barbosa* 496 (sp); *Marcano-Berti & Salcedo* 4-979 (10); *Marcelo Pena et al.* 1939 (6); *Marten et al.* 2818 (4); *McPherson* 8398 (13), 8405 (13), 8621 (13), 8894 (13), 8915 (13), 9536 (13), 9539 (13), 9554 (13), 12579 (13), 12702 (13), 13645 (13), 13673 (13); *Meier* 1196 (13), 1330 (10), 1341 (10), 1385 (10), 1403 (10), 1786 (10); *Meier & Berg* 3809 (10); *Meier & Gutierrez* 11594 (13); *Meier et al.* 3934 (13), 6432 (10), 6543 (13); *Mendez et al.* 164 (13), 345 (14?); *Monteagudo & Ortiz* 4621(3); *Monteagudo et al.* 3500 (3), 3641 (3), 3798 (5), 4490 (13), 5518 (3), 6784 (6), 7726 (6), 9281 (5), 9352 (3), 13110 (3), 13709 (3), 14133 (5), 15442 (13), 15913 (13), 16932 (13), 27663 (3); *Moran et al.* 5 (6), 92 (6); *Mutis* 2287 (13), 2293 (10), 5214 (13).
Navarro et al. 1626 (6); *Neill* 15374 (10), 15378 (6); *Neill et al.* 8452 (2), 11355 (13), 12697 (10), 13850 (10), 15329 (13); *Nunez et al.* 9069 (4).
Ollgaard et al. 57644 (13); *Orellana & Quispe* 1454 (3); *Ortiz et al.* 929 (3).
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