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Five new synonyms in *Epimedium* (Berberidaceae) from China

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Abstract

Five new synonyms in Chinese *Epimedium* are designated in the present paper. *Epimedium chlorandrum* is treated as a synonym of *E. acuminatum*; *Epimedium rhizomatosum* as a synonym of *E. membranaceum*; *Epimedium brachyrrhizum* as a synonym of *E. leptorrhizum*; *Epimedium dewuense* as a synonym of *E. dolichostemon*; and *Epimedium sagittatum* var. *oblongifoliolatum* as a synonym of *E. borealiguizhouense*.

Keywords

Epimedium, Berberidaceae, synonyms, China

Introduction

Epimedium L., the largest herbaceous genus of Berberidaceae, contains approximately 58 species distributed in temperate hilly or montane regions from Japan to Algeria with enormous gaps in between. China, where *Epimedium* reaches its zenith of diversity, possesses approximately 48 species, of which are all endemic except *E. koreanum* Nakai (Stearn 2002; Ying et al. 2011). The genus *Epimedium* has been insufficiently understood because of the morphological variation within and among some Chinese *Epimedium* species. As a result, some new *Epimedium* species were published which are, in fact, synonymous with existing species. In the present paper, based on extensive studies on Chinese *Epimedium* plants in herbaria, field investigations, and cultivation, we reduce the following four species and one variety: *Epimedium chlorandrum* Stearn, *E. rhizomatosum* Stearn, *E. brachyrrhizum* Stearn, *E. dewuense* S.Z. He & W.F. Xu, and *E. sagittatum* Maxim. var. *oblongifoliolatum* Z. Cheng, as new synonyms of five species of the genus.

Materials and methods

Herbarium specimens were examined from the following herbaria: CDCM, CDBI, GZTM, HGAS, HIB, HNNU, HWA, IBK, IMD, KUN, PE, SAU, SM, and SZ. Furthermore, pertinent images of type specimens were examined from K, P, and WU. The field investigations covered all of the type localities and the typical regions of the different morphologies of the species. Additionally, plants of these species were collected and transplanted to Wuhan Botanical Garden, the Chinese Academy of Sciences, for further study.

Taxonomic treatment

Epimedium acuminatum **Franch.**

Epimedium acuminatum Franch., Bull. Soc. Bot. France, 33: 109. 1886. Type: China. Guizhou, 1858, *Perny s.n.* (holotype, P!).

Epimedium chlorandrum Stearn, Kew Bull., 52(3): 660. 1997, Syn. nov. Type: China. Sichuan: Baoxing, cult. England. Hampshire: Kilmeston, Blackthorn Nursery, Apr. 1996, *Ogisu 94003* (holotype, K!).

Description. Herbs 25–80 cm tall. Rhizome compact, sometimes long-creeping, 2–5 mm in diam. Leaves basal and cauline, usually trifoliolate or occasionally unifoliolate; leaflets of trifoliolate leaves narrowly ovate to lanceolate, 3–18 × 1.5–7 cm, apex long acuminate, base cordate with lobes rounded or acute, those of the lateral leaflets very unequal; unifoliolate leaves ovate or broadly ovate, 8.7–20 × 6.8–11.5 cm, apex acuminate, base cordate with lobes equal, rounded or rarely acute; leaves leathery when mature, margin spinous-serrate with the spines 1–2 mm long, adaxially deep green, glossy, abaxially glaucous, papillose, with dense or sparse short appressed stout bristle-like hairs and sometimes densely sericeous. Flowering stem usually bearing 2 opposite trifoliolate leaves, less often with 3 whorled trifoliolate leaves or 2 opposite unifoliolate leaves, rarely with 2 opposite leaves with one trifoliolate and the other unifoliolate or 3 whorled unifoliolate leaves. Inflorescence compound with lower peduncles 2–5-flowered, loose few- or many-(10–55)-flowered, glabrous or occasionally glandular hairy; pedicels 1–4 cm. Flowers 3–5 cm in diam., yellow, rose-purple, pale violet, or white. Outer sepals blunt, outer pair ovate-oblong, ca. 3 × 2 mm, inner pair broadly obovate, ca. 4.5 × 4 mm. Inner sepals ovate-elliptic, 8–12 × 3–7 mm, apex acute. Petals much longer than inner sepals, horn-shaped, tapering from the swollen but lamina-less base, curving outwards, 1.5–2.5 cm. Stamens 3–4 mm; anthers yellow or green, ca. 2.5 mm, pollen yellow or green. Capsules ca. 2 cm.

Distribution and habitat. *Epimedium acuminatum* is widely distributed in Sichuan, Chongqing, Guizhou, and northern Yunnan. It usually occurs in forests, thickets, bamboo forests, and weedy slopes ranging from 270 to 2400 m in elevation.

Phenology. *Epimedium acuminatum* flowers from April to May, and fruits from May to June.

IUCN Red List category. Although *Epimedium acuminatum* has a relatively wide distribution in China; it should be designated as Vulnerable (VU) (IUCN 2013), because of exploitation for medicinal use, especially in Guizhou.

Notes. *Epimedium acuminatum* is one of the most widespread species in the genus, and exhibits much variation in morphology; therefore, it is not surprising that there are several synonyms associated with it. Léveillé (1909) published *Epimedium komarovii* H. Lév. upon only contrasting it with *E. sagittatum* Maxim., Stearn (1938) found that it was not distinct from *E. acuminatum* and reduced it into synonymy. *Epimedium simplicifolium* T.S. Ying was described by Ying (1975), only separating it from *E. acuminatum* in having unifoliolate, sericeous leaves. Upon extensive specimen examination, however, Zhang et al. (2011) found that the diagnostic characters of *E. simplicifolium* were within the range of morphological variations of *E. acuminatum* and placed *E. simplicifolium* into synonymy.

Epimedium chlorandrum was described by Stearn (1997) as having the inner sepals being slightly ascending, and not closely appressed to the petals, and the anthers and pollen as being green. However, observations from the type locality of *E. chlorandrum* show that the diagnostic character of the inner sepals as not closely appressed to the petals is not stable, and *E. acuminatum* is also found having inner sepals being slightly ascending, with green anthers and pollen. There is no difference in morphology for the two species, thus, *E. chlorandrum* is here treated as a new synonym of *E. acuminatum*. Additionally, extensive specimen examination and field investigation demonstrate that it is incorrect for Stearn (1997) to recognize the color of anther and pollen as diagnostic features in *Epimedium* because, besides *E. acuminatum*, other *Epimedium* species (e.g. *E. sagittatum*, *E. sutchuenense* Franch., *E. elongatum* Kom., and *E. leptorrhizum* Stearn) with yellow anthers and pollen are also found with green anthers and pollen.

Specimens examined. China. Chongqing: Fuling, *Fuling Med. Pl. Exped. 337* (SM), *358* (SM), *Y.L. Cao & F.D. Pu* 1291 (CDBI); Hechuan, *Hechuan Med. Pl. Exped. 193* (SM), *T.H. Tu* 5434 (PE); Jiangjin, *Jiangjin Med. Pl. Exped. 237* (SM), *Sichuan Econ. Pl. Exped. Jiang 30* (KUN, SM); Mt. Jinyun, *Z. He* et al. *1003* (SZ), *T.C. Pan & G.F. Wu 105* (PE); Nanchuan, *C.H. Hsiung 90021* (HIB, HWA, PE, SZ), *90058* (HIB, HWA, PE, SZ), *90331* (HWA, PE, SZ), *91045* (HWA, KUN, PE, SZ), *C.L. Li N1* (IMD), *N4* (IMD), *N6* (IMD), *F.T. Wang 10554* (PE), *G.F. Li 60306* (HIB, KUN, PE, SZ), *60324* (HIB, KUN, PE, SZ), *60358* (HIB, PE, SZ), *60411* (HIB, KUN, PE, SZ), *60514* (HIB, KUN, PE, SZ), *60923* (HIB, KUN, PE, SZ), *61022* (PE, SZ), *61255* (HIB, KUN, SZ), *61470* (PE, SZ), *L. Lin & B.L. Li 58* (IMD), *Mt. Jinfo Exped. 202* (PE), *N.L. Chü 1057* (PE, SZ), *S.C. Chen & K.Y. Lang 2104* (PE), *2164*

(PE), *2192* (PE), *S.X. Tan* 172 (PE), *Sichuan Veg. Exped. 165* (PE, SM), *273* (CDBI, PE, SM), *T.H. Tu 2763* (PE), *3116* (PE), *W.P. Fang 802* (PE), *Z.D. Chen* et al. *960108* (PE), *Z.H. Wan & C.Y. Chu 177* (IMD), *Z. Xia 33* (CDBI), *Z.Y. Liu 15500* (PE), *15574* (PE); Wulong, *B.L. Guo 523* (IMD), *S.Z. Zhu 1562* (SM). **Guizhou:** Anlong, *Guizhou Exped. 2469* (PE, HGAS), *B.L. Guo A70* (IMD), *A73* (IMD); Anshun, *Anshun Med. Pl. Exped. 146* (GZTM); Bijie, *X. Yang s.n.* (GZTM); Chishui, *B.L. Guo A77* (IMD), *Y.M. Wang 87-273* (GZTM); Dafang, *B.L. Guo 601* (IMD), *D.L. Yu & C.L. Liu 191-5* (GZTM), *Dafang Exped. 108* (HGAS), *Y.J. Zhang 402* (HIB); Daozhen, *Anon. 85-463* (GZTM), *85-185* (GZTM), *85-2069* (GZTM), *85-60013* (GZTM), *J.M. Yuan 31* (HGAS); Dushan, *Libo Exped. 1688* (HGAS); Fuquan, *J.Y. Li 59-2* (GZTM), *59-4* (GZTM); Guanling, *Guanling Exped. 146* (GZTM); Guiding, *B.L. Guo A90* (IMD); Guiyang, *Anon. 20* (HGAS), *B. Gu s.n.* (GZTM), *C. Sun 96003* (GZTM), *G.Z. Fan 6-1* (GZTM), *6-2* (GZTM), *6-3* (GZTM), *6-4* (GZTM), *6-5* (GZTM), *L. Lin & B.L. Li 10* (IMD), *M.Z. Yang 810061* (HGAS), *810079* (HGAS), *810138* (HGAS), *P. Zhao 762* (HGAS), *807* (HGAS), *S. Guizhou Exped. 42* (HGAS, KUN, PE), *S.Y. Xiao & X.W. Li 86079* (GZTM), *S.Z. He 90001* (GZTM); Hezhang, *Hezhang Exped. 135* (GZTM); Huishui, *G.M. Qin 37* (GZTM); Jiangkou, *L.X. Yang 203* (GZTM); Kaili, *S.Z. He 90010* (GZTM), *90011* (GZTM); Kaiyang, *Kaiyang Med. Exped. 166* (GZTM), *S.Z. He 90018* (GZTM); Liuzhi, *B.L. Guo A79* (IMD), *P. Su 156* (GZTM); Longli, *M.X. Wan 403031* (GZTM); Luodian, *Y.J. Zhang 426* (HIB), *427* (HIB), *428* (HIB); Nayong, *C.J. Li 86-010* (GZTM); Panxian, *Z.X. Pan s.n.* (GZTM); Qianxi, *Z.X. Wang & H.P. Xiang 7* (GZTM); Shiqian, *S.H. Xu 196* (GZTM); Shuicheng, *G.Z. Fan 9-10* (GZTM), *9-11* (GZTM); Songtao, *B.L. Guo A75* (IMD); Suiyang, *G.Z. Fan* et al. *9106* (GZTM), *9107* (GZTM), *S.F. Li s.n.* (GZTM), *S.Z. He & B. Gu 96410* (GZTM, PE), *Y.J. Chen 86-007* (GZTM); Tongzi, *B.L. Guo A13* (IMD), *X.P. Wang & P. Zhao 870212* (HGAS), *X.J. Zhang & Y.Q. Xu 97* (HIB), *Y.J. Zhang 422* (HIB), *Y. Tsiang 4994* (PE); Wuchuan, *Wuchuan Med. Exped. 870112* (GZTM), *Y.J. Zhang 164* (HIB), *166* (HIB); Xifeng, *S.Z. He 90012* (GZTM), *T.H. Yang 146* (GZTM); Xishui, *Anon. 279* (HGAS), *B.L. Guo A88* (IMD), *G.Z. Fan 9105* (GZTM), *9106* (GZTM), *9107* (GZTM), *9108* (GZTM), *9109* (GZTM), *9114* (GZTM); Xingyi, *B.L. Guo A95* (IMD), *T.X. Chen & L. Chen 106* (GZTM); Yinjiang, *X. Tang 172* (GZTM), *173* (GZTM), *Z.S. Zhang* et al. *401131* (PE, HGAS); Zhenfeng, *S.Z. He 9101* (GZTM); Zhenning, *S.Z. He & Y. Huang 9107* (GZTM), *Zhenning Exped. 156* (GZTM); Zheng'an, *J.M. Yuan 3* (HGAS), *4* (HGAS), *5* (HGAS), *6* (HGAS), *Q.H. Chen & T.L. Xu 9411* (HGAS); Ziyun, *B.L. Guo A67* (IMD), *A84* (IMD), *S.Z. He s.n.* (GZTM); Zunyi, *P.C. Tsoong 355* (KUN, PE). **Sichuan:** Baoxing, *Baoxing Med. Pl. Exped. 78-123* (SM), *Y.J. Zhang 386* (HIB), *387* (HIB), *388* (HIB), *389* (HIB); Changning, *Anon. 199* (SM); Chongzhou, *Anon. 590* (SM); Dujiangyan, *T.N. Liou 10060* (PE); Gaoxian, *Anon. 317* (SM); Gongxian, *Anon. 165* (SM); Guang'an, *Sichuan Econ. P1. Exp. Nan 127* (PE); Gulin, *C.Y. Pan & J.H. Chen 4470* (SM), *Gulin Exped. 589* (SM); Hongya, *B.L. Guo & K.W. Bao 97004* (IMD), *Hongya Exped. 952* (SM), *Sichuan Econ. Pl. Exped. Le 13* (KUN), *W.K. Bao 2298* (CDBI), *Y.J. Zhang 390* (HIB); Jiajiang, *Sichuan Econ. Pl. Exped. Le 8164* (PE, SM); Jiang'an, *Anon. 117* (SM), *K.Y. Lang 3002* (PE), *3061* (PE), *3069* (PE); Junlian, *Anon. 536* (SM); Leibo, *M.Y. He & C.M. Tan 116965* (SZ); Lushan, *G.Y. Zhong 1988-14* (SM), *1988-16* (SM), *Lushan Med. Pl. Exped. 78-398* (SM), *Y.J. Zhang 383* (HIB), *384* (HIB), *385* (HIB); Mabian, *D.Y. Hong* et al. *P.B84046* (PE), *Mabian Exped. 168* (SM); Meigu, *Sichuan Econ. Pl. Exped. Nan 6001* (PE), *Z.W. Yao 3794* (PE); Mingshan, *Mingshan Exped. 16* (SM); Mt. Omei, *B.L. Guo 88091* (IMD), *Bio. Dep., Sichuan Univ. 54207* (HIB), *C.H. Hsiung* et al. *30469* (PE), *33481* (PE), *C.H. Li 97-301* (PE), *C.S. Cheng 377* (KUN), *C.Y. Chu 331* (IMD), *D.Z. Fu 84262* (PE), *F.T. Wang 23329* (PE), *G.Y. Zhong 1988-25* (SM), *H.G. Xu 89463* (IMD), *89464* (IMD), *J.L. Hao 548* (IMD), *K.H. Yang 54343* (KUN, PE, SZ), *54207* (KUN, PE, SZ), *L.W. Wang & Z.Y. Zhang 824* (PE), *L.Z. Hu & P.Q. Duan 57-166* (SZ), *No. 236-Sichuan Exped. 201* (PE), *Mt. Omei Exped. 176* (SM), *P. Luo* et al. *1859* (SZ), *S.L. Sun 111* (HWA, KUN, SZ), *1405* (KUN, SZ), *1566* (SZ), *1615* (SZ), *2489* (KUN, SZ), *S.S. Chien 5499* (SZ), *S.X. Wang 401* (CDBI, PE), *S.Y. Chen* et al. *3033* (SM, SZ), *3080* (SM, SZ), *S.Z. Guo 403* (PE), *Sichuan Econ. Pl. Exped. Le 210* (PE), *Sichuan Med. Pl. Exped. 12121* (IMD), *Sichuan Veg. Exped. 477* (CDBI, PE), *Sino-Russia Exped. 1996* (PE), *2169* (PE), *T.H. Tu 42* (PE, SZ), *1902* (PE), *T.T. Yu 312* (PE), *W.C. Cheng 10151* (KUN), *10174* (KUN, SZ), *W.P. Fang 2138* (SZ), *14692* (HWA, KUN, SZ), *15803* (SZ), *15985* (SZ), *16038*(SZ), *16134* (SZ), *16411* (SZ), *16242* (SZ), *16793* (SZ), *18299* (HWA, SZ), *18338* (SZ), *18400* (SZ), *18583* (SZ), *T.C. Lee 4391* (SZ), *4424* (KUN, SZ), *X.B. Peng 6108* (PE), *Y.H. Tao 53876* (SZ), *53927* (SZ), *838* (PE), *Y.J. Zhang 398* (HIB), *399* (HIB), *412* (HIB), *414* (HIB), 444(HIB), *Y.X. Xiao 48108* (SZ), *48742* (SZ), *Y.Y. Wang* et al. *604012* (GZTM), *604013* (GZTM), *604014* (GZTM); Pingshan, *B.L. Guo 617* (IMD), *Bio. Dep., Sichuan Univ. 110147* (SZ); Qionglai, *Anon. 233* (SM); Tianquan, *D.Y. Peng 47070* (CDBI), *47073* (CDBI); Xingwen, *Sichuan Econ. Pl. Exped. Yi 1256* (KUN, PE), *Xingwen Exped. 77-162* (SM); Xu'yong, *B.L. Guo 602* (IMD), *L.S. Chen s.n.* (IMD), *G.Y. Zhong 1988-29* (SM), *M.F. Zhong & S.G. Tang 138* (SM), *Xu'yong Exped. 86* (SM), *Y.J. Zhang 401* (HIB); Ya'an, *G.H. Tang 65-7* (SM), *Y.J. Zhang 308* (HIB), *Y.Y. Wang* et al. *604008* (GZTM), *Ya'an Exped. 78-34* (SM), *554* (SM); Yongjing, *B.L. Guo 615* (IMD), *Yongjing Exped. 78-8* (SM). **Yunnan:** Weixin, *P. Huo 1076* (KUN); Yiliang, *Z.Y. Wu 60* (KUN).

Epimedium membranaceum K. Mey.

Epimedium membranaceum K. Mey., Repert. Spec. Nov. Regni Veg. Beih., 12: 380. 1922. Type: China. Sichuan: Dujiangyan, *Limpricht 1293* (isotypes, K!, WU!).

Epimedium rhizomatosum Stearn, Kew Bull., 53(1): 226. 1998. Syn. nov. Type: China. Sichuan: Leibo, Selenggong, alt. 2040 m, cult. England. Hampshire: Kilmeston, Blackthorn Nursery, July 1997, *Ogisu 92114* (holotype, K!).

Description. Herbs 20–65 cm tall. Rhizome compact or elongated. Leaves basal or cauline, trifoliolate; leaflets broadly ovate or narrowly ovate, 4–6 × 2–3 cm, apex acute or acuminate, margin with spines 1–1.5 mm, base cordate with lobes rounded or acute, those of lateral leaflets conspicuously oblique, subleathery, adaxially glabrous, abaxially glaucous, with scattered minute erect hairs. Flowering stem with 2 opposite or alternate leaves. Inflorescence paniculate, 9–40 cm long, 5–35-flowered, glandular; pedicels 1.5–2 cm. Flowers yellow, 4–6 cm in diam. Outer sepals green with base purplish. Inner sepals red, ovate-elliptic or narrowly ovate, 6–7 × 2.5–3 cm, apex acute. Petals pale yellow, much longer than inner sepals, subulate, 1.5–3.5 cm, lamina-less base. Stamens ca. 4 mm; anthers ca. 3 mm, yellow. Capsules ca. 2.5 cm.

Distribution and habitat. *Epimedium membranaceum* occurs in montane forests and thickets of Sichuan and the adjoining region of northern Yunnan, at elevations of 1200 to 2500 m.

Phenology. *Epimedium membranaceum* flowers from April to June, and fruits from May to July.

IUCN Red List category. *Epimedium membranaceum* should be designated as Least concern (LC) according to IUCN Red List criteria (IUCN 2013).

Notes. Ying (1975) placed *Epimedium membranaceum* into synonymy of *E. davidii* Franch., which was adopted by the Flora Reipublicae Popularis Sinicae (Ying 2001) and the Flora of China (Ying et al. 2011). However, the two species can be easily distinguished by petal shape, with the petals of *E. davidii* bearing obvious lamina while those of *E. membranaceum* have no lamina. Additionally, *Epimedium davidii* was treated as the type species of series *Davidianae* Stearn while *E. membranaceum* was referred to series *Dolichocerae* Stearn in the updated taxonomic system of *Epimedium* (Stearn 2002).

Epimedium rhizomatosum is much like *E. membranaceum*. In the protologue for *E. rhizomatosum*, Stearn (1998) distinguished it from *E. membranaceum* in rhizome shape, closeness of spines along the leaflet margin, inflorescence morphology, and number of flowers. *Epimedium membranaceum* had a compact rhizome with annual-growth shoots 1–2 cm long while *E. rhizomatosum* had an elongated rhizome and annual-growth shoots about 3–5 cm long; the leaflets of *E. membranaceum* had about 9–11 spines to 3 cm of leaflet margin whereas leaflets of the same size in *E. rhizomatosum* had about 15–17 spines to 3 cm of margin; *E. membranaceum* had a 30–40 cm long inflorescence with numerous well-separated flowers whereas *E. rhizomatosum* had a much shorter inflorescence with fewer, more crowded flowers. However, based on extensive investigation in herbaria and the field, it was found that *E. membranaceum* continuously varies in the morphology of these organs and the diagnostic features of *E. rhizomatosum* can fall into the variation range of *E. membranaceum*. For instance, *E. membranaceum* not only has compact but also slender and elongated rhizome in the type locality (even in one collection *X.J. He* et al. *131825* (SZ)).Therefore, *E. rhizomatosum* is here reduced as a new synonym of *E. membranaceum*.

Specimens examined. China. Sichuan: Beichuan, *Sichuan Econ. Pl. Exped. Mian 530* (SAU, SZ), *1149* (KUN, SM, SZ), *S. Jiang* et al. 7050 (PE); Butuo, *Butuo Med. Pl. Exped. 19* (SM); Dechang, *Grade 1974, SW Normal Univ. 12067* (CDBI, HWA, PE); Dujiangyan, *B.L. Guo 603* (IMD), *604* (IMD), *Z. He 12229* (HWA, PE), *F.T.*

Wang 20851 (KUN, PE), *X.J. He* et al. *131825* (SZ), *Y.J. Zhang 391* (HIB); Huidong, *Huidong Med. Pl. Exped. 1* (SM), *S.K. Wu 1433* (KUN, SM, SAU, SZ); Jiangyou, *Jiangyou Med. Pl. Exped. 223* (SM); Jinyang, *B.L. Guo 612* (IMD), *Jinyang Med. Pl. Exped. 440* (SM), *Y.J. Zhang 307* (HIB); Leibo, *M.Y. Fang 11740* (SZ), *S. Jiang* et al. *7534* (KUN, PE, SZ), *Sichuan Econ. Pl. Exped. Liang 26* (PE, KUN), *Sichuan Med. Pl. Exped. 27948* (SM), *K.P. Yin 83* (SZ), *Y.J. Zhang 303* (HIB); Maoxian, *B.L. Guo 529* (IMD), *88187* (IMD), *B.L. Guo & W.K. Bao 97017* (IMD), *C. Zhang* et al. *2004010* (PE), *Maowen Med. Pl. Exped. 183* (SM), *275* (SM), *S.H. Ma 65-331* (CDCM), *Sichuan Econ. Pl. Exped. E 166* (IMD), *5189* (CDBI, KUN, SAU, SM), *Z.L. Shen 89024* (IMD); Meigu, *Meigu Med. Pl. Exped. 154* (SM), *Sichuan Econ. Pl. Exped. Liang 6001* (PE); Ningnan, *Ningnan Med. Pl. Exped. 254* (SM); Pengzhou, *G.H. Jiang 200606001* (SM), *Q. Wang* et al. *yc013* (SZ), *yc017* (SZ), *W.Z. Zeng 25* (CDCM), *X.M. Lu 18* (CDCM); Pingwu, *Sichuan Econ. Pl. Exped. Mian 2195* (SM), *X.L. Jiang 10231* (PE, SZ); Qingchuan, *Qingchuan Exped. 594* (SM), *595* (SM), *Qingchuan Med. Pl. Exped. 2222* (SM), *3130* (SM); Shifang, *B.L. Guo 536* (IMD), *X.J. He* et al. *138339* (SZ), *Shifang Exped. 118* (SM); Wanyuan, *Sichuan Econ. Pl. Exped. Da 2323* (SAU); Xichang, *Q.E. Yang 93032* (PE); Yanbian, *Yanbian Exped. 295* (SM); Yanyuan, *Yanyuan Exped. 218* (SM); Zhaojue, *Zhaojue Exped. 90* (SM). **Yunnan:** Dongchuan, *S.B. Lan 250* (PE); Kunming, *J.H. Chen 679* (SM); Lijiang, *Y.Z. Zhao 20510* (KUN); Suijiang, *B.X. Sun* et al. *233* (PE, KUN); Weixi, *K.M. Feng 3510* (PE, KUN), *3383* (PE, KUN), *4371* (PE, KUN), *Qing-Zhi Exped. 6300* (PE, KUN), *6595* (PE, KUN), *Q.W. Wang 63581* (PE, KUN), *63697*(PE, KUN), *64285* (PE).

Epimedium leptorrhizum Stearn

Epimedium leptorrhizum Stearn, J. Bot., 71: 343. 1933. Type: China. Guizhou: Guiyang, *Bodinier 2184* (holotype, P!).

Epimedium brachyrrhizum Stearn, Kew Bull., 52(3): 659. 1997. Syn. nov. Type: China. Guizhou: Fanjingshan Mts., cult. USA. Massachusetts: Hubbardston, *Darrell Probst CPC 94.0495* (holotype, K!).

Description. Herbs 12–30 cm tall. Rhizome long-creeping, occasionally clump-forming, 1–2 mm in diam. Leaves basal and cauline, trifoliolate or occasionally unifoliolate; leaflets of trifoliolate leaves narrowly ovate or ovate, 3–10 × 2–5 cm, apex long acuminate, base deeply cordate with usually rounded lobes nearly touching, those of the lateral leaflets very unequal; unifoliolate leaves ovate or broadly ovate, 8−13.7 × 5−11 cm, apex acuminate, base cordate with lobes equal, rounded and rarely acute; leaves leathery, margin spinous-serrate, adaxially deep green, glossy, abaxially glaucous, papillose, and reddish pubescent along veins, especially dense at insertion of petioles and petiolules. Flowering stem with 1 leaf or 2 opposite leaves. Inflorescence racemose, 12–25 cm long, 4–12-flowered, glandular; pedicels 1–2.5 cm. Flowers ca. 4 cm in diam., white, tinged with rose or deep rose. Outer sepals green or purplish, outer pair ovate-oblong, 3–4 × ca. 2 mm, apex obtuse, inner pair broadly ovate, 4–5.5 × 3–4.5 mm, apex obtuse. Inner sepals white or pale rose, narrowly elliptic or lanceolate, 11–22 × 4–7 mm, apex acuminate. Petals slightly longer than inner sepals, almost white with base rose or deep rose, horn-shaped, up to 2.6 cm, tapering from the swollen but lamina-less base. Stamens ca. 4 mm, anthers ca. 3 mm, yellow or green. Capsules oblong, 1.5–2 cm.

Distribution and habitat. *Epimedium leptorrhizum* occurs in montane forests or thickets in Chongqing, Guangxi, Guizhou, Hubei and Hunan, at elevations of 600 to 1500 m.

Phenology. *Epimedium leptorrhizum* flowers from April to May, and fruits from May to June.

IUCN Red List category. *Epimedium leptorrhizum* should be designated as nearly threatened (NT) according to IUCN Red List criteria (IUCN 2013), because of exploitation for medicinal use.

Notes. Stearn (1997) published *Epimedium brachyrrhizum,* which had been only known from the type locality. In the protologue for *E. brachyrrhizum*, the major difference between *E. leptorrhizum* and *E. brachyrrhizum* was that the former had a very slender elongated rhizome while the latter bore a more compact clump-forming rhizome. However, examination of a series of *E. leptorrhizum* specimens shows that its rhizome is often slender and long-creeping but occasionally thicker and compact. In addition, we observed *E. leptorrhizum* and *E. brachyrrhizum* in herbaria, the field, and gardens, and did not observe any associated floral or foliar differences between the two species. *E. brachyrrhizum* is reduced here as a new synonym of *E. leptorrhizum*.

Specimens examined. China. Chongqing: Fengdu, *Anon. 109* (SM), *247* (SM); Shizhu, *Anon. 135* (SM), *202* (SM), *Y.J. Zhang 30* (HIB), *31* (HIB), *32* (HIB); Youyang, *Anon. 216* (SM), *503* (SM), *1510* (SM); Zhongxian, *J.X. Shi 637* (HWA). **Guangxi:** Quanxian, *Y.C. Chen 102* (IBK). **Guizhou:** Anshun, *Anshun Exped. 1548* (HGAS); Guiyang, *Anon. 45* (HGAS), *635* (IMD), *B.L. Guo 94018* (IMD), *S. Guizhou Exped. 77* (HGAS, PE, KUN); Jiangkou, *S.Z. He 90005* (HGAS); Kaili, *Y.J. Zhang 156* (HIB), *435* (HIB); Longli, *B.L. Guo A38* (IMD), *A81* (IMD), *D.Q. Zhang 19* (GZTM), *Y.Y. Wang 403030* (GZTM); Luodian, *Y.J. Zhang 429* (HIB); Meitan, *Anon. 254* (IMD), *Guizhou Med. Pl. Exped. 37* (IMD); Pingba, *Anshun Exped. 1548* (PE); Songtao, *B.L. Guo A87* (IMD), *A98* (IMD), *Y.J. Zhang 174* (HIB), *177* (HIB), *298* (HIB); Suiyang, *P. Zhao 452* (HGAS); Tongzi, *Y.K. Li 11171* (HAGS); Wuchuan, *J.M. Yuan & S.L. Yang 1* (HGAS), *2* (HGAS), *Y.J. Zhang 168* (HIB), *172* (HIB); Xifeng, *B.L. Guo A104* (IMD); Yinjiang, *Anon. 680* (HGAS), *S.Z. He s.n.* (IMD), *Y.J. Zhang 159* (HIB), *Z.S. Zhang* et al. *401219* (HGAS, PE). **Hubei:** *Enshi, H.J. Li 8738* (PE, HIB), *Y.J. Zhang 13* (HIB), *14* (HIB), *15* (HIB), *16* (HIB), *18* (HIB), *71* (HIB), *141* (HIB), *142* (HIB), *143* (HIB), *144* (HIB), *145* (HIB), *146* (HIB), *147* (HIB); Hefeng, *Y.J. Zhang 64* (HIB); Laifeng, *B.L. Guo A05* (IMD); Lichuan, *B.L. Guo & X.Z. Luo 89005* (IMD), *89009* (IMD), *A47* (IMD), *A52* (IMD), *A54* (IMD), *H.J. Li 11020* (HIB), *Y.J. Zhang 22* (HIB), *23* (HIB), *24* (HIB), *25* (HIB), *26* (HIB), *27* (HIB), *29* (HIB), *30* (HIB), *64* (HIB), *73* (HIB), *Z.C. Ye 25*

(HIB), *Z.E. Zhao 3226* (HIB), *3237* (HIB), *3238* (HIB), *3240* (HIB), *9053* (HIB); Xianfeng, *Y.M. Wang 6657* (HIB), *X.S. Zou 74010* (HIB); Xuan'en, *Y.J. Zhang 416* (HIB). **Hunan:** Baojing, *B.M. Yang 34B* (HNNU), *Y.J. Zhang 180* (HIB); Longshan, *B.L. Guo A99* (IMD); Sangzhi, *B.L. Guo A32* (IMD), *Sangzhi Insititute of Forestry Scinece 202* (KUN), *263* (KUN), *Hunan-Guizhou Exped. 3469* (KUN), *Y.J. Zhang 189* (HIB).

Epimedium dolichostemon Stearn

Epimedium dolichostemon Stearn, Kew Bull., 45(4): 685. 1990. Type: China. Chongqing: Shizhu, alt. 150 m, *Ogisu s.n.* (holotype, K!).

Epimedium dewuense S.Z. He, Probst & W.F. Xu, Acta Bot. Yunnan. 25(3): 281. 2003. Syn. nov. Type: China. Guizhou: Dejiang, in thickets on slopes, alt. 1350 m, 19 Apr. 2002, *S.Z. He* & *W.F. Xu 2419* (holotype, GZTM!; isotype, KUN!).

Description. Herbs 30–50 cm tall. Rhizome compact. Leaves basal or cauline, trifoliolate; leaflets narrowly ovate or lanceolate, 8–10 × 3–4.5 cm, apex long acuminate, margin spinous-serrate with the spines 0.5–1.5 mm, base deeply cordate with lobes acute or rounded, those of lateral leaflets very oblique, leathery, adaxially glabrous or pubescent, abaxially glaucous, glabrous or pubescent. Flowering stem with 2 opposite or rarely alternate leaves. Inflorescence paniculate, 15–20 cm long, 35–70-flowered, glabrous or glandular pubescent; pedicels 1–3 cm. Flowers ca. 2 cm in diam. with spreading inner sepals. Outer sepals purplish with margin white, outer pair ovate-oblong, 3.5–4.5 × 1.2–2.5 mm, apex obtuse, inner pair ovate, 4–5.5 × 2.8–3.5 mm, apex obtuse. Inner sepals white, narrowly elliptic or lanceolate, 8–14 × 2.5–5.5 mm, apex acuminate. Petals reddish purple, cucullate, much shorter than inner sepals, 3–4 mm, with blunt incurved spur and slight lamina base. Stamens conspicuously prolonged, ca. 8 mm; anthers ca. 2.5 mm; filaments 4.5–5 mm.

Distribution and habitat. *Epimedium dolichostemon* is distributed in Chongqing, northeastern Guizhou, and western Hubei, and usually occurs in forests, thickets, and weedy slopes, at elevations of 800 to 1400 m.

Phenology. *Epimedium dolichostemon* flowers from March to April, and fruits from April to May.

IUCN Red List category. *Epimedium dolichostemon* should be designated as nearly threatened (NT) according to IUCN Red List criteria (IUCN 2013), because of exploitation for medicinal use.

Notes. He and Xu (2003) recognized *E. dewuense* as a new species based only on the comparison with *E. sagittatum* but not with *E. dolichostemon*. According to the protologue of *E. dolichostemon* and *E. dewuense*, the two species can be distinguished by the shape and indumentum of leaflets: *E. dolichostemon* bears narrowly ovate leaves glabrous on both sides, while *E. dewuense* has wider leaves pubescent on both sides (Stearn 1990; He and Xu 2003). Based on investigations in herbaria and the field, morphological variation of leaflets between the two species is continuous, and *E. dewuense* is here treated as a new synonym of *E. dolichostemon*.

Specimens examined. China. Chongqing: Shizhu, *Y. Chen 59* (CDBI). **Guizhou:** Dejiang, *B.L. Guo A78* (IMD), *Y.J. Zhang 163* (HIB), *249* (HIB), *339* (HIB); Wuchuan, *S.Z. He* et al. *405001* (GZTM), *405002* (GZTM), *Y.J. Zhang 165* (HIB), *170* (HIB), *171* (HIB). **Hubei:** Jianshi, *Y.M. Wang 15* (HIB); Lichuan, *B.L. Guo A51* (IMD), *89008* (IMD), *89010* (IMD), *H.J. Li 11029* (HIB), *R.H. Huang 3725* (HIB), *Y.J. Zhang 247* (HIB), *248* (HIB), *334* (HIB), *Z.E. Zhao & Y.H. Wang 3201* (HIB); Xianfeng, *X.S. Zou 74009* (HIB).

Epimedium borealiguizhouense S.Z.He & Y.K.Yang

Epimedium borealiguizhouense S.Z. He & Y.K. Yang, J. Pl. Resourc. Environ. 2(4): 51. 1993, as "baieali-guizhouense". Type:—China. Guizhou: Yanhe, nearby brooklet in valley, alt. 300-500 m, 11 Apr. 1993, *S.Z. He 93001* (holotype, GZTM!).

Epimedium sagittatum Maxim. var. *oblongifoliolatum* Z. Cheng, Flora Hubeiensis, 1: 406. 2001. Syn. nov. Type:—China. Hubei: Enshi, alt. 400 m, 24 Apr. 1974, *X.S. Zou 74004* (holotype, HIB!).

Description. Herbs 40–80 cm tall. Rhizome compact. Leaves basal and cauline, trifoliolate; leaflets lanceolate or narrowly lanceolate, 13–18 × 2.5–4 cm, apex long acuminate, margin spinous-serrate, base shallowly cordate, terminal leaflet with subequal rounded lobes, lateral leaflets much oblique, inner lobes small, rounded or almost truncate, outer lobes larger, triangle, acuminate or acute, leathery, adaxially glabrous, abaxially densely strigose, densely pubescent, lanose, or glabrous. Flowering stem with 2 opposite or rarely 3 alternate leaves. Inflorescence paniculate, 30–40 cm long, many (up to 200) flowered, glabrous. Flowers small, 6–10 mm in diam. Outer sepals purplish, small, soon falling. Inner sepals white, ovate, 3–4 × 1.5–2.2 mm, apex acute. Petals yellow, calceiform, 2.2–3.2 mm. Stamens ca. 4 mm; anthers ca. 2.5 mm; filaments ca. 1.5 mm. Capsules ca. 1 cm.

Distribution and habitat. *Epimedium borealiguizhouense* is distributed in south central Chongqing, northeast Guizhou, western Hubei, and western Hunan. It usually occurs in forests, thickets, weedy slopes, and streamsides in valleys, at elevations of 300 to 800 m.

Phenology. *Epimedium borealiguizhouense* flowers from March to April, and fruits from April to May.

IUCN Red List category. *Epimedium borealiguizhouense* should be designated as nearly threatened (NT) according to IUCN Red List criteria (IUCN 2013), because of exploitation for medicinal use.

Notes. *Epimedium borealiguizhouense* is a member of series *Brachycerae* Stearn. Within this series, it is particularly similar to *Epimedium myrianthum* Stearn, but both are obviously different in the shape of the leaflets: *E. borealiguizhouense* bears lanceolate or narrowly lanceolate leaflets with the base of terminal leaflet shallowly cordate, the lateral leaflet is much more oblique with the inner lobe much smaller and rounded or almost truncate and the outer lobe triangular and acuminate or acute, while *E. myrianthum* usually has narrowly ovate leaflets with the base moderately cordate with a narrow sinus and the lateral leaflet is oblique with the lobes rounded or acute.

Epimedium borealiguizhouense was previously known only from the type locality, Yanhe, Guizhou. According to herbarium and field investigations, new localities of the species are recorded for Chongqing, Hubei, and Hunan. Furthermore, the indumentum on the abaxial surface of the leaflets varies from densely strigose to densely pubescent, lanose to glabrous. In addition, *Epimedium sagittatum* var. *oblongifoliolatum* published in Flora Hubeiensis (Fu 2001) is the same species as *E. borealiguizhouense* and is synonymized here.

Specimens examined. China. Chongqing: Changshou, *B.L. Guo 522* (IMD), *Y.J. Zhang 400* (HIB), *420* (HIB); Dianjiang, *Dianjiang Med. Pl. Exped. 82* (SM), *Y.J. Zhang 421* (HIB); Fengdu, *J.A. Wang & Y.X. Wang 49* (CDBI); Hechuan, *Hechuan Med. Pl. Exped. 731* (SM); Pengshui, *Anon. 214* (SM), *F.T. Pu & Y.L. Cao 255* (CDBI), *Y.J. Zhang 419* (HIB). **Guizhou:** Yanhe, *B.L. Guo A80* (IMD), *S.Z. He 93007* (GZTM), *93010* (IMD), *Y.J. Zhang 231* (HIB), *301* (HIB), *325* (HIB). **Hubei:** Enshi, *B.L. Guo & X.Z. Luo 89011* (IMD), *89014* (IMD), *Y.J. Zhang 20* (HIB), *62* (HIB), *399* (HIB), *415* (HIB); Laifeng, *Y.J. Zhang 417* (HIB); Xianfeng, *X.S. Zou 74011* (HIB). **Hunan:** Baojing, *Y.J. Zhang 411* (HIB).

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RESEARCH ARTICLE

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Preliminary phylogenetic analysis of the Andean clade and the placement of new Colombian blueberries (Ericaceae, Vaccinieae)

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Abstract

The blueberry tribe Vaccinieae (Ericaceae) is particularly diverse in South America and underwent extensive radiation in Colombia where many endemics occur. Recent fieldwork in Colombia has resulted in valuable additions to the phylogeny and as well in the discovery of morphologically noteworthy new species that need to be phylogenetically placed before being named. This is particularly important, as the monophyly of many of the studied genera have not been confirmed. In order to advance our understanding of the relationships within neotropical Vaccinieae and advice the taxonomy of the new blueberry relatives, here we present the most comprehensive phylogenetic analysis for the Andean clade. *Anthopterus*, *Demosthenesia*, and *Pellegrinia* are among the putative Andean genera recovered as monophyletic, while other eight Andean genera were not. The analyses also showed that genera that have been traditionally widely defined are non-monophyletic and could be further split into more discrete groups. Four newly discovered Colombian Vaccinieae are placed in the monophyletic *Satyria s.s.* and the *Psammisia* I clade. Although these new species are endemic to the Colombian Western Cordillera and Chocó biogeographic region and three are not known outside of Las Orquídeas National Park, they do not form sister pairs.

Keywords

Ericaceae, Vaccinieae, Andes, Molecular phylogeny, New species, Colombia

Introduction

In the neotropical regions, the most extensive radiation of the plant family Ericaceae took place in Colombia where there are 24 genera and 278 described species. Notably, about 55% of the Colombian Ericaceae are endemic to the country (Pedraza-Peñalosa unpubl.). Within Colombia, the greatest documented diversity of Ericaceae is found in the Western Cordillera and adjacent Chocó region, which belong to the Tropical Andes and Chocó biodiversity hotspots (Mittermeier et al. 1998; Myers et al. 2000), respectively. These hotspots have the highest angiosperm diversity in N South America (Morawetz and Raedig 2007), but despite their importance for the understanding of the genesis of the neotropical flora, entire lineages particularly rich in NW Colombia are missing in modern monographic and phylogenetic research, and not only in Ericaceae.

Over the past 40 years, major U.S. herbaria have observed a sharp decline (ca. > 85%; calculated between 1970–2009) in the number of Colombian specimens received and databased. This decline reflects the decrease in field-based projects and exchange of herbarium specimens due to a combination of safety concerns, complicated Colombian permitting legislation, and lack of funding.

It is only recently that Colombian Ericaceae are being included in molecular analyses (see *Disterigma* (Klotzsch) Nied. in Pedraza-Peñalosa 2009, 2010a, 2010b). The ongoing inventory of the vascular plants of Las Orquídeas National Park (LONP), strategically located in the confluence of the Colombian Tropical Andes and Chocó regions, has made available interesting new material of Ericaceae. LONP is a poorly known and isolated protected area in NW Antioquia within the general region with the greatest documented diversity and endemism of Ericaceae in the Neotropics (Luteyn 2002). Four new members of the tribe Vaccinieae stand out among the many other new plant species discovered in LONP. All of them are endemic to the Colombian Western Cordillera and Chocó biogeographic region, and three of them are endemic to LONP. Vaccinieae include the edible North American blueberries and South American *mortiños* and make up the bulk of Ericaceae in Colombia.

There are about 600 species of Vaccinieae in the Neotropics, currently placed in 30 genera, 28 of them endemic to the region (Luteyn 2002). Large-scale phylogenetic analyses of Vaccinieae are few. In a preliminary analysis of the entire tribe, Kron et al. (2002) found that the great majority of the neotropical taxa are resolved within an Andean clade. This clade has about 500 species (Pedraza-Peñalosa unpubl.) and includes species growing as far south as Bolivia. The only study of the N Andean blueberries is one that included 55 species and 14 Andean genera (Powell and Kron 2003). However, because Colombian taxa have been largely unavailable, Colombian species were largely absent from these studies.

Kron et al. (2002) and Powell and Kron (2003) are studies with different scopes, but both found a striking disparity between phylogenetic relationships and the current classification system, with 60–80% of the genera sampled resolved as not monophyletic. However, because tropical Ericaceae are very diverse, hard to collect and sometimes hard to sequence, phylogenetic analyses comprehensive enough to readdress generic limits are not available yet. In the absence of a phylogenetic based classification for Vaccinieae, the generic placement of novel species remains challenging, at best.

Morphology is most frequently the only tool available to determine the taxonomic identity of a new Vaccinieae and the morphology of the four new species from LONP place them in *Satyria* Klotzsch and *Psammisia* Klotzsch, both broadly-circumscribed groups that have been shown to be non-monophyletic. *Satyria* and *Psammisia* are both placed by nuclear and chloroplast molecular data within the Andean clade (Kron et al. 2002, Powell and Kron 2003). *Psammisia*, the second largest neotropical Ericaceae genus, is paraphyletic with respect to *Macleania* Hook., while the small-sized *Satyria* is polyphyletic. While the phylogenetic relationships of *Psammisia* and *Macleania* have not been addressed in more detail, molecular analyses revealed that the species of *Satyria* are placed in two clades that are not closely related to each other. *Satyria* from Central America and N South America are congeneric and form *Satyria* s.s. (including the type species, *S. warszewiczii* Klotzsch), whereas species of *Satyria* from S Peru and Bolivia cluster with representatives of *Thibaudia* Ruiz & Pav. ex J. St.-Hil. from the same geographic region, forming the *Thibaudia* clade, which is placed in a distant part of the phylogenetic tree (Powell and Kron 2003). All the previously mentioned groups, except for *Thibaudia*, are most diverse in N South America.

The objectives of this study are twofold, first, to provide the most comprehensive phylogenetic analysis yet for the entire Andean clade, second, to discover the evolutionary affinities of the novel taxa from LONP. These phylogenetic results will be used to guide their future naming. Although special emphasis has been placed in the representation of the neglected Colombian taxa, making of this dataset the largest published for neotropical Vaccinieae, more work is still necessary to elucidate intergeneric relationships within the Andean clade. Consequently, our results are still only preliminary, but they lay the groundwork for future detailed studies within and across Andean Vaccinieae. Lastly, although no attempt to reconstruct the evolution of morphological characters is made here, the morphology associated with the best-supported clades is briefly discussed when relevant.

Material and methods

Taxon sampling

Sequence data from 94 terminals (91 species), belonging to 20 putatively neotropical Vaccinieae genera, were analyzed. The sampling strategy followed that of Pedraza-Peñalosa et al. (2013), but with emphasis on taxa of Andean origin. Eighteen species endemic to Colombia were newly sequenced and for five other species that also grow outside Colombia, a population from Colombia was chosen. The sampled taxa exemplify different aspects of reproductive and vegetative morphology. They also represent the major clades recovered within Neotropical Vaccinieae in previous phylogenetic analyses, and also include species from the Caribbean/Mesoamerican clade. Emphasis was placed on sampling *Satyria*, *Macleania*, *Psammisia*, *Thibaudia* and *Cavendishia* Lindl. For polymorphic species hard to identify or those whose variation is insufficiently known, more than one specimen was sequenced. For the plastic *Satyria grandifolia* Hoerold, two specimens recently collected in LONP (NW Colombia), each representing a separate morphospecies, were sequenced. These were analyzed along with the sequence already available in GenBank and originally collected in SW Colombia. Two specimens were also sequenced of the very rare and morphologically insufficiently understood *Psammisia mediobullata* Luteyn & Sylva, endemic to a small region of NW Antioquia (Colombia). Trees were rooted with *Gaylussacia baccata* (Wangenh.) K.Koch, a species from a genus of extra-neotropical origin that is basal with respect to all New World taxa (Kron et al. 2002).

DNA extraction and sequencing

A combination of nuclear (nrITS, 651 aligned bp.) and plastid (5' end of *ndhF*, ca. 1225 aligned bp.; *matK*, 1331 aligned bp.) markers were selected because of their number of phylogenetically informative characters in previous studies (Kron et al. 2002, Powell and Kron 2003, Pedraza-Peñalosa 2009, 2010a, Pedraza-Peñalosa et al. 2013). All procedures used during the DNA extraction and sequencing have been published previously (Pedraza-Peñalosa 2009). Sequences were edited with Sequencher 5.2.3 (Gene Codes Corporation). For this study, 93 new molecular sequences were produced (permits DTSA 033 SFF Galeras y otros; Acceso a Recursos Genéticos Res. 734 de 30 de Abril de 2007; 35-2005-INRENA-IFFS-DCB), the rest were gathered from GenBank; all accession numbers are provided in Table 1.

Analytical methods

A multiple sequence alignment was produced using MUSCLE (Edgar 2004) and the model of sequence evolution was estimated with jModelTest 2 (Guindon and Gascuel 2003, Darriba et al. 2012). Maximum Likelihood (ML) estimation of the phylogenetic relationships was conducted using RAxML (Stamatakis 2006), employing one thousand replicates with stepwise random taxon addition, starting MP trees, the GTRGAMMA model of evolution, and 1000 bootstraps (BS) inferences. The best ML tree was visualized with FigTree 1.3.1 (http://tree.bio.ed.ac.uk/). The ML analyses were performed for each individual loci, partition (nuclear vs. plastid), and lastly, for the entire dataset.

Results

The resulting topologies of the individual, partitioned (nuclear vs. plastid), and combined best ML trees are in general agreement (trees not shown) and no significant

Table 1. Species of Vaccinieae studied with their corresponding voucher specimens and GenBank accession numbers (ITS, *matK*, *ndhF*). m = missing, RBGE = Royal Botanic Garden Edinburgh, RBGK = Royal Botanic Garden Kew, LONP = Las Orquídeas National Park.

Species	**DNA sample (GenBank)**
Anthopterus revolutus (Wilbur & Luteyn) Luteyn	Powell 20 (AY331866, AY331893, AY331920)
Anthopterus wardii Ball	Luteyn 15191 (AF382656, AF382746, AY331921)
Cavendishia grandifolia Hoerold (Subg. *Cavendishia*, sect. *Engleriana*, ser. *Engleriana*)	Luteyn 8023(AY331869, AY331896, AY331924)
Cavendishia adenophora Mansf. (Subg. *Cavendishia*, sect. *Engleriana*, ser. *Engleriana*)	Pedraza 1709 (KJ788222, KJ788253, KJ788191)
Cavendishia angustifolia Mansf. (Subg. *Cavendishia*, sect. *Engleriana*, ser. *Engleriana*)	Pedraza 1769 (KJ788223, KJ788254, KJ788192)
Cavendishia bomareoides A.C.Sm. (Subg. *Cavendishia*, sect. *Callista*)	Pedraza 1752 (KJ788224, KJ788255, KJ788193)
Cavendishia bracteata (Ruiz & Pav. ex J.St.-Hil.) Hoerold (Subg. *Cavendishia*, sect. *Cavendishia*, ser. *Cavendishia*)	Luteyn 14223 (AY331867, AY331894, AY331922)
Cavendishia capitulata Donn.Sm. (Subg. *Cavendishia*, sect. *Cavendishia*, ser. *Cavendishia*)	Powell 10 (AY331868, AY331895, AY331923)
Cavendishia complectens Hemsl. subsp. *striata* (A.C. Smith) Luteyn var. *cylindrica* Luteyn (Subg. *Cavendishia*, sect. *Cavendishia*, ser. *Imbricatae*)	Pedraza 1749 (KJ788225, KJ788256, KJ788194)
Cavendishia leucantha Luteyn (Subg. *Cavendishia*, sect. *Cavendishia*, ser. *Deciduae*)	Pedraza 1768 (KJ788226, KJ788257, KJ788195)
Cavendishia lindauiana Hoerold (Subg. *Cavendishia*, sect. *Callista*)	Pedraza 1766 (KJ788227, KJ788258, KJ788196)
Cavendishia martii (Meisn.) A.C.Sm. (Subg. *Cavendishia*, sect. *Quereme*)	Luteyn 15443 (AF382658, AF382747, AY331925)
Cavendishia micayensis A.C.Sm. (Subg. *Chlamydantha*)	Pedraza 1888 (KJ788228, KJ788259, KJ788197)
Cavendishia pilosa Luteyn (Subg. *Cavendishia*, sect. *Cavendishia*, ser. *Cavendishia*)	Pedraza 1743 (KJ788229, KJ788260, KJ788198)
Cavendishia pubescens (Kunth) Hemsl. (Subg. *Cavendishia*, sect. *Cavendishia*, ser. *Cavendishia*)	Pedraza 1038 (KJ788230, KJ788261, KJ788199)
Cavendishia quereme (Kunth) Benth. & Hook. f. (Subg. *Cavendishia*, sect. *Quereme*)	Pedraza 1707 (KJ788231, KJ788262, KJ788200)
Cavendishia tarapotana (Meisn.) Benth. & Hook. f. var. *tarapotana* Luteyn (Subg. *Cavendishia*, sect. *Cavendishia*, ser. *Cavendishia*)	Pedraza 1958 (KJ788232, KJ788263, KJ788201)
Cavendishia tryphera A.C.Sm. (Subg. *Cavendishia*, sect. *Engleriana*, ser. *Engleriana*)	Pedraza 1702 (KJ788233, KJ788264, KJ788202)
Ceratostema lanceolatum Bentham	Luteyn 15107 (AF382660, AF382749, m)
Ceratostema lanigerum (Sleumer) Luteyn	Luteyn 14216 (AY331870, AY331897, AY331926)
Ceratostema megabracteatum Luteyn	Luteyn 15037 (AF382661, AF382750, m)
Ceratostema rauhii Luteyn	Rauh 68468 (AY331871, AY331898, AY331927)
Ceratostema reginaldii (Sleumer) A.C.Sm.	Luteyn 14159 (AY331872, AY331899, AY331928)
Ceratostema silvicola A.C.Sm.	ABG 90-1101 (=Pedraza 1021) (AY331873, AY331900, AY331929)
Demosthenesia mandonii (Britton) A.C.Sm.	Luteyn 15433 (AF382664, AF382751, m)
Demosthenesia spectabilis (Rusby) A.C.Sm.	Luteyn 15474 (AF382665, AF382753, m)
Diogenesia alstoniana Sleumer	Luteyn 15196 (AF382672, AF382759, m)
Diogenesia racemosa (Herzog) Sleumer	Luteyn 15462 (AF382673, AF382760, AY331931)

Species	**DNA sample (GenBank)**
Disterigma agathosmoides (Wedd.) Nied.	Pedraza 1001/Luteyn 15191 (FJ001671, KC175470, FJ001710)
Disterigma pentandrum S.F.Blake	Pedraza 1201/Luteyn 15085 (FJ001693, KC175465, FJ001733)
Disterigma pseudokillipiella Luteyn	Pedraza 1143, 1066 (FJ001694, KC175471, FJ001735)
Disterigma rimbachii (A.C.Sm.) Luteyn	Pedraza 1018 (FJ001695, KC175463, FJ001736)
Disterigma trimerum Wilber & Luteyn	Luteyn 15568 (FJ001700, KC175464, FJ001741)
Gaylussacia baccata K.Koch	Floyd 858 (AF273713, m, m)
Gonocalyx costaricensis Luteyn	Luteyn 15228 (AF382678, AF382764, m)
Gonocalyx megabracteolatus (Wilbur & Luteyn) Luteyn	Luteyn 14817 (AF382682, AF382767, m)
Macleania bullata Yeo	Luteyn 15724 (AF382679, U89758, AY331937)
Macleania coccoloboides A.C.Sm.	Luteyn 15852A (AF382680, AF382765, AY331938)
Macleania cordifolia Benth.	Pedraza 1884 (AY331877, AY331904, AY331939)
Macleania floribunda Hook.	Pedraza 1882 (FJ001704, m, FJ001745)
Macleania insignis M. Martens & Galeotti	RBGK 1969-19236 (AF382681, AF382766, AY331940)
Macleania rupestris (Kunth) A.C.Sm.	Pedraza 1879 (KC175462, m, KC175457)
Notopora schomburgkii Hook.f.	Luteyn 15275 (AF382683, AF382768, AF419728)
Orthaea apophysata (Griseb.) A.C.Sm.	van der Kloet 37694 (AF382685, AF382770, m)
Orthaea venamensis Maguire, Steyermark & Luteyn	Luteyn 15277 (AF382687, AF382772, m)
Pellegrinia coccinea (Hoerold) Sleumer	Luteyn 15646 (KC175461, KC175468, KC175453)
Pellegrinia hirsuta (Ruiz & Pav. ex G.Don) Sleumer	Luteyn 15644 (KC175458, KC175466, KC175455)
Psammisia aberrans A.C.Sm.	Pedraza 1715 (KJ788234, KJ788265, KJ788203)
Psammisia breviflora (Benth.) Klotzsch	Pedraza 2133 (KJ788235, KJ788266, KJ788204)
Psammisia dolichopoda A.C.Sm.	Luteyn 15006 (AF382690, AF382775, AF419730)
Psammisia ecuadorensis Hoerold	Luteyn 15033 (AF382691, AF382776, AY331942)
Psammisia ferruginea A.C.Sm.	Pedraza 1706 (KJ788237, KJ788268, KJ788206)
Psammisia grandiflora Hoerold	Pedraza 1101 (KJ788238, KJ788269, KJ788207)
Psammisia sp. nov. 1	Salinas 865 (KJ788243, KJ788274, KJ788212)
Psammisia sp. nov. 2	Pedraza 2134 (KJ788244, KJ788275, KJ788213)
Psammisia mediobullata Luteyn & Sylva "PP 2005"	Pedraza 2005 (KJ788239, KJ788270, KJ788208)
Psammisia mediobullata Luteyn & Sylva "PP 2129"	Pedraza 2129 (KJ788240, KJ788271, KJ788209)
Psammisia oreogenes Sleumer	Betancur 12349 (KJ788236, KJ788267, KJ788205)
Psammisia pedunculata A.C.Sm.	Pedraza 1754 (KJ788241, KJ788272, KJ788210)
Psammisia ramiflora Klotzsch	Setaro 08M33 (KJ788242, KJ788273, KJ788211)
Psammisia sodiroi Hoerold	Luteyn 8021 (AY331878, AY331905, AY331943)
Psammisia ulbrichiana Hoerold	Luteyn 15170 (AY331879, AY331906, AY331944)
Satyria allenii A.C.Sm.	Luteyn 15292 (AF382692, AF382777, AY331945)
Satyria arborea A.C.Sm.	Pedraza 1741 (KJ788245, KJ788276, KJ788214)
Satyria boliviana Luteyn	Luteyn 15481 (AF382693, AF382778, AY331946)
Satyria bracteolosa A.C.Sm.	Pedraza 2411 (KJ788246, KJ788277, KJ788215)
Satyria cerander (Dunal) A.C.Sm.	Mori 25279 (AY331880, AY331907, AY331947)
Satyria grandifolia Hoerold	Luteyn 15204 (AF382694, AF382779, AY331948)
Satyria grandifolia Hoerold "PP 2350"	Pedraza 2350 (KJ788247, KJ788278, KJ788216)
Satyria grandifolia Hoerold "PP 2408"	Pedraza 2408 (KJ788248, KJ788279, KJ788217)
Satyria sp.	Powell 9 (AY331882, AY331909, AY331953)

Species	**DNA sample (GenBank)**
Satyria sp. nov. 1	Pedraza 2436 (KJ788251, KJ788283, KJ788220)
Satyria sp. nov. 2	Pedraza 1755 (KJ788252, KJ788282, KJ788221)
Satyria latifolia A.C.Sm.	Pedraza 1771 (KJ788249, KJ788280, KJ788218)
Satyria leucostoma Sleumer	Luteyn 15051 (AF382695, AF382780, AY331949)
Satyria meiantha Donn.Sm.	Luteyn 15236 (AF382696, AF382781, AY331950)
Satyria panurensis (Benth. ex Meisn.) Hook. f. ex Nied.	Luteyn 15247 (AF382697, AF382782, AY331951)
Satyria pilosa A.C.Sm.	Pedraza 2349 (KJ788250, KJ788281, KJ788219)
Satyria polyantha A.C.Sm.	Powell 83 (AY331881, AY331908, AY331952)
Satyria vargasii A.C.Sm.	Powell 75 (AY331883, AY331910, AY331954)
Satyria ventricosa Luteyn	Luteyn 15293 (AY331884, AY331911, AY331955)
Satyria warszewiczii Klotzsch	RBGE 781009 (AF382698, U61314, AY331956)
Themistoclesia sp. 1	Luteyn 15653 (m, KC175467, KC175456)
Thibaudia costaricensis Luteyn & Wilbur	Powell 16 (AY331887, AY331914, AY331963)
Thibaudia densiflora (Herzog) A.C.Sm.	Luteyn 15459 (AF382708, AF382790, AY331964)
Thibaudia floribunda Kunth	Luteyn 15090 (AF382709, AF382791, AY331966)
Thibaudia inflata Luteyn	Luteyn 15029 (AY331889, AY331916, AY331967)
Thibaudia jahnii S.F.Blake	Luteyn 15258 (AF382710, AF382792, m)
Thibaudia litensis Luteyn	Luteyn 15020 (AF382711, AF382793, AY331968)
Thibaudia macrocalyx J. Rémy	Luteyn 15444 (AY331890, AY331917, AY331969)
Thibaudia martiniana A.C.Sm.	Luteyn 15028 (AY331891, AY331918, AY331970)
Thibaudia pachyantha A.C.Sm.	Luteyn 15189 (AF382712, AF382794, AY331971)
Thibaudia parvifolia (Bentham) Hoerold	Luteyn 15212 (AF382713, AF382795, AY331972)
Thibaudia tomentosa Hoerold	Luteyn 15502 (AY331892, AY331919, AY331973)
Vaccinium crenatum (G.Don) Sleumer	Luteyn 14171 (AF382719, VCU89761, AF419742)

conflicts were detected. Thus, the results and discussion will focus on the best ML tree obtained from the combined analysis (Fig. 1). Only the more robust groups recovered by this analysis and those relevant to the placement of the new species from LONP will be discussed in detail.

The general topology of the most likely reconstruction (ln$L$= -13984.363979) is congruent with previous phylogenetic analyses of neotropical Vaccinieae. Here, some species from the Guyana Shield and the South American páramos are of extra-neotropical origin (98% bootstrap) and sister to a large neotropical clade. The neotropical clade (97% bootstrap) comprises a small Mesoamerican/Caribbean clade (100% bootstrap) sister to a large Andean clade (100% bootstrap), where the vast majority of the species are found. The Andean clade is divided into two major groups, named here A and B (Fig. 1).

Andean clade A (Fig. 1), is the larger of the two major groups, but it is the least supported (< 50% bootstrap). *Disterigma s.s.* (100% bootstrap) forms a tritomy with *Thibaudia p.p.* (including *Satyria* from the Central Andes, 100% bootstrap) and a clade that includes the Homoandrous and Continuous Pedicel (HmCP; equal stamens and pedicel continuous with the calyx; 100% bootstrap) and the Heteroandrous and Articulate Pedicel (HtAP; unequal stamens and pedicel articulated with the calyx;

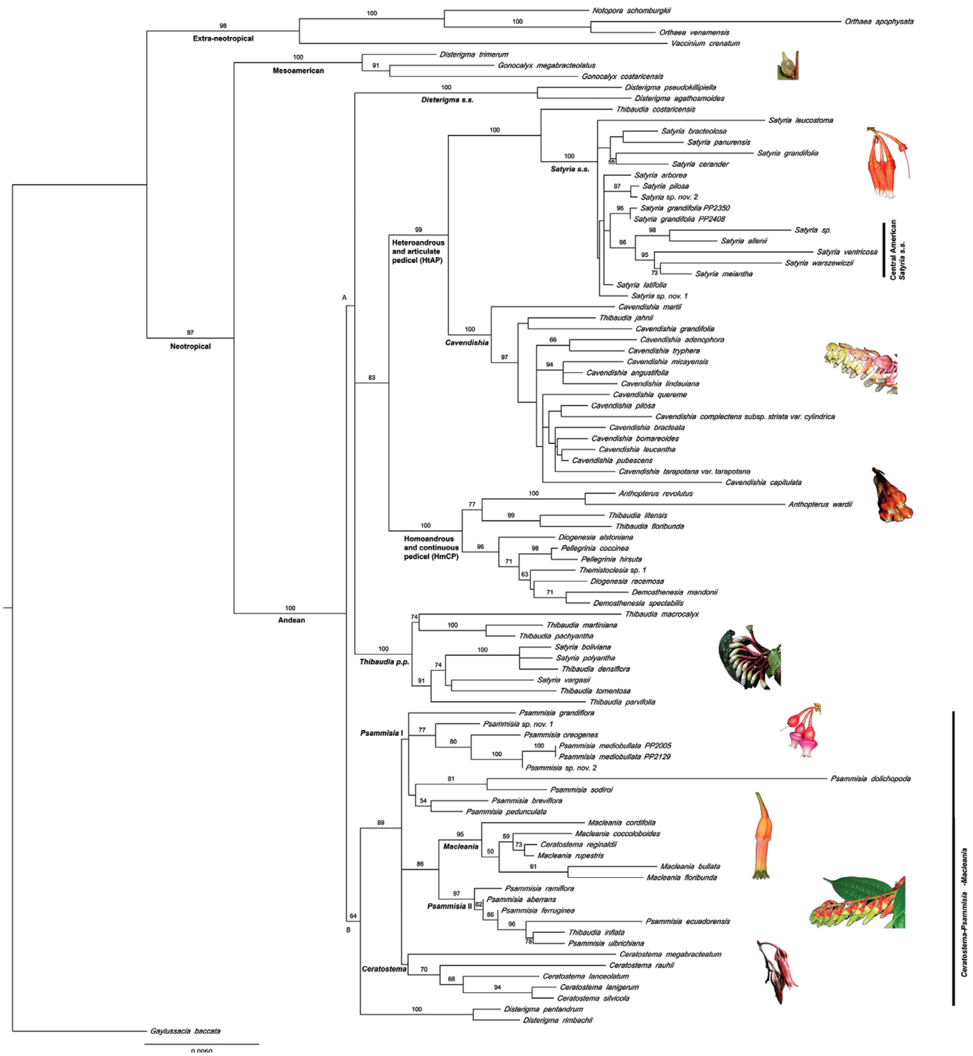

Figure 1. Phylogram of the best found Maximum likelihood hypothesis based on nuclear and plastid sequence data (ln*L*= -13984.363979). Bootstrap support values greater than 50% are shown in front of nodes.

99% bootstrap) clades. *Thibaudia* is polyphyletic with at least four independent origins within clade A and one species within clade B.

The HtAP group is the largest within clade A and *Cavendishia*, the most diverse of the neotropical genera (> 100 species), dominates it. *Cavendishia* is sister to the smaller *Satyria s.s.* (ca. 20 species). Sister to HtAP is the HmCP clade (*Anthopterus* + *Themistoclesia* + *Demosthenesia* + *Diogenesia* + *Pellegrinia* + *Thibaudia p.p.*), composed by putative genera that are very small or medium sized (5–30 species) (Fig. 1).

Andean clade B (64% bootstrap; Fig. 1) is made up of a clade previously denominated the Central Andes Segregated *Disterigma* (Pedraza-Peñalosa 2009, 2010a, 2010b) (100% bootstrap), sister to a tritomy (89% support) that contains the non-monophyletic *Ceratostema* Juss., *Macleania*, and *Psammisia*.

Overall, 73% of the genera of Andean origin (8 out of 11) for which more than one species was sampled were not monophyletic. The core *Disterigma* and *Satyria* clades have already been identified by previous studies, along with the species that need to be segregated from them (Powell and Kron 2003, Pedraza-Peñalosa 2009, 2010a); *Disterigma s.s.* was subsequently monographed (2010b). Therefore, *Disterigma s.l.* will not be further discussed. *Anthopterus* Hook. (100% bootstrap), *Demosthenesia* A.C.Sm. [including the type species, *Demosthenesia mandonii* (Britton) A.C.Sm., 71% bootstrap], and *Pellegrinia* Sleumer (98% bootstrap) are among the few Andean genera resolved as monophyletic. *Gonocalyx* Planch. & Linden (91% bootstrap) is another monophyletic group, but is of Mesoamerican origin (Fig. 1).

Satyria s.s. clade

This HtAP subclade includes the majority of the sampled *Satyria* and is sister to *Thibaudia costaricensis* Hoerold. *Satyria s.s.* is strongly supported (100% bootstrap; Fig. 1); it includes the type of the genus, *S. warszewiczii*. *Satyria leucostoma* Sleumer forms a tritomy with the rest of *Satyria s.s.* The only well-supported groupings within *Satyria s.s.* are species pairs and a small subclade made up by taxa from Central America (96% bootstrap). Two of the sampled new species from LONP, *S.* sp. nov. 1 and *S.* sp. nov. 2, are placed within *Satyria s.s.*

Cavendishia clade

In this clade (100% bootstrap; Fig. 1), *Cavendishia martii* (Meisn.) A.C.Sm. is strongly supported as sister to the rest. The only other well supported clade is the *C. micayensis*–*C. lindauiana* clade (≥ 94% bootstrap). *Thibaudia jahnii* S.F. Blake, from Venezuela, is included, and is sister to the Ecuadorean *C. grandifolia* Hoerold (support weak).

Thibaudia p.p. clade

Within this clade (100% bootstrap; Fig. 1), *Thibaudia macrocalyx*–*T. pachyantha* form a cluster (74% bootstrap) sister to a clade (91% bootstrap) that contains three species of *Satyria* mixed with other species of *Thibaudia*.

Psammisia–*Ceratostema*–*Macleania* clade

Within the Andean clade B, *Psammisia* is split in two clusters (Fig. 1). The largest of the groupings, *Psammisia* I clade (< 50% bootstrap), is part of a tritomy that also contains *Ceratostema* (< 50% bootstrap) and the *Psammisia* II + *Macleania* clade (86% bootstrap). *Psammisia* II (97% bootstrap) (including *Thibaudia inflata* Luteyn) is sister to *Macleania* (96% bootstrap). Neither *Ceratostema* nor *Macleania* are monophyletic as *C. reginaldii* (Sleumer) A.C.Sm. is derived within *Macleania*. The other two sampled new species from LONP are resolved within *Psammisia* I.

Discussion

The two main groupings within the Andean clade, clades A and B (Fig. 1), also appear in previous studies with large generic coverage (see Kron et al. 2002, Pedraza-Peñalosa et al. 2013). However, these studies differ in their generic sampling and the groups in which they disagree are either poorly supported or sampled, making detailed comparisons difficult. The following are the most significant findings.

HtAP clade

This strongly supported group (99% bootstrap; Fig. 1) is among the largest Andean Vaccinieae subclades with an estimated 170 species, most of them *Cavendishia*. Heteroandrous taxa are very distinctive within Vaccinieae and are characterized by having strongly unequal stamens in which the filaments and/or anthers of adjacent stamens (each corresponding to one of the two staminal whorls) alternate in length. When there are differences in anther size, dimorphism can be also expressed in anther shape (*Satyria s.s.*) and orientation of the tubule aperture (*Satyria s.s.*, *Cavendishia*). However, differences in this latter feature are poorly documented in species descriptions and are at times slight, and neither its extent nor its consistency is clear.

A close evolutionary relationship between *Satyria s.s.* and *Cavendishia* was first proposed by Smith (1932) who suggested that even though the genera are distinct, they form a separate group within Vaccinieae having staminal dimorphism in common. However, the nature of the dimorphism is quite different in each group, as pointed out below, and it should be further examined. Smith included the also dimorphic *Orthaea* within this group, but Andean species of *Orthaea* were not included in this analysis as it is currently being studied in detail (revision in preparation by N. R. Salinas).

Lastly, the HtAP species are characterized by having the pedicel articulate with the calyx (seen as a constriction at the point of attachment), a homoplasic feature that is traditionally used as part of the key characters useful to tell genera apart.

Satyria s.s. clade

Thibaudia costaricensis is sister to *Satyria s.s.*, a clade that is in agreement with the molecular circumscription of *Satyria* by Powell and Kron (2003). Both taxa have connate filaments (Fig. 1). *Satyria s.s.* species have in common markedly alternately unequal stamens with rigid dimorphic anthers, the longer of which have flaring tubules that are often ornamented or recurved into hooks; their filaments are equal in length (Powell and Kron 2003). Powell and Kron (2003) sampled 11 out of the 22 then recognized species and noted that the Colombian *Satyria* (10 species, 9 of them endemic) needed to be included in future studies to better elucidate evolutionary patterns. Seven Colombian species, including two new to science, are added to this analysis for a total of 18 *Satyria s.l.*

Fifteen morphospecies are placed within *Satyria s.s.*, mostly South American (Fig. 1). However, despite the increased taxonomic coverage, support at the basal nodes is weak and the only well-supported major subclade is that of the Central American species (*S. allenii–S. meiantha*, 96% bootstrap). The derived position of these Central American species indicate they are the result of relatively recent dispersals from a South American ancestor. However, in the case of *S. panurensis* (Benth. ex Meisn.) Hook. f. ex Nied., a species found from Mexico to southern Bolivia (including the Guianese Shield to the east) and not included within the Central American clade of *Satyria s.s.*, the direction of the migration of is not clear.

Although the new species are endemic to the same general region, have similar corolla colors and shape, and are the only *Satyria s.s.* known to have an ornamented calyx (winged and/or lobed), they are not sister species. *Satyria* sp. nov. 1, sister to a clade containing species from both Central and South America, is easily differentiated from all other *Satyria s.s.* because of its pseudoverticillate leaves. *S. pilosa* A.C.Sm., another newly sequenced species, present in Antioquia but also beyond, being endemic to the greater Chocó biogeographic region, is sister to *S.* sp. nov. 2 (87% bootstrap).

Some of the molecular-based relationships here obtained using a larger sampling of *Satyria s.s.* do not agree with some of the taxonomic rearrangements of a recent monographic study (Powell 2005). Although the proposed changes have not been formally published, the unpublished names and combinations have already appeared in taxonomic and record-based public databases, as well on annotations of herbarium specimens from several American and European herbaria. Hence the comments below.

Satyria warszewiczii is a species thought to be confined to Central America (southern Mexico to Panama), with a broad altitudinal gradient [(100–)300–2500 m] and consequently morphological variation (Luteyn and Wilbur 2005). Based on Principal Components Analyses of the morphological variation, Powell (2005) suggests that 11 species, mostly from South America, are indistinguishable from it and therefore should be synonymized.

Molecular data for *Satyria latifolia* A.C.Sm. and *S. ventricosa*, as well as two morphospecies of the variable *S. grandifolia* (Colombia–Peru) from NW Colombia , all putative synonyms of *S. warszewiczii* according to Powell (2005), were sampled. A third collection of *S. grandifolia* from SW Colombia, which was used in previous phylogenetic analyses (see Powell 2005, Powell and Kron 2003), was also analyzed.

The Central American *Satyria meiantha*, *S. warszewiczii*, and *S. ventricosa* form a clade (95% bootstrap; Fig. 1), in agreement with Powell's taxonomic proposal, and they may as well be conspecific, although terminal branch lengths are very long. However, they are more closely related to *S. allenii* A.C.Sm., which was considered by Powell (2005) a distinct species, than to either *S. latifolia* or *S. grandifolia*.

On the other hand, the two newly sequenced specimens of *Satyria grandifolia* from NW Colombia form a well-supported clade sister to the Central American *Satyria s.s.*, but with little support, while the *S. grandifolia* from SW Colombia is placed with species of extra-Andean distribution, although again with little support (Fig. 1). As for *Satyria latifolia*, this species is part of a poorly supported tetratomy and is not immediately related to either *S. warszewiczii* or any accession of *S. grandifolia*, as hypothesized. Moreover, there are no big differences between the samples of *S. grandifolia* from NW Colombia, whereas considerable changes have accumulated on the branches and terminals in their sister group, *S. warszewiczii* and relatives.

Altogether, the results suggest that the *Satyria grandifolia* from NW and SW Colombia are not conspecific. The herbarium vouchers of the *S. grandifolia* from NW Colombia were collected in the same biogeographic region (Chocó) where the type species was procured, about 200 km from the type locality. To rule out contamination of our sample, some molecular markers were independently re-sequenced and identical results were obtained. The herbarium voucher of the *S. grandifolia* from SW Colombia (*Luteyn 15204*) was collected much farther away from the type locality, but still within the Chocó biogeographic region. Unfortunately, because *Luteyn 15204* does not have flowers (only fruits), it is not possible to reassess its taxonomic identity.

In the same general area of *Luteyn 15204* there are specimens very similar to those from NW Colombia, however, others have floral and vegetative characteristics that subtly diverge from them and which have not been observed in other studied *S. grandifolia* collections. Without doubt Powell was right at pointing out that species delimitation within *Satyria s.s.* is complicated and that more fieldwork in western Colombia was advised.

It was also (Powell 2005) suggested that *Satyria arborea* A.C.Sm., endemic to Colombia, should be synonymized with *S. allenii*, endemic to Panama. However, in this analysis they are not sister species, with *S. allenii* placed at a more derived position within a well-supported clade that includes other Central American *Satyria s.s.* (Fig. 1). The newly sequenced *S. arborea* was collected relatively close to the type locality and it is easily differentiated from *S. allenii* by anther length (about twice as long in *S. arborea*). Anther length may be one of the best characters, beyond geographic distribution, to differentiate among these species, as other traditionally used features such as length of the petiole and pedicel and life form have been shown to be inadequate (Powell 2005).

Cavendishia clade

Filaments and anthers of adjacent stamens are of different lengths in *Cavendishia*, a diagnostic character that has been invoked by most of the taxonomic classifications of the neotropical Vaccinieae of the last century (Luteyn 1983, Smith 1932, Sleumer 1941). However, the *Cavendishia* clade also includes *Thibaudia jahnii* (but < 50% bootstrap) toward its base (Fig. 1), a taxon that lacks the characteristic heteroandrous morphology of the genus *Cavendishia* and of the entire HtAP clade. Besides sharing free stamens, there are no other apparent morphological characters that satisfactorily explain the placement of *T. jahnii* within this clade

Cavendishia has approximately 130 species, most of which are native/endemic to Colombia. The 15 species of *Cavendishia* here analyzed include representatives from the two currently recognized subgenera of *Cavendishia*: *Chalmydantha* and *Cavendishia*, as well as of four of the five sections of subgenus *Cavendishia* (*Forereoa* is missing), all but one of the series of section *Cavendishia* (*Uniflorae* is missing), and all but series *Lactiviscidae* of section *Engleriana* (see Table 1). Unfortunately, none of the subgenera, sections, or series of *Cavendishia* is resolved as monophyletic. However, it must be cautioned that the phylogenetic relationships recovered within *Cavendishia* are too poorly supported to draw strong conclusions and a more extended taxonomic/molecular sampling of it is needed.

From a more general point of view, taxa present in Central America have a more derived position, but unlike *Satyria s.s.* in which Central American species are clustered together, in *Cavendishia* the Central American species are dispersed throughout the clade [*C. lindauiana* Hoerold, *C. quereme* (Kunth) Benth. & Hook. f., *C. pubescens* (Kunth) Hemsl., *C. capitulata* Donn.Sm., *C. bracteata* Ruiz & Pav. ex J.St.-Hil.].

HmCP clade

The relationships recovered for this clade (Fig. 1) are consistent with those found by Pedraza-Peñalosa et al. (2013). Taxa in this clade all have equal stamens and their pedicels are continuous with the calyx, unlike the HtAP clade, the sister group. That being said, the sampled species of *Demosthenesia* A.C.Sm. have slightly unequal filaments, but not as markedly as in the HtAP clade.

The HmCP clade unites groups with diverse morphologies. The only monophyletic genera within it are relatively small (up to 12 spp.) and have contrasting geographic patterns: *Anthopterus* is widely distributed in the neotropics, while *Pellegrinia* and *Demosthenesia* are both endemic to a small area of the Peruvian and Bolivian Andes (Fig. 1). However, many subclades within HmCP are well supported and the two largest stand out. The four species of the *Anthopterus revolutus*–*Thibaudia floribunda* clade (77% bootstrap) have in common winged or angulate calyces and corollas, whereas the seven species of the *Diogenesia alstoniana*–*Demosthenesia spectabilis* clade (96% bootstrap) in contrast all have terete calyces and corollas.

Only one species of *Themistoclesia* Klotzsch was included in this analysis. However, *Themistoclesia* with articulate calyces have recently been described, but unfortunately, none of them was available for sequencing. These taxa also have other characteristics not previously thought to occur in the genus and it has been hypothesized they may represent a geographically and morphologically distinct clade (Pedraza-Peñalosa and Luteyn 2010). Thus, future analyses should sample in more detail the morphological diversity of *Themistoclesia*, as well as that of other members of the HmCP clade.

Thibaudia p.p. clade

All species in the *Thibaudia p.p.* clade have pedicels articulated with the calyx; it is precisely the presence of such articulation that initially defined *Thibaudia* section *Eurygania*, currently a synonym of *Thibaudia*. However, the staminal characters that seem to be important in defining other larger clades are absent here. This analysis supports Powell and Kron's (2003) assessment that species of *Satyria* in this clade, all endemic to S Peru and N Bolivia, should be segregated from *Satyria s.s.* (Fig. 1). The anther tubules of these *Satyria* do not diverge much distally, their sides being more parallel, and their tips lack ornamentations, so differing from *Satyria s.s.* (Powell 2005). The *Thibaudia* and *Satyria* species that cluster together all have equal or slightly unequal stamens and connate filaments.

On the other hand, although the *T. macrocalyx*–*T. pachyantha* subclade (74% bootstrap) also includes species with equal stamens, their filaments are free. Other characters that are alos shared by some of the members of the *Thibaudia p.p.* are thick corolla and calyx limb, anthers with poor distinction between tubules and thecae, thecae papillose and dehiscence by ventral clefts.

Psammisia–*Ceratostema*–*Macleania* clade

Psammisia s.l. contains species with terete to winged calyces; fused, free or coherent staminal filaments; short to long corollas; and pinnate or plinerved laminas. It also includes perhaps the greatest variety of corolla shapes of any neotropical Vaccinieae (tubular, obconic, urceolate, turbinate and depressed, hemispheric); and also a great variety of corolla colors (yellow, magenta, vermilion, dark wine, red, white, green, etc.) and color combinations (solid, bicolor, multicolor).

The unifying staminal features of *Psammisia s.l.* include stout anthers, free tubules, and connectives, the region where filaments adhere to the anthers, that are 2-spurred, alternately spurred (i.e. only one staminal cycle is spurred), or rarely unspurred. It is precisely because of the presence of spurs that Smith (1932) linked *Psammisia* to a group of *Macleania* whose connectives are faintly thickened distally. These thickened connectives were interpreted as a step toward the spurred condition observed in some *Psammisia s.l.* A morphological connection between members of *Psammisia* and *Macleania* is suggested by these results, as *Psammisia s.l.* is resolved in two clades, one of them sister to *Macleania*. However, the morphological basis of this relationship it is not yet known. As for the second grouping of *Psammisia s.l.*, it is part of a more basal tritomy. Unfortunately, because taxon sampling is still inadequate and the type species of the genus was not available for sequencing, it is uncertain which *Psammisia* clade will retain the name.

Psammisia I clade

Most of the sampled *Psammisia s.l.* are found within the *Psammisia I* clade (*P. grandiflora–P. pedunculata*, < 50% bootstrap), which is dominated by species from the N Andes (Fig. 1). *Psammisia dolichopoda* A.C.Sm. is the only species that is also present in Central America. However, ongoing studies suggest that it has considerable morphological variation and may represent more than one species (Pedraza-Peñalosa pers. obs.).

Two of the new species from LONP are placed here, within a clade (77% bootstrap) dominated by Colombian taxa; the only exception is the rare *Psammisia oreogenes* Sleumer, which was earlier thought to be exclusive to Ecuador but is now known to also occur in the Colombian portion of the Chocó biogeographic region (Fig. 1). The new species from LONP portray morphological characters that are either unusual in *Psammisia s.l.* (e.g., *P.* sp. nov. 1 has large leaves with pinnate venation) or previously unknown (i.e., *P.* sp. nov. 2 is the only known taxon with pseudoverticillate leaves). In general, the novel taxa are morphologically different and molecular sequence data indicate they are not immediately related.

It is difficult to find unifying morphological characters for *Psammisia I*. Moreover, the clade lacks support and has a tritomy at its base. Within it, only the *P.* sp. nov. 1–*P.* sp. nov. 2 subclade has moderate support (77% bootstrap). All its species share chartaceous to subcoriaceous leaves, pinnate venation, racemes with short rachises typically less than 1.6 cm long making the inflorescences look fasciculate, and medium sized corollas 8–22 mm long.

Psammisia II

Sequence data shows that *Psammisia* II taxa are more closely related to *Macleania* than to other congeneric species (Fig. 1). Unifying characteristics of the *Psammisia* II group comprise coriaceous leaves, plinerved venation, racemes with usually conspicuous rachises (1–26 cm long), and long corollas (17–40 mm). The inclusion of *Thibaudia inflata* within *Psammisia* II in a relatively derived position, deserves further scrutiny as its pedicel and calyx are continuous, whereas in most *Macleania*, and in all *Psammisia s.l.* it is articulated.

Furthermore, other morphological features seem to also help to differentiate between the *Psammisia* I and II clades. The leaves of *Psammisia* II have laminar glands at the base of the abaxial side, while the leaves of *Psammisia* I do not have basal glands, or when laminar glands are present, they are then spread through the entire abaxial surface (e.g., *P. sodiroi*, see Pedraza-Peñalosa et al. 2013). Anther morphology also seems to be helpful, with *Psammisia* II possessing well-developed tubules of a diameter similar to that of the theca, while in *Psammisia* I tubules are smaller and narrower, of a basal diameter only a fraction of the theca width.

Macleania clade

Macleania is sister to *Psammisia* II and there is good support for this clade and this relationship; the former clade includes *M. floridunda* Hook., the type species of the genus (Fig. 1). Because of its morphological range, Smith (1932) considered *Macleania* a coherent genus from which other genera were in the process of being derived. However, the subgenera *Aponema* and *Macleania*, which were thought to be morphologically well delimited, are not monophyletic. Moreover, although most sampled *Ceratostema* form a clade (but unsupported) placed within the basal tritomy of the *Psammisia–Ceratostema–Macleania* clade, *C. reginaldii* is resolved within *Macleania*.

As for *Ceratostema*, although as currently circumscribed is morphologically recognizable, it is not monophyletic and the sampled species fail to form a well supported clade. *Ceratostema* was one of the first genera to be erected, and because Ericaceae is a predominantly montane group with a high number of endemics, it is not difficult to imagine the challenges earlier taxonomists faced to procure sufficient specimens for their studies. Limited collections and field observations led to problematic generic classifications. Consequently, not only many species have been transferred out of *Ceratostema*, but also entire genera have been segregated from within it such as *Demosthenesia* and *Pellegrinia*. Both genera are here resolved as monophyletic and not closely related to any sampled *Ceratostema*. Unfortunately, both taxon (16 out of ca. 75 spp.) and molecular sampling are still insufficient to better discern the evolutionary relationships between *Macleania* and *Ceratostema*.

Conclusions

With the study of the undersampled Colombian taxa, a critical component of neotropical Vaccinieae, a more complete picture of the complexity of the phylogenetic relationships within the Andean Vaccinieae has emerged.

The molecular results suggest that the observed diversity of neotropical Vaccinieae is mostly due to the diversification of several clades of Andean origin that do not necessarily correspond to the current taxonomic classification. Several genera that have been traditionally broadly defined are resolved as non-monophyletic and it seems likely they could be further split into more discrete groups. All this points to the need for broad-scale comparative anatomical and morphological studies to reevaluate homologies, synapomorphies and clade support in general.

Indeed, although a cladistic analysis of morphological characters is premature at this point, it was still possible to identify morphological characters that seem to differentiate among some major clades and subclades. Most notable are the HtAP and HmCP clades, both strongly supported molecularly and easily diagnosable morphologically – they reflect the diversity of arrangements and morphologies of the stamens and flowers of Vaccinieae. However, although morphological characters may diagnose clades in one part of the tree, they may vary within a clade in another part of the tree. Such is the case of the fusion of staminal filaments, a character diagnostic for *Satyria s.s.*, the HmCP, and *Cavendishia* clades, but which is variable within the well-supported *Macleania* clade.

This analysis unequivocally places the newly discovered Colombian Vaccinieae within *Satyria s.s.* and the *Psammisia* I clade, 2 species in each clade, but not closely related to each other within their respective clades.

The small *Satyria s.s.* is a complex genus with species limits that are hard to elucidate. It is now clear that many morphological characters previously thought to differentiate species, especially those based on the scant voucher specimens available to earlier workers, do not work in the light of today's better documented intraspecific variation. Molecular results suggest that continuous characters (i.e., size) include informative data and can be used to distinguish species. Fieldwork in LONP suggests that characters that are not reported in herbarium labels and that cannot be recognized in herbarium specimens may be useful to work out species hard to differentiate (i.e. tridimensional shape of calyx, corolla, fruits, seed and embryo color) and these characters need to be reported on a regular basis.

Taxon sampling was nearly doubled in this analysis when compared to previous studies dealing with Andean species and robust monophyletic groups such as, *Anthopterus*, *Demosthenesia*, *Gonocalyx*, *Pellegrinia*, and *Satyria s.s.*, were identified within the Andean clade, although admittedly the first four genera included only two species each. However, *Gonocalyx*, present in both Central and South America, may be of Mesoamerican origin. Clearly, more exhaustive analyses are necessary to fully resolve intergeneric relationships, and even the monophyletic groups here discerned (with exception of *Satyria s.s.*) need better representation. Further phylogenetic work is obviously needed for the large and non-monophyletic *Psammisia s.l.*, *Macleania*, *Thibaudia s.l.* and *Ceratostema*, accompanied of field and herbarium work.

Lastly, it is also important to increase the representation of Central American species in order to further explore diversification and colonization of that region. In these results, there is evidence of multiple dispersals of Andean Vaccinieae to Central America and of at least one radiation within Central America (Central American *Satyria s.s.*) of a genus of Andean origin.

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RESEARCH ARTICLE

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New blueberry and *mortiño* relatives (Ericaceae) from northwestern Colombia

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Abstract

The inventory of the vascular plants of one of the richest and least studied floras, the Andean and Chocó regions of northwestern Colombia, targets Las Orquídeas National Park. As a result of field trips to areas never before collected, several epiphytic and small terrestrial shrubs in the family Ericaceae have been discovered in the Park's humid forests. Five new, morphologically remarkable species of Ericaceae (tribe Vaccinieae), are here described and illustrated. In a separate phylogenetic analysis, *Psammisia pinnata* Pedraza, *P. pseudoverticillata* Pedraza, *Satyria orquidiensis* Pedraza, and *S. pterocalyx* Pedraza, were placed by molecular sequence data within clades of the non-monophyletic genera *Psammisia* and *Satyria*; phylogenetic evidence for the placement of *P. sophiae* Pedraza is still lacking. Their affinities are here discussed, along with their preliminary conservation status.

Resumen

El inventario florístico de las plantas vasculares de una de las floras más ricas y menos estudiadas, los Andes y Chocó del noroccidente colombiano, se centra en el Parque Nacional Natural Las Orquídeas. Como resultado de trabajo de campo en áreas del parque nunca antes colectadas, se han descubierto varias especies epífitas y arbustivas de la familia Ericaceae, las cuales habitan los bosques húmedos de la reserva. Cinco nuevas especies de Ericaceae (tribu Vaccinieae), con peculiar morfología, son acá descritas e ilustradas. En un análisis filogenético separado y basado en datos moleculares, *Psammisia pinnata* Pedraza, *P. pseudoverticillata* Pedraza, *Satyria orquidiensis* Pedraza, y *S. pterocalyx* Pedraza, fueron asignadas a clados de los géneros no monofiléticos *Psammisia* y *Satyria*; para la asignación de *P. sophiae* Pedraza no hay evidencia filogenética. Tanto las afinidades, como el estado preliminar de conservación de las nuevas especies, son acá discutidos.

Keywords

Psammisia, *Satyria*, Vaccinieae, Chocó biogeographic region, Tropical Andes, Las Orquídeas National Park

Introduction

The Colombian Western Cordillera and adjacent Chocó region, which belong to the Tropical Andes and Chocó biodiversity hotspots (Mittermeier et al. 1998, Myers et al. 2000), respectively, have the highest angiosperm diversity in N South America (Morawetz and Raedig 2007). Despite their importance, entire lineages endemic to or particularly rich in western Colombia are missing in monographic and phylogenetic works, as collections from this region have not been readily accessible, especially outside of the country. This unfortunate situation has silently weakened the scope of botanical research, while also undermining strategic planning for conservation and development in the Tropical Andes and the Chocó biogeographic regions, the world's first and fifth priority areas for conservation (Churchill et al. 1995, Mittermeier et al. 1998, Mast et al. 1999, Myers et al. 2000, Orme et al. 2005).

To bring attention back to one of the richest and least studied floras, an inventory of the vascular plants of Las Orquídeas National Park (LONP) was undertaken. LONP is strategically located in the confluence of the Tropical Andes and Chocó, in the Department of Antioquia (Colombia). Nested in the western slope of the Western Cordillera, LONP (29,118 ha; practically the same size of Grenada) boast an enormous altitudinal gradient (ca. 300–3,450 m) and consequent range of vegetation. In general, the forests below 2,000 m are considered to be part of the Chocó phytogeographic region (Rangel-Ch. et al. 2004) while the remainder is Andean.

The ongoing inventory of the vascular plants of LONP particularly targets remote areas that have never been botanically explored before. In addition to trees, collecting is also focused on non-tree plants, especially those that are epiphytic and which are usually omitted from rapid floristic and vegetation assessments in the tropics. This holistic collecting strategy has resulted in the discovery of several new non-tree plant species, including five members of the family Ericaceae, all placed in the berry producing tribe Vaccinieae. These five new species are all restricted to the Colombian Western Cordillera and Chocó biogeographic region, and three of them are endemic to LONP. The new species are here described, illustrated, and discussed. Their preliminary conservation status is also included, based on the author's field experience and knowledge of Colombian herbarium collections worldwide.

Vaccinieae diversity in Colombia

Although Vaccinieae is geographically widespread, the greatest species diversity lies in the mountains of Papua New Guinea and the Neotropics, most prominently in the N Andes. In the Neotropics, there are 46 putative genera and more than 800 species of

Ericaceae and the great majority belong to the inferior-ovaried tribe Vaccinieae (Luteyn 2002); actually, 27 genera are native to the Neotropics and all are Vaccinieae. The members of Vaccinieae are better known by the edible and commercially important blueberry, from North America, and the *mortiño* [*Vaccinium floribundum* Kunth], from South America.

In the Neotropics, the most extensive radiation of Ericaceae took place in Colombia with 24 genera and 278 species documented, that is ca. 35 % of the neotropical Ericaceae. Notably, about 55 % of the Colombian species are endemic to the country (Pedraza-Peñalosa unpubl.). Within Colombia, the greatest diversity is found in Antioquia, where 18 genera and at least 116 species were recently documented (Pedraza 2011), before the discovery of the five new species from LONP here described. Although Colombia contains already described hyper-diversity, its Ericaceae flora still remains poorly known, with many suspected undescribed species from sea level to the páramo.

Placement and phylogenetic affinities of new species

The taxonomic placement of new Vaccinieae is difficult due to the striking disparity between generic-level phylogenetic relationships and current classification systems (Kron et al. 2002, Powell and Kron 2003, Pedraza-Peñalosa 2009, 2010). Therefore, to determine the generic placement of the new species, four were included in a comprehensive phylogenetic analysis of neotropical Vaccinieae, based on chloroplast and nuclear sequence data of 91 species (Pedraza-Peñalosa et al. 2015). Unfortunately, amplifications of the fifth new species (*Psammisia sophiae* Pedraza), which bears the most complex corolla structure, were not successful.

The molecular dataset was particularly rich in species of *Satyria* Klotzsch and *Psammisia* Klotzsch, both non-monophyletic and broadly defined groups, to which the five new species are initially assigned based on their overall morphology (Pedraza-Penalosa et al. 2015). However, the new species possess unusual characters for the genera in which they are provisionally placed: *P. sophiae* has a corolla morphology unique among neotropical Vaccinieae; *P. pinnata* Pedraza is among the few *Psammisia* s.l. with very large and pinnate leaves; *P. pseudoverticillata* Pedraza is the only species in the group with clustered leaves and one of the few with markedly angled calyces; *S. orquidiensis* Pedraza is the only species in the group with clustered leaves, while its calyx ribs and constrictions makes it one of two species of *Satyria* s.l. with ornamented calyces; and lastly, *S. pterocalyx* Pedraza is the only other species in the group with ornamented calyx and apparently the only one with a corolla throat both dramatically constricted and elongated into a tube.

Eighteen out ca. 24 currently recognized species of *Satyria* s.l. were analyzed. The resulting best ML tree unequivocally placed the two new species described here, *S. orquidiensis* and *S. pterocalyx*, within a group that comprises *Satyria* s.s. (Pedraza-Peñalosa et al. 2015). Despite the fact that *S. orquidiensis* and *S. pterocalyx* are endemic to the same region, have similar corolla colors, and are the only *Satyria* s.s. known to have an ornamented calyx (winged and/or lobed), they are not closely related to each other.

The non-monophyletic *Psammisia* was split in the molecular analysis (Pedraza-Peñalosa et al. 2015). The largest of the groupings, *Psammisia* I clade, was dominated by species from the northern Andes. *Psammisia pinnata* and *P. pseudoverticillata* were both placed within one of its subclades, one mostly composed of Colombian species. All the species in this subclade share chartaceous to subcoriaceous leaves with pinnate venation (the majority of *Psammisia* have plinerved and coriaceous leaves) and short racemes with a rachis typically less than 1.6 cm long, which give inflorescences a fasciculated appearance, their corollas are medium size (8–22 mm long). However, the molecular sequence data show that the newly described *Psammisia* are not closely related.

Unfortunately, at this time it is not known which clade in the *Psammisia* complex will retain the generic name, as *P. falcata* (Kunth) Klotzsch, the type species of the genus has not been sequenced yet. Thus, taxonomic and nomenclatural changes in *Psammisia* s.l. are anticipated. Moreover, because only 14 out of about 70 spp. of *Psammisia* species were analyzed, a broader sampling of the group and related genera is needed to better infer the relationships of the new species described here. Names are coined here in order that they may be used in future studies both of phylogeny and conservation of Colombian plants.

New species from Las Orquídeas National Park (Colombia)

***Psammisia pinnata* Pedraza, sp. nov.**

urn:lsid:ipni.org:names:77146695-1
Figures 1–3

Diagnosis. *Psammisia pinnata* stands out among all other *Psammisia* s.l. because its distinctive large leaves (among the largest in the genus) that are subcoriaceous to chartaceous, elliptic to oblong, sometimes slightly asymmetrical, and which have pinnate venation; its petioles are pulvinate. Also distinctive is its ridged bark and conspicuous raceme rachises, and the relatively long flowers with staminal filaments fused at their very base.

Type. COLOMBIA. Antioquia: Municipio Urrao. Corregimiento La Encarnación, Parque Nacional Natural Las Orquídeas, camino entre el páramo del Almorzadero y la cabaña de Calles, [6°31'N; 76°15'W. 1400 m], 31 Jul 2011 (fl, fr) *P. Pedraza-Peñalosa, J. Betancur, M. F. González, R. Arévalo, D. Sanín, A. Zuluaga, A. Duque & J. Serna 2491* (holotype: COL!; isotypes: HUA!, E!, MO!, NY! [NY02058401]).

Description. Terrestrial or epiphyte *shrubs*, more or less erect or with arching branches, 1.5 m tall; stems brown-black, ridged or subterete, with soft and small grooves twisting near nodes, glabrous, pith drying dark purple, most terminal branches usually hollow, and, at least in one occasion, inhabited by ants; twigs with a few deep ridges running lengthwise and often twisting near nodes, glabrous. Axillary buds compressed; prophylls 2, inconspicuous, valvate, ovate, 1.5–2 mm long, margin ciliolate, the hairs unicellular and eglandular (all indumentum composed of this type of hairs except when indicated), apex acute, glabrous. *Leaves* alternate; petiole subterete, thick and basally pulvinate, 1–2.8 cm long, glabrous; lamina subcoriaceous to chartaceous, elliptic to oblong, sometimes slightly asymmetrical (more evident in large leaves), (19–)23–45 × (5–)8.7–22 cm, base cuneate to sometimes nearly truncate, margin entire and eciliate except for the very young leaves with a handful of caducous apical hairs, apex (long or short) acuminate, glabrate with caducous hairs on both sides, adaxial hairs inconspicuous (< 0.5 mm long), abaxial hairs often affixed atop of what seem to be minute laminar glands; laminar glands only evident abaxially, drying black, sparse, small, and round; venation pinnate, with up to 5 visible orders in dry specimens, 8–11 secondaries per side, these alternate (rarely subopposite), evenly dispersed along the lamina, ascending, brochidodromous, intersecondaries present toward midsection, midrib and secondaries adaxially impressed and abaxially raised, tertiaries well marked (in mature leaves), parallel among themselves and inserted at ca. 80–90° with respect to midrib. *Inflorescence* an axillary, solitary, 5–11-flowered raceme, often cauliflorous; inflorescence bracts caducous, chartaceous, ovate, 1.2–1.8 × 1.7–3 mm, margin entire and eciliate, apex obtuse, glabrous on both sides, venation obscure; rachis pink or magenta (fuchsia), 9–16 mm long, glabrous; floral bract 1, persistent, chartaceous, white, ovate, 1–3 × 1.5–2.5 mm, margin entire and eciliate, apex obtuse to acute, glabrous on both sides, venation obscure; pedicel pink or magenta (fuchsia), articulated with calyx, 9–23 mm long, glabrous; bracteoles 2, persistent, medially to distally inserted, opposite, chartaceous, white, ovate, 1.3–1.6 × 1–1.2 mm, margin entire and eciliate and with one or two pairs of stout masses of fimbria, apparently glandular in nature, easily breakable, apex acute, glabrous on both sides, venation obscure. *Flowers* 5-merous, actinomorphic, diplostemonous. Calyx pink or magenta, the lobes whitish with black marginal glands, cupuliform and sometimes slightly flaring out apically (urceolate *in vivo*), 6–8.5 mm long, glabrous; tube cupuliform, terete, ca. 3.5 mm long; limb spreading when dry (erect *in vivo*), 3–4 mm long; lobes ovate, 1–1.8 × 2–3.5 mm long, glandular margin on each side of the lobe (excluding the apex) sometimes breaking into stout segments of fusing glandular fimbria (sensu Luteyn 1983), margin eciliate, apex acute; sinuses obtuse (U-shaped); aestivation unknown. Corolla white (in bud basally pink and distally white), fleshy, not bistratose, conic, terete, 17–22 mm long, ca. 4.5 mm diam., ca. 2.5 mm wide at throat, glabrous within and without; lobes ovate, 1.2–1.3 × 1.4–1.5 mm, apex acute; aestivation valvate. *Stamens* 10, equal (though one cycle very slightly shorter than the other by < 0.5 mm), 7–9 mm long, included, not adherent to corolla; filaments connate in basal 0.3–1.5 mm, 3–4.7 mm long, glabrous, marginally glabrous or glabrate, the hairs inconspicuous, ca. 0.1 mm long; anthers 7–8 mm long, connective spurless; thecae 4.5–5 mm long, prognathous, without basal appendage, papillate; tubules 2, free, straight, basally similar in width to thecae, 2.2–3 mm long, smooth, dehiscing by introrse slits almost as long as the tubules, 2.2–2.7 mm long. *Ovary* 5-locular; nectary not pulvinate, top of ovary flat or concave; style 17–20 mm long, included; stigma punctiform. *Berry* ca. 12 mm diam., turning green with age, the lobes yellowish and converging.

Figure 1. Illustration of *Psammisia pinnata*. **A** Branches with leaves and inflorescences; general aspect of the plant **B** Close-up of leaves with detail of hairs **C** Branch with inflorescences and flowers at and post anthesis **D** Immature inflorescence with floral buds **E** Immature flower with pedicel **F** Calyx post-anthesis **G** Stamens in lateral, abaxial, adaxial and views. [Drawn from the type and *P. Pedraza-Peñalosa et al. 2015*.]

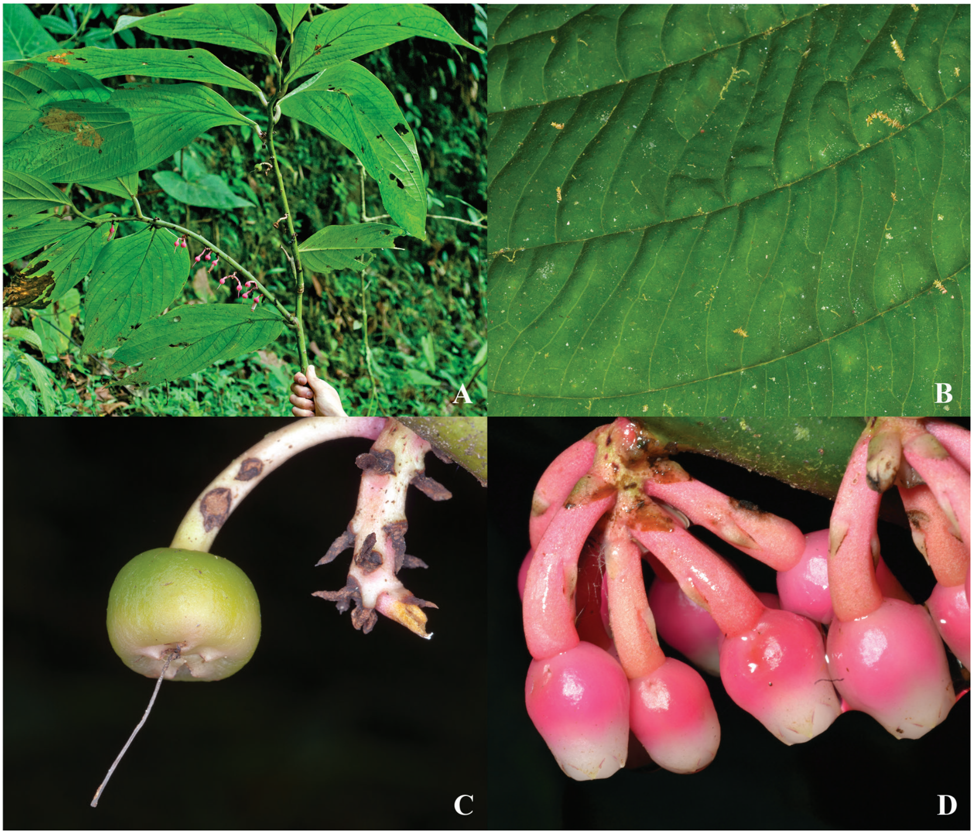

Figure 2. *Psammisia pinnata*. **A** Branches with leaves and inflorescences **B** Adaxial detail of leaf venation **C** Immature fruit attached to inflorescence axis **D** Floral buds, lateral view. [Photos by P. Pedraza-Peñalosa (**A–C**) and Nelson R. Salinas (**D**).]

Distribution and ecology. *Psammisia pinnata* is restricted to the rich humid premontane and montane forests of the Colombian Western Cordillera (Antioquia, Risaralda, and Valle del Cauca) where it is known to flower and fruit in January, April, and July. It grows at 950–1900 m.

Etymology. The species name indicates the characteristic pinnate leaf venation.

Preliminary conservation status. *Psammisia pinnata* occupies a large geographic area and ample altitudinal range, therefore there is no concern for its conservation status. However, it must be noted that Colombian Andes have alarming rates of deforestation and transformation, putting its natural vegetation under constant threat.

Discussion. *Psammisia pinnata* is perhaps morphologically close to *P. multijuga* Sleumer although it is clearly differentiable because of the soft bark grooves that twist near the nodes (vs. bark smooth in *P. multijuga*); dark purple branch pith (vs. white pith); elliptic to oblong (vs. ovate), apically acuminate (vs. abruptly acuminate [subcuspidato-acuminata]), and glabrous (vs. with inconspicuous hairs on both sides) leaves; black laminar glands evident (but small) abaxially (vs. few and inconspicuous);

Figure 3. *Psammisia pinnata*. **A** Immature inflorescences and abaxial side of leaf **B** Immature flowers. [Photos by P. Pedraza-Peñalosa (**A**) and Nelson R. Salinas (**B**).]

well-marked (abaxially) parallel tertiary venation, distinctively inserted at ca. 80–90° with respect to midrib (vs. not well-marked and reticulated); larger and fuller racemes with 5–11 flowers and rachises 9–16 mm long (vs. 2-flowered racemes and 2–4 mm long rachises [4–5-flowered fascicle in the protologue of *P. multijuga*]); glabrous calyces (vs. inconspicuously puberulous, the hairs eglandular and <0.5 mm long [glabrous in the protologue of *P. multijuga*]), with lobes with glandular margins (vs. eglandular); longer corollas (17–22 vs. 15 mm); basally connate staminal filaments, 3–4.7 mm long (vs. free, 2–2.5 mm long); tubules 2.2–3 mm long, dehiscing by slits almost as long as the tubules (vs. tubules 4.3–4.6 mm long, dehiscing by short slits 1.5 mm long).

Specimens examined. COLOMBIA. Antioquia: Municipio Urrao, Corregimiento La Encarnación, Vereda Calles, Parque Nacional Natural Las Orquídeas, finca de Alfonso Pino, entre la divisoria de las quebradas La Virola y El Bosque, al NW de la cabaña Calles, 6°31'35"N; 76°15'50"W, 1450–1470 m, 27 Jan 2011 (fl, fr), *P. Pedraza-Peñalosa et al. 2015* [COL! (2 sheets), HUA, MO, NY! (2 sheets)]; Parque Nacional Natural Las Orquídeas, sector Calles arriba, sitio El Macho, 6°32'22"N; 76°14'05"W, 1700–1750 m, 9 Dec 2013 (fl), *N. R. Salinas et al. 865* [COL, E!, HUA, LPB!, MO!, NY! (2 sheets)]; Near top of Cordillera Occidental on trail from Encarnación to Parque Nacional Natural Las Orquídeas, 1900–2100 m, 27 Jan 1979 (fl), *A. Gentry & A. Renteria 24641* (COL, MO!, NY!); Corregimiento Nutibara, region of Murrí, Nutibara-La Blanquita road, 1700–1800 m, 19 Apr 1988 (fl. buds), *J. L. Luteyn et al. 12002* (AAU, COL, HUA, MO, NY!), 950–1380 m, 20 Apr 1988 (fl. buds), *J. L. Luteyn et al. 12110* (COL, NY!). **Risaralda:** Municipio Mistrató, Inspección de Policia de Jeguadas, camino entre Jeguadas y Puerto de Oro, entre los sitios Curramaí y Pisones, 1200–1500 m, 3 Abr 1992 (fr), *J. Betancur et al. 3312* (COL, NY!). **Valle del Cauca:** Municipio Cali, Finca Zingara, km 18 de la carretera Cali-Buenaventura, km. 4 vía Dapa, Corregimiento La Elvira, 1900 m, 2 Abr 2000 (fl), *J. Giraldo-Gensini 903* (NY!).

***Psammisia pseudoverticillata* Pedraza, sp. nov.**
urn:lsid:ipni.org:names:77146696-1
Figures 4–6

Diagnosis. *Psammisia pseudoverticillata* can be easily differentiated from all other *Psammisia* s.l. by its leaves, which are clustered and seemingly verticillate, chartaceous, large, obovate, bullate *in vivo*, pinnate, decurrent at the base, and subtended by a basally pulvinated petiole. Its congested racemes bear flowers that are distinctive because of their large size, thickness and fleshiness; however, it must be noted that the flowers of this new species shrink significantly upon drying. The flowers of *P. pseudoverticillata* are also characterized by its color combination and angled calyces and corollas (calyces markedly angled).

Type. COLOMBIA. Antioquia: Municipio Urrao. Corregimiento La Encarnación, Vereda Calles, Parque Nacional Natural Las Orquídeas, camino Calles-La Encarnación, después de la confluencia del Río Polo y el Río Calles, antes del Río San Pedro, sitio La Quiebra, 6°30'31"N; 76°14'W, 1600–1850 m, 31 Jan–2 Feb 2011 (fl), *P. Pedraza-Peñalosa, J. Betancur, M. F. González, G. Giraldo, F. Gómez, A. Duque & J. Serna 2134* (holotype: COL!; isotypes: HUA!, NY! [NY02058402]).

Description. Terrestrial *shrubs* with arching branches, < 1 m tall; stems and twigs somehow flatten, caniculated lengthwise, apparently glabrous, the hairs inconspicuous (< 0.1 mm long), unicellular and eglandular (= minute hair type), bark brown and smooth. Axillary buds not observed. *Leaves* alternate, originated very close together, pseudoverticillate with clusters of 3–5 leaves separated by leafless sections several centimeters long; petiole caniculate, basally pulvinate, 4–12 mm long, glabrate, minute type of hair; lamina chartaceous, bullate *in vivo*, obovate, (17.5–)20.5–24 × (6.5–)12–14.2 cm (at least 24 cm long, apices incomplete), base attenuate and decurrent, margin entire and eciliate, apex missing in herbarium specimens but probably acuminate, glabrate on both sides, adaxially with caducous minute hairs, abaxially the hairs of arachnoid type, ca. 1 mm long, very thin, multicellular and eglandular; laminar glands absent; venation pinnate, with up to 4 orders visible adaxially in dry specimens, midrib adaxially impressed and abaxially raised, at least 9–11 secondaries per side, these alternate or subopposite, evenly dispersed along the lamina, ascending, adaxially flat and abaxially raised, brochidodromous, intersecondaries frequent. *Inflorescence* an axillary, solitary, 6–8-flowered raceme; inflorescence bracts, floral bract, and bracteoles alike, persistent, chartaceous, cream-reddish-colored, ovate, 1.6–1.8 ×

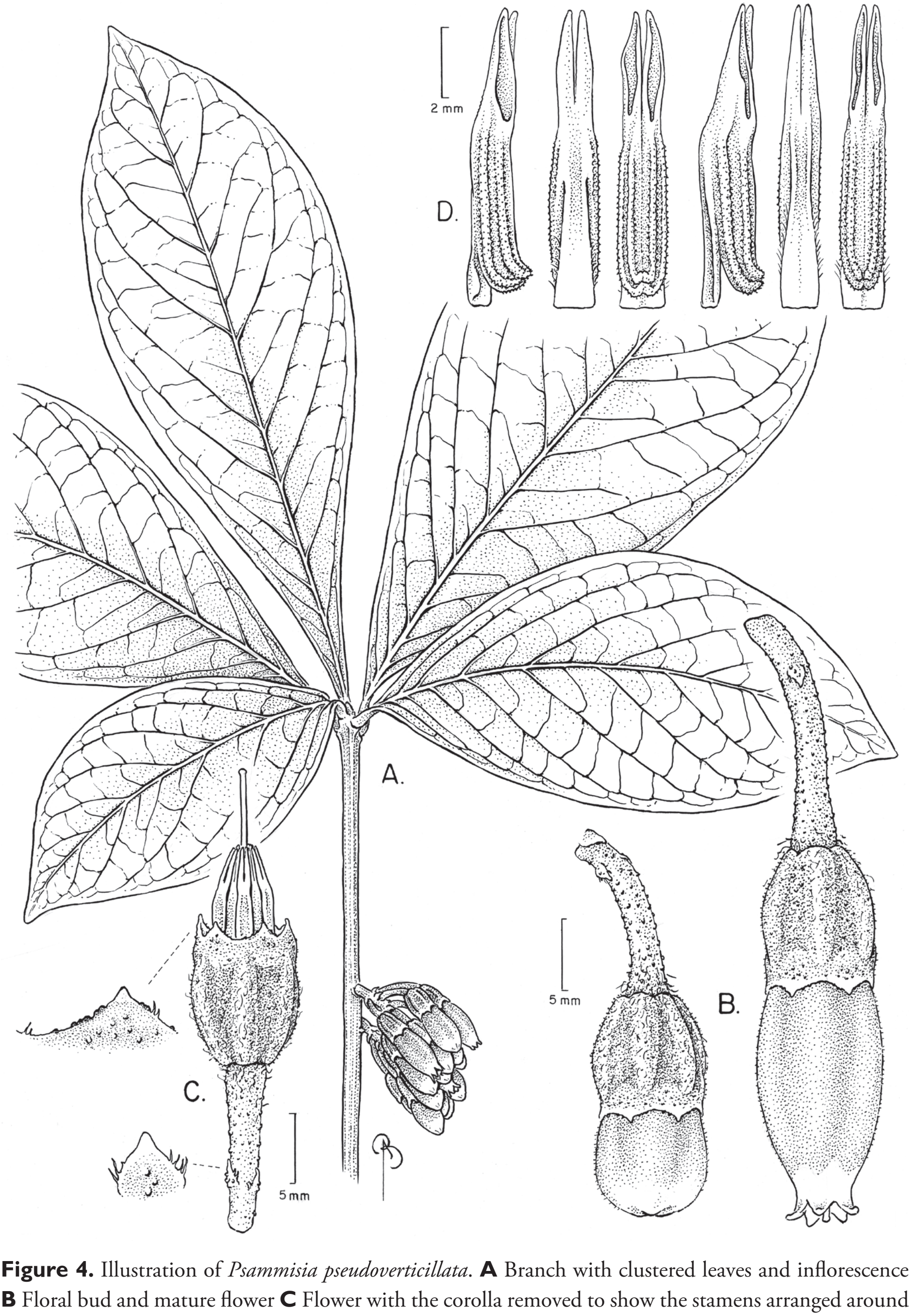

Figure 4. Illustration of *Psammisia pseudoverticillata*. **A** Branch with clustered leaves and inflorescence **B** Floral bud and mature flower **C** Flower with the corolla removed to show the stamens arranged around the style; details of the calyx lobes (above) and bracteoles (below) **D** Stamens in lateral, abaxial, adaxial and views. [Drawn from the holotype.]

Figure 5. *Psammisia pseudoverticillata*. **A** Clustered leaves **B** Inflorescences, side view. [Photos by P. Pedraza-Peñalosa.]

Figure 6. *Psammisia pseudoverticillata*. **A** Branch with leaves and inflorescences **B** Close up of flowers showing the angled calyces. [Photos by P. Pedraza-Peñalosa.]

1.5–2 mm, margin entire and inconspicuously ciliolate, the hairs of the minute type but a few are multicellular, apex obtuse or acute, glabrous on both sides, venation obscure, the bracteoles are different in having apex acute and more abundant marginal multicellular hairs that are fused in masses of fimbria toward the base; peduncle 4 mm long, rachis 5–10 mm long, both red-brown, glabrate, the hairs of the arachnoid type, also covered with minute, whitish warts *in vivo* (inconspicuous when dried, though imparting rough look); pedicel red-brown, articulate with calyx, 12–14 mm long (17 mm *in vivo*), with the same indumentum and warts of the rachis; bracteoles 2, basal, supopposite to alternate. *Flowers* 5-merous, actinomorphic, diplostemonous. Calyx red-brown, ellipsoid, 5-angled, the angles sharp and opposite to the sinuses, 8–9.2 mm long (10.5–11 mm *in vivo*), sparsely tomentulose with a combination of arachnoid and minute hair types, specially warty distally; tube ellipsoid, 6–7.4 mm long (8.5–9 mm *in vivo*); limb erect, 1.8–2 mm long; lobes deltate, 1 × 3.2 mm long, (1.5–1.7 × 4 mm *in vivo*), margin scariose (except at apex) and sometimes broken up in segments or with a few multicellular and eglandular hairs, apex acute; sinuses obtuse (U-shaped); aestivation unknown. Corolla dark pink with white throat and lobes, very fleshy, not bistratose, urceolate, 5-angled, 12–14 mm long (19 mm *in vivo*), 4–5.2 mm diam. (ca. 10 mm *in vivo*), 2.4–3 mm wide at throat (ca. 5 mm *in vivo*), puberulous without with a combination of arachnoid and minute hairs, the indumentum more abundant distally, glabrous within; lobes ovate, ca. 1.1 × 1.1 mm (ca. 2 × 2 mm *in vivo*), apex acute, reflexed at maturity; aestivation valvate. *Stamens* 10, equal, 8.7–9 mm long, included, not adherent to corolla; filaments free, long-triangular, 2.3–2.5 mm long, marginally glabrate, with minute hairs; anthers 8.3–8.5 mm long, connective spurless; thecae 4.1–4.5 mm long, slightly prognathous, without basal appendage, papillate; tubules 2, free, straight, 4–4.2 mm long, smooth, dehiscing by introrse slits, 2.7–3.5 mm long. Nectary not pulvinate, slightly concave *in vivo*, glabrous; style 15–17 mm long, included; stigma punctiform. *Berry* unknown.

Distribution and ecology. *Psammisia pseudoverticillata* is endemic to Antioquia (Colombia) and it is only known by the type specimen collected in Las Orquídeas National Park. It is known to flower in January and February. It grows in humid montane forests at 1600–1850 m.

Etymology. The species epithet refers to the clustered tendency of the leaves.

Preliminary conservation status. *Psammisia pseudoverticillata* it is only known by the type specimen collected in montane forests of Las Orquídeas National Park. Only one individual has been observed throughout several years of fieldwork. Currently, montane forest, and the park in general, suffer from degradation product of human activities (agriculture, selective logging, livestock), therefore I consider this species vulnerable due to the small area it occupies, its perceived scarcity, and current habitat threats.

Discussion. Apparently, *Psammisia pseudoverticillata* is the only in the genus with seemingly verticillate leaves; only *P. oppositiflora* Luteyn has opposite or subopposite leaves. *Psammisia pseudoverticillata* is morphologically closer to *P. orthoneura* but the latter is differentiated because of its evenly distributed glabrous leaves (vs. leaves clustered, glabrate with minute hairs in *P. pseudoverticillata*); obscurely articulate pedicels or apparently continuous with the calyx (vs. articulate); shorter (7–8 mm long), cupuliform, terete calyces (vs. 8–11 mm long, ellipsoid, with 5 well-defined angles); terete and shorter corollas (12–13 mm long vs. 5-angled, 12–19 mm long); and its staminal connectives with obsolete spurs (according to protologue) (vs. without spurs). A plant collected in La Serranía de los Paraguas (Valle del Cauca, Municipio El Cairo), where several Ericaceae novelties have recently been found (Pedraza-Peñalosa 2008), was identified by James L. Luteyn as *P.* aff. *orthoneura*. This specimen (*Luteyn 12330*) may belong to *P. pseudoverticillata*. However, the flowers are too immature to make an accurate identification given slight differences in leaf shape.

Psammisia sophiae Pedraza, sp. nov.

urn:lsid:ipni.org:names:77146697-1
Figures 7, 8

Diagnosis. *Psammisia sophiae* differs from other *Psammisia* s.l. because of its extraordinary flowers of complex morphology and unusual color combination. The distal half of the globose corolla has five pronounced projections or ribs, which in combination with the Christmas candy cane color pattern impart the species its distinctive and unique look.

Type. COLOMBIA. Antioquia: Municipio Urrao, Corregimiento La Encarnación, Parque Nacional Natural Las Orquídeas, camino entre el páramo del Almorzadero y la cabaña Calles, [6°31'N; 76°15'W, 1400 m alt], 31 Jul 2011 (fl), *P. Pedraza-Peñalosa, J. Betancur, M. F. González, R. Arévalo, D. Sanín, A. Zuluaga, A. Duque & J. Serna 2490* (holotype: COL!; isotype: NY! [NY02058403]).

Description. Terrestrial or epiphytic *shrubs*, more or less erect, 0.5–0.6 m tall; stems vinaceous and shiny, terete to subterete, glabrous, bark smooth; twigs subterete, glabrous. Axillary buds compressed; prophylls 2, inconspicuous, valvate, ovate, 1–1.2 mm long, margin eciliate, apex acute, glabrous. *Leaves* alternate; petiole caniculate (more so distally), pulvinate almost along entire length, 1.4–2.2 cm long, glabrous; lamina subcoriaceous, very smooth and flexible, elliptic, 19–34.5 × 4.5–12.5 cm, base attenuate and decurrent, margin entire and eciliate, apex acuminate, discolor *in vivo* with the abaxial side contrastingly light green, when dry the abaxial side is still lighter but with a dark marginal band, adaxially apparently glabrous, the hairs inconspicuous (< 0.5 mm long), unicellular and eglandular (all indumentum composed of this type of hair except when indicated), abaxially puberulous, the hairs with swollen bases that give them the aspect of minute punctuations; laminar glands absent; venation pinnate, with up to 3 visible orders in dry specimens, midrib adaxially raised and abaxially flat, 9–13 secondaries per side, these alternate or subopposite, evenly dispersed along the lamina, ascending, adaxially and abaxially slightly raised, brochidodromous. *Inflorescence* an axillary, solitary, 3–5-flowered raceme; inflorescence bracts, floral bract, and bracteoles alike, persistent, chartaceous, ovate, 1.2–1.4 × 1–1.5 mm, margin entire and eciliate, apex acute, glabrous on both sides, venation obscure; rachis magenta (fuchsia), 1.8–3 mm long, glabrous, a few inconspicuous warts at base; pedicel magenta (fuchsia), articulate with calyx, 7.5–13 mm long, glabrous although a few, small, glandular hairs at articulation; bracteoles 2, basal, opposite, only differing from other bracts in having an inconspicuous glandular margin. *Flowers* 5-merous, actinomorphic, diplostemonous. Calyx magenta (fuchsia) with the lobes whitish (more so in bud), cupuliform, 7.5–8 mm long

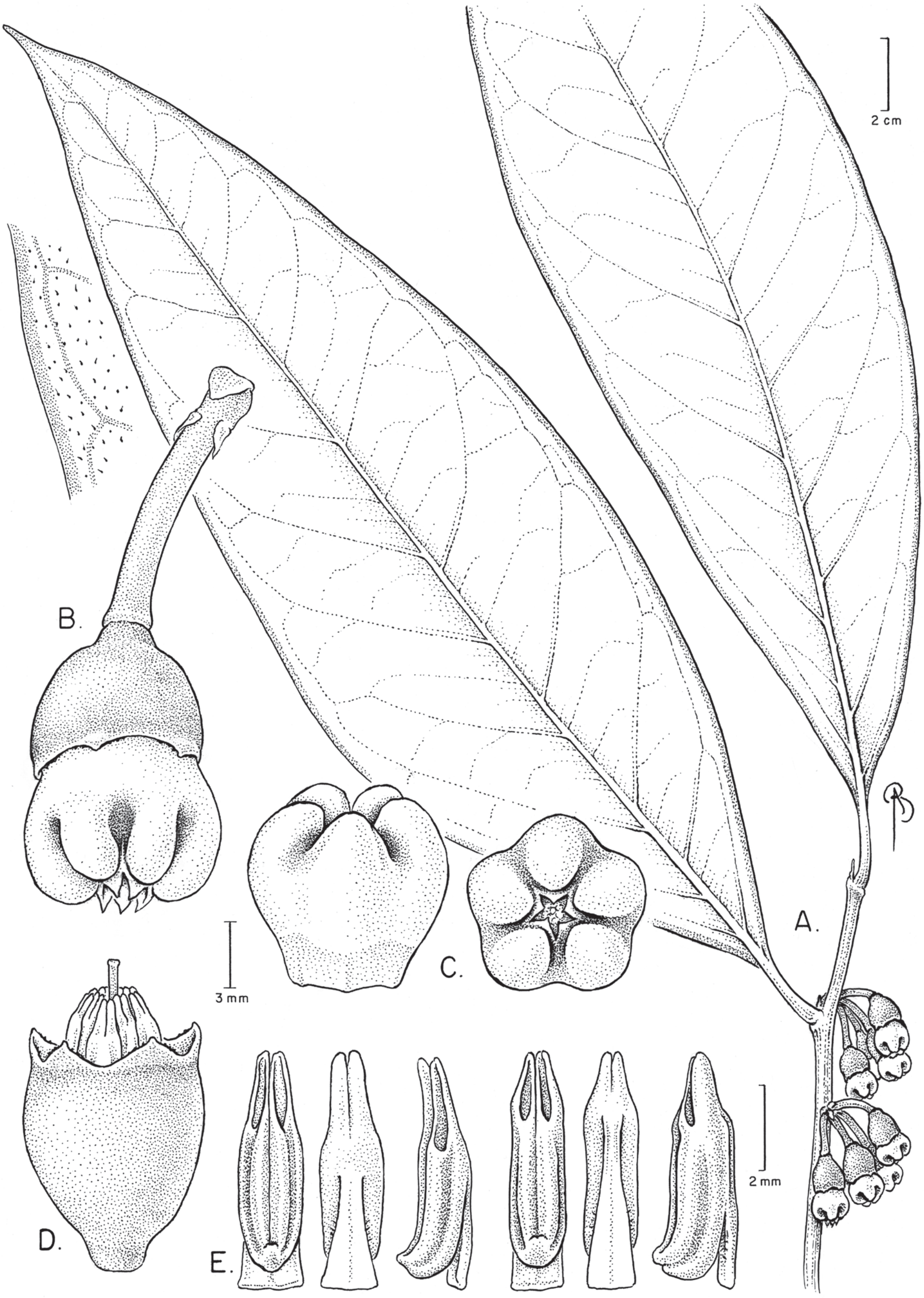

Figure 7. Illustration of *Psammisia sophiae*. **A** Branch with leaves, inflorescences and details of the darker colored leaf margin abaxially **B** Complete flower with pedicel and bracteoles **C** Lateral and top views of the corolla **D** Flower with the corolla removed to show the stamens arranged around the style **E** Stamens in abaxial, adaxial, and lateral views. [Drawn from the type.]

Figure 8. *Psammisia sophiae*. **A** Floral buds (top view) showing the distal ribs of the white corollas, which are magenta between the ribs **B** Top view of the inflorescence showing a flower at anthesis **C** Side view of the inflorescence showing a flower at anthesis **D** Branch with leaves, inflorescences and a detail of the pulvinate petioles. [Photos by P. Pedraza-Peñalosa.]

(10.5–11 mm *in vivo*), glabrous; tube cupuliform, terete, 5.5–5.8 mm long (7.8–8.5 mm *in vivo*); limb erect, 2–2.2 mm long (2–3.2 mm *in vivo*); lobes deltate, 1.1 × 2.5 mm long (1.2–1.5 × 3.5–4 mm *in vivo*), with a thin glandular margin (excluding apex and sinuses) that is inconspicuous in dry specimens, margin eciliate, apex blunt acute; sinuses obtuse (U-shaped); aestivation unknown. Corolla fleshy, not bistratose, globose (but wider in the apical half), basal half terete, apical half with 5 deep, wide and blunt ribs that surpass the corolla lobes by 1.5–2 mm and which slightly connivent distally, the ribs opposite to corolla lobes, 4 mm long, 2 mm wide; basic corolla color dull white but magenta between the ribs, from their bases up to the lobes sinuses, and continuing along the very margin of the lobes, the color pattern is such that when observed from the top, the corolla seem to have stripes with a color combination that is reminiscent of a Christmas candy cane, total corolla length 10 mm (7.5 mm long in immature flowers), ca. 8 mm diam. (ca. 11 mm *in vivo*), ca. 2 mm wide at throat, glabrous within and without; lobes deltate, 1–1.5 × 1.5–1.6 mm, apex acute, slightly reflexed; aestivation valvate. *Stamens* 10, equal, ca. 5.5 mm long, included, not adherent to corolla; filaments free, triangular, 2–2.2 mm long, adaxially inconspicuously glabrate, abaxially glabrous; adjacent anthers differing moderately in width, ca. 5.2 mm long, the innermost with an incipient bump on each side of the connective; thecae 3.2–3.7 mm long, prognathous, without basal appendage, papillate; tubules 2, free, straight, 1.5–2 mm long, smooth, dehiscing by introrse slits almost as long as the tubules, 1.2–2 mm long. *Ovary* 5-locular; nectary not pulvinate or evident, top of ovary completely flat; style ca. 7 mm long, included; stigma punctiform. Immature *berry* green, 8 mm diam.; seeds numerous, isodiametric, black when dry, with mucilaginous coat; embryo apparently white.

Distribution and ecology. *Psammisia sophiae* is endemic to Antioquia (Colombia) and it has only been collected in Las Orquídeas National Park. It is known to flower in December and July and fruit in January. It grows in conserved humid premontane forests at 1160–1400 m.

Etymology. Named after my daughter, Sofia Varón, an equally beautiful bloom.

Preliminary conservation status. *Psammisia sophiae* is only known from collections made in Las Orquídeas National Park. Despite collecting in that protected reserve for many years only a few specimens have been procured. This species seems to prefer conserved premontane forests. Currently, these forest, and the park in general, specially toward lower elevations, suffer from degradation product of human activities (agriculture, selective logging, livestock). I consider this species vulnerable due to the small area it occupies, its perceived scarcity, and current habitat threats.

Discussion. Although vegetatively similar, *P. sophiae* can be told apart from *P. panamensis*, not only because of their strikingly dissimilar flowers (obconic, terete, and with transversal bands of red, black and white in the latter), but also because the leaves of *P. panamensis* are glabrous and when dried, the lamina has a black-bluish tint on both sides (vs. hairs present, lamina drying brownish with a distinctive dark marginal band abaxially in *P. sophiae*), its petioles are not caniculate (vs. caniculate), and its rachis, bracts, bracteoles, and pedicel are longer.

Specimens examined. COLOMBIA. Antioquia: Municipio Frontino, Parque Nacional Natural Las Orquídeas, Finca La Guadalupa, Quebrada Horacio, afluente del Río Venados, 1160 m, 1 Dec 1986 (fl), *R. Callejas et al. 2937* (NY!). Municipio Urrao, Corregimiento La Encarnación, Vereda Calles, Parque Nacional Natural Las Orquídeas, cabaña Calles, 6°31'09.1"N; 76°15'08.4"W, 1357 m, 25 Jan 2011 (fr), *P. Pedraza-Peñalosa et al. 1951* (COL!, MO!, NY!); Corregimiento La Encarnación, Vereda Calles, Parque Nacional Natural Las Orquídeas, finca de Alfonso Pino, entre la divisoria de las quebradas La Virola y El Bosque, al NW de la cabaña Calles, 6°31'35"N; 76°15'50"W, 1450–1470 m, 27 Jan 2011 (fl, fr), *P. Pedraza-Peñalosa et al. 2014* (COL!).

Satyria orquidiensis Pedraza, sp. nov.
urn:lsid:ipni.org:names:77146698-1
Figures 9–11

Diagnosis. *Satyria orquidiensis* has many distinctive characters and it differs from other species in the genus because its leaves, which are clustered (up to 8 leaves) and seemingly verticillate (the only one in the genus), oblanceolate, large, and basally subcordate. The abundant and large flowers of this new species also stand out because of the big ribs on the calyx tube and the sharp transversal constriction between the limb and tube, which gives the entire calyx a broad campanulate shape. The long obconic corolla (up to 4.4 cm long) is orange and green at the tip. Both calyx and corolla are covered with a fine glabrate indumentum.

Type. COLOMBIA. Antioquia: Municipio Urrao. Corregimiento La Encarnación, vereda Calles, Parque Nacional Natural Las Orquídeas, finca de Alfonso Pino, en la divisoria de aguas entre las quebradas La Virola y El Bosque, al noroccidente de la cabaña de Calles, 6°31'35"N; 76°15'50"W, 1450–1470 m, 27 Jan 2011 (fl, fr), *Paola Pedraza-Peñalosa et al. 2016* (holotype: COL!; isotypes, CAS!, CUVC, E!, HUA, MO!, NY! [NY02058404], PSO).

Description. Epiphytic *shrub*, lianoid; stems brown-grey, terete, glabrous, bark smooth; twigs terete, smooth, glabrous. Axillary buds compressed; prophylls 2, valvate, lanceolate, inconspicuous, 2.5–4.5 mm long, margin eciliate, apex acuminate, abaxially puberulous, the hairs inconspicuous, ca. <0.2 mm long, eglandular and unicellular (all indumentum composed of this type of hairs except when indicated). *Leaves* alternate but apparently pseudoverticillate, originating in clusters of (2–)5–8 leaves separated by leafless sections 11.5–17.5 cm long; petiole terete, pulvinate, 3–6 mm long, glabrate; lamina coriaceous, elliptic, sometimes oblanceolate, (14–)18.7–28 × (3–)5–8 cm, base subcordate, margin entire and eciliate, apex acuminate, adaxially glabrous, abaxially glabrate (but appearing glabrous), the hairs inconspicuous, (< 0.2 mm long), caducous but with persistent bases that are red and swollen, apparently multicellular and glandular; laminar glands inconspicuous, basal, rounded; venation plinerved (acrodromous), suprabasal, with 3–4 visible orders (consistently well-marked up to 3th order) in dry specimens, prominent lateral veins 2(–3) per side, subopposite or alternate, concentrated in the basal third, ascending, brochidodromous, midvein and secondaries adaxially impressed and abaxially raised. *Inflorescence* a 4–6-flowered raceme, more than one raceme arising from an axillary pad (pincushion like), often cauliflorous; inflorescence and floral bracts alike, persistent, chartaceous, ovate, 0.5–2.6 × 0.8–1.2 mm, margin entire and ciliolate, the hairs inconspicuous and eglandular, apex acute to acuminate, adaxially glabrous, abaxially glabrate, venation obscure; rachis orange, 4–8.5 mm long, glabrate, warts abundant and minute; pedicel dark or lightly orange, articulate with calyx, 1.9–2.3 cm long (3 cm when fruiting), basally (1–1.2 mm diam.) less than half the diameter of apex (3–4.5 mm) (*in vivo* 2 mm basally, 5–7 mm apically), with the apex becoming discoid and almost as wide as the calyx tube, glabrate, minute warts present at very base both *in vivo* and when dry; bracteoles

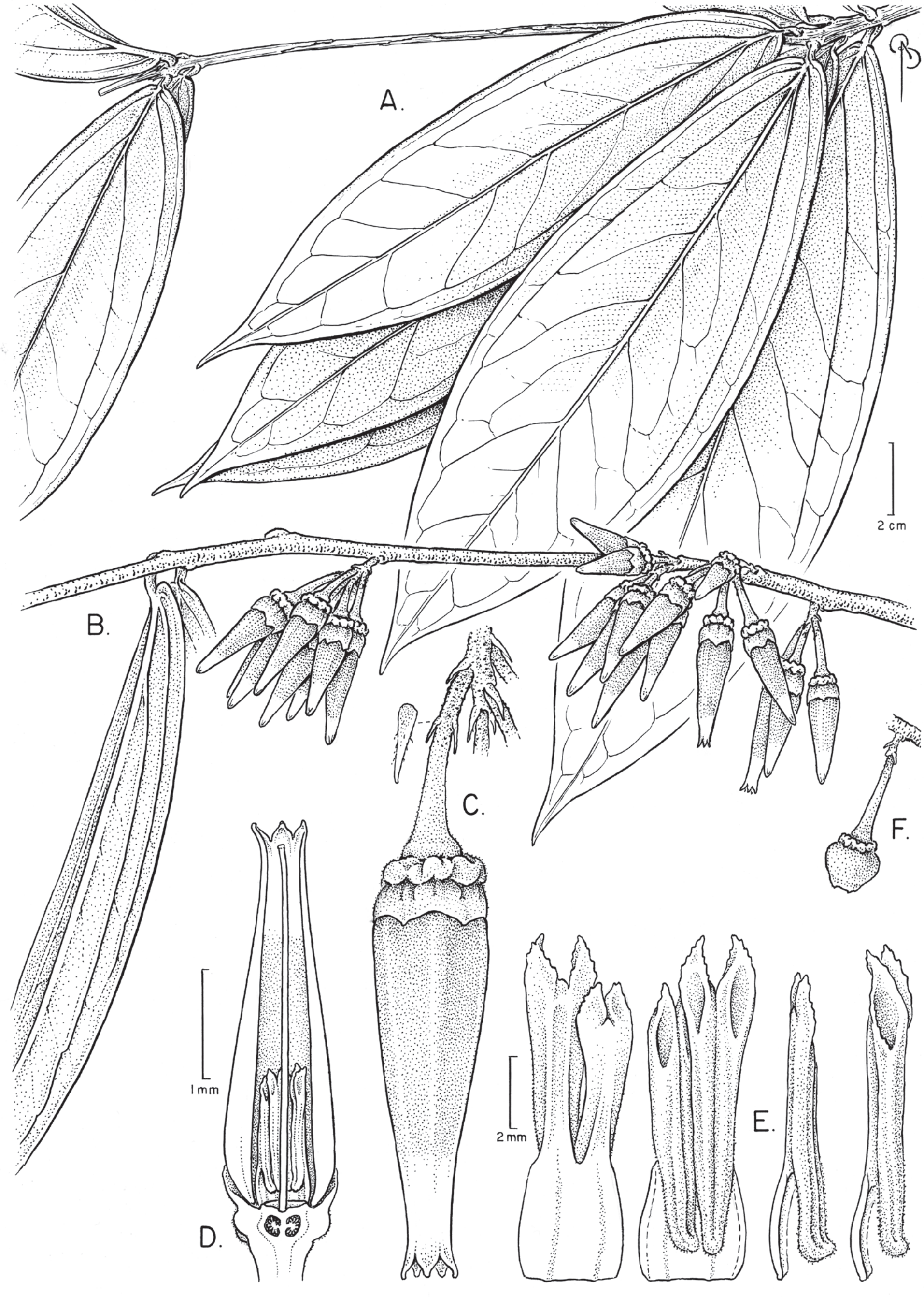

Figure 9. Illustration of *Satyria orquidiensis*. **A** Branch with clustered leaves **B** Branch with inflorescences **C** Flower attached to the rachis with detail of a bracteole **D** Longitudinal section of a flower **E** Stamens in abaxial, adaxial, and lateral views, respectively **F** Fruit. [Drawn from the type, *P. Pedraza-Peñalosa et al. 2436* and *2447*.]

Figure 10. *Satyria orquidiensis*. **A** Branch with clustered leaves, adaxial side **B** Branch with clustered leaves, abaxial side **C** Cauliflorous inflorescences **D** Nearly mature (right) and immature fruits (left). [Photos by P. Pedraza-Peñalosa.]

2, basal, supopposite to opposite, chartaceous, ovate, 2–2.4 × 0.6–0.8 mm, margin entire and ciliolate, the hairs inconspicuous, caducous and eglandular, apex acuminate, glabrous on both sides, venation obscure. *Flowers* 5-merous (some calyces 6-merous), actinomorphic, diplostemonous. Calyx dark or light orange, campanulate, with a marked transversal constriction between limb and tube, inconspicuously 5-angled, the angles alternating with lobes, conspicuously ribbed in the tube and with softer ribs in the limb, 4.1–5.8 mm long (6–7.2 mm *in vivo*), glabrate, the hairs inconspicuous, <0.1 mm long; tube oblate, 2–2.2 mm long (2.5–3 mm *in vivo*); limb slightly flaring, 2.1–3.6 mm long (3.5–4.7 mm *in vivo*); lobes deltate, 1–2 × 3.5–4.5 mm long (1.6–2 × 5 mm *in vivo*), margin entire, eglandular, and eciliate, apex acute; sinuses practically flat (broadly U-shaped *in vivo*); aestivation valvate. Corolla basal two thirds orange, apical third green, fleshy, not bistratose, obconic, 3.2–4 cm long (3.4–4.4 cm *in vivo*), 1–1.2 cm diam. (1–1.1 cm *in vivo*), 3 mm wide at throat (4.7–5.5 mm *in vivo*), inconspicuously 5-angled, glabrate without, the hairs inconspicuous, <0.1 mm long, glabrous within; lobes ovate, 1.5–2 × 1–2 mm, but sinuses often further

Figure 11. *Satyria orquidiensis.* **A** Flowers at anthesis with detail of a longitudinal section **B** Close-up of flowers showing the ornamented calyces. [Photos by P. Pedraza-Peñalosa.]

tearing toward end of anthesis and the lobes then oblong and 4.8–7 × 1–2 mm, apex acute, not strongly reflexed at maturity; aestivation valvate. *Stamens* 10, dimorphic, staminal cycles with different anther lengths and dehiscence orientation, included, not adherent to corolla. Long stamens 10–11.2 mm long; filaments connate into a tube, straight, 3.5–4 mm long, glabrous or distally glabrate on the abaxial side, the hairs a handful, inconspicuous, multicellular and apparently eglandular; anthers 9–9.5 mm long, slightly prognathous, narrowing at base and widening at apex, without a clear distinction between tubules and thecae; thecae 6–6.5 mm long, without basal appendage, minutely papillate at least basally; tubules 2, free, turned inwards like bull's horns, 3 mm long, smooth, dehiscing by latrorse elliptical slits 3 mm long, distal margin ornamented with small and irregular lobes. Short stamens 9–10 mm long, same shape, indumentum and features as long stamens except when indicated; filaments 3.5–4 mm long; anthers 8–8.5 mm long; thecae 5.5 mm long; tubules pointing upwards and without space between them, 2.5–3 mm long, dehiscing by introrse elliptical slits 2.5–3 mm long. Nectary not pulvinate, slightly concave to flat, glabrous; style white, 2.6–3.7 cm long, included; stigma punctiform. *Berry* cream-colored and ribbed when immature, turning purple at maturity.

Distribution and ecology. *Satyria orquidiensis* is endemic to Antioquia (Colombia) and it only known from collections from Las Orquídeas National Park. It is known to flower in January and fruit in January and July. This species grows in the canopy of humid premontane and montane forests at 880-1470 m, but it is possible that it could be found at lower altitudes as well.

Etymology. Named after Las Orquídeas National Park (Colombia), where the species is endemic to.

Preliminary conservation status. *Satyria orquidiensis* it is only known by specimens collected in Las Orquídeas National Park. It is commonly observed in conserved premontane and montane forests, but because it is a liana normally found high in the canopy, only a few collections exits. Because the observed abundance within the protected area I consider this species of least concern.

Discussion. Morphologically, *Satyria orquidiensis* and *S. pterocalyx* stand out within the genus and have more similarities among themselves than with other species; these are the only species in the genus with conspicuous wings and/or ribs on their calyces. Although their large corollas share similar colors and obconic shape, they can be easily differentiated because *S. orquidiensis* has corollas inconspicuously 5-angled (vs. terete in *S. pterocalyx*), orange with green lobes (vs. red-orange with the tube and lobes green-whitish) that gradually decrease in diameter toward the lobes (vs. dramatically constricted at the throat which is elongated into a tube ca. 8 mm long). Also, the dark or light orange (vs. light green) calyces of *S. orquidiensis* are conspicuously ribbed on the tube and sharply constricted between the limb and tube (vs. calyces 5-winged, tube with two basal lobes in each of the facets demarked by the wings, not transversally constricted). Vegetetatively, these two new species are even more distinct as *S. orquidiensis* has leaves that are clustered and seemingly verticillate (vs. not clustered in *S. pterocalyx*), larger [(14–)18.7–28 cm long vs. 14–18 cm], basally subcordate (vs. obtuse or cuneate), apically acute to acuminate (long acuminate, acumen 1.8–2.8 cm long), and with inconspicuous basal laminar glands (vs. absent).

Specimens examined. COLOMBIA. Antioquia: Municipio Frontino, Vereda Venados Abajo, Parque Nacional Natural Las Orquídeas, sector Venados, sitio La Miquera, 6°32'28.1"N; 76°18'05.3"W, 1000–1030 m, 27 Jul 2011 (fr), *P. Pedraza-Peñalosa et al. 2436* [COL!, NY! (2 sheets)]; Municipio Frontino, Vereda Venados Abajo, Parque Nacional Natural Las Orquídeas, sector Venados, sitio La Esperanza, cuenca de la quebrada Arenales, 6°42'06.8"N; 76°18'46.03"W, 880-920 m, 29 Jul 2011 (fl), *P. Pedraza-Peñalosa et al. 2447* (COL!, MO!, NY!).

***Satyria pterocalyx* Pedraza, sp. nov.**

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Figures 12, 13

Diagnosis. *Satyria pterocalyx* can be easily differentiated among all other species in the genus by the following combination of characters. Its leaves are elliptic, often slightly asymmetric with the apex slanted to one side, large (14–18 cm long) and apically long acuminate (acumen 1.8–2.8 cm long). Its calyces are light green, 5-winged, with each of the facets of the calyx demarked by the wings containing two basal lobes that together look like an inverted m. In dry specimens, the pedicels have inconspicuous warts. Its corollas are very characteristic, terete, obconic and noticeably constricted at

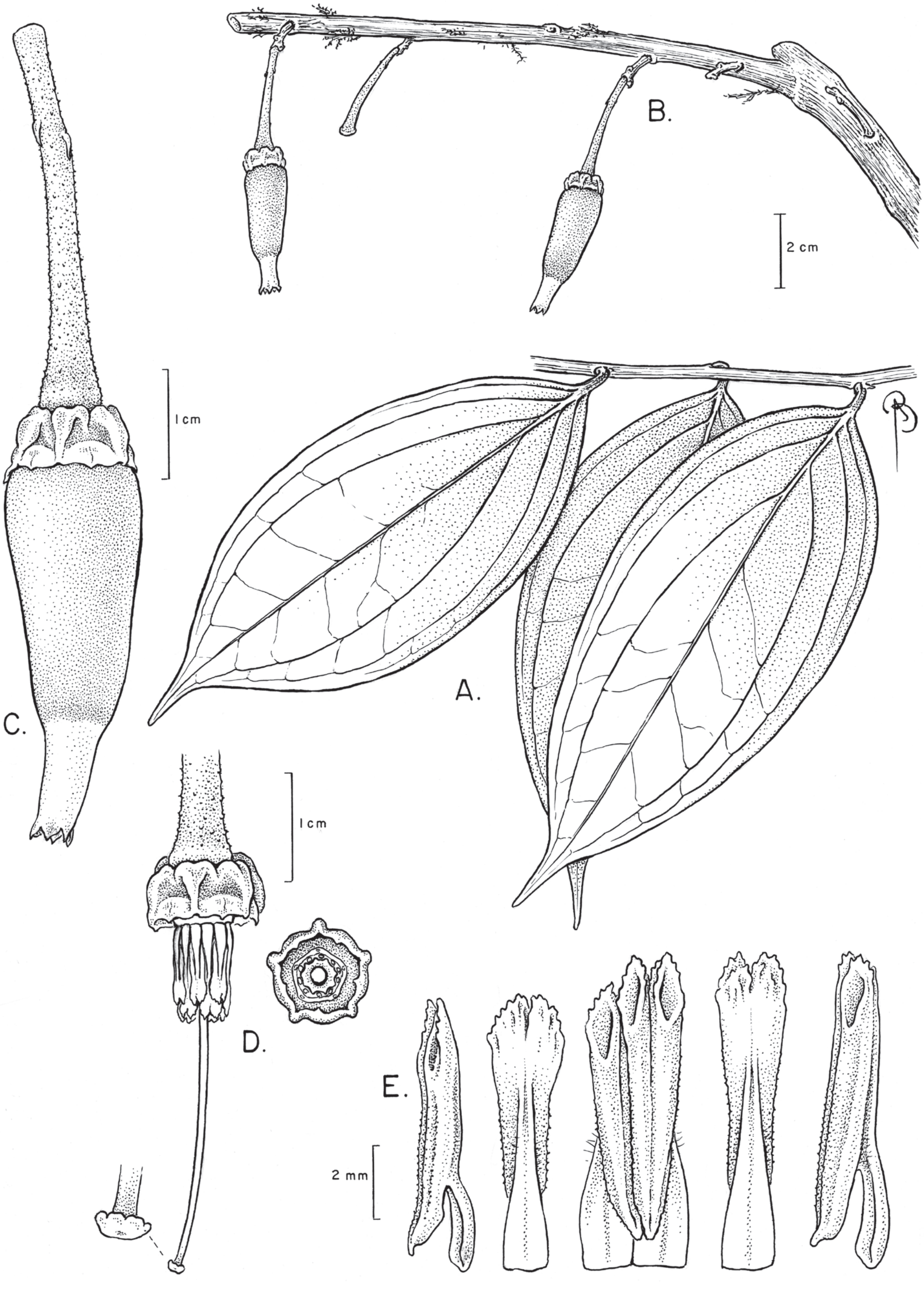

Figure 12. Illustration of *Satyria pterocalyx*. **A** Branch with leaves **B** Branch with flowers **C** Flower with pedicel **D** Flower with the corolla removed to show the stamens arranged around the style; detail of the nectary from above and of the stigma **E** Stamens in abaxial, adaxial, and lateral views. [Drawn from the type.]

Figure 13. *Satyria pterocalyx*. **A** Branch with leaves and flowers **B** Flowers at anthesis. [Photos by P. Pedraza-Peñalosa.]

the throat, which is then elongated into a tube ca. 8 mm long; the corolla is red-orange with the tube and lobes green-whitish.

Type. COLOMBIA. Antioquia: Municipio Urrao, Vereda La Magdalena, camino de herradura desde La Magdalena al Río Ocaidó, pasando por el Alto del Caballo, cuencas ríos Orougo, Orougito y Ocaidó, 6°14'05"–6°16'55"N; 76°13'24"–76°15'14"W, 1730–2150 m, 13 Dec 2007 (fl), *P. Pedraza-Peñalosa, J. Betancur, F. Gómez & O. Laverde 1755* (holotype: COL!; isotypes: HUA!, MO!, NY!).

Description. Epiphytic *shrub*, lianoid; stems brown-grey, terete, glabrous, bark smooth; twigs subterete, smooth, glabrate, the hairs inconspicuous (< 0.1 mm long), unicellular and eglandular (all indumentum composed of this type of hairs except when indicated). Axillary buds compressed; prophylls 2, valvate, lanceolate, conspicuous, 3.6–4.1 mm long, margin eciliate, apex acuminate, glabrous. *Leaves* alternate; petiole terete, not pulvinate, 6–8 mm long, glabrescent; lamina coriaceous, elliptic, often slightly asymmetric with the apex slanted to one side, 14–18 × 5.8–7.3 cm, base obtuse or cuneate, margin entire and eciliate, apex long acuminate (acumen 1.8–2.8 cm long), adaxially glabrous, abaxially glabrate, the hairs inconspicuous, (< 0.1 mm long), multicellular and eglandular; laminar glands absent; venation plinerved (acrodromous), suprabasal, with 3–4 visible orders in dry specimens, prominent lateral veins 2(–3) per side, subopposite, concentrated in the basal third, ascending, brochidodromous, midvein and secondaries adaxially impressed and abaxially raised. *Inflorescence* a axillary, solitary, raceme with at least 2 flowers, cauliflorus; inflorescence bracts, floral bract, and bracteoles alike, persistent, chartaceous, ovate, 1–1.6 × 0.5–1 mm, margin entire and ciliolate, the hairs inconspicuous, caducous and eglandular, apex acute to acuminate, glabrous on both sides, venation obscure; rachis green, 5–12 mm long, glabrous; pedicel orange, articulate with calyx, 2.6–3 cm long, basally less than half the diameter of apex (*in vivo* 1.5 mm vs. 4.5 mm, respectively), glabrescent, with inconspicuous warts basally (not evident *in vivo*); bracteoles 2, basal, supopposite to alternate. *Flowers* 5-merous, actinomorphic, diplostemonous. Calyx light green, oblate (more or less campanulate when dry), 3.8–5.6(–7.7) mm long (6.2–6.5 mm *in vivo*), 5-winged, the wings alternating with lobes, minutely puberulous; tube oblate, 3–3.2(–5.2) mm long (3.5–4.1 mm *in vivo*), the base conspicuously lobed, each facet of the calyx demarked by the wings contains two basal lobes that together look like an inverted m; limb more or less erect, 1.6–2(–2.5) mm long (2.4–3.3 mm *in vivo*); lobes deltate, 0.8–1 × 3–3.5 mm long (0.5–1.2 × 4–6 mm *in vivo*), margin entire, eglandular, and eciliate, apex obtuse; sinuses obtuse (U-shaped) to almost flat; aestivation unknown. Corolla red-orange with the tube and lobes green-whitish, fleshy, bistratose, obconic and noticeably constricted at the throat which is elongated into a tube (ca. 8 mm long), terete, 2.8–3(–4) cm long, 1.2–1.3 cm diam., 2.7–3 mm wide at throat (4 mm *in vivo*), inconspicuously puberulous without with a combination of hairs minute (< 0.5 mm long), eglandular and unicellular, along with a few hairs eglandular and multicellular, glabrous within; lobes deltate, 1.1 × 1.2–1.5 mm (lanceolate, 4.3 × 2 mm *in vivo*), apex acute, not strongly reflexed at maturity; aestivation unknown. *Stamens* 10 (all measurements *in vivo*), dimorphic, staminal cycles with different anther lengths and dehiscence orientation, included, not adherent to corolla. Long stamens 9.8–10.8 mm long; filaments connate at base, straight, 3–4 mm long, glabrate, the hairs inconspicuous and eglandular, the marginal ones unicellular, the abaxial ones multicellular, very scarce and distally concentrated, adaxial side glabrous; anthers 8.6–10.1 mm long, narrowing at base and widening at apex, without a clear distinction between tubules and thecae; thecae 5.9–7.1 mm long, without basal appendage, papillate at base, smooth at apex; tubules 2, free, pointing upwards, 2.5–3 mm long, smooth, dehiscing by latrorse elliptical slits 2.2–2.5 mm long, abaxial side and margin ornamented with irregular epidermal projections. Short stamens 8.3–9.5 mm long, same shapes, indumentum and features as long stamens except when indicated; filaments 3–3.5 mm long; anthers 7.5–9.4 mm long; thecae 5.2–6.4 mm long; tubules 2.3–3 mm long, dehiscing by introrse elliptical slits 2.2–2.5 mm long. Nectary pulvinate, not too prominent, glabrous; style 2.8–3.2 cm long, included; stigma discoid. *Berry* unknown.

Distribution and ecology. *Satyria pterocalyx* is restricted to the biologically rich montane forests of Western Colombia (Antioquia, Choco). It is known to flower in December and January.

Etymology. Species named after the rare winged calyces.

Preliminary conservation status. *Satyria pterocalyx* is known from two localities far apart (from adjacent departamentos) that confer it a not so small geographic range. However, after botanizing for several years in Antioquia, this species remains only known by two individuals. Although collected a few miles from Las Orquídeas National Park, *S. pterocalyx* has not been found within the protected area. Currently, Colombian montane forest suffer from degradation product of human activities (agriculture, selective logging, livestock, mining, etc.), therefore I consider this species vulnerable due to its perceived scarcity and current habitat threats.

Discussion. The morphological differences and similarities between *Satyria pterocalyx* and *S. orquidiensis* are discussed under the latter.

Specimens examined. COLOMBIA. Choco: Alto del Buey, 1200–1800 m, 8 Jan 1973 (fl), *A. Gentry & E. Forero 7311* (NY!).

Acknowledgments

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RESEARCH ARTICLE

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Studies of Malagasy *Eugenia* – IV: Seventeen new endemic species, a new combination, and three lectotypifications; with comments on distribution, ecological and evolutionary patterns

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Abstract

Seventeen new endemic species of the genus *Eugenia* L. (Myrtaceae) are proposed from Madagascar, including: *E. andapae* N. Snow, *E. barriei* N. Snow, *E. bemangidiensis* N. Snow, *E. calciscopulorum* N. Snow, *E. delicatissima* N. Snow, Callm. & Phillipson, *E. echinulata* N. Snow, *E. gandhii* N. Snow, *E. hazonjia* N. Snow, *E. iantarensis* N. Snow, *E. malcomberi* N. Snow, *E. manomboensis* N. Snow, *E. obovatifolia* N. Snow, *E. ranomafana* N. Snow & D. Turk, *E. ravelonarivoi* N. Snow & Callm., *E. razakamalalae* N. Snow & Callm., *E. tiampoka* N. Snow & Callm., and *E. wilsoniana* N. Snow, and one new combination, *Eugenia richardii* (Blume) N. Snow, Callm. & Phillipson is provided. Detailed descriptions, information on distribution and ecology, distribution maps, vernacular names (where known), digital images of types, comparisons to morphologically similar species. Preliminary assessment of IUCN risk of extinction and conservation recommendations are provided, including Vulnerable (4 species), Endangered (2 species), and Critically Endangered (4 species). Lectotpyes are designated for *Eugenia hovarum* H. Perrier, *Eugenia nompa* H. Perrier, and *E. scottii* H. Perrier respectively.

Résumé

Dix-sept nouvelles espèces endémiques du genre *Eugenia* L. (Myrtaceae) sont proposées pour Madagascar, incluant *E. andapae* N. Snow, *E. barriei* N. Snow, *E. bemangidiensis* N. Snow, *E. calciscopulorum* N. Snow, *E. delicatissima* N. Snow, Callm. & Phillipson, *E. echinulata* N. Snow, *E. gandhii* N. Snow, *E. hazonjia* N. Snow, *E. iantarensis* N. Snow, *E. malcomberi* N. Snow, *E. manomboensis* N. Snow, *E. obovatifolia* N. Snow, *E. ranomafana* N. Snow & D. Turk, *E. ravelonarivoi* N. Snow & Callm., *E. razakamalalae* N. Snow & Callm., *E. tiampoka* N. Snow & Callm., et *E. wilsoniana* N. Snow, ainsi qu'une nouvelle combination, *E. richardii* (Blume) N. Snow, Callm. & Phillipson. Des descriptions détaillées, des informations sur la distribution et l'écologie, des cartes de distribution, des noms vernaculaires (quand ils sont connus), des images digitalisées des types, des comparaisons avec les espèces morphologiquemnet proches et une évaluation préliminaire du risque d'extinction selon l'UICN ainsi que des recommendations de conservation sont fournies. Des lectotypes sont désignés pour *Eugenia hovarum* H. Perrier, *Eugenia nompa* H. Perrier et *Eugenia scottii* H. Perrier.

Keywords

Biogeography, conservation, *Eugenia*, *Eulemur fulvus*, leaf cutter bees, Madagascar, Myrtaceae, new species, systematics, vernacular names

Introduction

This paper is the fourth in a series devoted to clarifying the systematics of Malagasy *Eugenia* L. (Snow 2008, 2011; Snow et al. 2012), which until the work of Miller (2000) and Labat and Schatz (2002) had been dormant for five decades since early treatments by Perrier de la Bâthie (1953a,b). Its purpose is to propose seventeen new species, make a new combination, and lectotypify three names. It also provides detailed species descriptions with comparisons to morphologically similar taxa, distribution maps, vernacular names, digital images of types, and preliminary conservation assessments following IUCN Red List Categories and Criteria (2012).

Materials and methods

Type specimens of all nearly described species of *Eugenia* from Madagascar have been examined. All Malagasy specimens of *Eugenia* housed at MO (abbreviations following Thiers (2015)) have been viewed by NS (through May 2014), as have all duplicates housed at his institution (KSP). Specimens housed at G and P have been studied by MC and PP. Duplicates of many specimens housed at KSP also have been consulted by NS. Specimens cited here also were compared against all material of *Eugenia* from the Comoros and Mascarenes housed at MO through May 2014. All specimens housed at MO should have duplicates at P and TAN given existing exchange agreements, although none at TAN have been seen by the authors. Accession numbers of specimens (where indicated) follow the herbarium acronym with a hyphen, whereas barcode numbers are enclosed in square brackets.

Species descriptions include all information that can be interpreted with confidence and, given available information, are more or less in parallel. The species concept and criteria follow previous applications (Snow 1997; Snow et al. 2003). Terminology largely follows earlier works for Malagasy *Eugenia* (e.g., Snow et al. 2012) but with greater consistency regarding general terminology (Beentjie 2010). Terms specific to Myrtaceae have been minimized, but may include anthopodium, metaxyphyll, brachyblast, bracteole, monad, and triad, given their descriptive utility in Myrtaceae (see Briggs and Johnson 1979). The collection number cited for each specimen follows immediately after the senior collector, in accordance with most database systems now in use. Geocoordinates in square brackets were determined retrospectively by various workers.

Hotlinks to holotypes on Tropicos® are included in lieu of illustrations of the new species. In addition, scanned images for all barcoded specimens from P are available online through the MNHN Vascular Plant Database (http://science.mnhn.fr/institution/mnhn/collection/p/item/search/form). Photos of living material are included when available. The conservation status of each species was assessed following IUCN Red List Categories and Criteria (IUCN 2012). The calculations of Area of Occupancy (AOO), Extent of Occurrence (EOO) and number of subpopulations follow the methodology of Callmander et al. (2007), using a grid cell size to calculate AOO of 3 × 3 km.

Results and taxonomic treatments

Eugenia andapae N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146886-1
holotype (Figure 1): http://www.tropicos.org/Image/100314911

Frutex usque ad 9 m altus; ramuli complanati, glabri; folia usque ad 19 × 11.5 cm, obovata vel late elliptica, basi cordata vel rotundata, nervo medio supra sulcato, nervis secundariis infernis elevatis.

Type. MADAGASCAR. Prov. Antsiranana: Sud-Ouest d'Andapa, Réserve Spéciale d'Anjanaharibe-Sud. Ambodisatrana, aux environs des sommets, 14°32'45"S, 49°35'15"E, 809–1364 m, 25 May–3 June 1994, D. Ravelonarivo 206 + Raymond & Bekamisy (holotype: MO-6277713!; isotypes: KSP [KSP000041]!, P [P05097480]!, TAN).

Description. Shrubs or trees 4–12 m tall; bark of main bole unknown. Vegetative and reproductive parts mostly glabrous except as noted. Branchlets laterally compressed, the terminal internode sometimes with a distal sulcus but becoming rounded, smooth, minutely and sparsely short-sericeous but soon glabrous, oil glands faint and moderately common but soon fading; emerging (youngest) internodes sometimes bearing 1–2 pairs of opposite to broadly ovate bracts 1.5–4.0 mm long. Leaves opposite, thinly coriaceous (dried material cracking with only moderate pressure), discolorous, matte above and below, venation brochidodromous. Axillary colleters absent. Petioles 3–4 mm long, slightly striate below, flattened above, epunctate. Leaf blades

Holotype of: Eugenia andapae N. Snow

Ref.

Missouri Botanical Garden (MO)

MADAGASCAR

MYRTACEAE
Eugenia

Antsiranana

Sud-Ouest d'Andapa, Réserve Spéciale d'Anjanaharibe-Sud. Ambodisatrana, aux environs des sommets.
14°32'45"S 49°35'15"E 809-1364m

Arbuste de 5m de haut. Fruits bacciformes, le plus souvent couronnés par le reste du calice. Avec: Raymond et Bekamisy. Plantes préservées en alcool.
25 mai-3 juin 1994

D. Ravelonarivo et al. 206
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 1. Holotype specimen of *Eugenia andapae* (MO).

(15–)18.5–25 × (7–)13.5–14 cm, broadly elliptic to broadly obovate, base cordate and somewhat clasping (or rounded), surface and margin flat, apex obtuse to broadly acute, tip acuminate (or rarely retuse), secondary veins more or less straight, 11–15 per side protruding prominently below and arising at 25–55° angles and connected by slightly arching (but also prominent) inner marginal veins, tertiary veins relatively well-spaced but projecting only slightly (dried material); adaxial surface glabrous, oil glands faint (use magnification), sparse to common, more or less flush and darkish (dried), midvein sulcate; abaxial surface glabrous, midvein projecting prominently throughout and punctate (especially proximally) or epunctate, secondary veins projecting prominently, straight or only curving slightly towards margin, the secondaries connected at their ends by moderately arching connecting veins, tertiary veins projecting but less so than secondaries, intramarginal vein of same thickness as tertiaries, 1.5–5 mm from margin at midpoint of blade. Inflorescence (material scant) a monad; flowers cauliflorous, arising from short brachyblasts (< 3 mm long) above nodes on naked branches. Pedicels 8–32 mm long (possibly elongating after fertilization), 0.7–2.0 mm wide, somewhat compressed laterally, longitudinally striate, somewhat flexuous (bending with light touch), habit unknown, moderately glandular (glands faint), anthopodium and metaxyphylls absent. Bracteoles narrowly to broadly ovate, 1.5–2.5 × 0.5–1 mm, minutely and sparsely hairy dorsally and apically (hairs clear or whitish with some reddish). Hypanthium campanulate, 3.0–3.3 mm long, 3–4 mm wide at base of calyx lobes, densely but very shortly sericeous in proximal half (hairs reddish-brown) but glabrous distally; ovary apex glabrous. Calyx lobes 4 and often tearing irregularly towards hypanthium, up to 3.5 mm long × 4.5 mm broad (at base), irregularly hemispherical, glabrous on both faces apart from occasional minute hairs, evidently reflexed irregularly in anthesis. Petals 4 (material scant), 5.5–19.0 × ca. 10 mm, narrowly to broadly obovate, glabrous, epunctate, rose to violet. Staminal ring 3.5–4.0 mm in diameter (rounded or somewhat squarish), sparsely short hairy (hairs whitish). Stamens ca. 140 (estimated from scars on ring), multiseriate; filaments up to 10 mm long; anthers globular, ca. 0.8 mm long. Fruit 23–35 × 21–50 mm, depressed globular to globose, glabrous, base and apex rounded or apex crowned by calyx lobes, pinkish-reddish.

Phenology. Flowering in February and March; fruiting March through November.

Etymology. The species occurs in the Andapa Basin.

Distribution. Known in northeast Madagascar in and around the Anjarahabe-Sud and Marojejy protected areas (Figure 7).

Habitat and ecology. Humid forests, riparian areas and near summit of Ambodisatrana; ca. 200–1540 m.

Conservation status. With an Extent of Occurrence (EOO) of 1586 km^2, and Area of Occupancy (AOO) of 45 km^2 and five subpopulations, two of which are situated within the protected area network (Anjanaharibe-Sud, Marojejy), *Eugenia andapae* is assigned a preliminary risk of extinction of "Vulnerable" [VU B1ab(iii)+2ab(iii)] following the IUCN Red List Categories and Criteria (IUCN 2012).

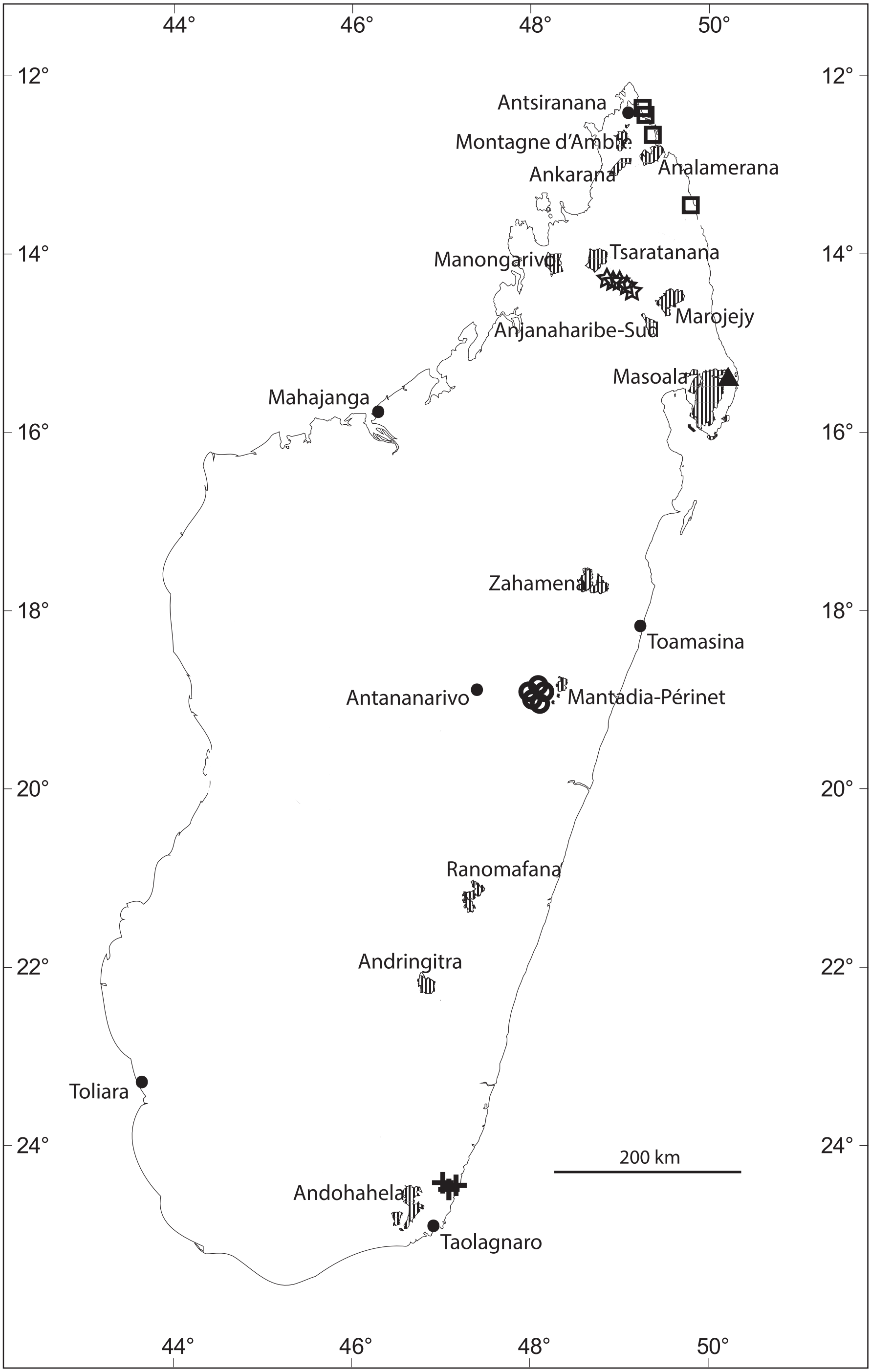


Figure 2. Distribution of new *Eugenia* species in Madagascar with selected Protected Areas (hatched): *E. bemangidiensis* (crosses), *E. razakamalalae* (triangle), *E. richardii* (squares), *E. tiampoka* (stars), and *E. wilsoniana* (circles).

Comments. The calyx lobes of this species tear towards the hypanthium during anthesis (see also *E. lacerosepala* N. Snow and *E. ambanizanensis* N. Snow). In this regard *Eugenia andapae* is similar to taxa first described by Scott (1979) from the Mascarenes in *Monimiastrum* A.J. Scott, which were reduced to synonymy under *Eugenia* (Snow 2008). The relatively long and broadly elliptic to obovate leaf blades with cordate bases, and the relatively straight and projecting abaxial secondary veins are diagnostic among other species of *Eugenia* in Madagascar. On herbarium material the abaxial tertiary veins also protrude slightly despite being thin. The label of the type specimen indicates that the fleshy fruits typically are crowned by the calyx lobes, although this was not true for the specimen from the Beamalona River.

Specimens examined. MADAGASCAR. Prov. Antsiranana: Vallée inférieure de l'Androranga, affluent de la Bemarivo (NE), aux environs d'Antongondriha, à la base du massif du Betsomanga, [14°15'30"S, 49°44'00"E], 200 m, 17-20 Nov. 1950, H. Humbert 24234 + R. Capuron (P [P05208578]); Quartier d'Ambodisatrana, SW d'Andapa, Réserve Spéciale d'Anjanaharibe-Sud, suivant la piste au bord de la rivière de Beamalona, vers la chaîne d'Anjanaharibe dans la réserve, 14°38'30"S, 49°25'30"E, 1235 m, 23 Mar. 1995, D. Ravelonarivo 694 + R. Rabesonina (MO). Andapa, Anjialavabe, Ankiakabe, 14°09'50"S, 49°22'47"E, 952 m, 11 Feb. 2007, R. Razakamalala 3234 + D. Ravelonarivo, C. Rakotovao, Jacky & José (G, K, MO-6175410, P [P04885355]). Prov. Mahajanga: Amparihy, Ruisseau d'Andasinanantsomanga, 14°55'38"S, 49°25'50"E, 1199 m, 23 Feb. 2008, P. Bernard 860 + J. Ramiadana & J. Jocelyn (MO-6432613).

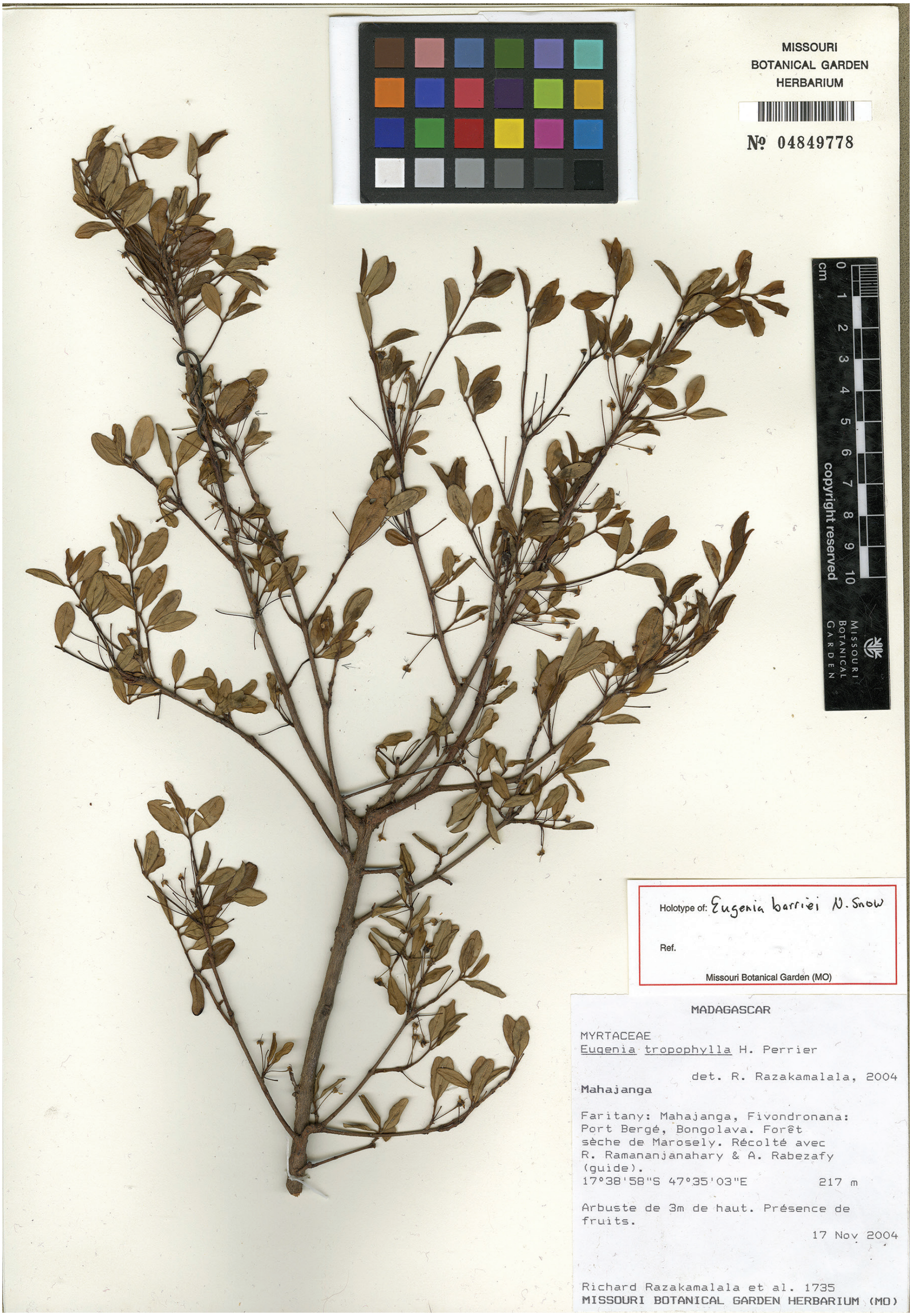
***Eugenia barriei* N. Snow, sp. nov.**

urn:lsid:ipni.org:names:77146887-1
holotype: (Figure 3): http://www.tropicos.org/Image/100314913

Haec species a congeneris madagascariensibus pedicellis gracilibus delicatis, foliis tenuiter coriaceis, floribus minutis atque hypanthio dense villoso distinguitur.

Type. MADAGASCAR. Prov. Mahajanga: Fiv. Port Bergé, Marosely, Bongolava, 15°38'58"S, 47°35'03"E, 217 m, 17 Nov. 2004, R. Razakamalala 1735 + R. Ramananjanahary & A. Rabezafy (holotype: MO-4849778!).

Description. Shrubs to 3 m tall; bark of main bole unknown. Vegetative and reproductive parts (where indicated) bearing a moderately dense, shortish indumentum, the individual trichomes dibrachiate or not, appressed to somewhat reflexed (appearing villous), frequently irregularly contorted, whitish or reddish. Branchlets laterally compressed but becoming rounded, smooth, moderately short villous (hairs mostly reflexed and not dibrachiate) becoming glabrous, oil glands common and prominent (after indumentum falls away). Leaves opposite, mostly occurring in 2–4 pairs along seasonal growth of branchlet, thinly coriaceous, venation brochidodromous (invisible to obscure), discolorous, somewhat glossy above but matte below. Axillary colleters



MISSOURI
BOTANICAL GARDEN
HERBARIUM
№ 04849778

Holotype of: Eugenia barriei N. Snow
Ref.
Missouri Botanical Garden (MO)

MADAGASCAR

MYRTACEAE
Eugenia tropophylla H. Perrier
det. R. Razakamalala, 2004
Mahajanga

Faritany: Mahajanga, Fivondronana: Port Bergé, Bongolava. Forêt sèche de Marosely. Récolté avec R. Ramananjanahary & A. Rabezafy (guide).
17°38'58"S 47°35'03"E 217 m

Arbuste de 3m de haut. Présence de fruits.
17 Nov 2004

Richard Razakamalala et al. 1735
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 3. Holotype specimen of *Eugenia barriei* (MO).

absent. Petioles 1.7–2.5 mm long, broadly sulcate above, moderately hairy towards base adaxially in sulcus. Leaf blades 0.9–2.0 (–2.7) × 0.6–0.9 cm, narrowly elliptic or elliptic to narrowly obovate, base cuneate, surface flat to slightly and irregularly (but broadly) sinuous on drying, margin flat or drying slightly revolute, apex obtuse; abaxial surface glabrescent, oil glands common (use magnification) and drying brownish and slightly sunken, midvein flush and becoming imperceptible towards apex; abaxial surface sparsely glabrescent, oil glands relatively sparse to moderate and somewhat less prominent than adaxially, secondary veins few and barely perceptible, the secondaries connected at their ends by a slightly arching pseudo-intramarginal vein 0.3–0.8 mm from leaf margin (i.e., lacking an intramarginal vein distinct from pseudo-intramarginal vein). Inflorescence a monad; the base of the flowering branchlets each with (2–)4–6 flowers arising alternately, each flower subtended by a short, hairy and somewhat ovate to broadly triangular caducous bract. Pedicels (5–)10–15(–20) mm long, 0.3–0.5 mm wide, round in transverse section, stiff, ascending, sparsely hairy (especially near base) to nearly glabrous, moderately glandular throughout, anthopodium present or absent. Bracteoles 2, linear, 1.0–1.2 × 0.3–0.5 mm, sparsely hairy. Hypanthium cupulate 2.0–2.5 mm long, 1.4–1.8 mm wide at base of calyx lobes, densely short-hairy, oil glands absent or sparse (and obscured by hairs); ovary apex glabrous. Calyx lobes 4, 1.5–1.9 mm, broadly ovate to rounded, glabrous on both faces apart from sparse apical hairs (white or reddish), strongly reflexed in athesis. Petals 4 (material scant), ca. 2.5 mm × 2 mm, obovate to widely obovate, glabrous on both faces apart from sparse apical hairs (contorted irregularly), oil glands absent. Staminal region (i.e., lacking a well-defined staminal ring) 1.6–1.8 mm diameter in anthesis, sparsely hairy (trichomes simple); stamens 35–45; filaments 1.5–2.5 mm; anther sacs 0.5–0.7 mm long, globose, basifixed, eglandular. Style 2.5–2.8 mm, glabrous or sparsely hairy basally; stigma narrow and only slightly capitate. Fruit unknown.

Etymology. The specific epithet honors Dr. Fred Barrie (b. 1948) of the Missouri Botanical Garden in recognition of his contributions to our knowledge of *Eugenia* and other genera of Mesoamerican Myrtaceae (e.g., Barrie 2004, 2005).

Phenology. Flowering confirmed only for the middle of November; fruiting likely late November through December.

Distribution. Known only from near Port Bergé in Mahajanga Province (Figure 4).

Conservation status. With only one collection known from Central-western Madagascar collected in an unprotected and threathened dry forest, *Eugenia barriei* is assigned a preliminary risk of extinction of “Critically Endangered” [CR A3c] following the IUCN Red List Categories and Criteria (IUCN 2012). In the absence of effective protection and the high human pressure on these forests, it is unlikely that the forest will persist beyond 3 generations of *Eugenia barriei* (ca. 30 years).

Comments. The type specimen of *Eugenia barriei* initially was determined as *E. tropophylla* H. Perrier. The latter species and the varieties described by Perrier de la Bâthie (1953a,b) do not represent a single taxon, which even a cursory glance at the numerous syntypes (at P) will reveal.

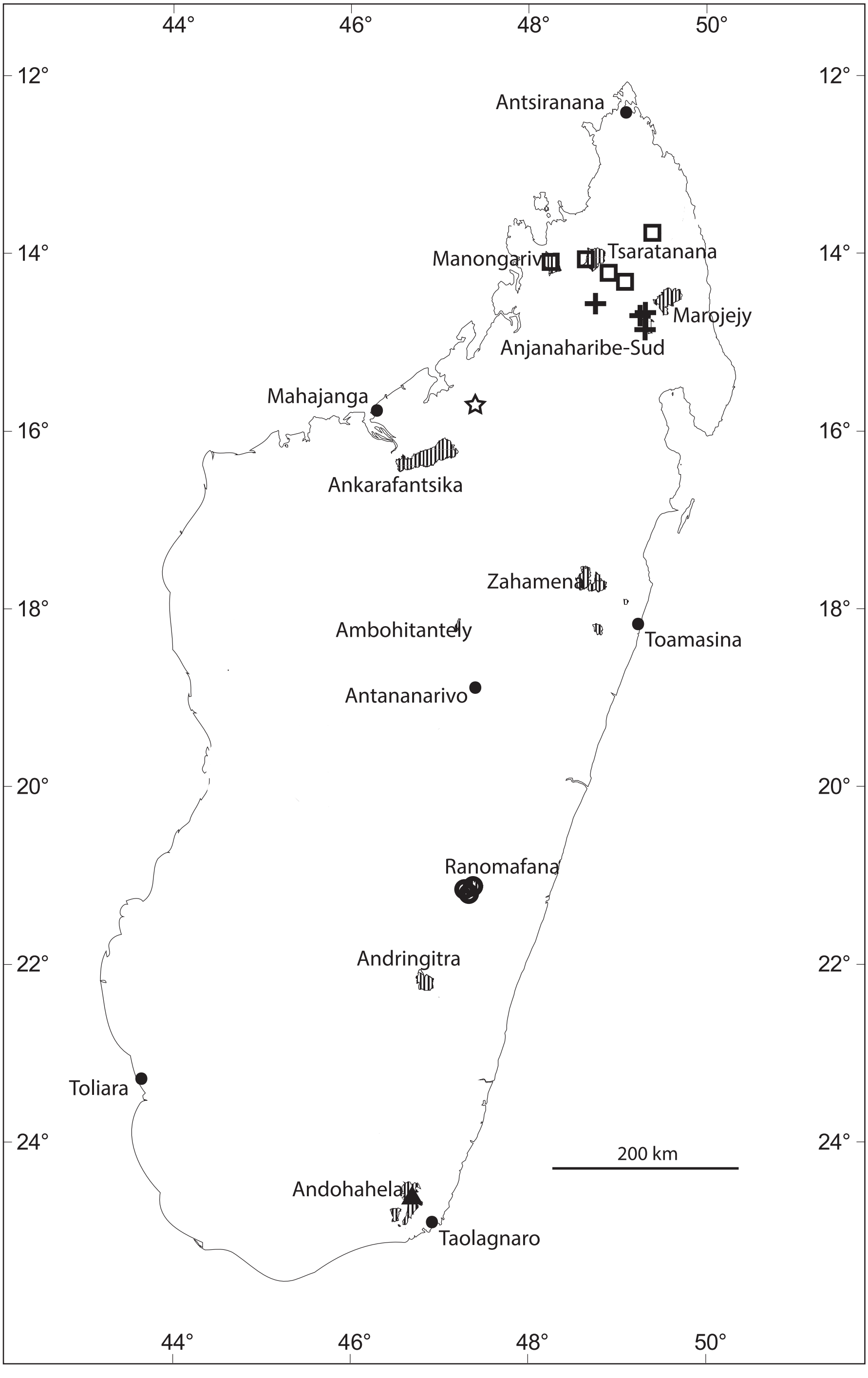


Figure 4. Distribution of new *Eugenia* species in Madagascar with selected Protected Areas (hatched): *E. barriei* (star), *E. delicatissima* (squares), *E. malcomberi* (triangle), *E. ranomafana* (circles), and *E. ravelonarivoi* (crosses).

Among taxa from southeastern Africa, *Eugenia barriei* resembles some specimens of *E. capensis* subsp. *gracilipes*. In particular, the slender pedicels of a specimen from Malawi (Chapman 6570 [MO]) have a similar but less dense indumentum on the branchlets, pedicels and hypanthium. Other differences of the Chapman specimen include longer and more densely and prominently punctate leaves, and inflorescences that mostly arise from ramiflorous brachyblasts.

Eugenia barriei also has gross morphological similarity to the widespread and relatively common west African species *E. leonensis* Engler & Brehmer (e.g., D.K. Harder 3372 et al. [MO] from Ghana), but it differs from that species by the generally glabrous aspect of the latter. Likewise, *E. barriei* somewhat resembles *E. mufindiensis* Verdc. by virtue of the indumentum of the branchlets, but the latter differs by its much more densely punctate leaves (above and below), the glabrous hypanthium, and a narrower and more deeply sulcate petiole (e.g., M.A. Mwangoka 5945 + H. Mgalla [MO]).

Eugenia bemangidiensis N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146888-1
Holotype: (Figure 5): http://www.tropicos.org/Image/100314916

Haec species Eugeniae wilsonianae N. Snow *similis, sed ab ea inflorescentiis fasciculatis caulifloris distinguitur; etiam ad altitudines inferiores crescit.*

Type. MADAGASCAR. Prov. Toliara: Anosy, Taolagnaro, Iaboko, Antsotso Avaratra, 24°34'35"S, 47°12'28"E, 25 m, 13 Dec. 2007, R. Razakamalala 4056 + D. Rabehevitra, M. Maka, Roger & B. Mara (holotype: MO-6335452!; isotypes: P [P06490265]!, TAN).

Description. Shrubs 3–4 m; bark of main bole more or less smooth but somewhat flaking, brown to gray. Foliage and reproductive parts glabrous except where noted. Branchlets terete, light brown (dried), smooth, oil glands sparse to moderate (but indistinct). Leaves mostly concentrated near branch tips, coriaceous, slightly discolorus, surfaces matte. Axillary colleters lacking. Petioles 3–4(–5) mm, slightly sulcate above, elgandular. Leaf blades 6–10 × 1.7–3.5 cm, narrowly elliptic to narrowly ovate, base rounded, apex acute to acuminate or a few falcate, margin flat, oil glands not seen (dried material); adaxial midvein broadly but shallowly sulcate, secondary veins indistinct to prominent (with magnification), intramarginal vein 0.5–1.8 mm from edge at midpoint of leaf blade. Inflorescences cauliflorous, arising from amorphous knobby protrusions (short shoots?) at or near nodes; flowers triads, monads, or fascicled (and possibly a few short botryoids); pedicels 1.5–6 mm, flexuous. Bracteoles 2 or absent, ca. 0.5 × 0.5 mm, broadly triangular to broadly rounded, ascending to divergent, stiff. Hypanthium 2.5–4.0 mm, cupuliform, oil glands common but small. Sepals 4, 2–3.0 × 3.5–4 mm, semi-circular to broadly elliptic or oblate, apex broadly rounded to obtuse, lobes very sparsely and minutely ciliate distally, moderately glandular; persistent and crowning (at least) young fruits. Petals 4 (material limited), 5–6 × 3–4

Holotype of: *Eugenia bemangidiensis N. Snow*

Ref.

Missouri Botanical Garden (MO)

MADAGASCAR
MYRTACEAE [222]
Eugenia

Toliara: Anosy Region

Toliara, Anosy, Taolagnaro, Iaboko, Antsotso Avaratra. Récoltés avec D. Rabehevitra, M. Maka, Roger & B. Mara.
24°34'35"S 047°12'28"E 25 m

Arbuste 3 m, fleurs cauliflores.

13 Dec 2007
Richard Razakamalala & et al. 4056
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 5. Holotype specimen of *Eugenia bemangidiensis* (MO).

mm, widely elliptic to obovate, glabrous to sparsely and minute ciliate distally, glands sparse to moderate but faint (in dried material). Stamens 50–75, multiseriate; staminal disk short-hairy; ovary apex glabrous but distinctly punctate; filaments 2–5 mm; anthers 0.5–0.8 mm, elliptic, sub-basifixed, connective apex eglandular. Styles 6–7 mm; stigma narrow (scarcely if at all capitate). Fruits ca. 10–15 × 10–15 mm, (material possibly not fully mature) subglobose to globose, base sometimes sharply tapered, glabrous, dark bluish-black (dried).

Etymology. The epithet is derived from the place name *Bemangidy*, a biologically rich region within the provisional Protected Area of Tsitongambarika.

Phenology. Flowering commencing November and December; fruiting likely commencing by late December or early January (unconfirmed).

Distribution. Known only from southeast Madagascar in Toliara Province, ca. 55 km northeast of Taolognaro, in Tsitongambarika (Fig. 2).

Habitat and ecology. Label information is sparse, but based on recent satellite imagery, evidently occurring in moderately to highly disturbed hilly areas that retain thin remnants of forest in ssome drainages and on steeper slopes, the type gathering located some 0.5 km east of much less disturbed primary forests that occur on steeper slopes, the paratype gathering in highly disturbed sites; elevation ca. 25–110 m.

Conservation status. With only three collections known, an AOO of 9 km^2 and one subpopulation, which is situated outside the current protected area network, *Eugenia bemangidiensis* is assigned a preliminary risk of extinction of "Critically Endangered" [CR A3c+B1ab(iii)] following the IUCN Red List Categories and Criteria (IUCN 2012). All the known material of the species was collected in the proposed new protected area of Tsitonggambarika in the south-east (Fig. 2). The new species seems to have a highly restricted distribution and the lowland evergreen tropical forests where the species grows is under threat. Its definitive protection would likely allow this species to be downlisted to "Endangered".

Comments. The leaf morphology of *Eugenia bemangidiensis* resembles *E. wilsoniana* (see discussion above). However, the short-pedicellate, fasciculate, and cauliflorous infloresences of *E. bemangidiensis* differ from the axillary, long-pedicellate flowers of *E. wilsoniana*. The type gathering at ca. 25 m elevation of *E. bemangidiensis* is approximately 645 km south of the most southerly collections of *E. wilsoniana*, the latter of which occur at middle elevations of ca. 980–1100 meters.

An indetermined fruiting specimen (Rakotovao 241 [MO-6437191]) from Near Ivohibe approximately 260 km north of the type gathering of *E. bemangidiensis*, which appears to have ramiflorous (and possibly cauliflorous) inflorescences, may be related, although it occurs at 1210 m, far above the known occurrences of *E. bemangidiensis*.

Specimens examined. MADAGASCAR. Prov. Toliara: Iaboko, Antsotso, forêt Ivohibe, 24°33'52"S, 47°14'5"E, 26 Nov. 2005, R. Razakamalala 2326 + E. Ramisa & B. Mara (MO-6433204, P [P06490266]); *ibid. loc.*, 24°34'16"S, 47°12'06"E, 8 Dec. 2007, R. Razakamalala 3799 + D. Rabehevitra, M. Maka, Roger & B. Mara (MO-6308460, P [P04827649]).

Eugenia calciscopulorum N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146889-1
holotype (Figure 6): http://www.tropicos.org/Image/100314917
living material: http://www.tropicos.org/Image/100128169;
http://www.tropicos.org/Image/100128168

Haec species quoad faciem habitumque Eugeniae richardii (Blume) N. Snow *et al. et* E. hazonjia N. Snow *subsimilis, sed ab eis lamina foliari grosse sinuata, lobis calycinis roseo-albidis atque petalis subroseis distinguitur.*

Type. MADAGASCAR. Prov. Antsiranana: Mahavanona, Andranomanitra, 12°23'27"S, 49°20'01"E, 11 Dec. 2004, S. Rakotonandrasana 883 + R. Randrianaivo, A. Rakotondrafara, C. Christian & J. Be (holotype: MO-6245566!; isotypes: CNARP, KSP [KSP000016]!, P [P04885354]!, TAN).

Description. Trees to 6 m; dbh 13 cm; bark of main bole unknown. Herbage glabrous except as noted. Branchlets rounded; oil glands sparse to common but indistinct; first epidermal layer soon flaking irregularly and drying grayish; later-forming bark smooth, light brown or light gray, frequently cracking horizontally. Leaves coriaceous, mostly concentrated near branch tips; opposite to disjunct opposite, discolorous, surfaces matte. Foliar colleters absent. Petioles 3–4 mm, terete or somewhat sulcate proximally when young, broadening and flattening somewhat distally at base of blade. Leaf blades (1.7–)2.0–4.3 × 1.8–3.0 cm, broadly elliptic (mostly) or a few ovate, base rounded to slightly cuneate, apex obtuse to somewhat acute, margins more or less flat, surface overall broadly sinuous; adaxial midvein sulcate lower 1/3–1/2 becoming flush distally, oil glands common to dense but becoming faint with maturity; abaxial surface oil glands sparse to common but faint at maturity and relatively small, secondary veins relatively indistinct, intramarginal vein 1–2 mm from margin of leaf at midpoint of blade, faint. Inflorescence terminal or axillary, of 1–3 monads per leaf axil. Pedicels 7–15 mm, relatively stiff. Bracteoles 2; ca. 0.5–1.0 mm, ovate, stiff, sparsely short-pubescent distally (trichomes ca. 0.1 mm long). Hypanthium 1.5–2.0 mm, cupuliform to obconic, densely glandular. Calyx lobes 4, 2–3 mm, elliptic to oblong, apex rounded, whitish to pink when fresh, oil glands common and prominently. Petals 4 (material scant), 6–11 × 5–7 mm, elliptic to widely elliptic, sparsely short-ciliate apically, pinkish, oil glands common. Stamens ca. 70–90, multiseriate; filaments 5–8 mm, whitish; anthers 0.6–0.8 mm, globose to elliptic, sub-basifixed, yellowish, the connective bearing a single apical oil gland; staminal disk squarrish, ca. 3 mm across, sparsely short-hairy. Styles 7–9 mm; stigma narrow. Fruits unknown.

Etymology. *Calci* and *scopulorum* combine to form a genitive plural masculine noun, in reference to the locality at the base of a calcareous (limestone) cliff.

Phenology. Flowering December; fruiting most likely late December through January (unconfirmed).

Distribution. Known only from the type gathering in north-eastern Madagascar in Antsiranana, in the Montagne des Français limestone massif (Figure 7).

Figure 6. Holotype specimen of *Eugenia calciscopulorum* (MO).

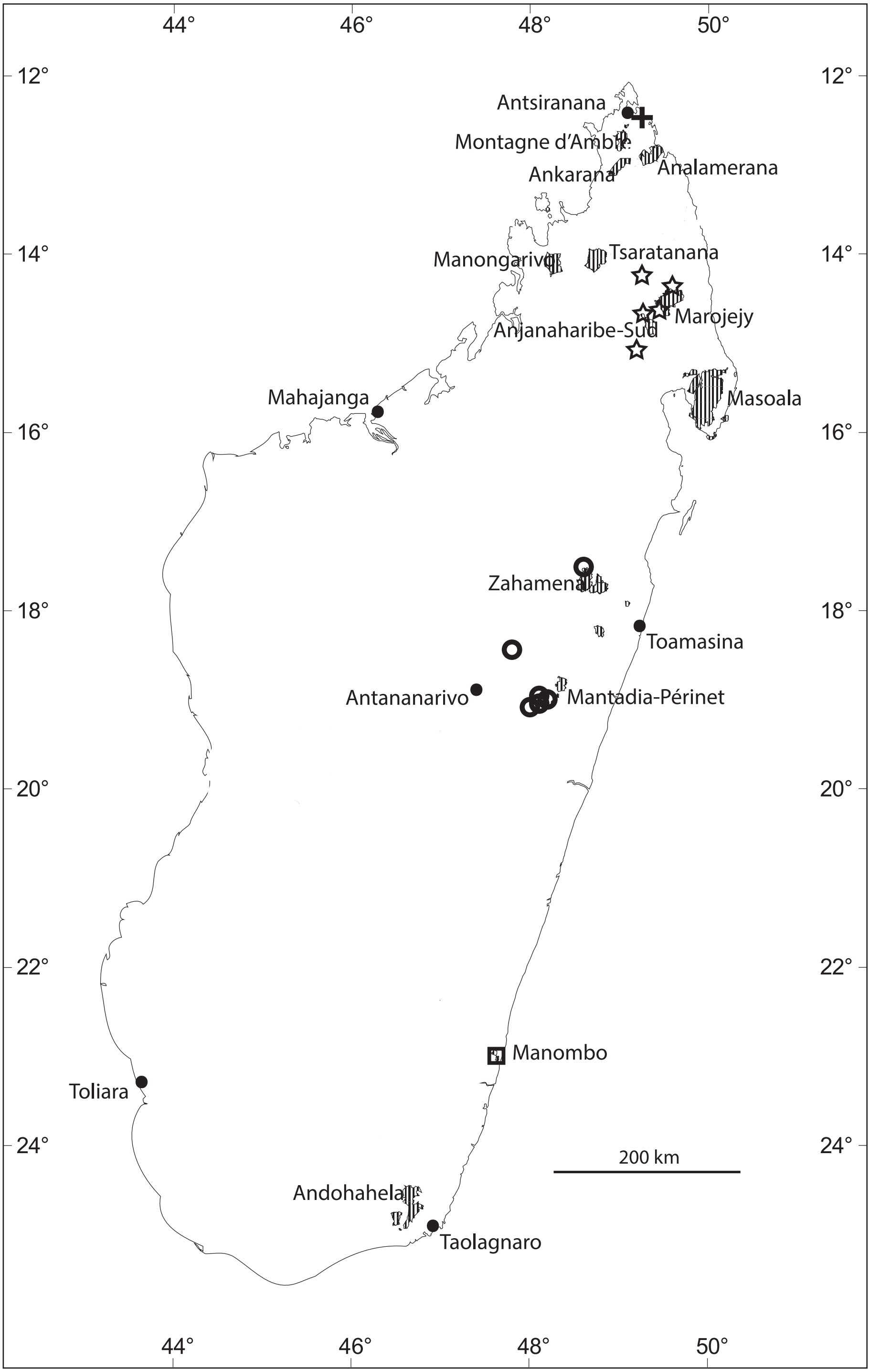


Figure 7. Distribution of new *Eugenia* species in Madagascar with selected Protected Areas (hatched): *E. andapae* (stars), *E. calciscopulorum* (cross), *E. echinulata* (circles), and *E. manomboensis* (square).

Habitat and ecology. Degraded dry forest at the foot of a cliff over calcareous substrates; ca. 410 m.

Conservation status. The species was said to be abundant at the type gathering. However, with only one collection known, an AOO of 9 km^2 and one subpopulation, which is situated within a proposed protected area that currently holds a temporary protection status (Montagne des Français), *Eugenia calciscopulorum* is assigned a preliminary risk of extinction of "Critically Endangered" [CR A3c+B1ab(iii)] following the IUCN Red List Categories and Criteria (IUCN 2012). The species seems to have a highly restricted distribution and the dry deciduous forests around Montagne des Français is mostly degraded as a result of human activities and is under serious threat. Definitive protection of those dry forests likely would allow the species to be downlisted to "Vulnerable".

Comments. See *Eugenia richardii* for similar species.

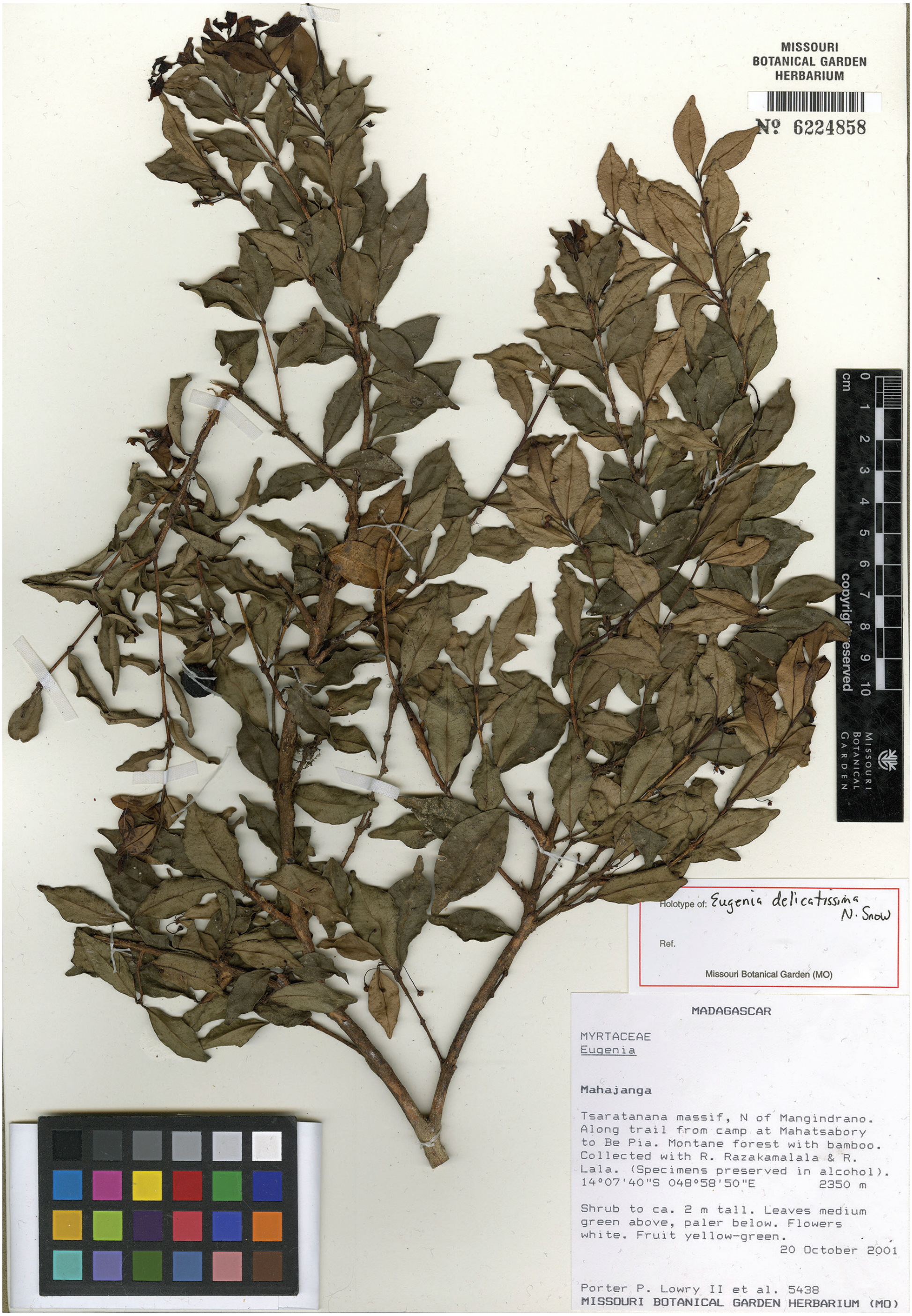
Eugenia delicatissima N. Snow, Callm. & Phillipson, sp. nov.

urn:lsid:ipni.org:names:77146890-1
holotype (Figure 8): http://www.tropicos.org/Image/100314909

Haec species a congeneris madagascariensibus lamina foliari tenuiter coriacea irregulariter sinuosa atque pedicello gracili delicato distinguitur.

Type. MADAGASCAR. Prov. Mahajanga: Tsaratanana massif, N of Mangindrano, along trail from camp at Mahatsabory to Be Pia, 14°07'40"S, 48°58'50"E, 2350 m, 20 Oct. 2001, P.P. Lowry II 5438 + R. Razakamalala & R. Lala (holotype: MO-6224858!; isotypes:P [P05208430]!, TAN).

Description. Shrubs to treelets 2–4 m tall; bark of main bole smooth, light brownish or grayish. Plants glabrous or (where noted) sericeous (hairs dibrachiate, reddish). Branchlets laterally compressed, sparsely hairy upon emergence but becoming glabrous, oil glands faint, sparse or occasional and of uniform size, flush or only slightly protruding, smooth, light brown or gray. Leaves evenly distributed along branchlets, thinly coriaceous, venation brochidodromous, strongly discolorous, matte above and below. Axillary colleters if present then soon deciduous. Petioles 4.0–6.5 mm long, slightly to deeply sulcate above, sparsely glabrescent, eglandular. Leaf blades (18–)30–52 mm × (8–)18–25 mm, narrowly elliptic to elliptic (or occasionally broadly elliptic), base cuneate to strongly cuneate, margin flat to slightly revolute (dry), surface slightly irregularly wavy (sometimes including along midvein), apex acute to acuminate, tip obtuse to mostly acute or acuminate or slightly falcate; adaxial surface glabrous, oil glands faint, dense and of uniform size, midvein sulcate but becoming flush distally; abaxial surface glabrous, oil glands faint, sparse to occasional and of different sizes, vein connecting tips of secondaries near margin slightly arching arching only slightly, 0.5–0.9 mm from margin at midpoint of leaf blade. Inflorescence terminal, axillary or ramiflorous, consisting of short brachyblasts with 1–3 pairs of monads, often 2 or



Holotype of: *Eugenia delicatissima* N. Snow

Ref.

Missouri Botanical Garden (MO)

MADAGASCAR

MYRTACEAE
Eugenia

Mahajanga

Tsaratanana massif, N of Mangindrano. Along trail from camp at Mahatsabory to Be Pia. Montane forest with bamboo. Collected with R. Razakamalala & R. Lala. (Specimens preserved in alcohol). 14°07'40"S 048°58'50"E 2350 m

Shrub to ca. 2 m tall. Leaves medium green above, paler below. Flowers white. Fruit yellow-green.
20 October 2001

Porter P. Lowry II et al. 5438
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 8. Holotype specimen of *Eugenia delicatissima* (MO).

more brachyblasts per axil or point of insertion (on naked branches), or monads arising in axils. Pedicels 3–11 mm long, 0.3–0.4 mm thick, stiff to somewhat flexuous, ascending to sometimes reflexed, glabrous or very sparsely short-hairy, lightly striate, round, oil glands sparse and faint, anthopodia and metaxyphylls absent. Bracteoles 0.8–1.3 mm long, less than 0.5 broad (at base), very narrowly triangular to ovate, normally persisting in anthesis, sparsely hairy (or merely ciliate). Hypanthium obconic, (0.8–)1.2–1.3 mm long, 0.9–1.0 mm broad at apex beneath base of calyx lobes, sparsely hairy to glabrous, smooth, oil glands sparse to common and protruding. Calyx lobes 4, 1.3–1.9 mm long, broadly ovate to rounded, sparsely ciliate, sparsely glandular, greenish. Petals 4, 2.8–4.4 × 1.6–1.8 mm, obovate to broadly elliptic, glabrous or sparsely ciliate apically, white, oil glands sparse to common, of uniform size and somewhat protruding below. Staminal disk ca. 1.8 mm in diameter, sparsely hairy. Stamens 15–25; filaments 3–4 mm long; anther sacs ca. 0.5 mm long, globose to subcylindrical, dorsifixed, brown, connective with an apical gland. Style 4–5 mm long, glabrous; stigma narrow. Fruit 0.9–1.4 × 0.8–1.6 cm, subglobose to globose, texture smooth, rounded or tapered at base, glabrous, greenish but drying blackish, calyx lobes reflexed flat against apex.

Etymology. A superlative of *delicata* in Latin, in reference to the thin, almost thread-like pedicels.

Vernancular name. Rotramadinika (Rakoto 294).

Phenology. Flowering in late October through at least early November; fruiting November.

Distribution. Known from the northern mountains of Madagascar in and around the Manongarivo and Tsaratanana protected areas and in the Sorata region (Fig. 4).

Habitat and ecology. High elevation montane forests with bamboo; 1100–2350 m.

Conservation status. With an EOO of 3278 km^2, an AOO of 36 km^2 and four subpopulations, two of which are situated within the protected area network (Manongarivo, Tsaratanana), *Eugenia delicatissima* is assigned a preliminary risk of extinction of “Vulnerable” [VU B1ab(iii)+2ab(iii)] following the IUCN Red List Categories and Criteria (IUCN 2012). At the summit of Beampoko *Eugenia delicatissima* was indicated as being rare (Rakotovao 2565).

Comments. *Eugenia delicatissima* is part of an apparent species group characterized by thinly coriaceous, sinuous leaf blades and slender, often elongate and delicate pedicels.

The thinly coriaceous, sinuous leaf blades of *Eugenia delicatissima* are somewhat suggestive of *E. echinulata*, but the fruits of *E. delicatissima* are smooth (e.g. Randriambololomamonjy 270), unlike the highly irregular (warty to echinate) texture of of *E. echinulata*.

The slender pedicels are similar to those of *Eugenia tropophylla* H. Perrier, a highly heterogenous species that Perrier de la Bâthie (1953a: 167) initially described with three subspecies, none of which match *E. delicatissima*. The taxonomy of *E. tropophylla* needs serious revision and will be the subject of a forthcoming publication.

An indetermined specimen of *Eugenia* from Mayotte in the Comoros (Barthelat 992 [G, K, MO]) also has slender pedicles, but they are much shorter than those of *E.*

delicatissima. The leaf blades of the Barthelat specimen are longer and the bases rounded, unlike the cuneate bases of *E. delicatissima*. Taxa from eastern and southern Africa with delicate pedicels include *E. capensis* (Eckl. & Zeyh.) Sonder subsp. *gracilipes* F. White (e.g., P. van Wyk BSA 2844 [MO] from Zimbabwe and J.D. Chapman 6570 [MO] from Malawi). Another species from Africa with delicate pedicels that differs from *E. delicatissima* in various traits is *E. congolensis* De Willd & T. Durand (e.g., J. Madidi 642 et al. [MO] and F. Bujo 602 [MO] from Congo). None of these, however, are good morphological matches for *E. delicatissima*.

Specimens examined. MADAGASCAR. Prov. Antsiranana: Massif du Manongarivo, [13°59'24"S, 48°22'12"E], c. 1600 m, 1909, Perrier de la Bâthie 6503 (P [P05258587]); Sommet de Beampoko, Ambohimirahavavy, 14°13'55"S, 49°08'23"E, 2137 m, 21 Nov. 2005, C. Rakotovao 2565 (G, MO-6174672); Vohemar, Andrafainkona, Ampsarahina, forêt de Maromaniry située à 5 km au N d'Ampiarahina, 13°38'49"S, 49°32'13"E, 1177 m, 7 Nov. 2007, O. Randriambololomamonjy 270 + R. Razakamalala & Jaowind (MO-6186659); Massif du Tsaratanana, crête (et ses abords) séparant les bassins du Sambirano et de la Mahavavy, entre l'Andohanisamborano et la cote 2362, 9-10 Nov. 1966, Service Forestier 27019 (P [P05097488]).

Eugenia echinulata N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146891-1
holotype (Figure 9): http://www.tropicos.org/Image/100314922
living material: http://www.tropicos.org/Image/100306108

Haec species inter congeneros madagascarienses fructibus maturis valde echinulatis distinguitur.

Type. MADAGASCAR. Prov. Toamasina: zone d'occupation controlée d'Antenina, sur piste entre Antenina et Ankosy, à 2 km du village d'Antenina, 17°30'00"–17°29'47"S, 48°46'19"E–48°45'35"E, 917 m, 1 Feb. 2002, L.M. Randrianjanaka 702 + N.M. Andrianjafy (holotype: MO-5786207!; isotypes: P, TAN).

Description. Shrubs or trees 1.5–4 m tall; dbh 4–5 cm; bark of main bole brown, somewhat cracking. Foliage and flowers glabrous except as noted. Branchlets terete to laterally compressed, drying light brown to gray, smooth, oil glands occasional but barely visible. Leaves slightly discolorous, more or less evenly distributed, margins coarsely sinuous, venation brochidodromous, surfaces matte. Axillary colleters absent. Petioles 4–6 mm long, slightly suclate, eglandular. Leaf blades (3.0–)3.8–6.5 × (1.0–)1.6–3.5 cm, narrowly elliptic or narrowly ovate to elliptic, base cuneate, apex acute to acuminate; adaxial midvein sulcate proximally but becoming flush distally, oil glands dense but faint, sometimes protruding slightly on dried material; abaxial surface midvein prominently raised, oil glands common to dense and of uniform size but faint, sometimes slightly protruding (dried material). Inflorescence ramiflorous or axillary. Flowers solitary or clustered into short brachyblasts; brachyblasts 2–5 mm long, densely short-bracteolate, sparsely covered with twisted, whitish-maroon trichomes. Pedicles 5–7.5 mm, glabrous. Flower material scant. Hypanthium ca. 3 mm, coarsely large-pustullate (warty), light green or yellowish-green in bud. Calyx lobes 4 (rose-colored in bud), 3–4 mm, elliptic to broadly ovate or rounded, glabrous, mostly persisting and crowning fruit. Petals not seen; said to be pink (Antilahimena 8858). Stamens not seen; anthers said to be yellow with white filaments (Ahtilahimena 8858). Style not seen. Berry 1.3–1.8 × 1.0–1.5 cm, globose to subglobose, coarsely rugose-warty when fresh but drying echinulate (with with short sharp points), densely glandular when younger, green when immature, drying nearly black. Seeds in mature fruit 1; ca. 10–11 mm, globular, outer seed coat elgandular.

Etymology. The specific epithet comes from the Latin *echinulatus* (having very small prickles) in reference to the prickly, dried, mature fruits that are unique for the genus in Madagascar.

Vernacular name. Rotra (Antilahimena 6841).

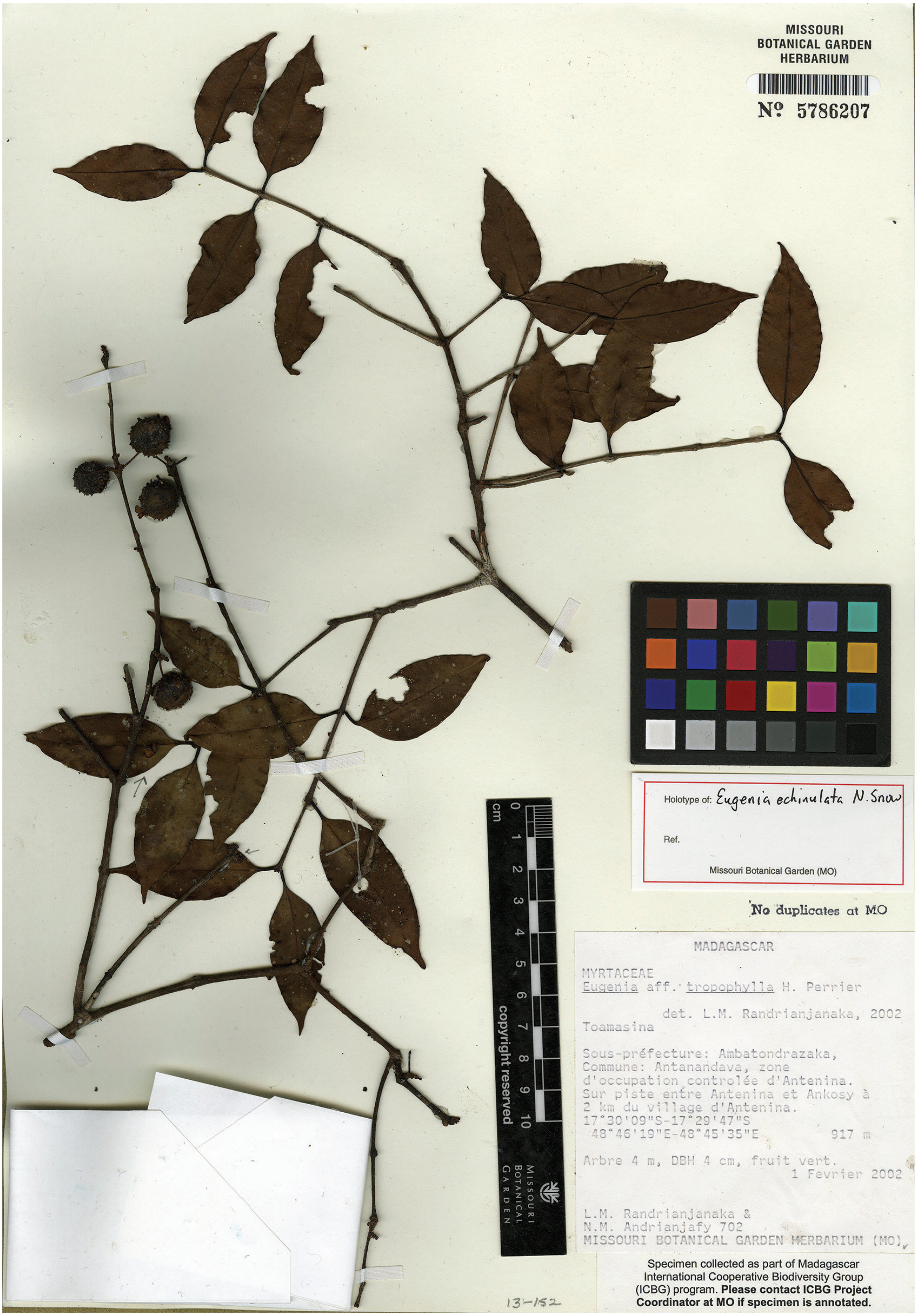
Phenology. Flowering December; fruiting January and February.

Distribution. Known from the eastern escarpment of Madagascar in the Toamasina Province around Analamazaotra and Ambatovy and in the highlands at Anjozorobe in Antananarivo Province (Fig. 7).

Habitat and ecology. Dense humid evergreen forests; ca. 915–1350 m.

Conservation status. One collection indicated the species as being abundant in its area of collection (Randrianaivo 1463 et al.). However, with an EOO of 4,372 km^2, an AOO of 72 km^2 and three subpopulations, two of which are situated within the protected area network (Analamazaotra, Zahamena), *Eugenia echinulata* is assigned a preliminary risk of extinction of “Vulnerable” [VU B1ab(iii)+2ab(iii)] following the IUCN Red List Categories and Criteria (IUCN 2012).

Specimens examined. MADAGASCAR. Prov. Antananarivo: Reg. Analamanga, Anjozorobe, Ambongamarina, Ampamoa, à 10 km au Nord-Est d’Anjozorobe, prolongement N de la fôret d’Antsahabe, 18°23'19"S, 47°55'49"E, 1352 m, 15 Feb. 2007, R. Randrianaivo 1463 + L. Vary, François, Jacques & Rakoto (MO-6440448). Prov. Toamasina: Alaotra-Mangoro, Fkt: Menalamba, Ambatovy, 1168 m, 18°50'11"S, 48°18'44"E, 22 Jan. 2007, P. Antilahimena 5170 et al. (MO-5786207, KSP [KSP000006], P [P00730617]); *ibid. loc.,* 18°52'25"S, 48°20'44"E, 979 m, 4 Oct. 2008, P. Antilahimena 6566 et al. (MO, P, TAN); *ibid. loc*., 18°52'28"S, 48°17'37"E, 1010 m, 10 Nov. 2008, P. Antilahimena 6841 + M. Ratolojanahary, B.A. Ratodimanana, M. Randrianarivony, M. Ratovomanana & F. Edmond (MO, P, TAN); *ibid. loc*., 18°52'30"S, 48°17'35"E, 970 m, 10 Nov. 2008, P. Antilahimena et al. 6854 (MO, P, TAN); *ibid. loc*., 18°55'22"S, 48°25'39"E, 1013 m, 21 Dec. 2013, Antilahimena 8858 + Rabarison, Honoré, Félix, Randrimitantsoa Jean & V. Razafindrahaja (MO, P, TAN); Phelps Dodge project site, ca. 15 air-km NE of Moramanga, ca. 11 km E of Antanambao. Ambatovy, SE valley (Ambohimanga), 18°51'34”S, 48°18'25”E, 1050 m, P.J. Rakotomalaza 1208a (MO, P [P00730620]); Analamazaotra, Ambatovy, 18°56'10”S, 48°25'33”E, 11 Dec. 2013, Ramahenina 276 et al. (MO); Ambatovy, forêt de Savihara, 18°52'06"S, 48°16'43"E, 22 Feb. 2010, D. Razafimelison 10 et al. (P



MISSOURI
BOTANICAL GARDEN
HERBARIUM
№ 5786207

Holotype of: *Eugenia echinulata N. Snow*

Ref.

Missouri Botanical Garden (MO)

No duplicates at MO

MADAGASCAR

MYRTACEAE
Eugenia aff. tropophylla H. Perrier

det. L.M. Randrianjanaka, 2002
Toamasina

Sous-préfecture: Ambatondrazaka,
Commune: Antanandava, zone
d'occupation controlée d'Antenina.
Sur piste entre Antenina et Ankosy à
2 km du village d'Antenina.
17°30'09"S-17°29'47"S
48°46'19"E-48°45'35"E 917 m

Arbre 4 m, DBH 4 cm, fruit vert.
1 Fevrier 2002

L.M. Randrianjanaka &
N.M. Andrianjafy 702
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Specimen collected as part of Madagascar International Cooperative Biodiversity Group (ICBG) program. **Please contact ICBG Project Coordinator at MO if specimen is annotated.**

13-152

Figure 9. Holotype specimen of *Eugenia echinulata* (MO).

[P00730618]); Alaotra-Mangoro, Moramanga, Andasibe, Réserve Spécial d'Analamazaotra, Circuit Indri 1, 18°56'20"S, 48°25'09"E, 947 m, 14 Dec. 2013, H.M.J. Rasoazanany 541 + H. Razafindraibe, B. Ramandimbisoa & Rakotondravelo (MO, P, TAN).

Comments. *Eugenia echinulata* is unknown in flower apart from one remnant hypanthium on the holotype. However, the coarsely sinuate leaf blades and acuminate apices, coupled with the warty mature fruits, are diagnostic and unknown in combination elsewhere among Malagasy congeners. Whereas *E. muscicola* H. Perrier has narrowly elliptic leaves, its leaf margins are more or less planar. A number of similar sterile collections from this area may be this taxon.

The texture of the fruit is coarsely rugulose-warty (see link above to image of living material), but the warty protrusions collapse to a large extent and upon drying and then assume a sharper, echinulate texture.

Eugenia gandhii N. Snow, sp. nov.

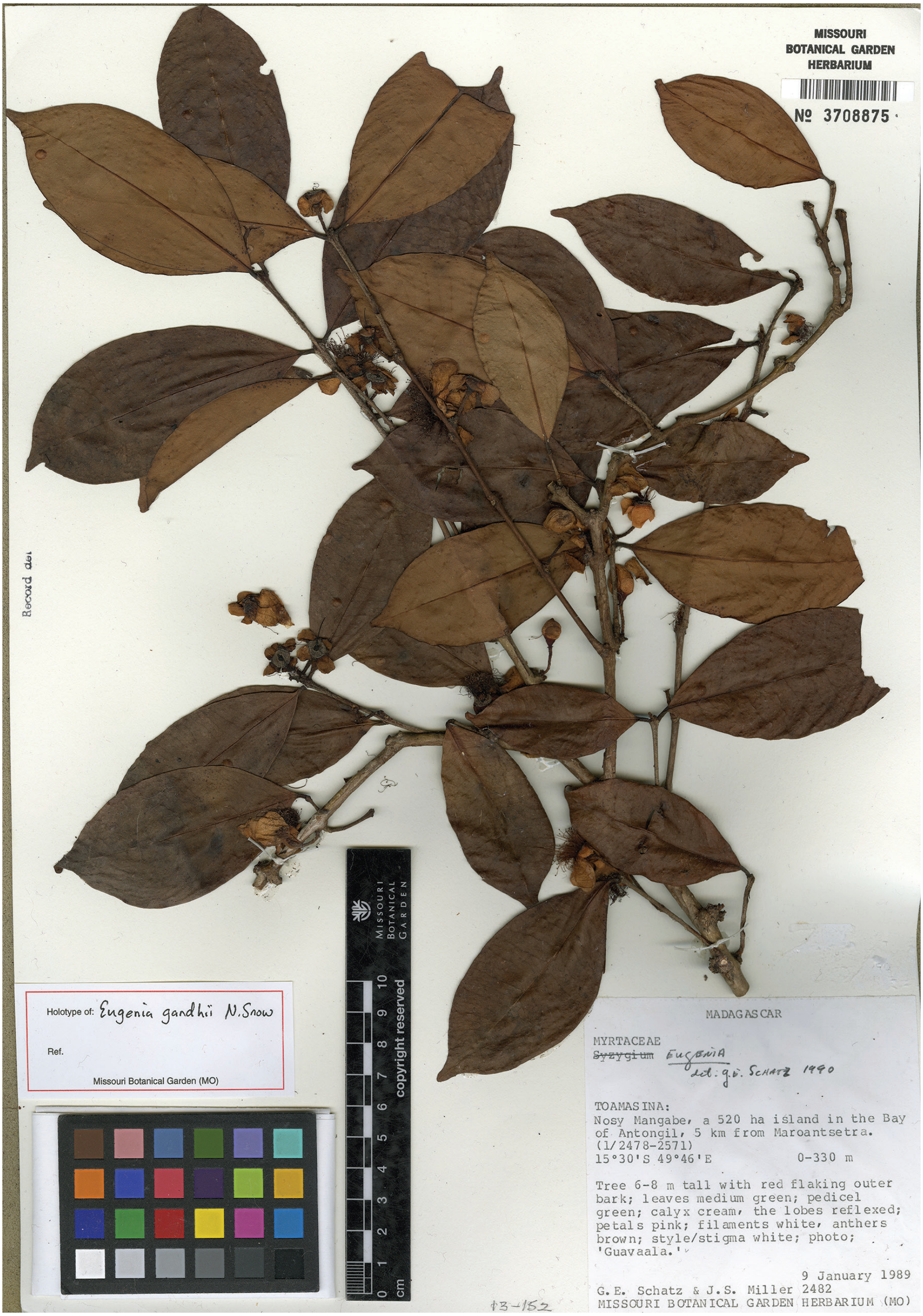
urn:lsid:ipni.org:names:77146892-1
holotype (Figure 10): http://www.tropicos.org/Image/100314906
living material: http://www.tropicos.org/Image/100160915

Haec species a congeneris madagascariensibus lamina foliari tenuiter coriacea elliptica usque obovata dense sed inconspicue glandulosa apice acuta acuminatave distinguitur.

Type. MADAGASCAR. Prov. Toamasina: Nosy Mangabe, a 520 ha island in the Bay of Antongil, 5 km from Maroantsetra, 15°30'S, 49°46'E, 0–330 m, 9 Jan. 1989, G.E. Schatz 2482 + J.S. Miller (holotype: MO-4805069!; isotypes: MO-3708875!, P [P05260197]!, TAN).

Synonym. *Eugenia arthroopoda* Drake var. *ambalavensis* H. Perrier in Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 4(2): 177. 1953. Nom. inval. (lacking Latin diagnosis, ICN, Art. 39.1, McNeill et al. 2012).

Description. Shrubs to trees, 3–12 m. Trunk 3–8 cm dbh; outer bark of main bole reddish, papery to flakey and peeling. Foliage and reproductive parts glabrous except where noted. Branchlets terete to laterally compressed, reddish when fresh but drying brownish or grayish, glabrous but prominently glandular, the epidermis smooth but soon peeling (dried specimens) and often thin and narrow grayish strips or even threads. Leaves opposite, medium green (fresh), slightly to strongly discolorous, venation brochidodromous, thinly coriaceous (easily cracking when dried), surfaces matte. Axillary colleters lacking. Petioles 2.8–6 mm, slightly sulcate distally. Leaf blades (5.5–)9–16 × 2.5–6.0 cm, elliptic to occasionally obovate, base cuneate, apex acute to mostly acuminate or caudate, margins flat; adaxial surface glabrous, densely punctate (glands small and best seen with magnification); abaxial surface similar, lateral veins indistinct to prominent; intramarginal vein 1–3.5 mm from margin at midpoint of blade. Inflorescence terminal, axillary, or ramiflorous, of soliltary monads or in fascicles of 2–3 flowers. Pedicels 9–29 mm long × 0.8–1.2 mm thick, stiff, moderately glandu-



MADAGASCAR

MYRTACEAE
~~Syzygium~~ Eugenia
det. G.E. Schatz 1990

TOAMASINA:
Nosy Mangabe, a 520 ha island in the Bay of Antongil, 5 km from Maroantsetra.
(1/2478-2571)
15°30'S 49°46'E 0-330 m

Tree 6-8 m tall with red flaking outer bark; leaves medium green; pedicel green; calyx cream, the lobes reflexed; petals pink; filaments white, anthers brown; style/stigma white; photo; 'Guavaala.'

9 January 1989
G.E. Schatz & J.S. Miller 2482
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 10. Holotype specimen of *Eugenia gandhii* (MO).

lar, ascending to erect, green. Bracteoles narrowly ovate to broadly rounded, 0.5–1.3 × 1.0–1.2 mm, stiff but thin, glabrous to minutely and sparsely sericeous on margin, often persistent in fruit. Hypanthium 4–5 mm long, cupuliform, densely glandular (some glands larger proximally). Calyx lobes 4, 6–9 × up to 11 mm, broadly elliptic to rounded, cream-colored (fresh), reflexed in flower, persistent and often crowning the fruit. Petals 4, 11–14 × up to 12 mm, widely elliptic to widely obovate (narrowly greatly at base), sparsely and minute ciliate marginally, densely glandular (glands of variable size but typically large proximally). Stamens 250–300, multiseriate, exserted; staminal disk short-hairy (trichomes slightly ferrugineous); filaments 8–15 mm, white; anthers globose, 0.3–0.5 mm, brownish, bearing a single large apical gland. Ovary apex glabrous but somewhat glandular. Style 8–10 mm; stigma narrow (scarcely if at all swollen). Berries 2.5–4.0 × 3.0–4.0 cm, subglobose to globose, purplish or violet (drying nearly black). Locules 2; placentation axile. Seeds up to 20 mm long and wide (available material possibly not fully mature), up to 6 per fruit, evidently often somewhat flattened, cotyledons and hypocotyl barely if at all differentiated.

Etymology. The species honors Dr. Kanchi N. Gandhi (b. 1948) of Harvard University Herbaria, North American editor of the *International Plants Names Index*, and an expert of botanical nomenclature who has assisted colleagues with the proper usage of botanical Latin and interpretation of the Code over many years.

Vernacular names. Gavoala (Ravelonarivo 103); gavoalabe.

The name "guaavaala" appears on one specimen, but native speakers inform us that it is a nonsensical name based on a combination of the common English name *guava* (for members of *Psidium*, a Neotropical genus) and *ala*, meaning locally "of the forest".

Phenology. Flowering January through June; fruiting March through November.

Distribution. Endemic to northeast Madagascar, recorded from the Island of Nosy Mangabe, the Masoala Peninsula, and in and around the Anjaniharibe Reserve (Figure 11).

Habitat and ecology. Humid and typically dense forests; 0–1424 meters.

Conservation status. With an "Extent Of Occurrence" (EOO) of 9,504 km^2, an "Area Of Occupancy" (AOO) of 45 km^2 and five subpopulations, three of which are situated within the protected area network (Anjanaharibe-Sud, Marojejy and Nosy Mangabe), *Eugenia gandhii* is assigned a preliminary status of "Least Concern" [LC] following the IUCN Red List Categories and Criteria (IUCN 2012).

Comments. Perrier de la Bâthie's *E. arthroopoda* H. Perrier var. *ambalavensis* H. Perrier was based on a single collection from the lowlands just to the south of Marojejy Reserve, but we have little doubt that it is conspecific with the material we include in *E. gandhii*, which ranges from the nearby Anjaniharibe Reserve to the southwest of Marojejy to the Masoala peninsula and Nosy Mangabe farther south.

The thinly coriaceous leaf blades of *Eugenia gandhii* are suggestive of *Eugenia vatomandrensis* H. Perrier, which thus far is known as a coastal species from near Vatomandry north towards Soanierana (Perrier 1953a). However, the leaves of *E. vatomandrensis* are rounded to subcordate and nearly sessisle, which contrast with the distinctly petiolate, cuneate leaf blades of *E. gandhii*.

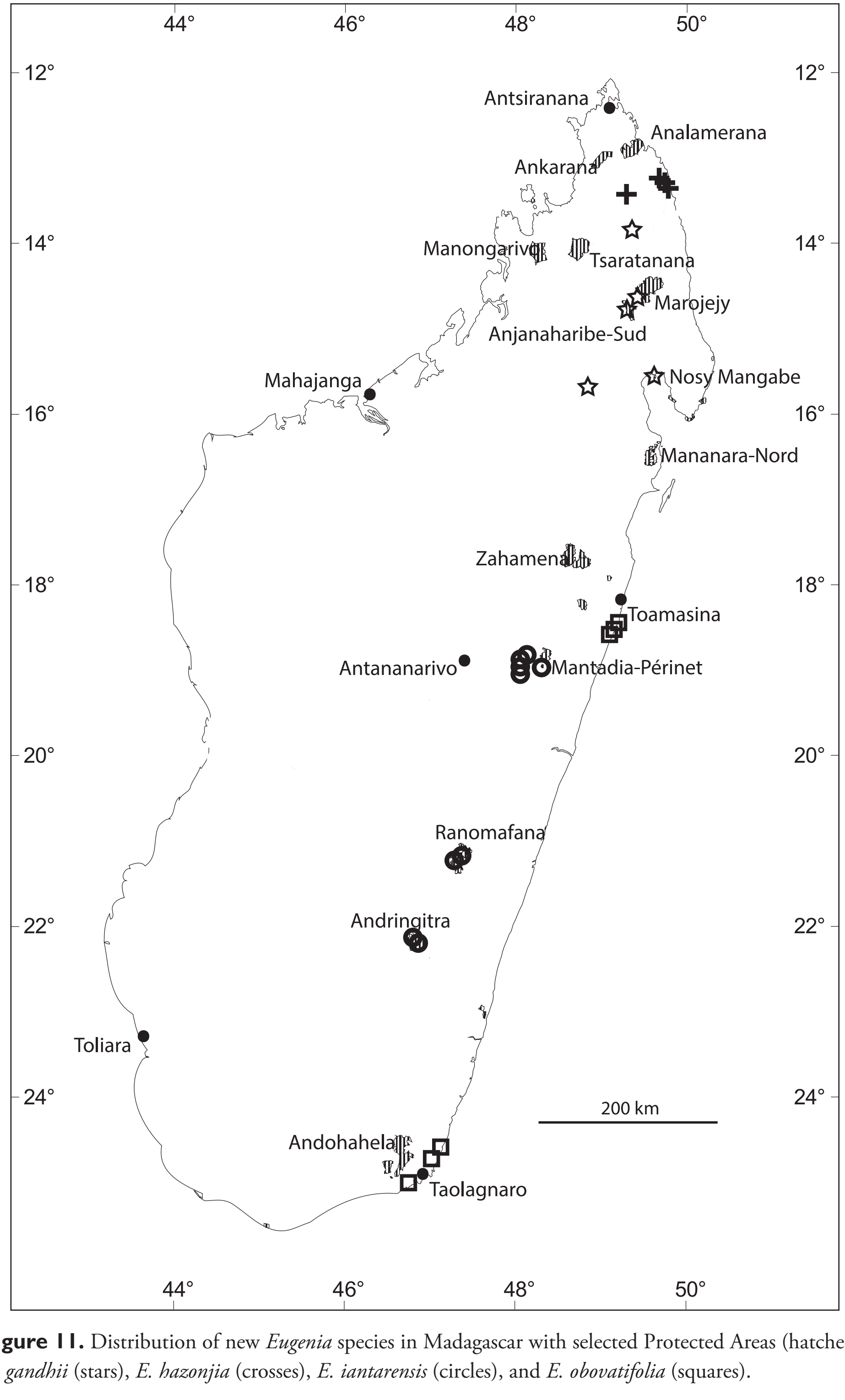


Figure 11. Distribution of new *Eugenia* species in Madagascar with selected Protected Areas (hatched): *E. gandhii* (stars), *E. hazonjia* (crosses), *E. iantarensis* (circles), and *E. obovatifolia* (squares).

Specimens examined. MADAGASCAR. Prov. Antsiranana: Vallee de la Lokoho (Nord-est), près d'Amalavanonio, 9-10 January 1949, H. Humbert + G. Cours 22804 (P [P00118089, P00118090]!); Réserve Spéciale d'Anjanaharibe-Sud, aux environs du sommet, 1161–1424m, 14°46'15"S, 49°28'00"E, 21 Mar.–7 Apr. 1994, D. Ravelonarivo 103 et al. (KSP [KSP000010, KSP000011], MO-6135429, P [P04884879]); Réserve Spéciale Anjanaharibe-Sud, Ambodisatrana, aux environs des sommets, 14°32'45"S, 49°35'15"E, 809–1364 m, 25 May–3 Jun. 1994, D. Ravelonarivo et al. 174 (KSP [KSP000013]); Réserve Spéciale d'Anjanaharibe-Sud, village d'Andranotsarabe, suivant la route Nationale d'Andapa-Bealanana de la piste vers à l'W, Ambatomainty, Camp No. 2, 14°44'42"S, 49°27'42"E, 1185–1335 m, 3 Nov. 1994, D. Ravelonarivo 516 + P. Rabesonina (KSP [KSP000012], P[P04885352]); Réserve Spéciale Anjanaharibe-Sud, suivant la piste pour Ambalaheva, haute rivière d'Andramonta, 14°36'40"S, 49°24'12"E, 628–1879 m, 22 Feb. 1996, D. Ravelonarivo et al. 929 (KSP [KSP000015, KSP000014], MO-6135429, P [P05208458]). Toamasina: Maroantsera Tampolo, Péninsule Masoala, env. 1 km NW du camp (site du posé du radeau), 15°42'77"S, 48°58'25"E, 100–200 m, 1 Nov. 2001, O. Poncy 1548 + S. Rapanarivo (K, P [P00373064], TEF); Nosy Mangabe, 5 km from Maroantsetra in the Bay of Antongil, 15°30'S, 49°46'E: all sterile specimens collected by G.E. Schatz + A. Gentry from 13–23 April 1988: 2010 (MO-3599534), 2020 (MO-3599524), 2100 (MO-3598203), 2137 (MO-3598167; P [P05156045]), 2197 (MO-3596402), 2210 (MO-3596403), 2261 (MO-3597989), 2294 (MO-3597957), 2296 (MO-3597954).

Eugenia hazonjia N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146893-1
holotype (Figure 12): http://www.tropicos.org/Image/100314908

Haec species a congeneris madagascariensibus ramificationis ordinatione V-formi, lamina foliari elliptica vel late elliptica basi cuneata apice rotundata usque late acuta, costa adaxialiter plana atque bracteolis cupulatis base latis distinguitur.

Type. MADAGASCAR. Prov. Antsiranana: Fiv. Vohemar. Fir: Nosibe. Fkt: Anjiabe, 13°04'42"S, 49°54'13"E, 25 m, 2 Nov. 2002, J. Rabenantoandro 1089 + R. Rabevohitra, G. McPherson, H. Ranarivelo, C. Claude & M. Sola (holotype: MO-6038336!, isotype: P [P05208261]!).

Description. Shrubs or small trees 2–5 m; dbh 5 cm; bark of main bole unknown. Herbage glabrous except as noted. Branchlets strongly laterally compressed on emergence but becoming terete, drying light brown to light gray, sometimes slightly striate, oil glands sparse. Leaves mostly evenly distributed, coriaceous, venation brochidodromous, discolorous, surfaces matte and sometimes slightly undulate. Axillary colleters absent. Petioles 1–3 mm, flattened adaxially, sometimes slightly sulcate basally. Leaf blades (2.0–)2.5–4.0 × (1.0–)1.5–3.3 cm, elliptic to broadly elliptic, base cuneate, apex rounded or obtuse to (occasionally) broadly acute, margins usually slightly rev-

MADAGASCAR

MYRTACEAE
Eugenia aff. scottii

but K glab pal. 15 mm

Antsiranana
Fiv: Vohemar. Fir: Nosibe. Fkt: Anjiabe. Forêt littoral sur sable d'Anaborano près du Lac Sahaka. Récolté avec: R. Rabevohitra, G. McPherson, H. Ranarivelo, Jean Claude (guide), M. Sola (CLS). Echantillons préserves en alcool.
13°04'42"S 049°54'13"E 25 m

Petit arbre, 5 m, calice vert jaune, corolle rose. Nom local: Hazonjia.
2 Novembre 2002

J. Rabenantoandro et al. 1089
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Holotype of: Eugenia hazonjia N. Snow

Ref.

Missouri Botanical Garden (MO)

Figure 12. Holotype specimen of *Eugenia hazonjia* (MO).

olute; adaxial surface oil glands common to dense but faint, midvein flush; abaxial surface midvein flush except proximally, oil glands common to dense (sometimes faint), secondary veins indistinct, intramarginal vein 1–2 mm from edge at midpoint of blade. Inflorescence of terminal or axillary monads, these solitary, paired, or (especially at apex) fasciculate. Pedicels 8–18 mm, ascending, stiff. Bracteoles 2, 1.0–1.5 mm, broadly ovate and cuplike (sometimes keeled), rigid, minutely and sparsely ciliate proximally (use magnification). Hypanthium 2.5–3.0 mm, cupuliform, oil glands dense. Calyx lobes 4, 3–5 mm, broadly rounded, apex obtuse, sparsely short ciliate, prominently glandular, greenish. Petals 4, 8–11 × 6–7 mm, obovate to broadly obovate, glabrous, pink. Stamens >150, multiseriate, staminal disk densely short-hairy; filaments 5–9 mm; anthers 0.6–0.9 mm, ellipsoid, basifixed, connectives with a single (but faint) apical gland. Styles up to 8 mm; stigma narrow and scarcely if at all capitate. Fruits unknown.

Etymology. Named after the local vernacular name *hazonjia*, which is recorded on two specimen labels.

Phenology. Flowering September through December; fruiting unknown.

Distribution. Known from Antsiranana Province in north-eastern Madagascar approximately 30 km northwest of Vohemar and in the Daraina region (Fig. 11).

Habitat and ecology. From littoral forest on sand and dry deciduous forest; 15–1015 m.

Conservation status. With an EOO of 39 km^2, an AOO of 27 km^2 and two subpopulations, one of which is located within in the temporarily protected Loky-Manambato area, *Eugenia hazonjia* is assigned a preliminary risk of extinction of "Endangered" [EN B1ab(iii)+2ab(iii)] following the IUCN Red List Categories and Criteria (IUCN 2012). The new species appears to be hightly restricted in its distribution, and the lowland evergreen tropical and littoral forests where it grows is under threat. Its definitive protection likely would allow downlisting to "Vulnerable".

Comments. *Eugenia hazonjia* somewhat resembles *E. urschiana* H. Perrier, but the latter has longer petioles and shorter pedicels. It resembles even more closely a specimen (Rabevohitra 5044 et al.) form the eastern side of Ile Sainte Marie approximately 420 km south, but which has a moderately dense indumentum on the hypanthium and pedicels of dibrachiate, ferrugineous trichomes, and a staminal disk with significantly longer and more erect trichomes.

Specimens examined. MADAGASCAR. Prov. Antsiranana: Vohemar, Nosibe, Fkt: Anjiabe, Anaborano, Fôret littorale d'Analabe, Mosorolava, 13°05'41"S, 49°54'21"E, 24 Sept. 2004, H. Manjakahery 17 (MO-6308382); Vohemar, Nosy-Be, Anjiabe, forêt de Lac Sahaka, Anaborano, 13°04'49"S, 49°54'14"E, 9 Dec. 2007, R. Randrianaivo 1505 + S. Randrianasolo, R. Rakotondrajaona, V. Beninjara, C. Claude, Cyprien & M. Sola (G, MO-6250496); Loky Manambato, Daraina, forêt d'Antsahabe, 13°12'59"S, 49°32'47"E, 1015 m, 1 Dec. 2004, Gautier 4799 (G, P [P05094974]); *ibid. loc.*, 900 m, 6. Dec. 2004, L. Gautier 4842 + L. Nusbaumer (G [G00019226], P [P04827946], TEF n.v.).

Eugenia iantarensis N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146894-1
holotype (Figure 13): http://www.tropicos.org/Image/100314910
living material: http://www.tropicos.org/Image/100146017

Haec species a congeneris madagascariensibus foliis abaxialiter secus costae partem proximalem glandulis oleiferis manifestis ornatis, fructu permagno atque seminibus testa externa profunde sulcata convolutaque distinguitur.

Type. MADAGASCAR. Prov. Fianarantsoa: Andringitra, Camp I, ca. 45 km S of Ambalavao, east bank of Iantara River, along Ambalamanenjana-Ambatomboay trail, edge of Andringitra Reserve, 22°13'20"S, 47°01'29"E, 20 m, 15–21 Nov. 1993, B. Lewis 776 + J. Raharimalala, G. Rahajasoa, M. Randriambololona & J. McDonagh (holotype: MO-6224855!]; isotypes: KSP [KSP000052]!, P, TAN).

Description. Shrubs or trees, 3–9 m tall; dbh 6–10 cm; bark of main bole unknown. Vegetative and reproductive parts glabrous or (as noted) moderately to densely sericeous (trichomes dibrachiate and ferrugineous). Branchlets somewhat compressed laterally but becoming terete, becoming irregularly wrinkled in age, oil glands common, prominent and somewhat protruding initially but fading with age, grayish brown. Leaves concentrated mostly at branchlet tips, only 1–2 leaves produced during seasonal growth, the pairs ca. 1–1.5 cm distant; blades coriaceous, venation brochidodromous, surface and margin flat or slightly sinuous, somewhat discolorous, matte above and below. Axillary colleters absent. Petioles 6.5–10.5 mm long, rounded above, eglandular, shedding an outer (grayish or light brownish) epidermal layer with age. Leaf blades (9)11.5–22 × (3.4)5–8.7 cm, elliptic (or infrequently narrowly elliptic, narrowly obovate or obovate), base cuneate, apex obtuse; adaxial surface oil gland dense, easily seen with magnification, midvein sulcate but becoming flush apically, secondary veins protruding slightly; abaxial surface sparsely to moderately sericeous (hairs dibrachiate, ferrugineous) but becoming glabrous, oil glands common (notably less dense than adaxial), midvein protruding (and with punctate glands, especially proximally), punctate, striate, secondary veins somewhat protruding (moreso than on adaxial surface), intramarginal vein connecting tips of secondaries arching moderately, 1.5–3.3 mm from margin at laminar midpoint. Inflorescence of terminal, axillary or ramiflorous monads, solitary to paired or occasionally in few-flowered fascicles. Pedicels 8–21 mm long (in fruit), 1.8–3.5 mm wide, round in transverse section, rigidly stiff, ascending, sparsely hairy (use high magnification) or evidently glabrous, eglandular, somewhat striate, the epidermis reddish and eventually cracking in small irregular flakes, anthopodia and metaxyphylls lacking. Bracteoles (only one seen) evidently broadly triangular, ca. 2 mm long. Calyx lobes 4, 5.5–8.8 mm long, broadly rounded, apex obtuse, hairy towards based but otherwise more or less glabrous adaxially, moderately to densely hairy abaxially, bifacially glandular, persisting in fruit and tearing somewhat beneath the based as fruit matures, green to cream-colored or magenta above. Petals violet (Ratolojanahary 88). Staminal disk (in mature fruit) 7–16 mm wide, glabrous. Stamens (estimated from basal scars) 150+. Style (material scant) ca. 9 mm long, glabrous; stigma narrow (scarcely if at all capitate). Ovary 2-locular; placentation axile; ovules up to 5 per locule and radiating from central position. Berries 3.2–4.1 × (1.6)2.4–5.0 cm, irregularly globose and often with 3-numerous irregular lobes (from maturing seeds), densely shortly sericeous, pale green immature becoming grayish-brown when fresh but drying light rusty-brown by virtue of indumentum, outer wall embedded with numerous straight, more or less evenly spaced vertical veins extending between base and apex. Seeds 3–15 per fruit (up to 8 per locule), 17–25 mm long, up to ca. 15 mm thick (shrinking considerably away from seed coat during drying), radiating out from placenta (narrowed towards attachment point); seed coat thickly membranous to somewhat leathery, eglandular, separating easily from embryo, surface drying irregularly bullate, light reddish brown; cotyledons evidently completely fused.

Etymology. The specific epithet is a Latinization of the Iantara River, location of the type gathering.

Vernacular names. Rotramena vaventiravina (Kotozafy 922); rotra (Antilahimena 6914).

Phenology. Flowering March through November; fruiting November and December.

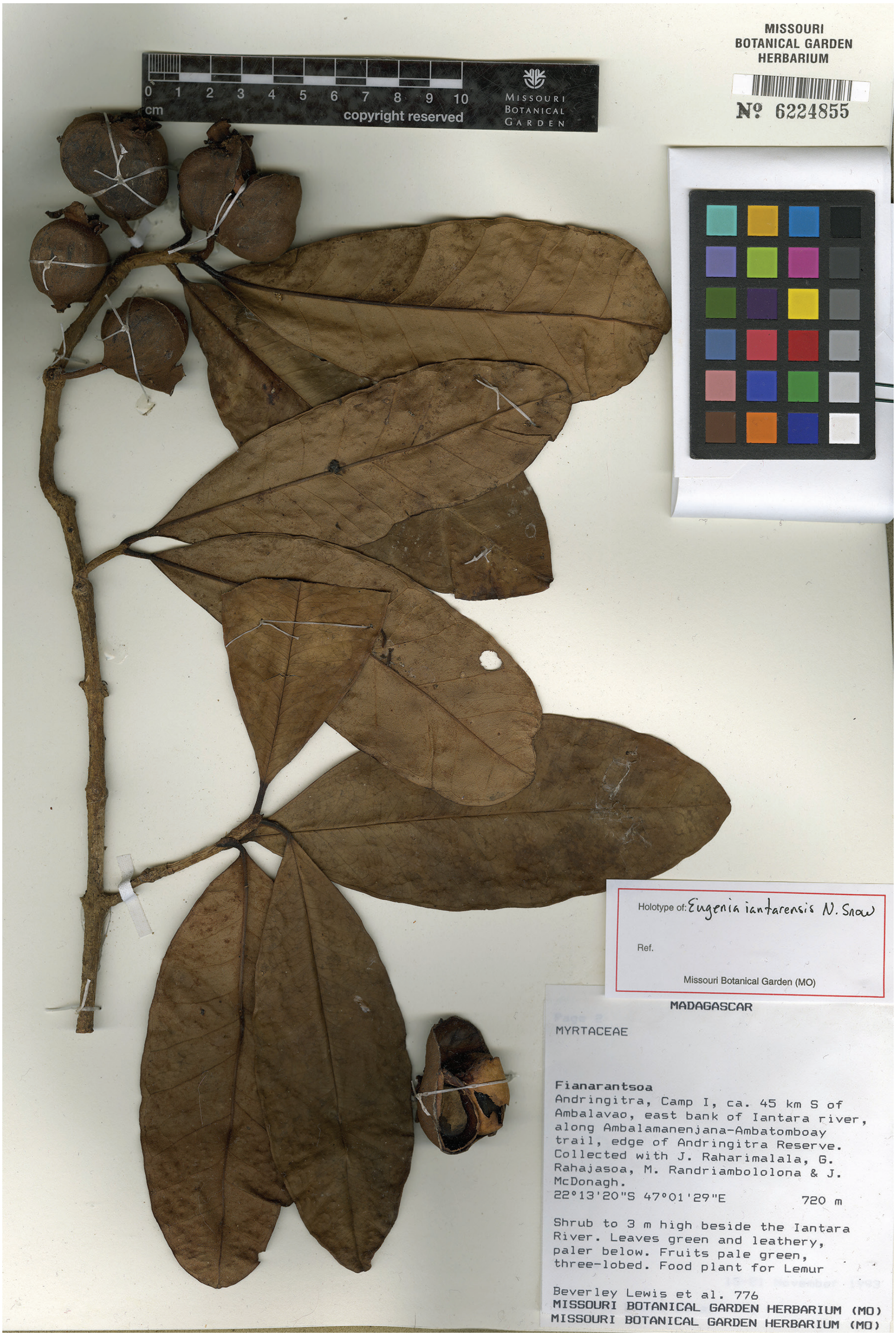
Distribution. Known from the eastern escarpment of Madagascar in Finarantsoa and Toamasina provinces around and in the Andringitra, Ranomafana and Analamazaotra Special Reserve (Fig. 11).

Habitat and ecology. Evidently along or near rivers in humid forest, sometimes in disturbed areas; from 770–1210 m. The type collection indicates the plant, presumably the large fruits, is used by the Common brown lemur, *Eulemur fulvus*.

Conservation status. With an EOO of 4,892 km^2, an AOO of 81 km^2 and three subpopulations, all of which are situated within the protected area network (Andringitra, Ranomafana and Analamazaotra), *Eugenia iantarensis* is assigned a preliminary status of "Least Concern" [LC] following the IUCN Red List Categories and Criteria (IUCN 2012).

Comments. The flowering and early fruiting material (Toamasina Province) and mature fruiting material (Finarantsoa) are disjunct and the flowering material is somewhat incomplete (no petals), but apart from slightly shorter leaves in Toamasina the specimens match well.

Mature fruits are among the largest yet known among Malagasy *Eugenia*, and the large number of seeds per fruit (up to 13) is considerably greater than that commonly seen for *Eugenia* worldwide or in Madagascar. The testa in dried material becomes highly furrowed-convoluted to resemble the surface of a human brain, likely due only in part to shrinkage from dessication. A similar testal morphology was recently described in *Eugenia alletiana* Baider & Florens from Mauritius (Baider and Florens 2013), although the testa of that species at maturity was said to be as firm as the texture of wood. The selective pressures underlying the evolution of such a thick and tough testa are worthy of consideration in light of the observation on the holotype label that the trees are used by brown lemurs. The walls of the fruit and testa frequently have bore holes of an unknown insect of ca. 2 mm diameter.



Holotype of: Eugenia iantarensis N. Snow

Ref.

Missouri Botanical Garden (MO)

MADAGASCAR

MYRTACEAE

Fianarantsoa
Andringitra, Camp I, ca. 45 km S of Ambalavao, east bank of Iantara river, along Ambalamanenjana-Ambatomboay trail, edge of Andringitra Reserve. Collected with J. Raharimalala, G. Rahajasoa, M. Randriambololona & J. McDonagh.
22°13'20"S 47°01'29"E 720 m

Shrub to 3 m high beside the Iantara River. Leaves green and leathery, paler below. Fruits pale green, three-lobed. Food plant for Lemur

Beverley Lewis et al. 776
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 13. Holotype specimen of *Eugenia iantarensis* (MO).

Specimens examined. MADAGASCAR. Prov. Fianarantsoa: Parc National de Ranomafana, 21°15'S, 47°25'E, 1045 m, 5 Dec. 2007, J. Renoult Ma07-225 (P [P05208539]); Parc National de Ranomafana, Parcelle II d'Ambodiamontana, Parcelle II de Talatakely, 21°16'S, 47°26'E, 950 m, 14 Mar. 1995, A. Kotozafy 922 (KSP [KSP000050, KSP000051], MO-04940615, P [P05208460]); Andringitra RN. Ivohibe, à l'W d'Ambarongy, au NE du campement no. 3, sur la piste à l'E du campement no. 3 vers le campement no. 4, 22°13'22"S, 46°58'18"E, 1210–1625 m, 8–11 Dec. 1994, C. Rakotovao 287 (MO-6224856, MO-5474705 [carpo.], P [P04884880]). Prov. Toamasina: Ampitambe, Ambatovy, Sahaviara forest, 18°52'19"S, 48°16'43"E, 1035 m, 9 Nov. 2005, P. Antilahimena 4143 & F. Edmond (MO, P [P05094984]); Ampitambe, Ambatovy, 18°51'39"S, 48°16'27"E, 943 m, 15 Dec. 2005, P. Antilahimena 4384 (MO, P [P00730616]); Ambatovy, Antaralava Besalampy forest, 18°53'15"S, 48°16'09"E, 950 m, 15 Nov. 2008, Antilahimena 6905 (MO-6447003, P [P00730615]); Ambatovy, Sahaevo, 18°50'26"S, 48°16'3"E, 982 m, 23 Nov. 2008, P. Antilahimena 6914 + B.A. Ratodimanana, D. Ravelonarivo, E. Félix & M. Ratovomanana (MO-6447031); Fkt: Ambohibolakely, forêt d'Amparihy, corridor Forestier Analamay Mantadia, 18°47'28"S, 48°22'46"E, 1001 m, 23 Apr. 2012, C. Rakotovao 5783 (P [P00730613]); Ampitambe, Ambatovy, forêt d'Ampadidifanantsy, 18°51'46"S, 48°16'32"E, 975 m, 27 Oct. 2008, M. Ratolojanahary 88 (MO-6453743, P [P04680790]); Forêt d'Analamazaotra, [18.56'S, 48.26'E], 3 Dec. 1934, Ursch 20 (P [P05208538]).

Eugenia malcomberi N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146895-1
holotype (Figure 14): http://www.tropicos.org/Image/100314912

Haec species a congeneris madagascariensibus folia grandia habentibus foliis late ellipticis ad basem rotundatis plerumque plus quam 15 cm longis distinguitur.

Type. MADAGASCAR. Prov. Toliara: NW of Tolagnaro, Reserve Naturelle Integrale #11 (Andohahela) parcelle I, NW of Eminiminy, beside River Itrotroky, 24°38'S, 46°46'E, 500–1000 m, 6–13 Feb. 1993, S. Malcomber 2117 + H. van der Werff, C. Hemingway, M. van Bergen, S. Rapanarivo, P.J. Rakotomalaza, O. Andrianantoanina & B. Randriamampionona (holotype: MO-6277745!; isotypes: KSP [KSP000046]!, P [P05131986]!, TAN).

Description. Trees to 6 meters tall; bark of main bole unknown. Indumentum (where noted) of vegetative and reproductive material sericeous (hairs dibrachiate and typically reddish or brownish). Emerging (youngest) branchlets laterally compressed, sparsely hairy, glandular, color uncertain; older branchlets becoming terete, soon glabrous, mostly eglandular, becoming brownish-gray, smooth. Leaves evenly distributed along branchlets (nodes greater than 9 cm apart), coriaceous, venation brochidodromous, strongly discolorous, matte above and below. Axillary colleters present (type A;

Holotype of: Eugenia malcomberi N. Snow

Ref.

Missouri Botanical Garden (MO)

MADAGASCAR

MYRTACEAE
Eugenia

TOLIARA
NW of Tolanaro, Reserve Naturelle Integrale #11 (Andohahela) parcelle I, NW of Eminiminy, beside River Itrotroky. Plants preserved in alcohol. With H. van der Werff, C. Hemingway, M. van Bergen, S. Rapanarivo, P.J. Rakotomalaza, O. Andrianantoanina & B. Randriamampionona.
24°38'S 46°46'E 500–1000 m

Tree 6 m tall; flowers white; fruit green.

6-13 February 1993
S. Malcomber 2117
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 14. Holotype specimen of *Eugenia malcomberi* (MO).

Snow et al. 2003) on youngest emerging leaves, otherwise absent. Petioles 8–11 mm long, flattened above, sparsely hairy upon emergence but becoming glabrous, glandular (particularly above adjacent to blade). Leaf blades 14.7–22.6 × (9.3–)10.0–)12.5 cm, broadly elliptic (mostly) or ovate, base rounded, margin and blade surface flat, apex and tip acute; abaxial surface sparsely hairy at emergence becoming glabrous, oil glands prominent (becoming less so), midvein broad (1.5–2.0 mm wide) and flush at emergence but becoming slightly sulcate in older leaves at least proximally; abaxial surface glabrous, oil glands sparse to moderate on laminar surface but common on midvein, midvein protruding but becoming flush or nearly so towards apex, secondary and intramarginal veins prominent, the veins connecting secondaries also prominent and broadly arching; intramarginal vein relatively faint, irregularly sinuous and 2–3 mm from midpoint at laminar margin. Inflorescence mostly ramiflorous or axillary, fasciculate clusters and comprised monads and triads to 5–7-flowered cymes. Bracteoles 1.1–1.8 mm × ca. 0.5 mm, ovate, sparsely hairy, glandular, mostly persisting during anthesis. Hypanthium 4.3–4.5 × 4.0–5.3 mm wide below base of calyx lobes, cupulate, sparsely to moderately hairy especially towards base, oil glands common to dense. Calyx lobes 4, 3.5–6.5 mm long, rounded to broadly obovate, apex obtuse, sparsely ciliate, oil glands moderately common and projecting (especially lower surface), consisting of two longer (inner) lobes and two shorter outer lobes (the bases of the outer lobes covering the bases of the inner lobes in bud), evidently whitish in flower. Petals 4 (5 on one flower), 11–17.5 × 6–12 mm, obovate to widely obovate, glabrous, white, oil glands sparse to common and pronounced. Staminal ring ca. 3.5–4.5 mm in diameter, glabrous. Stamens (estimated) 100–150; filaments 5–13 mm long; anther sacs 0.7–0.9 mm long, globose to subcylindrical; connective bearing one faint apical gland or eglandular. Ovary apex glabrous. Style 10–13 mm long, glabrous, eglandular; stigma narrow (barely if at all swollen). Berries not seen, indicated as being green on specimen label.

Epynomy. The new species honors Dr. Simon Malcomber (b. 1967), who collected the type material and nearly two thousand specimens from Madagascar in the early 1990s.

Phenology. Flowering in early February; fruiting probably late February through at least mid-March.

Distribution. Known only from the type gathering in Toliara in parcelle I of the Reserve Naturelle Integrale #11 northwest of Taolognaro, in south-western Madagascar. This region is near the southern terminus of the humid forests that occur east of the main escarpment that run latitudinally along much of the length of Madagascar (Fig. 4).

Habitat and ecology. The species was collected in a riverine habitat in a rainforest. Some of the (undistributed) type material is heavily clothed in epiphytic mosses, Hymenophyllaceae, and lichens.

Conservation status. *Eugenia malcomberi* occurs in the Andohahela protected area (parcel I). No indication was provided on the label about its relative abundance at the time it was collected. Google™ Earth imagery (April 2013) shows a more or less continuous band of primary forest extending ca. 42 km south and ca. 135 km northeast, and ca. 10 km wide (east to west) at comparable elevations from the type locality. Considering its occurence in a nature reserve in fairly rugged terrain with considerable topographic relief, but also because it is known only from a single subpopulation with an AOO of 9 km^2, *Eugenia malcomberi* is assigned a preliminary risk of extinction of "Vulnerable" [VU D2] following the IUCN Red List Categories and Criteria (IUCN 2012).

Comments. The petals during anthesis are quite large relative to the size of the flower buds, suggesting that they enlarge rapidly during early anthesis.

Eugenia manomboensis N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146896-1
holotype (Figure 15): http://www.tropicos.org/Image/100317960

Haec species a congeneris madagascariensibus petiolo longo, lamina foliari grandi elliptica, pedicello crasso atque fructu grandi globulari laevi distinguitur.

Type. MADAGASCAR. Prov. Fianarantsoa: Région Atsimo-Atsinanana, Dist. Farafangana, comm. Ankarana, Réserve Spéciale de Manombo, parcelle I, forêt d'Anaviavy, 23°00'S, 47°44'E, 12 m, 17 Sep. 2005, R. Razakamala 2136 (holotype: MO-2590168! isotypes: KSP [KSP000043]!, P [P04776395]!, TAN).

Description. Trees to 8 m tall. Foliage glabrous and without evident oil glands except as noted. Branchlets round to somewhat laterally compressed, drying brown to light brown; bark smooth but cracking slightly longitudinally. Leaves stiffly coriaceous, opposite or sometimes three per node, evenly distributed along branchlets, discolorous, somewhat glossy adaxially, matte abaxially. Axillary colleters absent. Petioles 25–35 mm, terete or slightly sulcate. Leaves 16–18 × 6.5–10.5 cm, elliptic, base slightly cuneate to mostly rounded, apex obtuse, surface and margin more or less flat; adaxial surface with impressed midvein in lower ½ to 2/3, becoming flush distally; abaxial surface with dense but small oil glands (faint, use high magnification); secondary veins indistinct, arising at 40–50° angle but mostly too faint to count with confidence; intramarginal vein indistinct to barely visible, 1.5–2.5 mm from margin at midpoint of blade. Inflorescence up to 7 cm, structure uncertain but evidently of triads or botryoids, these solitary in leaf axils. Pedicels 4–14 mm, stiff and thick. Flowers mostly unknown. Calyx lobes (from dried fruit) 4, 3–5 mm, broadly rounded (much broader than long in fruit), persistent in fruit. Fruit 25–30 × 25–30 mm, globose.

Etymology. The specific epithet is derived from the Réserve Spéciale de Manombo, the only known occurrence of this prominent species.

Phenology. Fruiting mid September; likely flowering by August (unconfirmed).

Distribution. Known only from the type gathering in south-eastern Madagascar in Fianarantsoa from Réserve Spéciale de Manombo, near the coast (Fig. 7).

Figure 15. Holotype specimen of *Eugenia manomboensis* (MO).

Habitat and ecology. Dense, humid, low-altitude forest over lateritic soils.

Conservation status. *Eugenia manomboensis* occurs in the Réserve Spéciale of Manombo. Considering its occurrence in a natural reserve, but also because it is known only from single subpopulation (AOO of 9 km2), *Eugenia malcomberi* is assigned a preliminary risk of extinction of "Vulnerable" [VU D2] following the IUCN Red List Categories and Criteria (IUCN 2012).

Comments. Large-leaved but indetermined speicmens of Malagasy *Eugenia* with large fruits have not been matched closely with flowering material in some cases. However, given that none of the larger-leaved species have petioles as thick or as long as *Eugenia manomboensis*, no others are known from near the type locality, and no large-leaved species present globular fruits of this size, it appears that this species has not been named previously.

It seems likely that the large fruits of this tree are consumed by local widelife.

Eugenia obovatifolia N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146897-1
holotype (Figure 16): http://www.tropicos.org/Image/100314904

Haec species a congeneris madagascariensibus foliis anguste obovatis atque inflorescentiis glabris saepe ramifloris distinguitur.

Type. MADAGASCAR. Prov. Toliara: Fokontany: Sainte Luce, 24°46'15"S, 47°10'15"E, 5 m, 5 Nov. 2003, J. Rabenantoandro 1592 + A. Monja (holotype: MO-6038332!; isotypes: P [P04885376]!, TAN).

Description. Trees 5–14 m; dbh 14–28 cm; bark of main bole unknown. Indumentum (where indicated) of short, ferrugineous, dibrachiate hairs that become increasingly white or grayish. Branchlets rounded laterally compressed, densely short-hairy becoming glabrescent; light brown to light gray (dried). Leaves concentrated near branch tips, coriaceous, surfaces matte. Axillary colleters absent. Petioles 4–8 mm, terete, pubescent when emerging. Leaf blades (3.0–)4.5–6.5 × 1.5–2.5 cm, narrowly obovate (or infrequently ovate); base narrowly cunate; apex obtuse or somewhat acute; margins flat but drying somewhat revolute; adaxial surface glabrous or moderately hairy (especially proximally), oil glands dense (but small; use magnification) on emergence but becoming less visible, midvein slightly sulcate to flush; abaxial surface moderately hairy, oil glands dense but faint; secondary veins 8–15, alternating along midvein, faint; intramarginal vein not visibile. Inflorescences ramiflorous, less than 1.5 cm long, solitary or more commonly fasciculate, of monads, triads, or short botryoids. Pedicels 1–5 mm, stiff, ascending, sparsely hairy to glabrous. Bracteoles 2, ovate, 0.5-1.0 × < 0.5 mm, rigid, sparsely hairy on margins. Hypanthium 2–3 mm, cuplate to obconic, glabrous to densely ferrugineous-hairy, densely glandular (glands relatively large). Calyx lobes 4, 1.5–2 mm, two each relatively large and small, broadly rounded (much broader than long), apex obtuse, sparsely minutely hairy marginally near apex,

Holotype of: Eugenia obovatifolia N. Snow

Ref.

Missouri Botanical Garden (MO)

Eugenia

MADAGASCAR

MYRTACEAE
Eugenia cloiselii H. Perrier

det. J. Rabenantoandro, 2003
Toliara

Fivondronana: Fort-Dauphin, Firaisana: Mahatalaky, Fokontany: Sainte Luce. Forêt littorale sur sables de Sainte Luce, bloc S9 près du premier marécage. Echantillon préservé en alcool.
24°46'15"S 47°10'15"E 5 m

Arbre de 14m de haut, dhp: 28cm. Présence de fruits vert-pâles.
05 Nov 2003

Johny Rabenantoandro & A. Monja 1592
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 16. Holotype specimen of *Eugenia obovatifolia* (MO).

otherwise glabrous, greenish to cream colored. Petals 5–8 × 5–6 mm, elliptic to ovate, glabrous, whitish to pink or violet, oil glands sparse but easily visible. Stamens ca. 30–50, multiseriate; staminal disk short-hairy, ca. 1.5 mm diameter; filaments 3–5 mm, white; anthers ca. 0.5 mm, globular, basifixed, eglandular, light yellow. Styles 5–7 mm, glabrous; stigma narrow. Berries not seen, but labels indicate pale green (probably immature).

Etymology. In reference to the shape of the leaf blades.

Vernacular name. Ropsay (Rabenantoandro 366).

Phenology. Flowering September, November, and January; fruiting August through December.

Distribution. East-central Madagascar in Toamasina Province and south-eastern in Toliara Province from Mandena to Sainte Luce (Fig. 11).

Habitat and ecology. Littoral forest over sand; elevation ca. 5–53 m.

Conservation status. With an EOO of 8,333 km^2, an AOO of 63 km^2 and four subpopulations, none of which are situated within the protected network, *Eugenia obovatifolia* is assigned a preliminary risk of extinction of "Endangered" [EN 2ab(i, iii, iv)] following the IUCN Red List Categories and Criteria (IUCN 2012). The new species seems to be restricted to the highly threaten littoral forests and none of the known populations are currently protected.

Comments. *Eugenia obovatifolia* has a general resemblance to *E. arenicola* H. Perrier, *E. hazompasika* H. Perrier, and *E. cloiselii* H. Perrier given its ramiflorous, more or less fasciculate inflorescences. The four species also grow in relative proximity in southeastern and eastern Madagascar, often in sandy littoral forests, and may form a species complex that ranges approximately 1300 km between Taolognaro and Sainte Luce along the coast and somewhat inland to Vatomandry.

Eugenia obovatifolia differs from *E. arenicola* by its more or less glabrous leaves, whereas those of the latter are densely ferrugineous-hairy upon emergence and retain much of the indumentum on the abaxial surface. *Eugenia obovatifolia* differs each from *E. cloiselii* and *E. hazompasika* by virtue of the glabrous (or nearly so) inflorescences, which contrast with the hairy inflorescences of the latter two.

Several indetermined specimens cannot be confidently placed yet given variation in leaf morphology and indumentum (e.g., Razanatsima 31 + Ranaivojaona; Ranaivojaona 1177 + Razanatsima; Razanatsima 711 + Céléstin; Rakotovao 3755 et al. [all at MO]). However, including all of these taxa and specimens into one highly heterogenous species likely would equate to the inappropriate lumping of several independently evolving lineages.

Specimens examined. MADAGASCAR. Prov. Toamasina: Fokontany: Andravokoditra, 18°34'53"–18°34'20"S, 49°14'42"–49°14'54"E, 7 Jan. 2003, R. Ludovic 228 & F. Rakotoarivony (MO-6038324); Hotel Pangalan on Lake Ampitabe, west of Andranokoditra, 18°35'S, 49°14'E, S.K. Pell 607 + J.D. Mitchell & A. Randrianasolo (MO-5887243); Fokontany: Andranonkoditra Vohibola du côté de l'hôtel Pangalane, 18°35'32"S, 49°14'02"E, 11 Feb. 2003, J. Rabenantoandro 1248 + R. Rabevohitra, P. Lowry, R.Razakamalala & S. Lowry (MO-6038325); Ambinaninony, Andranokoditra, Akinin'ny nofy, 18°34'12"S, 49°14'18"E, 3 Aug. 2003, R. Razakamalala 664 & D. Rabehevitra (MO-6038323); Ambila-Lemaitso, 18°49'S, 49°08'E, 14 Dec. 1967, Service Forestier 28034 (B, BR, G, K, MO-6321087, NY, WAG). Prov. Toliara: Mandena, Jardin Botanique, M16-QMM, Ampasy, Taolagnaro, 24°57'05"S, 47°00'11"E, 26 Sep. 2000, J. Rabenantoandro 241 + P. Lowry, R. Rabevohitra, L. Randrihasipara, & E. Ramisy (MO-5598572); Saint-Luce (Manafiafy), S9, Mahatalaky, Taolagnaro, 24°46'30"S, 47°10'20"E, 16 Dec. 2000, J. Rabenantoandro 366 + F. Lucien & E. Ramisy (MO-5728973); Manambaro, Petriky, 25°03'43"S, 46°52'06"E, 15 Nov. 2006, Ramison 33 (MO-6427490).

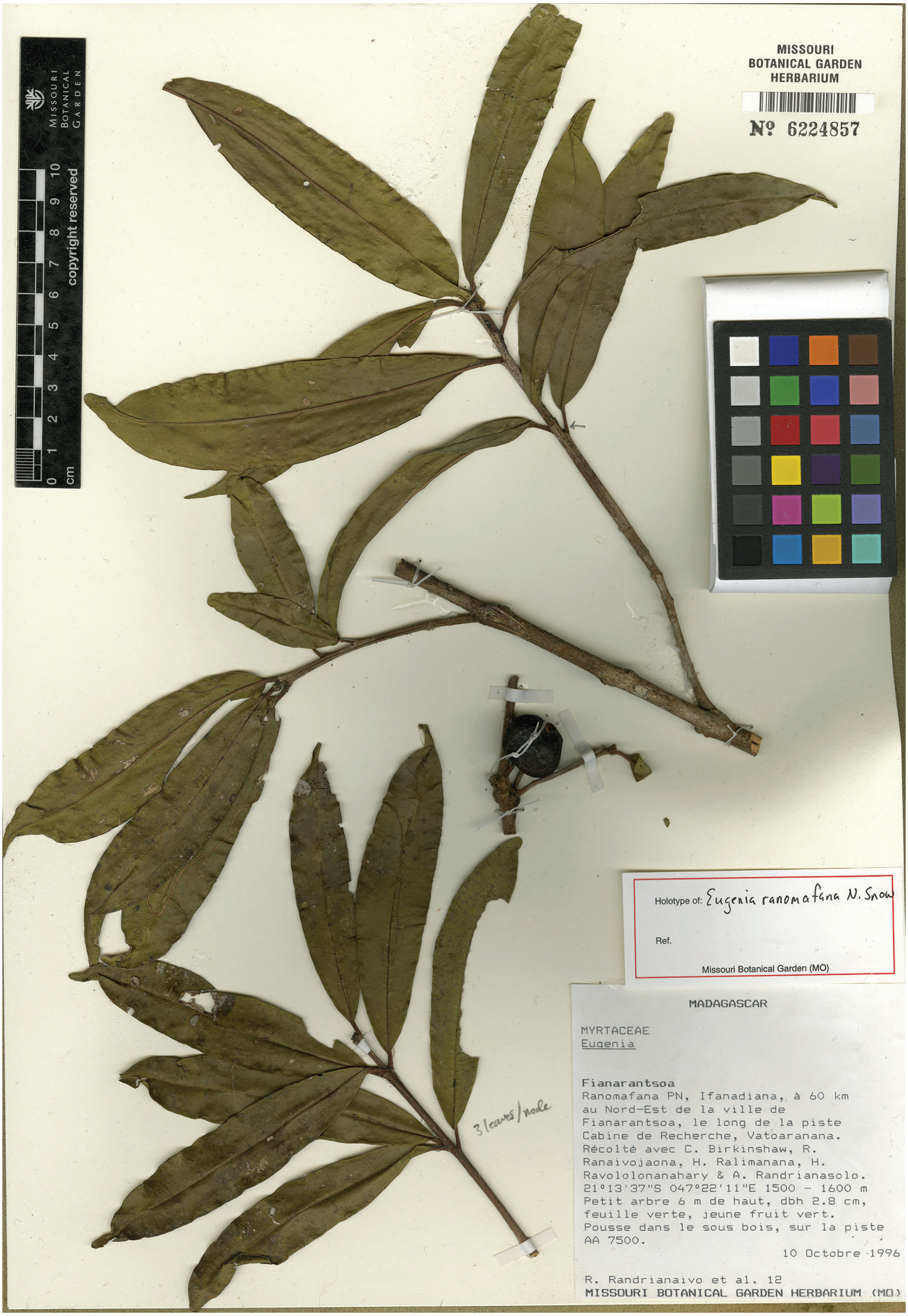
Eugenia ranomafana N. Snow & D. Turk, sp. nov.

urn:lsid:ipni.org:names:77146898-1
holotype (Figure 17): http://www.tropicos.org/Image/100314914

Haec species a congeneris madagascariensibus ramulis in sectione transversali non profunde sed late sulcatis, foliis saepe 3- vel 4-verticillatis atque hypanthio sub anthesi discoideo distinguitur.

Type. MADAGASCAR. Prov. Fianarantsoa: Ranomafana PN, Ifanadiana, à 60 km au Nort-Est de la ville de Fianarantsoa, le long de la piste Cabine de Recherche, Vatoaranana, 10 Oct. 1996, 21°13'37"S, 47°22'11"E, 1500–1600 m, R. Randrianaivo 12 et al. (holotype: MO-6224857!; isotypes: KSP [KSP000044, KSP000045]!; P [P04885335]!, TAN).

Description. Shrubs or trees, 3–8 m tall; dbh 2.8 cm; bark of main bole unknown. Foliage and flowers glabrous except as noted below. Branchlets laterally compressed to terete but sometimes trigonal in cross section, and irregularly and broadly and prominently sulcate on one or more sides, flaring distally below nodes but becoming rounded; smooth but sometimes striate, sparsely serciceous (trichomes reddish and dibrachiate) but soon glabrous, epidermis reddish or maroon on emergence but becoming irregularly and finely brown-gray mottled (dried material). Leaves opposite to disjunct opposite or whorled in 3s or 4s, concentrated near branch tips; coriaceous; venation brochidodromous; surfaces concolorous, matte; lateral veins 20–32 on each side, arising at an angle of 65–75° from the midrib. Axillary colleters lacking. Petioles 3–7(–12) mm, deeply sulcate adaxially, prominently striate-rugose (especially abaxially), eglandular. Leaf blades (4.4–)6.0–16.0 × (1.9)2.8–3.3 cm, narrowly elliptic, often conduplicate (dried material) in lower ca. 20%, base mostly rounded (sometimes cuneate), apex obtuse but sometimes slightly falcate, margin and surface somewhat sinuous; adaxial midvein deeply sulcate throughout, eglandular; abaxial surface eglandular except on midvein (glands moderately dense and somewhat indistinct); secondary veins consisting of (16–)25–32 pairs, indistinct but slightly raised, diverging at wide angle from midvein; intramarginal vein indistinct, 1.5–2.5 mm from margin of leaf at midpoint of blade. Inflorescence of solitary, paired, or fasciculate and ramiflorous monads. Pedicels (4.5–)8–17 mm, stiff but thin, terete to slightly compressed. Bracteoles 2, 0.5–0.7 × ca. 0.2–0.5 mm, broadly



Holotype of: Eugenia ranomafana N. Snow

Ref.

Missouri Botanical Garden (MO)

MADAGASCAR

MYRTACEAE
Eugenia

Fianarantsoa
Ranomafana PN, Ifanadiana, à 60 km au Nord-Est de la ville de Fianarantsoa, le long de la piste Cabine de Recherche, Vatoaranana. Récolté avec C. Birkinshaw, R. Ranaivojaona, H. Ralimanana, H. Ravololonanahary & A. Randrianasolo. 21°13'37"S 047°22'11"E 1500 – 1600 m Petit arbre 6 m de haut, dbh 2.8 cm, feuille verte, jeune fruit vert. Pousse dans le sous bois, sur la piste AA 7500.

10 Octobre 1996

R. Randrianaivo et al. 12
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 17. Holotype specimen of *Eugenia ranomafana* (MO).

ovate, apex rounded, horizontal to reflexed in fruit, occasionally a few short trichomes. Hypanthium 0.5–1.5 mm long; initially cupuliform but becoming discoid (prominently flattened from above) during and after anthesis, glabrous, oil glands common, cream-colored (fresh). Calyx lobes 4 (but of unequal lengths), the two shorter lobes broader than long, ca. 1.5 × 2.2 mm broad at base, the two longer lobes hemispherical, ca. 2 × 2 mm, glandular, pale green (fresh), persisting or deciduous in fruit, ascending or crowing mature fruit. Petals 4, ca. 4 mm × 3.2 mm, broadly obovate to broadly elliptical, pink, with 9 veins arising from the base. Staminal disk diameter (in fruit) 3.5–5.0 mm; glabrous. Stamens ca. 60–80; filaments (1.5–)4–6 mm, cream-colored; anther sacs ca. 0.5 mm, subglobose to globose, connective apex eglandular; staminal disk glabrous. Style ca. 4–6 mm; stigma narrow. Fruit 11–18 × 8–23 mm, subglobose with irregular lobes (but not costate), base rounded, green (young fresh) but drying dark bluish-black, locules 2, placenta capitate, placentation axile, ovules radiating from center of placenta. Seeds 3–4 per fruit; outer coat leathery, highly contorted, drying to a light yellowish-brown ("fawn") or dull brownish-yellow ("tawny", Beentje 2010).

Etymology. From Ranomafana National Park.

Phenology. Fruiting October and November; flowering May.

Distribution. Known from three collections in Ranomafana National Park in Fianarantsoa Province, southeast-central Madagascar (Fig. 4).

Habitat and ecology. Growing in the undergrowth or subcanopy in humid forests, ca. 950–1600 m. The collection by Turk notes its occurrence with trees of the genera *Weinmannia* L., *Tambourissa* Sonn., *Decarydendron* Danguy, *Ephippiandra* Decne., *Ocotea* Aubl. and *Cryptocarya* R. Br., and understory with *Psychotria* L. and *Oncostemum* A. Juss.

Conservation status. With only three collections known, an AOO of 9 km^2 and one subpopulation, which is situated within the protected area network (Ranomafana), *Eugenia ranomafana* is assigned a preliminary risk of extinction of "Vulnerable" [VU D2] following the IUCN Red List Categories and Criteria (IUCN 2012).

Comments. This species was first recognized as undescribed by Turk (1997) as part of a dissertation studying plants in Ranomafana National Park, who approved of and collaborated with its publication here.

With its narrowly elliptic leaf blades with mostly rounded leaf bases, *Eugenia ranomafana* resembles mostly closely *Eugenia wilsoniana*, the nearest occurrence of which is ca. 280 km northeast. *Eugenia wilsoniana* differs by its shorter stature, leaf margins being flat to only slightly sinuous, longer and thinner (on average) pedicels, presence of axillary colleters, and a hairy staminal disk. In addition, *E. ranomafana* differs by its often trigonous branchlets and the frequent occurrence of 3–4 leaves per node.

Specimens examined. MADAGASCAR. Prov. Fianarantsoa: Ranomafana National Park, parcelle 3, S of National Road 25 at 7 km W of Ranomafana; Talatakely trail system, 21°15'30"S, 47°25'00"E, 950–1150 m, 4 May 1993, D. Turk 436 + J. Randrianasolo, J. Solo, & D. Randriamanatenta (MO, KSP); Ranomafana National Park, Talatakely parcel, Trail System F-TBT-B, 21°15'S, 47°25'E, P. Fritsch 1643 et al. (CAS, MO-6287616).

Eugenia ravelonarivoi N. Snow & Callm., sp. nov.

urn:lsid:ipni.org:names:77146899-1
holotype (Figure 18): http://www.tropicos.org/Image/100314919

Haec species a congeneris madagascariensibus foliis apice abrupte cupidatis caudatisve atque inflorescentiis ramifloris dense fasciculatis distinguitur.

Type. MADAGASCAR. Prov. Antsiranana: SW d'Andapa, Réserve Spéciale Anjanaharibe-Sud, suivant la piste pour Ambalaheva, haute rivière d'Andramonta, 14°36'40"S, 49°24'12"E, 628–1879 m, 22 Feb. 1996, D. Ravelonarivo et al. 930 (holotype: MO-6135426!; isotypes: KSP [KSP000007, KSP000008]!, P [P04885351]!, TAN).

Description. Shrubs or trees, 3–12 meters; bark of main bole unknown. Herbage glabrous except as noted. Branchlets laterally comprssed and shallowly 2-grooved on each side when young below petioles, oil glands common but indistinct, epidermis smooth, green drying light brown. Leaves evenly distributed along branchlets, opposite to disjunct opposite, thinly coriaceous to thickly membranous, discolorous, surfaces matte. Axillary colleters absent. Petioles 7–10 mm, narrowly and deeply sulcate (especially distally). Leaf blades (5.5–)7.5–14 × 3.3–4.8 cm, mostly elliptic but some broadly elliptic or narrowly oblong, base cuneate, apex obtuse, or acuminate and often falcate, margins flat but slightly undulate (dried); adaxial surface midvein deeply but narrowly sulcate to nearly the apex, secondary veins numerous but faint, oil glands absent; abaxial surface lakcking oil glands, secondary veins faint, slightly raised, diverging at ca. 80°; intramarginal vein 0.5–1.5 mm from margin at midpoint of blade. Inflorescences of moderately dense fascicles of monads arising from short brachyblasts, these evidently ramiflorous or cauliflorous (uncertain given that all are detached on herbarium sheets); pedicels 9–15 mm, rigid, irregularly glandular. Bracteoles 2, ca. 0.5–0.8 mm, triangular to ovate, often obscure. Hypanthium ca. 2–2.5 mm, cupuliform to discoid (somewhat flattened) in anthesis, prominently glandular. Calyx lobes 4, 2.0–5.0 mm, broadly oblong to oblate or rounded, often dimorphic (2 shorter, 2 longer), apex broadly rounded, petaloid, oil glands sparse (and mostly abaxial). Petals 4 (material scant), up to 5 mm; indicated as pinkish on a paratype. Staminal ring more or less square, ca. 4 mm per side, sparsely short hairy (use magnification) and glandular. Stamens (material scant) numerous; anthers ca. 0.5 mm, ellipsoid. Styles 6–11 mm, thin, sparsely glandular (especially proximally); stigma narrow. Berries 24–35 × 30–50 mm (dried), subglobular, greenish (mature or nearly so); seeds 1–3, 16–22 × 25–30 mm, subglobular; embryo globular, hypocotyl and cotyledons not differentiated; testa thinnish, drying light brown.

Phenology. Flowering January through April; fruiting March through November.

Distribution. In the northern mountains of Madagascar in Antsiranana and Mahajanga provinces (Fig. 4).

Habitat and ecology. In mid-elevation, wet eastern forests often over granite or gneiss; elevation approximately 630–1880 m but needing confirmation.

Etymology. It is a pleasure to name this species in honor of Désiré Ravelonarivo (b. 1966), a prolific collector of specimens in Madagascar. Désiré is native to the An-

Figure 18. Holotype specimen of *Eugenia ravelonarivoi* (MO).

dapa basin, where he collected the type specimen of *Eugenia andapae* and the only known fruiting specimen of this new species (D. Ravelonarivo 489 & R. Babesonina).

Vernacular name. Gavoalehely (Ravelonarivo 930); gavoala (Ravelonarivo 103).

Conservation status. With an EOO of 436 km^2, an AOO of 36 km^2 and three subpopulations, two of which are situated within the protected area network (Anjanaharibe-Sud), *Eugenia ravelonarivoi* is assigned a preliminary risk of extinction of "Vulnerable" [VU D2] following the IUCN Red List Categories and Criteria (IUCN 2012).

Comments. The label of the type gathering indicates "rougeâtres" (reddish) for petals, but this is doubtful and probably was meant for pinkish, which accords with information on the label of a paratype.

Among existing species, the leaf morphology of *Eugenia ravelonarivoi* resembles that of *E. alatroensis* H. Perrier and *E. vatomandrensis* H. Perrier, but the bases of their leaves are subsessile to sessile, which contrasts with the distinctly petiolate leaves of *E. ravelonarivoi*. In addition, the often cuspidate-caudate aspect of the leaf apex of new species is much more pronounced than of those two species, whose tips are barely (if at all) cuspidate.

Eugenia antongilensis H. Perrier has cuspidate apices on the blade, but it is a much longer leaf with shorter petioles. *Eugenia musicola* H. Perrier also resembles *E. ravelonarivoi*, especially given the membranous to weakly coriaceous texture of the leaf blades; however, the pedicels of the former are much thinner and more lax, and its petioles are shorter and much less (if at all) sulcate adaxially. *Eugenia diospyroides* differs with its generally larger flowers and leaves, and leaves having a rounded apex.

The new species also closely resembles *Eugenia radiciflora* in leaf morphology, but that species is said to have solitary flowers with pedicels only 2–3 mm long, which does not match the fasciculate brachyblasts of *E. ravelonarivoi*. The leaves of *Eugenia ravelonarivoi* also superficially resemble those of *E. gandhii*, but the latter has densely punctate leaf blades and solitary flowers. Finally, *Eugenia ravelonarivoi* resembles closely some evidently undescribed taxa

Dr. David Gordon, an entomologist at Pittsburg State University, indicates that the visible damage on the leaves of some specimens may be from leaf cutter bees (Family Megachilidae), which often damage leaves in this manner to obtain material for the construction of their nests.

Additional specimens. MADAGASCAR. Prov. Antsiranana: SW d'Andapa, Réserve Spéciale d'Anjanaharibe-Sud, aux enrivons de sommet, 14°46'15"S, 49°28'00"E, 1112–1424 m, 21 Mar.–7 Apr. 1994, Ravelonarivo 103 + F. Rasoavimbahoaka, B.T. Rafaliarimanana, H. Rasitefarinina & Motera (P [P04884879]); Massif de l'Anjanaharibe (pentes et sommet N) a l'W d'Andapa (Haut Andramonta, Bassin de Lokoho), [14°37'S, 49°25'E], 900 m, 10 Dec. 1950–9 Jan. 1951, H. Humbert 24576 + R. Capuron & G. Cours (P [P05208600]); Sud-Ouest d'Andapa, Réserve Spéciale d'Anjanaharibe-Sud, village d'Andranotsarabe, suivant la route Nationale d'Andapa-Bealanana de lat piste vers à l'oueste, Ambatoomainty, Camp No. 2, 14°44'22"S, 49°27'42"E, 3 Nov. 1994, 1185–1335 m, D. Ravelonarivo 489 & R. Babesonina (KSP [KSP003115, KSP003116], P [P05208456]). Prov. Mahajanga: Ankaizinana, [14°30'S, 48°55'E], 1400 m, 20 Apr. 1923, R. Decary 2009 (P [P00118106]).

***Eugenia razakamalalae* N. Snow & Callm., sp. nov.**

urn:lsid:ipni.org:names:77146900-1
holotype (Figure 19): http://www.tropicos.org/Image/100314920

Haec species a congeneris madagascariensibus lamina foliari rigide coriacea late elliptica usque obovata utrinque ad paginas (nec ad margines tantum) nonnihil sinuosa atque glandulis densis folii paginam abaxialem pedunculos hypanthium lobos calycinos petala necnon fructum ornantibus distinguitur.

Type. MADAGASCAR. Prov. Antsiranana: Fokontany: Anjia, Ambato, 15°17'26"S, 50°20'28"E, 37 m, 25 Feb. 2001, R. Razakamalala 67 + S. Rakotoarisoa, A. Rasolohery & P. Antilahimena (holotype: MO-6277747!; isotypes: KSP [KSP000003]!; P, TAN).

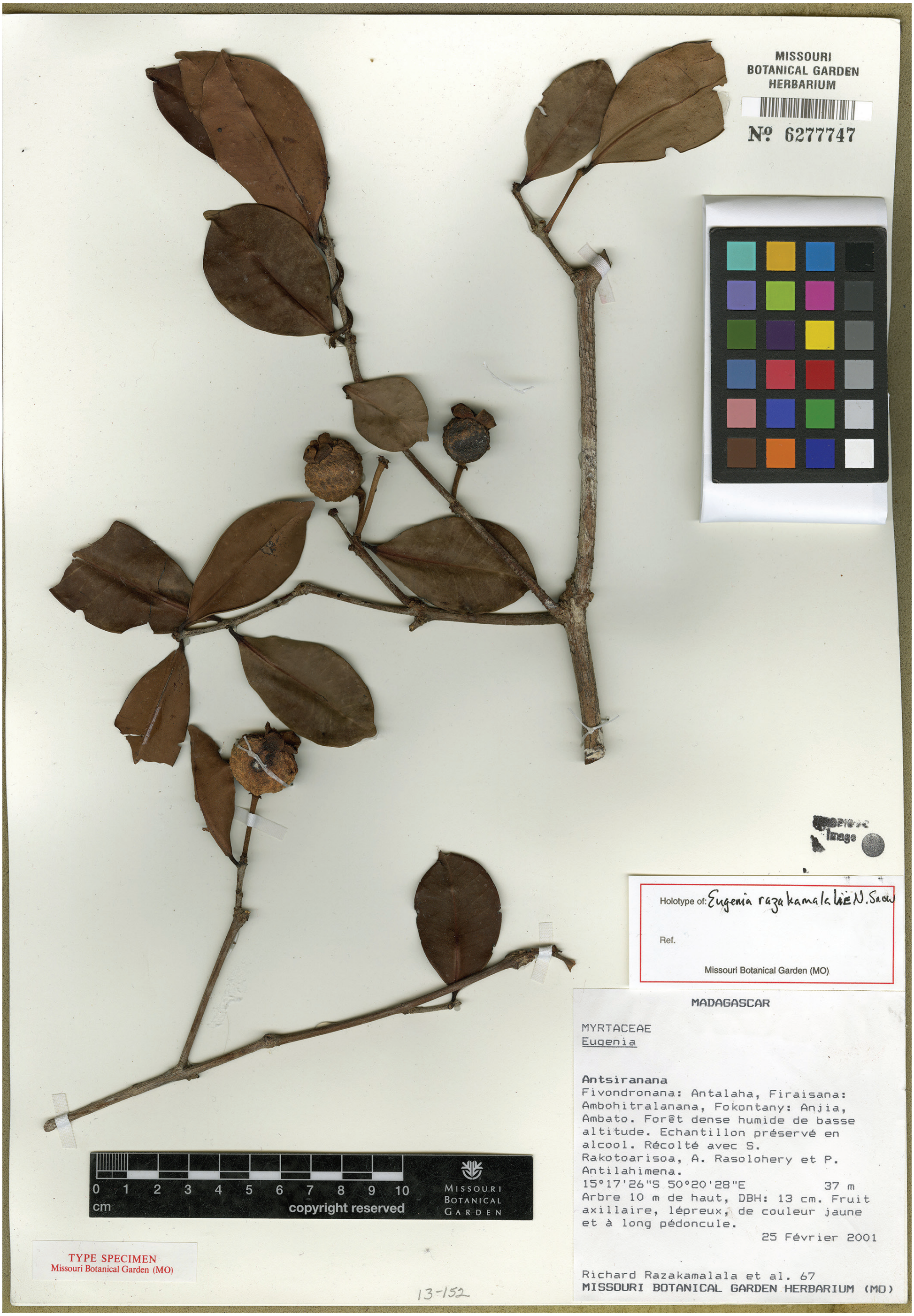
Description. Trees to 10 m; dbh up to 13 cm; bark of main bole unknown. Plants glabrous throughout. Branchlets laterally compressed; youngest epidermis drying light brown to light gray but soon peeling and flaking to reveal reddish-brown color (dried); oil glands of epidermis prominent and common. Leaves stiffly coriaceous, mostly concentrated near branch tips, medium green and slightly discolorous, irregularly sinuous, surfaces matte. Axillary colleters absent. Petioles 3–5 mm, becoming slightly sulcate distally and broadening towards apex. Leaf blades 3.5–9.0 × 2.5–5.0 cm, broadly elliptic to obovate or broadly obovate, base cuneate, apex obtuse to somewhat acute; adaxial surface with midvein broadly but shallowly sulcate in the lower half, becoming flush distally; oil glands absent; abaxial surface oil glands common to dense but small and faint and fading with maturity (visible only with magnification), secondary veins somewhat indistinct, intramarginal vein indistinct and ca. 0.5–1.0 mm from margin at midpoint of blade. Inflorescence terminal or axillary, monads 1–3 in each axil. Pedicels 15–25 mm, relatively thick (1.2–2.0 mm at maturity), ascending to erect, rigid. Bracteoles 2, 1–2 mm, ovate, stiff, persistent and more or less divergent in fruit. Hypanthium 3.5–5 mm, cupulate, oil glands common to dense. Calyx lobes 4, 5–8 mm, broadly rounded, apex obtuse, densely glandular, persistent and crowning the fruit, stramineous or rufous-beige (fresh). Flowers unknown. Berries 1.5–1.8 × 2.0–2.3 cm, subglobular to globular, densely glandular, slightly verrucose (dried), yellowish (possibly not fully mature).

Etymology. It is a pleasure to name this species in honor of Richard Razakamalala (b. 1962), a Malagasy botanist who has collected over seven thousand specimens of plants from Madagascar since 2001. His prolific collecting efforts have contributed significantly to our increased knowledge of the Malagasy flora. Four of his *Eugenia* collections are designated as type specimens in this publication.

Phenology. Fruiting late February.

Distribution. Known only from the type gathering in Antsiranana Province, north-eastern Madagascar, about 14 km west of the coast in the Masoala Peninsula (Fig. 2).

Habitat and ecology. In dense humid lowland forests over quartzite from ca. 35 m elevation.



Holotype of: Eugenia razakamalalae N. Snow

Ref.

Missouri Botanical Garden (MO)

MADAGASCAR

MYRTACEAE
Eugenia

Antsiranana
Fivondronana: Antalaha, Firaisana: Ambohitralanana, Fokontany: Anjia, Ambato. Forêt dense humide de basse altitude. Echantillon préservé en alcool. Récolté avec S. Rakotoarisoa, A. Rasolohery et P. Antilahimena.
15°17'26"S 50°20'28"E 37 m
Arbre 10 m de haut, DBH: 13 cm. Fruit axillaire, lépreux, de couleur jaune et à long pédoncule.
25 Février 2001

Richard Razakamalala et al. 67
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 19. Holotype specimen of *Eugenia razakamalalae* (MO).

Conservation status. With only one collection known from just outside the Masoala protected area, *Eugenia razakamalalae* is assigned a preliminary risk of extinction of "Endangered" [EN 2ab(i, iii, iv)] following the IUCN Red List Categories and Criteria (IUCN 2012). It is highly probable that the new species occurs within Masoala National Park, and is therefore protected.

Comments. The leaf morphology *of Eugenia razakamalalae* resembles that of *Eugenia arthroopoda* H. Perrier var. *ambalavensis* H. Perrier, an invalid name given the lack of a Latin diagnosis in the protologue (Perrier de la Bâthie 1953a). However, the pedicels, hypanthium and calyx lobes of Humbert 22,804 (a syntype of var. *ambalavensis*) have a dense, uniform, appressed rusty indumenta that is also present on the outer surface of the petals, apart from an approximately 1 mm wide glabrous margin. In contrast, the pedicels in fruit of *E. razakamalalae* are glabrous (flowering material is unknown).

Snow (2011) discussed some morphological characters of the type gathering of *E. razakamalalae* relative to those of *E. lacerosepala* N. Snow, the latter of which is known only from its type gathering ca. 300 km north-northwest. The two species are similar in having fruits that are borne atop stiff and relatively long pedicels that are prominently and densely glandular, in having a slightly verrucose texture, and in being crowned by prominent calyx lobes. However, the narrowly obovate and shorter (2.1–3.5 cm) leaves of *E. lacerosepala* are quite unlike those of *E. razakamalalae*.

Eugenia richardii (Blume) N. Snow, Callm. & Phillipson, comb. nov.

urn:lsid:ipni.org:names:77146902-1

Isotype: http://sonneratphoto.mnhn.fr/2012/08/23/1/P00118150.jpg

Basionym. *Jossinia richardii* Blume in Mus. Bot. 1: 123. 1851. **Type.** MADAGASCAR. Prov. Antsiranana: forêt à Vohémar, [13°21'30"S, 50°00'30"E], comm. 1837, J.M.C. Richard 119 (holotype: L [L0009467]!; isotype: P [P00118150]!).

Description. Shrubs 2–4 m tall; ca. 4 cm dbh; bark of main bole rough, grayish-brown. Branchlets terete, lightish gray-brown (dried); internodes short, (0.5–)1.5–2.3 cm; epidermis smooth but becoming fissured and flaking on older internodes, indumentum moderately dense of minutely dibrachiate trichomes; oil glands common, and somewhat prominent, and protruding above surface. Leaves mostly evenly distributed along branchlets, coriaceous, slightly discolorous, surfaces matte. Axillary colleters absent. Petioles 1–2 mm, slightly sulcate but mostly flush adaxially, glabrous. Leaf blades 2.5–4.5 × 1.6–2.5 cm, elliptic; base rounded to somewhat cuneate; apex broadly obtuse to rounded; margins slightly revolute; adaxial surface glabrous, oil glands dense upon emergence but fading as blade thickens, midvein broadly but slightly sulcate proximally; abaxial surface resembling adaxial, secondary veins indistinct or not visible, intramarginal vein 1.0–1.5 mm from margin at midpoint of blade. Inflorescence a monad arising in terminal leaf axils. Anthopodia (short internode between base of hypanthium and subtending bracteoles) present, 1–2 mm. Pedicels 1.0–1.4 mm, firm but slightly bowed, glabrous. Bracteoles 2, 0.8–1.0 × ca. 1.0 mm, ovate, minutely hairy on margins near apex. Hypanthium 4–5 mm, cupuliform to obconic, glabrous but evidently exuding salt, oil glands common to dense; ovary apex densely short-hairy. Calyx lobes 4, ca. 4 × 4 mm (material limited), oblong, apex obtuse, glabrous, greenish. Petals 9–10 × 6–9 mm, widely elliptic to widely obovate, sparsely short-ciliate on margins, thin (nearly transluscent), pinkish, oil glands sparse to common but prominent. Stamens ca. 70–100, multiseriate; anthers ellipsoid, 0.6–0.8 mm, sub-basifixed, connective with a single apical gland. Filaments 3–9 mm, white; ovary apex densely short-hairy. Styles 9–10 mm, glabrous; stigma narrow. Berries unknown.

Phenology. Flowering August; fruiting January and likely commencing in late August (unconfirmed).

Distribution. Known from the north-eastern coastal region of Madagascar in Antsiranana Province, from Orangéa to about 140 km along the coast near Vohemar (Fig. 2).

Habitat and ecology. Littoral forests over sand, inland from the ocean shore less than 1 km; elevation 10 m.

Conservation status. With an EOO of 358 km^2, an AOO of 36 km^2 and three subpopulations, one of which is situated within a proposed protected area that currently holds a temporary protection status (Oronjia), *Eugenia richardii* is assigned a preliminary risk of extinction of "Endangered" [EN B1ab(iii)+ B2ab(iii)] following the IUCN Red List Categories and Criteria (IUCN 2012). The species seems to have a highly restricted distribution in dry deciduous forests over sand. The area around Oronjia is mostly degraded as a result of human activities and is under serious threat. A definitive protection of the dry deciduous forests over sand of Oronjia would likely enable the species to be downlisted from the current risk of extinction to "Vulnerable".

Comments. *Eugenia richardii* most closely resembles two species, including *Eugenia vanwykiana* N. Snow, which differs by its larger leaves with cuneate bases (Snow et al. 2012). The second fairly close match is *Eugenia calciscopulorum*, which occurs significantly farther inland (ca. 11 km) than *E. richardii* and at a higher elevation (ca. 410 m) and over limestone, compared to the sandy substrates of *E. richardii*. The leaves of *E. calciscopulorum* have more pronounced secondary veins above and below, retain the pronounced glands into the mature leaf stage, and have a more pronounced petiole.

Eugenia richardii also resembles *E. quadriflora* H. Perrier, which is known from a single collection in 1961 from east of Lake Alaotra. Both species have thickly coriaceous, densely glandular leaf blades with irregularly undulating surfaces and moderately to strongly recurved margins, and simple flowers arising terminally. However, the leaves of *E. quadriflora* are sessile with strongly and irregularly recurved blades (although this may reflect to some degree its condition when pressed and dried); in contrast, the leaf blades of of *E. richardii* are distinctly but shortly petiolate and slightly recurved.

Elsewhere, the leaf morphology of *Eugenia richardii* somewhat resembles that of *Eugenia neofasciculata* Bennet from Mauritius (formerly *E. fasciculata* Guého & A.J. Scott). Based on comparison digitally with an isotype (Lorence DL 1214 (P [P00390098]!), the species are similar by virtue of stiffly coriaceous, densely punctate, obovate-elliptic leaf blades with slightly undulating surfaces and recurved margins that arise from relatively short petioles. However, whereas the adxial petiolar surface of *E. richardii* is flat, that of *E. neofasciculata* is somewhat sulcate. In addition, the inflorescence of *E. richardii* is a terminal pair of flowers with one arising in each leaf axil, whereas that of *E. neofasciculata* is conspicuously fasciculate (mostly) on naked branches or within leaf axils.

Specimens examined. MADAGASCAR. Prov. Antsiranana: Vohémar, [12°16'24"S, 49°23'20"E], s.d., L.H. Boivin 2697 (=J.M.C. Richard 134) (P [P00118153]); Orangéa, [12°14'S, 49°22'E], 1–100 m, 22 Jan. 1960, G. G. Cours 5394 (P [P05097489]; Env. de Diégo-Suarez, Orangéa, [12°14'S, 49°22'E], 1–100 m, 22 Jan. 1960, H. Humbert 32245 + G. Cours (P [P05576991]); Ramena, Baie des Sakalava, 3.5 km à l'E du Fokontany Ankorikihely, 12°16'24"S, 49°23'20"E, 17 Aug. 2004, J.B. Leopold 27 + L.J. Razafitsalama, R. Guittou, J. Be, & V. Benjara (CNARP, KSP [KSP000005], MO-6245567, P [P05208542], TAN); Andrafiabe, presqu'île entre Ambolobozobe et Ambolobozokely, 12°29'39"S, 49°34'04"E, 9 Feb. 2005, F. Ratovoson 965 + R. Guittou & D. Elifara (G, MO-6028974, P [P05208572]); Vohémar, [13°21'30"S, 50°00'30"E], s.d., J.M.C. Richard 75 (P [P00118148, P00118149]).

Eugenia tiampoka N. Snow & Callm., sp. nov.

urn:lsid:ipni.org:names:77146901-1
holotype (Figure 20): http://www.tropicos.org/Image/100314918
Living material: http://www.tropicos.org/Image/76837

Haec species Eugeniae thouvenotianae H. Perrier simillima, sed ab ea lamina foliari glandulis oleiferis punctatis abaxialiter ornata atque pedicellis multo brevioribus distinguitur.

Type. MADAGASCAR. Prov. Antsiranana: Doany, en aval des deux côtes de la rivière Ambalanirano. Ambohimirahavavy, 14°13'43"S, 49°08'07"E, 2011 m, 19 Nov. 1995, C. Rakotovao 2511 + Jaovazaha & Tsarajery (holotype: MO-6174870!; isotypes: G [G00341423]!, P [P05260190]!, TAN).

Description. Trees 8–18 m; dbh 12–60 cm; bark of main bole unknown. Indumentum of foliage and floral parts dibrachiate, short and appressed, ferrugineous, denser upon emergence but becoming (often) nearly glabrous (or as indicated below). Branchlets rounded to laterally compressed, greenish fresh but drying light brown to light gray; epidermis thin and peeling away in thin strips or flakes, oil glands absent to sparse and indistinct. Leaves discolorous, margin sometimes strongly revolute and irregularly sinuous, venation reticulate, emerald and somewhat glossy adaxially, citrine and matte abaxially, concentrated near branch tips. Axillary colleters occasionally present. Petioles (2.5–)5–10, narrowly and deeply sulcate adaxially, elgandular. Leaf blades 4.0–6.8 × 2.3–.8 cm, elliptic to obovate, base cuneate, apex obtuse or occasionally retuse; adaxial surface remaining at least sparsely sericeous when fully emerged (trichomes closely appressed), oil glands common to dense but faintly visible, midvein deeply and narrowly suclate proximally becoming flush distally; abaxial surface indumentum as above, oil glands not as dense but much more prominent, secondary

MADAGASCAR
MYRTACEAE
Eugenia goviala H. Perrier

det. R. Razakamalala & C. Rakotovao, 200
Antsiranana: SAVA Region

Sava, Andapa, Doany. En aval des deux côtés de la rivière Ambalanirano. Ambohimirahavavy.
14°13'43"S 049°08'07"E 2011 m

Grand arbre de 18m de haut, dbh: 15cm. tige frise blanchâtre. Face inférieure des feuilles vert-claires. Présence de fleurs: sépales vert-claires, pétales jaune-claires, courbés vers l'extérieur, nombreuses étamines à filet jaune-claire sur une inflorescence axillaire. Peu fréquente.
19 Nov 2005
Charles Rakotovao, Jaovazaha & Tsarajery
2511
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Holotype of: Eugenia tiampoka N. Snow

Ref.

Missouri Botanical Garden (MO)

Missouri Botanical Garden

This specimen is part of the «**Biogeography and endemism of the Northern Humid Mountains of Madagascar**» project.

An intensive botanical inventory of this essentially unknown region was undertaken to improve our understanding of biogeographical relations and patterns of endemism on the principal northern massifs and to evaluate their role as centers of speciation.

Could you please send any new determination to:
martin.callmander@mobot-mg.org

Figure 20. Holotype specimen of *Eugenia tiampoka* (MO).

veins indistinct to somewhat prominent, intramarginal vein 1.0–1.5 mm from margin at midpoint of leaf blade (but often obscured by revolute margin). Inflorescence 2–5 cm long, mostly axillary or ramiflorous, sometimes terminal, consisting of triads, botryoids, or less commonly metabotryoids or pseudo-umbels of 4–5 flowers apically clustered on peduncle; peduncles mostly solitary but often opposite in leaf axils or on naked branches, mostly ascending and somewhat stiff but also sometimes flexuous. Pedicels 1–2 mm long. Bracteoles absent; bract-like structures surrounding triads of flowers when inflorescence is emerging but these soon deciduous. Hypanthium 1.5–2.5 mm, obconic, densely hairy and densely punctate. Calyx lobes 4, (1.2–)1.5–1.8 mm, broadly rounded, apex obtuse, mostly glabrous above to sparsely sericeous, moderately sericeous dorsally and on margins below, deciduous in fruit, light green when fresh. Petals 4, 4–7 mm, obovate, minutely and sparsely ciliate apically (use magnification) but otherwise glabrous, oil glands sparse to moderate. Stamens 20–45, exserted; staminal disk glabrescent; ovary apex glabrous; filaments 4–7 mm, yellowish-white; anthers 0.4–0.6 mm, globose to subelliptic, basifixed, eglandular; style 4–5 mm, stigma narrow and scarcely if at all capitate. Fruit (material limited), ca. 2.2 × 2.2 cm, globose, glabrate, green when young drying nearly black; outer layer leathery and prominently glandular. Seed 1 at maturity (material scant), round from above but laterally compressed (due to pressing?), ca. 16 × 16 × 9 mm; embryo not differentiated into distinct cotyledons or epicotyl.

Etymology. The specific epithet is derived from elements of the native language of northern Madagascar, in which *ampoka* means mosses. *Eugenia tiampoka* thus means the “*Eugenia* that likes mosses”.

Phenology. Flowering October through February; fruiting by early April, likely commencing by March and extending through May.

Distribution. Northern Madagascar in Antsiranana Province in the northern mountains (Fig. 2).

Habitat and ecology. Mid- to high-altitude humid forests laden with mosses, sometimes along river banks; 1990–2300 m in the northern highlands of Madagascar. A team of botanists lead by MC conducted a series of field expeditions between 2005 and 2008 to explore the flora and vegetation of this long-neglected region, during which more than 4,400 collections were made, yielding material of several plant species new to science (Callmander et al. 2008, 2009, 2012).

Conservation status. With an EOO of 71 km^2, an AOO of 45 km^2 and two subpopulations, neither of which is within the protected area network, *Eugenia tiampoka* is assigned a preliminary risk of extinction of “Endangered” [EN B1ab(iii)+2ab(iii)] following the IUCN Red List Categories and Criteria (IUCN 2012).

Comments. The leaves reportedly are aromatic (Birkinshaw 950, Rakotovao 2398). One specimen is said to have a nectariferous disk (Randriarivelo 350). A specimen of 30 m stature (Ravelonarivo 647) from the same general area and also said to be aromatic, but growing at 1700 m, has a slightly different aspect to the leaves, also may be this species.

The morphological gestalt of the leaves and inflorescences resemble most closely those of *E. thouvetiana* H. Perrier, which however lacks the punctate oil glands of the abaxial leaf surface, and which has much longer pedicels subtending the individual flowers than those of *E. tiampoka*. The type locality of *E. thouvetiana* is located in Analamazaotra-Andasibe in Toamasina Province, some 525 km south of the southernmost known collection of *E. tiampoka*. *Eugenia tiampoka* also somewhat resembles *Eugenia hazompasika* H. Perrier, the latter of which has much longer, broader and stiffer leaves with a less abruptly cuneate base.

Specimens examined. MADAGASCAR. Prov. Antsiranana: 13 km N of Mangindrano, Tsaratanana Massif, SW ridge of Andomanisambiraro, 14°08'41"S, 48°57'53"E, 2150 m, 17 Oct. 2001, C. Birkinshaw 950 + R. Lala (KSP [KSP000048, KSP000049], P [P05156041]); Crête E d'Ambohimirahavavy, 14°12'15"S, 49°05'54"E, 2278 m, 3 Nov. 2005, C. Rakotovao 2398 + Jaovazaha & Torize (G, MO-6202095); Sommet de Beampoko, Ambohimirahavavy, 14°13'55"S, 49°08'23"E, 2137 m, 21 Nov. 2005, C. Rakotovao 2566 + Jaovazaha & Tsarajery (G, MO-6174671, P [P05260203]); Doany, forêt d'altitude d'Ambohimirahavavy, 14°13'41"S 49°08'14"E, 1991 m, 18 Nov. 2005, C. Randrianarivelo 350 + J. Randriantiavina & Torize (G, MO-6081166), KSP [KSP000047], P [P05260189]); Fokontany: Ampanompy, Ampanompy, 14°08'31"S, 48°58'04"E, 2050–2300 m, 5 Apr. 2001, R. Razakamalala 99 + R. Ranaivojaona, F. Ratovoson, A. Rasolohery, A. Andriamaniry & Mahavory (KSP [KSP000047]!).

Eugenia wilsoniana N. Snow, sp. nov.

urn:lsid:ipni.org:names:77146903-1
holotype (Figure 21): http://www.tropicos.org/Image/100314905

Haec species Eugeniae bemangidiensi N. Snow *simillima, sed ab ea inflorescentia axillari longipedicellata distinguitur; etiam ad altitudines superiores crescit.*

Type. MADAGASCAR. Prov. Toamasina: Alaotra Mangoro Reg., Moramanga, Ambohibary, Ampitambe, 18°48'55"S, 48°16'37"E, 1103 m, 14 Oct. 2008, R. Rakotondrajaona 649 (holotype: MO-6419537!); isotypes: P, TAN).

Description. Shrubs or trees, (1–)2–6 m. Trunk dbh ca. 2 cm (measurements few); bark of main bole fissured, maroon. Indumentum where present of highly asymmetric and short, ferrugineous, dibrachate hairs. Branchlets laterally compressed, smooth, sparsely puberulous, drying light brown to greenish, punctate glands absent. Leaves opposite or disjunct opposite, mostly concentrated near tips of branches; venation reticulate; blades thinly coriaceous, dark green above and lighter green below. Axillary colleters obscure when present. Petioles 3–5 mm, deeply and narrowly sulcate adaxially, laterally compressed, elgandular, glabrescent (especially abaxially), longitudinally striate initially but thickening and becoming somewhat latitudinally striate with age. Leaf blades 4.0–12.5 × 1.4–3.0 cm, narrowly elliptic to narrowly ovate, base rounded and slightly constricted-conduplicate above petiole, apex acute, margins flat;

adaxial surface glabrous, eglandular, midvein narrowly but deeply sulcate lower 2/3–4/5; abaxial surface like adaxial except: midvein protruding, sometimes prominently glandular and longitudinally striate, secondary veins faint to prominent, arising only 10–20° from midvein, tertiary veins faint to nearly as prominent as secondaries; intramarginal vein 1.0–1.5 mm from leaf edge at midpoint of blade. Inflorescence terminal, axillary, or arising on naked branch of current year's growth. Flowers solitary, or occasionally as up to four arising from short brachyblasts; pedicels 6–12 × ca. 0.5 mm, glabrous, strongly laterally compressed (especially distally), longitudinally striate, sparsely to moderately glandular. Bracteoles 2, 0.6–1.1 mm, narrowly ovate to ovate, sparsely hairy abaxially and apically, rigid, somewhat ascending to appressed against base of hypanthium. Hypanthium 2.5–4.0 mm, cupuliform, sparsely hairy becoming glabrous, sparsely to moderately (but only faintly) glandular. Calyx lobes 4, 4–5 × 3–5 mm, oblate to broadly elliptic, apex broadly obtuse to rounded, minutely and sparsely ciliate in upper half, prominently glandular, greenish when fresh. Petals 4, 4–5 × 2–3 mm, widely elliptic to ovate, sparsely short-ciliate upper 1/2–1/3, faintly and somewhat sparsely glandular, whitish or pinkish. Stamens exserted, staminal disk ca. 4 mm diameter, more or less square from above, short-hairy, adjacent ovary apex glabrous; filaments 2–3 mm; anthers 0.8–1.0 mm, elliptic, yellow, sub-basifixed, apical gland between connectives lacking. Styles 7–8 mm, glabrous; stigma narrow and scarcely if at all capitate. Berries (immature?) 12–15 × 12–15 mm, globular, greenish.

Etymology. In honor of Dr. Peter G. Wilson (b. 1950) of the Royal Botanic Gardens in Sydney, Australia; colleague, collaborator, and long-time student of Myrtaceae (e.g., Wilson and Waterhouse 1982; Wilson et al. 2005; Snow and Wilson 2010; Wilson 2011).

Vernacular name. Hazompasina (Antilahimena 4935); Rotra (Ravelonarivo 3148).

Phenology. Flowering mid-October through mid-November; fruiting October and November.

Distribution. East-central Madagascar in Toamasina Province, occurring near Analamazaotra National Park (Fig. 2).

Habitat and ecology. In humid, sometimes disturbed forests at middle altitudes from ca. 980–1103 m.

Conservation status. With five collections known, an AOO of 9 km^2 and one subpopulation that is situated outside the protected area, *Eugenia wilsoniana* is assigned a preliminary risk of extinction of "Critically Endangered" [CR A3c+B1ab(iii)] following the IUCN Red List Categories and Criteria (IUCN 2012). Current data suggest the species has a narrow distribution, and the montane evergreen tropical forests where the species grows are threatened by mining activities. The discovery of this species in one of the nearby protected areas probably would allow downlisting to "Endangered".

Comments. The leaf and floral morphologies of *Eugenia wilsoniana* are suggestive of *Eugenia diospyroides* H. Perrier. However, *E. wilsoniana* has much shorter leaves and a hairy staminal ring, in contrast with the much larger leaves and glabrous staminal ring of *E. diospyroides* (e.g., Randriatifika 118 et al. [KSP]). This new species resembles even more closely another newly described species herein, *E. bemangidiensis*, which differs by its caulifforous inflorences occurring in tight, relatively short fascicles, secondary

Holotype of: Eugenia wilsoniana N.Snow

Ref.

Missouri Botanical Garden (MO)

MADAGASCAR
MYRTACEAE [222]
Eugenia

Toamasina: Alaotra-Mangoro Region

Alaotra Mangoro, Moramanga, Ambohibary, Ampitambe. Forêt humide de moyenne altitude d'Ankosy à 6 km d'Ambohimanarivo. Récoltés avec M. Ratolojanahary, H. Raveloniaina & J. Mamitiana.
18°48'55"S 048°16'37"E 1103 m

Arbuste 3 m, DBH: 2 cm, écorce à fissure longitudinale, calice vert, corolle rose.

14 Oct 2008
Roland Rakotondrajaona 649
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Figure 21. Holotype specimen of *Eugenia wilsoniana* (MO).

veins on the leaf blades arising at steeper angles, and occurring in a different habitat at much lower elevations some 750 km southeast from the presently known occurrences of *E. wilsoniana*. Moreover, the foliage and floral parts of *E. bemangidiensis* are entirely glabrous, the abaxial laminar midvein protrudes less prominently, the adaxial laminar sulcus is not as deep or narrow, and its adaxial petiolar sulcus is broader and shallower than those of *E. wilsoniana*.

Specimens examined. MADAGASCAR. Prov. Toamasina: Ambatovy, Sahaevo forest, 18°50'26"S, 48°16'33"E, 11 Nov. 2006, P. Antilahimena 4935 & F. Edmond (MO-6338238); ibid. loc., 18°50'26"S, 48°16'34"E, 23 Nov. 2008, P. Antilahimena 6912 + B.A. Ratodimanana, D. Ravelonarivo, E. Félix & M. Ratvomanana (MO-6447030); Ambatovy, Antaniditra, 18°49'11"S, 48°16'53"E, 13 Oct. 2008, R. Bernard 1154 (MO); Ampitambe, Ambatovy, 18°49'06"S, 48°17'06"E, 1041 m, 13 Oct. 2008, R. Rakotondrajaona 642 + M. Ratolojanahary (MO-6419531); Mararano, Marovoay, 18°48'10"S, 48°17'59"E, 14 Nov. 2008, D. Ravelonarivo 3148 (MO-6447573).

Lectotypifications

Many species of *Eugenia* in Madagascar described by Perrier de la Bâthie (1953a) eventually will require lectotypification to establish coherent species concepts and avoid nomenclatural confusion. We have reviewed all of the existing published small-leaved *Eugenia* species in Madagascar and the currently available specimens, and have seen some additional material that has helped to clarify species delimitations. Here we lectotypify three names to help clarify species' boundaries and nomenclature.

Lectotypification is particularly important for *Eugenia scottii*, since the protologue included twelve syntype collections that clearly included more than one taxon. *Eugenia hovarum* H. Perrier and *Eugenia scottii* H. Perrier were described for relatively small-leaved species occuring mostly in the mountainous parts of Madagascar, and both were based on multiple syntypes (Perrier de la Bâthie 1953a).

Eugenia scottii H. Perrier in Mém. Inst. Sci. Mad., Sér. B, Biol. Vég. 4(2): 168-169. 1953. **Lectotype** (designated here): MADAGASCAR. Prov. Antsiranana: Massif du Tsaratanana et haute vallée du Sambirano, Mt. Andilabe, 2300 m, Nov.-Dec. 1937, H. Humbert 18501 (lectotype: P [P00118145]!; isolectotype: P [P00118146]!).

Perrier de la Bâthie (1953a: 169) referred to *Eugenia scottii* as having a large number of forms that he could not distinguish taxonomically ("…*un très grand nombre de formes que nous n'avons pu distinguer*"). In light of the material now available, we believe that the specimens can be assigned comfortably to five different species, four of which already have valid names. Among the syntypes, we have chosen Humbert 18501 at 2300 m elevation from the Tsaratanana Massif in Antsiranana Province as the lectotype because it is among the better flowering syntype collections, and represents a species that cannot be assigned to any other published taxon. None of the syntypes at

P were annotated specifically by Perrier de la Bâthie as the type, or designated as such in his original description or subsequently in the Flora treatment (Perrier de la Bâthie 1953b). Humbert 18501 comprises two sheets at P, so we designate the slightly more copious of the two (P [P00118145]), which bears an original hand-written label .as the lectotype. The other specimen with a printed label (P [P00118146]), as an isolectotype. As we now circumscribe *Eugenia scottii*, it is restricted to mountain summits and ridges in ericoid shrubland and rocky areas, mostly over 2000 m a.s.l. on Tsaratanana and Marojejy. It includes two other original syntypes of *E. scottii*: Humbert 18389 and Humbert + Cours 23709.

Among the specimens that we exclude from *Eugenia scottii* is material that can be accommodated in *E. cassinoides* Lam., a species from the littoral forest in the south-east (Perrier de la Bâthie 6486); *E. richardii* (e.g., Boivin 2697, Richard 75, Richard 119), a species from low elevation dry forest in the north-east (the needed new combination of which is provided in this article); *E. petrikiensis* N. Snow & Randriat. (Scott Eliott 2847) from Fort Dauphin; and a new, as yet undescribed species from the mountains of the south-east at mid elevation in the Mandrare basin (Humbert 6503, 6685, 6835), and probably also includes the last syntype, Humbert 11965, from Kalambatritra.

Additional specimens examined: MADAGASCAR. Prov. Antsiranana: Réserve Naturelle Intégrale du Marojejy, versant W et SW du sommet de Marojejy, 14°27'S, 49°44'E, 2040 m, 15 Nov. 1996, Rakotomalaza 918 et al. (G, MO, P [P05208453]); Massif du Tsaratanana, hauts sommets de l'Amboabory à l'Antsianongatalata, 2300-2609 m, Nov.-Dec. 1937, H. Humbert 18389 (P [P00118147]); Sommet oriental du Massif du Marojejy, à l'W de la Haute Manantenina, affluent de la Lohoho, 1850-2137 m, 26 March–2 Avril. 1949, H. Humbert 23709 + G. Cours (P [P00118154]).

Excluded syntypes: MADAGASCAR. Prov. Antsiranana: Vohemar, L.H. Boivin 2697 (= J.M.C. Richard 134) (syntype: P [00118153]!); Vohémar, [12°16'24"S, 49°23'20"E], s.d., J.M.C. Richard 75 (syntypes: P [P00118148, P00118149]!); Vohémar, [12°16'24"S, 49°23'20"E], comm. 1837, J.M.C. Richard 119 (syntypes: L [L0009467]!, P [P00118150]!). Prov. Fianarantsoa: massif de Kalambatitra (centre S), Mt. Analatsitendrika, Nov. 1933, H. Humbert 11965 (syntypes: P [P00118151, P00118152]!); près de l'embouchure du Matitana (SE), Oct. 1911, H. Perrier de la Bâthie 6486 (syntype: P [P00118144]!). Prov. Toliara: Haute vallée du Mandrare (SE), 600-900 m, 8–15 Nov. 1928, H. Humbert 6503 (syntypes: P [P00118141, P00118142]!); Bassin sup. du Mandrare (SE), du col de Vavara à la vallée du Manambolo, 700–1200 m, 20–22 Nov. 1928, H. Humbert 6685 (syntype: P [P00118140]!); Bassin sup. du Mandrare (SE), Mt. d'Amboahangy près d'Esira, 1000–1150 m, 25 Nov. 1928, H. Humbert 6835 (syntypes: P [P00118139, P00118138]!); Fort Dauphin, s.d., Scott Eliott 2847 (syntype: P [P00118137]!).

Eugenia hovarum H. Perrier in Mém. Inst. Sci. Mad., Sér. B, Biol. Vég. 4(2): 170. 1953. **Lectotype** (designated here): MADAGASCAR. Prov. Antananarivo: env. de Manjakandriana, comm. 1932, Perrier de la Bâthie 14007 (lectotype: P [P00118032]!;

isolectotype: P [P00118031]!). **Syntype:** MADAGASCAR. Prov. Antananarivo: Imerina, comm. 20 Nov. 1889, Campenon s.n. (P [P00118033]!).

Perrier de la Bâthie (1953a: 170) only cited two syntypes that clearly belong to species that we consider to be *Eugenia hovarum*. Not atypically, Perrier de la Bâthie made no indication of which should be regarded as the holotype, but his own collection (Perrier de la Bâthie 14007) is the more complete of the two, comprises two separate sheets at P, and bears a detailed collection locality information, unlike the other syntype, and is here designated as the lectotype.

Additional specimen examined: MADAGASCAR. Prov. Antsiranana: Parc National de Ranomafana, ca. 4 km E of Vohiparara, 21°13'32"S 47°26'43"E 1170 m, 5 Nov. 1993, Schatz 3531 (MO, P [P05208543]).

Eugenia nompa H. Perrier in Mém. Inst. Sci. Mad., Sér. B, Biol. Vég. 4(2): 181. 1953. **Lectotype** (designated here): MADAGASCAR. Prov. Antsiranana: Dist. Ambanja, Beangona (haut Sambirano), [14°03'00"S 48°42'15"E], 24 Oct. 1947, Réserves Naturelles 1275 (lectotype: P [P00118008]!; isolectotype: P [P00118007]!). **Syntypes:** MADAGASCAR. Prov. Antsiranana: env. du Mt. Tsaratanana, Nov. 1912, Perrier de la Bâthie 5481 (P [P00118004, P00118005, P00118006]!).

The species concept for *Eugenia nompa* H. Perrier has been uncertain. Because the syntypes were clearly designated by Perrier de la Bâthie (1953a), we lectotypify one of these to clarify its diagnostic characters, which include: leaf blades narrowly elliptic, apex acute; midvein deeply and narrowly sulcate lower 75%+; margins somewhat sinuous; inflorescence of somewhat elongate cymes or sparsely-flowered botryoids, terminal or axillary in clusters, the whole (at least when young) covered with a ferrugineous indumentum.

Perrier de la Bâthie (1953a) also described *Eugenia nompa* var. *arborea* H. Perrier, an invalid name based on Perrier de la Bâthie 16261. The inflorescence structure of those specimens differ considerably from the lectotype recognized above, and it is still unclear whether specimens designated as this variety can be confidently placed in extant taxa.

Additional specimen examined: MADAGASCAR. Prov. Antsiranana: District Ambanja, Canton: Marovato. Réserve Naturelle 4 (Tsaratanana), 21 Sept. 1953, Réserve Naturelle 5750 (P [P05097466]).

Discussion

The eighteen species of *Eugenia* newly proposed here increases the known number of native species in Madagascar from approximately 46 to 68, all of which are endemic. Of these, 32 (approximately half) have been described in the last fifteen years (Miller 2000; Snow 2008, 2011; Snow et al. 2012 and this paper). Specimens of the introduced and possibly naturalized Neotropical species *Eugenia uniflora* L. and *E. brasiliensis* Lam. have been confirmed by the first author (housed at MO). Both species produce edible fruits, and the former also is used as a hedgerow. The paucity of collections suggests that these species are not widely planted.

Many of the original descriptions by Perrier de la Bâthie (1953a) of Malagasy *Eugenia* were relatively incomplete, and many of his infraspecific names are invalid. Because preliminary studies suggest some of those infraspecific taxa are worthy of recognition, new names will be necessary in future combinations after additional study.

Malagasy *Eugenia* have a relative paucity of easily diagnostic, qualitatively different morphological character states compared to some baccate genera of Myrtaceae (e.g., Snow et al. 2003; Snow 2008), including the related genus *Syzygium*. For example, few species of *Eugenia* have winged or quadrangular branchlets, apically attenuate calyx lobes, costate fruits, or other qualitatively distinct character states that recur in many other baccate genera, and which simplify identifications and the writing of keys (e.g., Snow 2008; Snow et al. 2001, 2008). Although additional undescribed species are known with a high degree of confidence, further research and more collections will be needed to produce a complete taxonomic treatment of the genus for Madagascar.

Despite additional new species of *Eugenia* remaining to be described and other gaps in knowledge of Malagasy taxa, tentative patterns of distribution, ecological preferences and evolution are beginning to emerge (Snow et al. 2014). One: Moderately high levels of specific diversity of *Eugenia* can occur in relatively localized areas, such as the approximately 15 species (including some undescribed) between Taolagnaro and Sainte Luce on the southeast coast. Two: Most *Eugenia* occupy one of three general areas: i) high altitudes in the northern mountainous massifs; ii) humid forests in the vicinity of eastern escarpment; or iii) in drier lowland habitats near the eastern coast. Three: Most species of *Eugenia* in Madagascar have relatively limited geographic ranges. This contrasts with some Malagasy species of *Syzygium* Gaertn., the other genus of Myrtaceae native to Madagascar, which includes some widely distributed species, such as *S. bernieri* (H. Perrier) Labat & Schatz, *S. lububre* (H. Perrier) Labat & Schatz, *S. micropodum* (Baker) Labat & Schatz, *S. parkeri* (Baker) Labat & Schatz, *S. phiyllyreifolium* (Baker) Labat & Schatz, *S. sakalavarum* (H. Perrier) Labat & Schatz, and two other species in need of new names (Byng 2014; Byng et al. in press). Given that many species of *Eugenia* are relatively short trees or shrubs, in contrast with many of *Syzygium* that are canopy or emergent species, the average dispersal distance of fruits of *Eugenia* species may be considerably less than *Syzygium*. Four: No species of *Eugenia* is an ecological dominant, although some species can be locally common, such as *E. echinulata* and *E. obovatifolia*. Five: Cauliflory (flowers arising on main bole) and ramiflory (flowers arising on naked branches below leaves) are common methods of floral presentation, and often occur largely in lieu of terminal or axillary presentations. Cauliflory and ramiflory presumably reflect selective pressures for pollination and/or fruit dispersal. Six: All known species have whitish, cream-colored, or pinkish-magenta petals. In contrast, red, yellow, orange, purple or blue petals are unknown. While almost nothing is known about the pollination biology of Malagasy *Eugenia*, the petal colors likely reflect selection pressures of generalized pollinators such as bees. Seven: Selection has sometimes favored relatively large fruits and embryos (e.g., *E. andapae*, *E. manomboensis*, *E. iantarensis*, *E. guillotii*, *E. manomboensis*, *E. ravelonarivoi*), which suggests consumption of and dispersal by mammals or large birds. Lemurs (this paper; Snow et al. 2012) are among the known consumers, and information concerning bird consumption would be appreciated by the first author. Field studies documenting the pollinators of flowers and consumers of fruits of *Eugenia* (and *Syzygium*) would be valuable graduate theses. Eight: Although dioecy in *Eugenia* is well known from western and southern Africa and adjacent areas (van Wyk and Lowry 1988; Bernardini et al. 2014, J. Byng, pers. comm. 2014), this reproductive system has not yet been documented among Madagascar members of *Eugenia*.

Many species of Malagasy *Eugenia*, including several proposed here, are Threatened, Endangered, or Critically Endangered following IUCN Criteria and Recommendations (IUCN 2012). In view of rapidly continuing deforestation in Madagascar, the occurrence of many from five or fewer collections, and that some species are known from only flowering or fruiting material, additional collecting of *Eugenia* should remain a high priority.

We believe that at least ten or more additional species remain to be described, and stress here that more material of other species would enhance our knowledge of taxonomy, distribution, and conservation priorities. Duplicate material of Malagasy *Eugenia* sent to the first author at the T.M. Sperry Herbarium (KSP) for future studies would be greatly appreciated.

Corrigendum: The correct collection number for the paratype specimen of *Eugenia vanwykiana* N. Snow is Razakamalala 1234 et al. The protologue incorrectly cited the collection number as 1324 (Snow et al. 2012).

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