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Taxonomic revaluation of the *Polylepis pauta* and *P. sericea* (Rosaceae) from Ecuador

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Abstract

We conducted a taxonomic revaluation of the *Polylepis pauta* and *P. sericea* complexes in Ecuador, recognizing five species, three of which are described as new: *Polylepis humboldtii* sp. nov., *P. loxensis* sp. nov., *P. longipilosa* sp. nov., *P. ochreata*, and *P. pauta*. We provide descriptions of all species, full specimen citations, and updated keys to genus *Polylepis* in Ecuador and to the *P. pauta* and *P. sericea* complexes in general.

Resumen

Realizamos una reevaluación taxonómica de los complejos *Polylepis pauta* y *P. sericea* en Ecuador, reconociendo cinco especies en estos complejos, tres de las cuales se describen como nuevas: *Polylepis humboldtii* sp. nov., *P. loxensis* sp. nov., *P. longipilosa* sp. nov., *P. ochreata* y *P. pauta*. Proporcionamos descripciones detalladas de todas las especies, citas completas de los especímenes y claves actualizadas para el género *Polylepis* en Ecuador y los complejos *P. pauta* y *P. sericea* en general.

Keywords: Morphology, taxonomy

Introduction

Polylepis Ruiz & Pavón (1794:80) (Rosaceae) is an iconic tree genus of the high Andes, representing the natural forest vegetation of the tropical Andes above about 3500 m elevation and forming the highest treelines in the southern hemisphere at over 4800 m (Hoch & Körner 2005, Kessler *et al.* 2014). *Polylepis* forests have been strongly affected by human land use for millennia, leading to massive forest fragmentation and the modification of plant assemblages (Hensen 2002, Sylvester *et al.* 2017). Today, they are the focus of conservation action and reforestation projects such as Andes Action of the Global Forest Generation.

Taxonomically, the genus *Polylepis* has long been challenging due to high morphological plasticity, extensive hybridization, and polyploidization (Romoleroux 1996, Schmidt-Lebuhn *et al.* 2006, 2010). In the first modern revision of the genus, Simpson (1979) recognized 15 broadly delimited species. Later work gradually split up these species to arrive at more morphologically and biogeographically well-defined units, for example separating *P. tarapacana* Philippi (1891: 21) from *P. tomentella* Weddell (1857[1861]: 237) (Simpson 1986), *P. microphylla* (Wedd.) Bitter (1911: 611) from *P. weberbaueri* Pilger (1906: 535) (Romoleroux 1996), *P. rugulosa* Bitter (1911: 638) from *P. besseri* Hieronymus (1895: 312) (Kessler 1995a), *P. lanata* (Kuntze) Kessler & Schmidt-Lebuhn (2006: 69) and *P. triacontandra* Bitter (1911: 630) from *P. racemosa* (Kessler 1995b), and *P. incarum* (Bitter) Kessler & Schmidt-Lebuhn (2006: 69) and *P. subtusalbida* (Bitter) Kessler & Schmidt-Lebuhn (2006: 69) from *P. besseri* (Kessler 1995b). In addition, several new species have since been described, such as *P. neglecta* Kessler (1995b: 140), *P. canoi* Mendoza (2005: 104), and *P. pacensis* Kessler & Schmidt-Lebuhn (2006: 67), so that in 2006, the latter authors recognized 26 species. Since then, two further species have been described (Valenzuela and Villalba 2015, Boza *et al.* 2019).

Under Simpson's (1979) classification, the most widespread species of the genus was *P. sericea* Weddell (1857:238), ranging from Venezuela to Bolivia. The recognition that two forms that would both be included under this concept of *P. sericea* co-occur widely in central Peru without obvious signs of hybridization or intergradation prompted Boza *et al.* (2019) to revise this species group, recognizing five mostly geographically separate species, one of which was newly described. Based on a cursory examination of limited Ecuadorean material, they recognized a single species in the *sericea* complex for Ecuador, namely *P. ochreata* (Wedd.) Bitter (1911: 597). Upon revising the specimens at the herbarium QCA, one of us (KR) recognized that this classification does not adequately cover the variability of the species complex in Ecuador.

In addition to *P. sericea*, the species *P. pauta* Hieronymus (1895: 313) has also been taxonomically troublesome. Simpson (1979) already remarked that it is possible to morphologically differentiate various geographical populations. In Ecuador, in particular, the ecologically well-studied populations to the east of Quito (Cierjacks *et al.* 2007a,b), have either been identified as *P. pauta* or as hybrids between *P. pauta* and *P. sericea* (Simpson 1979, Romoleroux 1996). These taxonomic problems among *Polylepis* in Ecuador prompted us to undertake a joint revision of the herbarium collections, coupled with field work at several sites in Ecuador in September and December 2019. The aim of this study thus was to clarify the taxonomy of the species of the *Polylepis sericea* and *P. pauta* complexes in Ecuador. As a result, here we present an identification key, descriptions along with ecological information, illustrations, geographical distribution, and discussions the affinities between the species.

Methods

Field collections and herbarium specimens deposited in AAU, GOET, LOJA, MO, and QCA (Thiers, continuously updated), as well as taxonomic literature (Bitter 1911, Simpson 1979, Romoleroux 1996) were examined. The morphological descriptions and measurements were taken from dried specimens (Table 1). Conservation status was assigned using IUCN criteria (2015), combining field information, bibliographic data on habitat and geographic distribution based on herbarium specimens.

Species delimitation in *Polylepis* is challenging because of the taxonomic difficulties implied by hybridization and polyploidization, and previous studies on *Polylepis* have used different species concepts. Simpson (1979) used a very broad species delimitation, recognizing only 15 species in the entire genus, and six native species in Ecuador. Later workers have regarded this classification as too broad to describe the natural variation in the genus, resulting in subsequently finer species delimitations, increasing the numbers of species to seven in Ecuador (Romoleroux 1996) and 26 overall (Kessler & Schmidt-Lebuhn 2006). Here, based on de Queiroz (1998) and Davis and Heywood (1973), we applied a rather narrow species concept based on identifying morphologically, ecology, and biogeographically distinct entities, which provides a better basis for targeted conservation and management action.

Results

As a result of our studies, we here propose a revised classification of the *Polylepis pauta* and *sericea* complexes in Ecuador, recognizing five species, three of which are described as new. In particular, the newly described species *P. humboldtii* and *P. loxensis* have very small ranges and population sizes, so that they urgently deserve further study. We designate neotypes for *Polylepis pauta* and its synonym *P. stuebelii*. Therefore, we consider that the genus *Polylepis* in Ecuador includes eleven species, including the two species *P. longipilosa* and *P. pauta* belonging to *P. pauta* complex, and with the three species *P. humboldtii*, *P. loxensis* and *P. ochreata* in *P. sericea* complex.

Key to the species of *Polylepis* in Ecuador

1. Lower leaflet surfaces sparsely to densely sericeous or densely lanate 2
- Lower leaflet surfaces pannose, villous, or with small, matted, glandular hairs, not sericeous (except on the leaflet margins of *P. reticulata*) 7
2. Lower leaflet surfaces densely lanate, hairs 1.1–2.5 mm long 3
- Lower leaflet surfaces sparsely to densely sericeous, hairs 0.2–0.9 mm long 4
3. Leaflets elliptic, 1.7–2.8 × 0.7–1.4 cm; 13–16 flowers per inflorescence *P. lanuginosa*
- Leaflets ovate, 1.4–2.2 × 0.4–0.5 cm; 19–29 flower per inflorescence *P. longipilosa*

4. Lower leaflet surfaces sparsely sericeous; margins of the leaflets crenate *P. pauta*
 - Lower leaflet surfaces densely sericeous; margins of the leaflets entire to serrate 5
 5. Leaves 2.6–3.6 × 2.1–3.2 cm; leaflets broadly obovate with serrate margins *P. loxensis*
 - Leaves 4.3–7.0 × 3.4–4.3 cm long; leaflets elliptic to narrowly elliptic with entire or slightly serrate margins 6
 6. Leaves with 3–4 lateral leaflet pairs; stipular sheaths densely sericeous *P. humboldtii*
 - Leaves with 4–7 lateral leaflet pairs; stipular sheaths glabrous or sparsely sericeous *P. ochreata*
 7. Leaves with 1 lateral leaflet pair; leaflet apices round, obtuse, or emarginate 8
 - Leaves with (1–)2–6 lateral leaflet pairs; leaflet apices deeply emarginate 9
 8. Leaflets 1.4–2.7 × 0.4–0.7 cm; leaflet margins crenate; leaflet apices obtuse to emarginate; lower leaflet surfaces pannose *P. incana*
 - Leaflets 2.3–3.9 × 0.7–1.5 cm; leaflet margins serrate; leaflet apices round; lower leaflet surfaces sparsely to densely tomentose.. *P. racemosa*
 9. Stipular sheaths and leaflet margins sericeous; leaflets pannose below *P. reticulata*
 - Stipular sheaths and leaflet margins pannose or villous; leaflets pannose or lanose below 10
 10. Lower leaflet surfaces and stipular sheathes villous intermixed with short, matted, dark red multicellular hairs; hypanthium in fruit with irregular ridges *P. microphylla*
 - Lower leaflet surfaces and stipular sheathes pannose; hypanthium in fruit with small flattened spines *P. weberbaueri*

Key to all species of the *Polylepis pauta* and *sericea* species complexes

1. Lateral leaflets 4–7 pairs; lower leaflet surfaces sparsely sericeous or densely lanate, usually with longer hairs on the veins (*P. pauta* complex) 2
 - Lateral leaflets 2–7 pairs; lower leaflet surfaces densely villous or densely sericeous, usually with even hair length throughout (*P. sericea* complex) 4
 2. Leaflets (1.8–)2.4–3.5 × 0.8–1.0(–1.2) cm; leaflet margins serrate; Peru *P. serrata*
 - Leaflets (1.1–)1.4–2.2 × 0.4–0.6 cm; leaflet margins entire to crenate; Ecuador .. 2
 3. Leaflets ovate; lower leaflet surfaces densely lanate with whitish silky hairs 1.1–1.6 mm long; 19–29 flowers per inflorescence; northern Ecuador *P. longipilosa*
 - Leaflets elliptic; lower leaflet surfaces sparsely sericeous with whitish hairs 0.4–0.9 mm long; 9–15(–21) flowers per inflorescence; northeastern Ecuador *P. pauta*
 4. Lower leaflet surfaces densely villous; Colombia *P. frontinensis*
 - Lower leaflet surfaces densely sericeous; Venezuela to Bolivia 2
 5. Leaflet margins slightly crenate; Peru *P. albicans*
 - Leaflet margins entire to serrate; Venezuela to Bolivia 3
 6. Leaflets (2.4–)3.4–3.9 × (0.8–)1.1–1.5 cm; lower leaflet surface hairs 1.3–1.7 mm long, yellowish; central Peru to Bolivia
 *P. canoi*
 - Leaflets 1.2–3.0 × 0.5–1.0 cm; lower leaflet surface hairs 0.2–1.0 mm long, silky, whitish; Venezuela to central Peru 4
 7. Lateral leaflets 3–7 pairs; lower leaflet surface hairs 0.2–0.6 mm long; Ecuador 5
 - Lateral leaflets 2–3 pairs; lower leaflet surface hairs 0.6–1.0 mm long; Venezuela, Colombia, central Peru 7
 8. Leaflets broadly obovate; upper leaflet surfaces with a few hairs on the midvein; inflorescences (3.5–)4.3–10.5(–12.2) cm long, with 9–27 flowers; southern Ecuador *P. loxensis*
 - Leaflets narrowly elliptic to elliptic; upper leaflet surfaces glabrous; inflorescences 8.1–20.4 cm long, with 21–49 flowers; southern Colombia to central Ecuador 6
 9. Leaves with 3–4 lateral leaflet pairs; stipular sheaths apically acute with spurs, densely sericeous (adult and juvenile) on the upper surface; central Ecuador *P. humboldtii*
 - Leaves with 4–7 lateral leaflet pairs; stipular sheaths apically acute, glabrous to sparsely sericeous (adult) or densely sericeous (juvenile) on the upper surface; southern Colombia to northern Ecuador *P. ochreata*
 10. Leaflets 0.5–0.7 cm wide; upper leaflet surfaces with some hairs on the midveins to densely sericeous with silky hairs throughout; inflorescences 7.2–8.1 cm long, with 5–6(9) flowers; Peru *P. argentea*
 - Leaflets 0.8–1.0 cm wide; upper leaflet surfaces glabrous; inflorescences 3.3–4.5 cm long, with 9–15 flowers; Venezuela, Colombia *P. sericea*

Taxonomic treatment

Polylepis humboldtii T.Boza, K.Romol. & M.Kessler, sp. nov. (Fig. 1)

Type:—ECUADOR. Chimborazo: Lagunas de Atillo, 02°08' S 78°34' W, 3465 m, 17 December 2019, *K. Romoleroux et al.* 6199 (holotype QCA!, isotypes Z!).

This species differs from *Polylepis sericea* Weddell (1987) in having shorter hairs on the leaflets (0.2–0.4 mm versus 0.7–1.0 mm) and longer inflorescences with more flowers (13.0–20.4 cm, 23–29 flowers versus 3.3–4.5 cm, 9–15 flowers).

TABLE 1. Summary of quantitative characters separating the Ecuadorian species in the *P. sericea* and *P. pauta* complexes.

Character	<i>P. longipilosa</i>	<i>P. laxensis</i>	<i>P. humboldtii</i>	<i>P. ochreatum</i>	<i>P. pauta</i>
Number of lateral leaflet pairs	(4)5–6	3–4(–5)	3–4	4–7	4–5(–6)
Leaf length (cm)	(3.8–)4.3–7.3	2.6–3.6	4.5–6.3	(3.9–)4.4–7.0	3.2–4.9
Leaf width (cm)	2.4–4.5	2.1–3.2	3.4–4.3	2.9–4.7	2.2–3.0
Rachis	Densely sericeous	Densely sericeous	Densely sericeous	Glabrous–densely sericeous	Sparingly sericeous
Leaflet shape	Ovate	Broadly obovate	Elliptic	Narrowly elliptic	Elliptic
Leaflet length (cm)	1.4–2.2	1.2–1.6	1.8–2.8	1.6–3.0	(1.1–)1.4–1.6
Leaflet width (cm)	0.4–0.5	0.5–0.8	0.6–0.9	0.5–0.7	0.5–0.6
Leaflet margin	Entire–slightly crenate	Serrate	Entire	Entire–slightly serrate	Crenate
Leaflet apex	Emarginate–acute	Emarginate	Emarginate	Emarginate	Emarginate
Leaflet hairs (upper surface)	Glabrous	Glabrous–few hairs in mid depression	Glabrous	Glabrous	Glabrous–sparingly sericeous
Leaflet hairs (lower surface)	Densely lanate	Densely sericeous	Densely sericeous	Densely sericeous	Sparingly sericeous on mid veins
Leaflet hair length (mm)	1.1–1.6	0.2–0.6	0.2–0.4	0.3–0.5	0.4–0.9
Inflorescence length (cm)	(6.8–)11.1–16.6	(3.5–)4.3–10.5(–12.2)	13.0–17.9(–20.4)	8.1–15.5(–17.4)	(8.1–)12.6–14.3(–19.3)
# of flowers	19–29	9–27	23–29	(21–)26–49	9–15(–21)
# of stamens	8–10	7–9	9–15	9–13	9–15
Style length (mm)	1.6–2.0	1.7–2.0	1.9–2.9	2.1–2.6	2.2–3.0

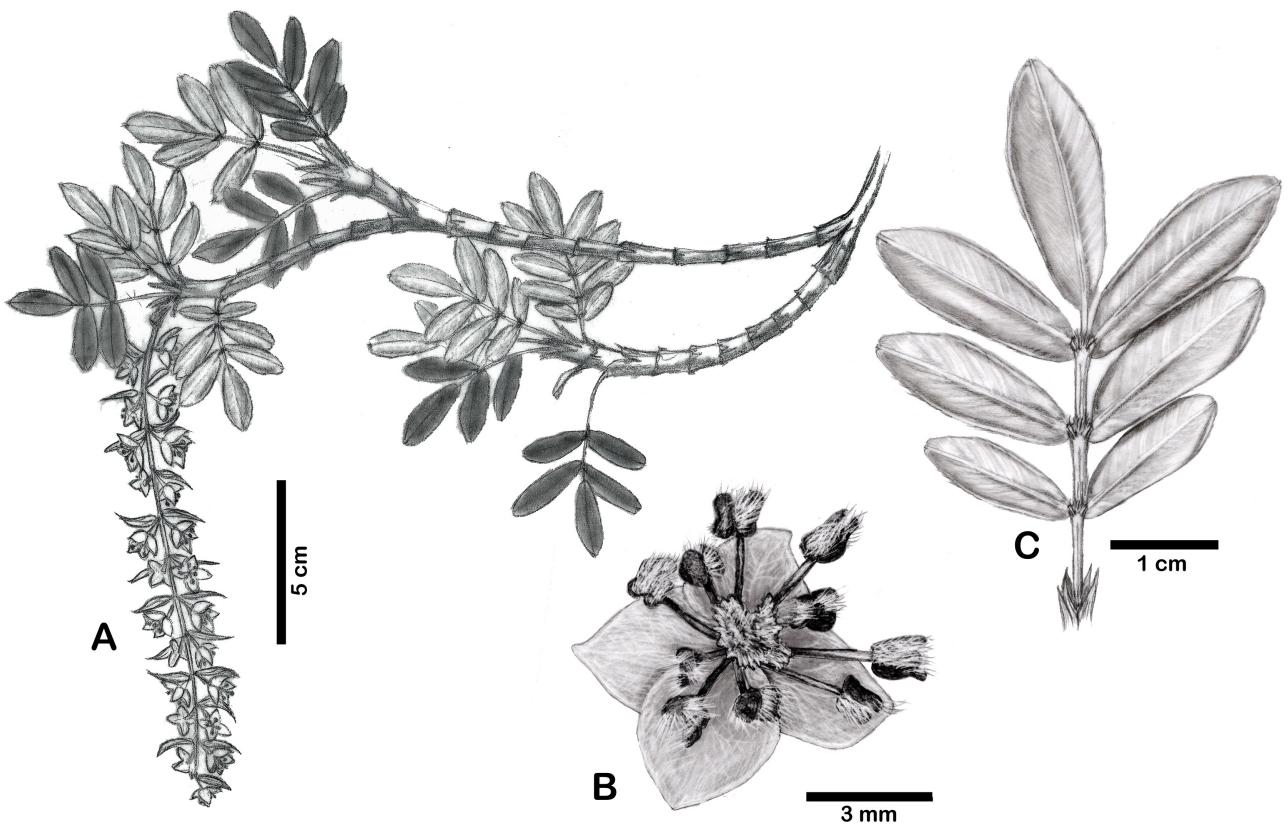


FIGURE 1. *Polylepis humboldtii*. A. Flowering branch (*Cárate et al. 188*). B. Leaf, seen from the underside (*Cárate et al. 185*). C. Flower (*Romoleroux et al. 6199*). A, C drawn by V. Popp, B drawn by M. Kessler.

Trees 4–12 m tall. **Leaves** strongly congested at the branch tips, imparipinnate with 3–4 pairs of lateral leaflets, obtrullate in outline, 4.5–6.3 × 3.4–4.3 cm; rachises densely sericeous, points of leaflet attachment with a tuft of long, straight whitish hairs; stipular sheaths apically acute with spurs, densely sericeous in the upper surface; leaflets elliptic in outline, second pair from the terminal leaflet the largest, one of this pair 1.8–2.8 × 0.6–0.9 cm; margins entire, apically emarginate, basally unequally cordate; upper leaflet surfaces glabrous; lower leaflet surfaces densely sericeous with whitish hairs 0.2–0.4 mm. long. **Inflorescences** pendant, 13.0–17.9(–20.4) cm long, bearing 23–29 flowers; floral bracts 9.3–11.1 mm long, narrowly triangular, densely sericeous on the outer surface; rachises glabrous. **Flowers** 7.4–8.4 mm diam.; sepals 4, ovate, green, densely sericeous outside; stamens 9–15, anthers orbicular, with a dense tuft of straight white hairs on the upper half; styles fimbriate, 1.9–2.9 mm long. **Fruits** turbinate, with variable numbers and placement of flattened spines, densely sericeous; 3.3–5.1 × 3.1–7.4 mm including spines.

Distribution, habitat and ecology:—*Polylepis humboldtii* is restricted to Chimborazo province in Ecuador. It occurs in small populations at 3800–4000 m elevation. It grows in mixed Andean forest with *Escallonia myrtilloides* L.f., *Miconia salicifolia* Bonpl. ex Naudin, *Gynoxys* sp., *Berberis* sp., *Diplostephium hartwegii* Hieron, *Ceratostema alatum* (Hoerold) Sleumer, *Hypericum* sp., *Brachyotum ledifolium* (Desr.) Triana, *Cortaderia nitida* (Kunth) Pilger, *Carex pichinchensis* Kunth, *Rubus nubigenus* Kunth, *Puya* sp., and *Elaphoglossum ovatum* (Hook. & Grev.) T.Moore (Fig. 2).

Conservation status:—The area of occupancy (AOO) for *Polylepis humboldtii* is estimated as 4 km², and it is known just from the type location in Ecuador and a nearby site. Although it is protected within Sangay National Park, burning of the páramo grassland matrix likely affects the remaining *Polylepis* forest patches. Therefore, we assess *P. humboldtii* as Critically Endangered (CR B2a, C2).

Etymology:—We name this species after Alexander von Humboldt, whose description of the vegetation zonation of Volcán Chimborazo, close to where this species is found, represents one of the milestones of biogeographical research. Incidentally, we first recognized this species in the herbarium just two days after von Humboldt's 250th birthday.

Additional specimens examined:—**ECUADOR.** Chimborazo: Alausí, Achupallas, alrededores, 2°17'S 78°39'W, 3300 m, 11 July 2013, J. Caranqui 2565 (QCA!); Lagunas de Atillo, 2°8'S 78°34'W, 3465 m, 13 April 2009, D. Cárate et al. 184 (QCA!), 185 (QCA!), 188 (QCA!).

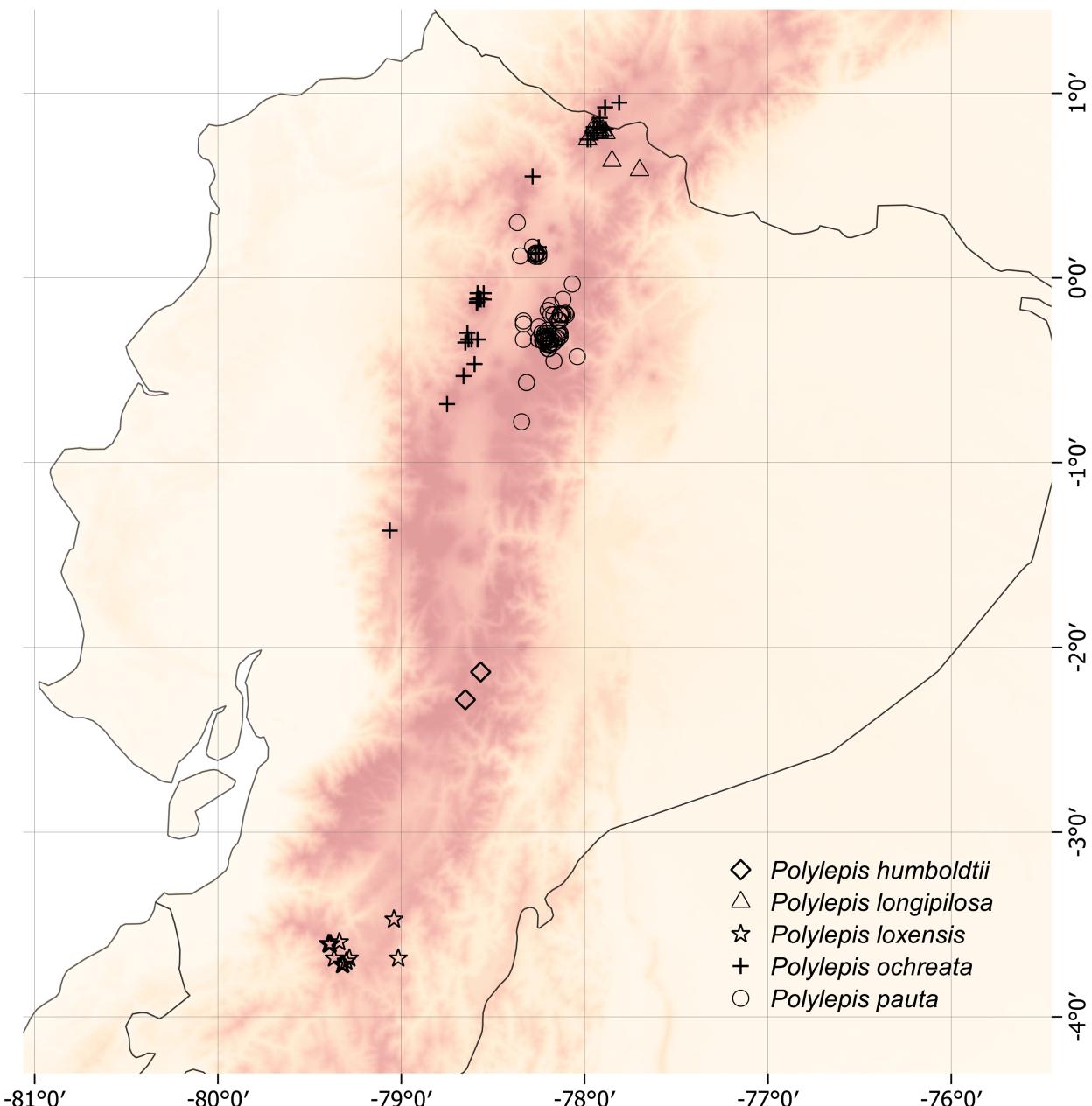


FIGURE 2. Geographical distribution of the species of the *Polylepis pauta* and *P. sericea* complexes in Ecuador and adjacent Colombia.

Notes. *Polylepis humboldtii* resembles *P. sericea* (sensu Boza *et al.* 2019) in having similar leaflet shape, margin, apex and upper and lower leaflet surfaces hairs type and density. However, it has shorter lower leaflet surface hairs 0.2–0.4 mm long, and longer inflorescences 13.0–20.4 cm long with more flowers (23–29), whereas *P. sericea* has lower leaflet hairs 0.7–1.0 mm long and inflorescences 3.3–4.5 cm with 9–15 flowers. Additionally, *P. humboldtii* occurs in the central Ecuadorean Andes, whereas *P. sericea* is distributed from western Venezuela to central Colombia.

***Polylepis longipilosa* T.Boza, K.Romol. & M.Kessler, sp. nov. (Fig. 3)**

Type:—ECUADOR. Carchi: Cantón Montúfar, Loma El Corazón (Bretaña), al sureste de Huaca, al este de la Colonia Huaqueña, Río Minas, 00°35'N 077°42'W, 3200–3500 m, 9 April 1989, Tipaz 35 (holotype QCA!, isotypes AAU!, MO!).

This species differs from the morphologically closest species *Polylepis ochreata* (Wedd.) Bitter (1911) in having ovate leaflets, longer lower leaflet surface hairs, stipular sheaths apically truncate, and shorter styles.

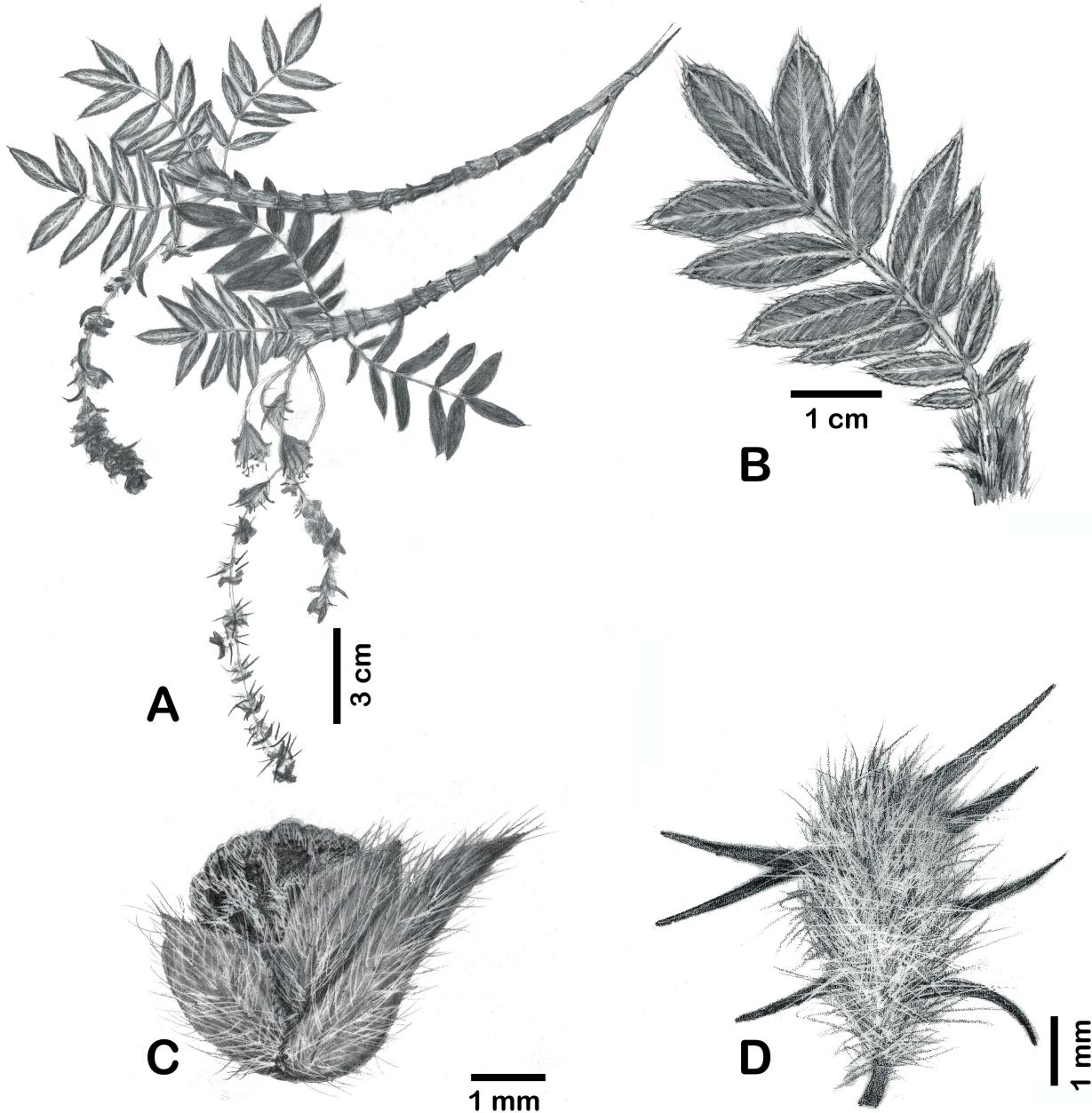


FIGURE 3. *Polylepis longipilosa*. A. Flowering branch (*Tipaz 35*). B. Leaf seen from the underside (*Laegaard 54965*). C. Flowerbud (*Tipaz 35*). D. Fruit (*Tipaz 35*). Drawn by M. Kessler.

Trees 5–10 m tall. **Leaves** strongly congested at the branch tips, imparipinnate with (4–)5–6 pairs of lateral leaflets, obtrullate in outline, (3.8–)4.3–7.3 × 2.4–4.5 cm; rachises densely sericeous, points of leaflet attachment with a tuft of long, straight whitish to yellowish hairs; stipular sheaths apically truncate, densely sericeous in the upper surface; leaflets ovate in outline, second pair from the terminal leaflet the largest, one of this pair 1.4–2.2 × 0.4–0.5 cm; margins entire to slightly crenate with 6–7 teeth, apically slightly emarginate seem like acute by the prolongation of hairs, basally unequally cordate; upper leaflet surfaces glabrous; lower leaflet surfaces densely lanate with whitish silky hairs 1.1–1.6 mm long. **Inflorescences** pendant, (6.8–)11.1–16.6 cm long, bearing 19–29 flowers; floral bracts 6.1–9.4 mm long, narrowly triangular, glabrous on the outer surface; rachises densely sericeous. **Flowers** 4.8–5.5 mm diam.; sepals 4, ovate, green, glabrous outside; stamens 8–10, anthers orbicular, with a dense tuft of straight white hairs on the upper half; styles fimbriate, 1.6–2.0 mm long. **Fruits** turbinate, with variable numbers and placement of flattened spines, densely sericeous; 3.9–6.7 × 4.3–7.5 mm including spines.

Distribution habitat and ecology:—*Polylepis longipilosa* is restricted to northwestern Ecuador (Carchi). It grows in humid páramo habitats at 3200–3900 m. It often co-occurs with *P. ochreata* with which it hybridizes (Romoleroux

1996). It grows in mixed forest with *Espeletia pycnophylla* Cuatrec., *Weinmannia* sp. and *Oreopanax* sp. (Boada *et al.* 2008) (Fig. 2).

Conservation Status:—The estimated extent of occurrence (EOO) for *Polyplepis longipilosa* is 265 km² and the AOO is 32 km². It is known from four locations. No conservation actions are taken at present. The Andean forest and páramos in Carchi province have in recent years come under increasing threat from timber cutting and forest burning, and advancement of the agricultural frontier, which has contributed to the fragmentation and destruction of high Andean ecosystems (Boada *et al.* 2008). Therefore, based on its degraded and fragmented distribution, we assess *P. longipilosa* as Critically Endangered (CR A2a, B1a+B2a, C1+C2a).

Etyymology:—The species epithet *longipilosa* refers to the characteristic long hairs of the species.

Additional specimens examined:—ECUADOR. Carchi: Tulcán, carretera Túlcan-Tufiño-Maldonado-Chical col. en km 12 de Tufiño, cerca de las lagunas, 00°48'N 077°55'W, 3900 m, 23 April 1993, A. Freire F. & E.O. Andersen 2547 (AAU!); road Tulcán-Maldonado, near Volcán Chiles, 00°48'N 077°56'W, 3850–4000 m, 16 August 1985, S. Laegaard 54965 (AAU!, MO!, QCA!), 54967A (AAU!), 54967B (AAU!), 54967C (AAU!), 54967D (AAU!, QCA!), 54967E (AAU!, QCA!), 54967F (AAU!, QCA!); along the road from Tulcán to Volcán Chiles, 3900 m, 6 October 1995, P. Sklenář & V. Kosteckova 14124 (QCA!); camino Tufiño, sitio Agua Hediondas, en la base del Volcán Chiles, límite con Colombia, 00°48'N 077°54'W, 3500 m, 8 November 1993, W.A. Palacios 11847 (AAU!, MO!, QCNE); carretera entre Tulcán y Maldonado, faldas del Volcán Chiles, punto más alto del cruce de carretera, 00°45'N 077°59'W, 3800 m, 19 May 1991, W.A. Palacios & D. Rubio 7349 (AAU!, MO!); southern slopes of Volcán Chiles, 00°49'N 077°57'W, 3600 m, P.M. Ramsay 911 (QCA!, QCNE); route de Tufiño a Maldonado, 10 km après Tufiño, zone très humide, 3850 m, 06 July 1988, C. Huttel 1390 (QCA!); carretera San Gabriel-Shután alto, 3500 m, 25 March 1989, J.L. Jaramillo A. 10862 (QCA!); comuna La Esperanza, páramo de El Artezón, sector Monte Redondo, 3789 m, 18 September 2007, S. Salgado 220B (QCA!), 239A (QCA!).

Notes:—The populations of *Polyplepis* from southern slopes of Volcán Chiles and on the road between Maldonado and Tulcán in Carchi have been previously identified either as *P. ochreata* (Simpson 1979, Romoleroux 1996, as *P. sericea*) or *P. pauta* (Romoleroux 1996). Certainly, *P. longipilosa* resembles *P. ochreata* in having 4–6 lateral leaflet pairs, a similar density of hairs, and sometimes slightly emarginate leaflet apices. However, it has ovate leaflets with longer, lanate lower surface hairs (1.1–1.6 mm), and shorter styles (1.6–2.0 mm), whereas *P. ochreata* has narrowly elliptic leaflets with sericeous lower surface hairs 0.3–0.5 mm long, and styles 2.1–2.6 mm long. *Polyplepis longipilosa* is also morphologically similar to *P. pauta*. The most obvious differences between these two species are lower leaflet surface hair density and type (densely lanate vs. sparsely sericeous) and length (1.1–1.6 mm vs. 0.4–0.9 mm), inflorescence length (6.8–16.6 cm vs. 8.1–19.3 cm), number of flowers (19–29 vs. 9–21), and style length (1.6–2.0 mm vs. 2.2–3.0 mm).

Polyplepis loxensis T.Boza, K.Romol. & M.Kessler, sp. nov. (Fig. 4)

Type:—ECUADOR. Loja: Laguna Chinchilla, 03°36'20"S 079°23'08"W, 3610 m, 21 December 2019, T.E. Boza E. & C. Medina 3185 (holotype: QCA!; isotypes: Z!, CUZI!).

Resembles *Polyplepis ochreata* (Wedd.) Bitter (1911) by having emarginate leaflet apices and subcordate leaflet bases, and similarly dense, short, white silky hair on the lower leaflet surfaces, but differs by the number of leaflet pairs (3–4(–5) vs. 4–7), shorter inflorescences (3.5–12.2 cm vs. 8.1–17.4 cm) bearing 9–27 vs. 21–49 flowers, fewer stamens (7–9 vs. 9–15), and shorter styles (1.7–2.0 mm vs. 2.1–2.6 mm),

Trees 4–10 m tall. Leaves strongly congested at the branch tips, imparipinnate with 3–4(–5) pairs of lateral leaflets, obtrullate in outline, 2.6–3.6 × 2.1–3.2 cm; rachises densely sericeous, points of leaflet attachment with a tuft of long, straight whitish hairs; stipular sheaths apically truncate, densely sericeous in the upper surface; leaflets narrowly to broadly obovate in outline, second pair from the terminal leaflet the largest, one of this pair 1.2–1.6 × 0.5–0.8 cm; margins serrate at apex with 3–4 teeth, apically emarginate, basally unequally cordate; upper leaflet surfaces glabrous with few hairs on mid depression; lower leaflet surfaces densely sericeous with whitish silky hairs 0.2–0.6 mm. long. Inflorescences pendant, (3.5–)4.3–10.5(–12.2) cm long, bearing 9–27 flowers; floral bracts 5.5–6.3 mm long, narrowly triangular, densely sericeous on the outer surface; rachises densely sericeous. Flowers 4.4–5.2 mm diam.; sepals 4, ovate, green, densely sericeous outside; stamens 7–9, anthers orbicular, with a dense tuft of straight white hairs on the upper half; styles fimbriate, 1.7–2.0 mm long. Fruits turbinate, with variable numbers and placement of flattened spines, densely sericeous; 1.7–3.0 × 1.4–1.5 mm including spines.

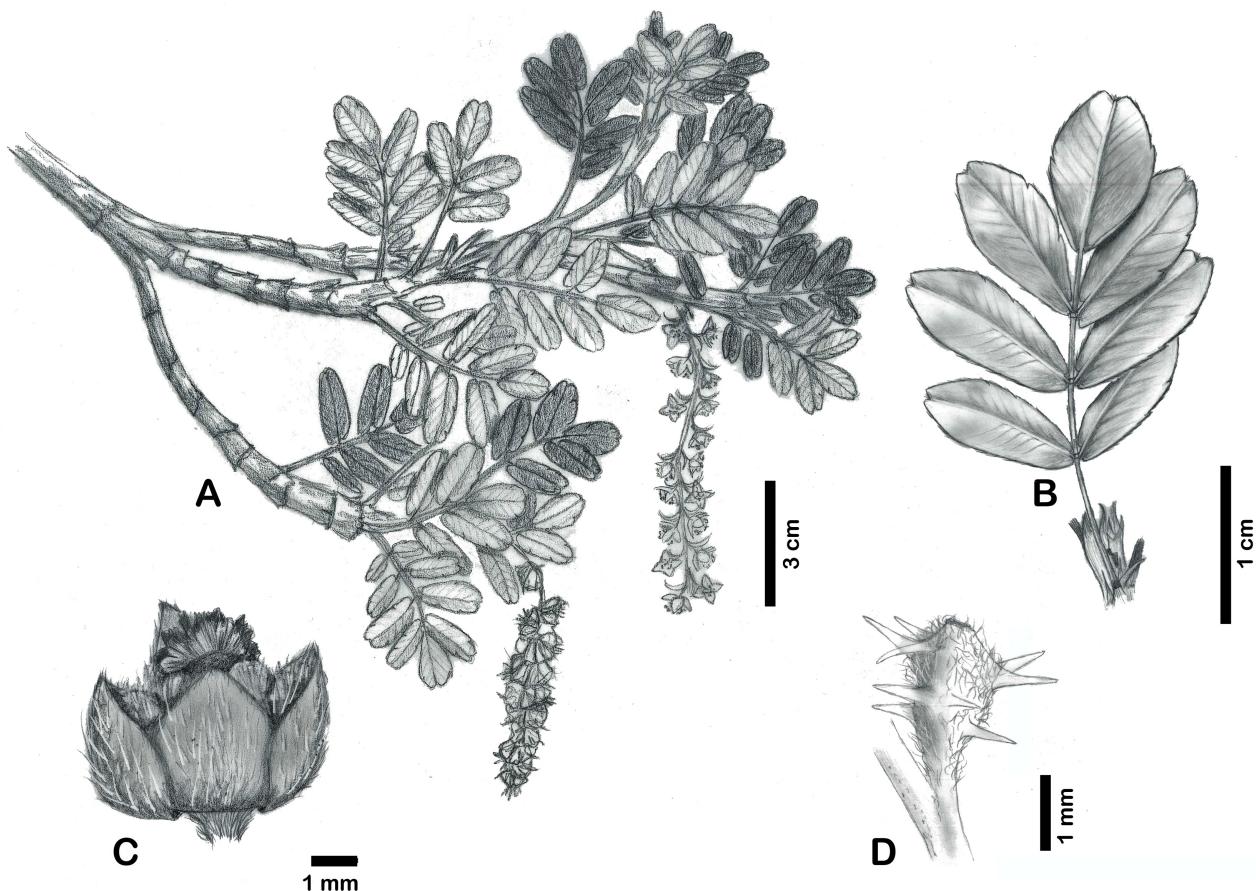


FIGURE 4. *Polylepis loxensis*. A. Flowering branch (*Sklenář & Laegaard 7096*). B. Leaf seen from the underside (*Sklenář & Laegaard 7096*). C. Flower (*Sklenář & Laegaard 7096*). D. Fruit (*Laegaard & Vicente 19109*). Drawn by V. Popp.

Distribution, habitat and ecology:—*Polylepis loxensis* is restricted to southwestern Ecuador from southern Azuay (Nabón) to northern Loja (Fierro Urco and Laguna Chinchilla). The species occurs in the humid páramo at 2650–3700 m elevation. It is often associated with *Gynoxys cuicochensis* Cuatrec., *Brachyotum ledifolium* Triana, and *Weinmannia glabra* L.f. (Fig. 2).

Conservation status:—The estimated EOO for *Polylepis loxensis* is 728 km² and the AOO is 32 km². It is known from six locations. It occurs in areas subject to continuing fragmentation and habitat degradation from livestock grazing, gold mining concessions and large extensions of pine plantations. Indeed, during our field work, we failed to find the species at some sites where it had been historically collected. We assess *P. loxensis* as Critically Endangered (CR A2a, B1a+B2a, C2a).

Etymology:—The name refers to the province of Loja, to which this species is largely restricted.

Additional specimens examined:—**ECUADOR.** Azuay: Nabón, 3°28'20"S 79°02'24"W, 2800–3300 m, 15 November 2008, S. Salgado 1419 (LOJA!); Loja: Loja, Fierro Urco, 03°36'20"S 079°23'08"W, 3610 m, 19 December 2019, T.E. Boza E. & C. Medina 3184 (QCA!, Z!, CUZ!); Fierro Urco, Saraguro-Loja, km 12.4 turnoff towards Fierro Urco, km 23.8, 03°43'10"S 079°19'18"W, 3840 m, 6 December 1994, P.M. Jørgensen et al. 1240 (AAU!, LOJA!, MO!); road San Lucas-Saraguro, km 9, turn off to Fierro Urco, 11 km to the pass, 03°43'03"S 079°19'25"W, 3630 m, 4 November 2000, P.M. Jørgensen et al. 2228 (QCA!); ca 10 km along road to Fierro Urco, 03°41'S 079°01'W, 2850 m, 8 September 1998, S. Laegaard 19109 (AAU!, LOJA!, QCA!); Fierro Urco, grass páramo 12 km to the left (northbound) from the Panamericana highway, 03°43'S 079°19'W, 3600–3650 m, 9 June 1999, P. Sklenář & S. Laegaard 7096 (AAU!, GOET!); ca km 12 along paramo road to Fierro Urco, 03°41'S 079°01'W, 3650 m, 9 June 1999, S. Laegaard & P. Sklenář 20279 (AAU!, LOJA!, QCA!); páramo of Fierro Urco SW of Saraguro, 03°43'S 079°19'W, 3500 m, 21 November 1996, G.P. Lewis, P. Lozano & B. Merino 2121 (AAU!); road Loja-Cuenca, km 50, track to Fierro Urco, km 5–7, 03°41'S 079°17'W, 3150–3350 m, 25 October 1996, G.P. Lewis & P. Lozano 2724 (AAU!, LOJA!, MO!, QCA!); road Loja-Saraguro, km 52, track to Fierro Urco, km 10, 03°42'S 079°18'W, 3350–3450 m, 17 January 1997, G.P. Lewis et al. 2932 (AAU!, LOJA!, MO!); road Loja-Saraguro, 8.5 km N of San Lucas, track

to Fierro Urco, km 11, 03°43'10"S 079°19'18"W, 3550 m, 15 January 1998, G.P. Lewis & C.E. Hughes 3804 (AAU!, LOJA!, MO!, QCA!); Fierro Urco, 03°41'S 079°22'W, 3700 m, 11 January 1995, P. Lozano 172 (LOJA!); Saraguro, Laguna Chinchilla, 03°36'20"S 079°23'08"W, 3610 m, 21 December 2019, T.E. Boza E. & C. Medina 3186 (QCA!, Z!, CUZ!), cerro Chinchilla, parroquia Celén, 03°35'44"S 079°20'17"W, 3000 m, 19 September 1984, J. Jaramillo A. 7332 (QCA!), 7335 (GB, QCA!); Laguna Chinchilla, 03°36'17"S 079°23'49"W, 11 November 2008, S. Salgado et al. 1392 (LOJA!), 1394 (LOJA!).

Notes:—*Polyplepis loxensis* can be distinguished from the most similar species *P. ochreata* by the number of leaflet pairs (3–4(–5)), shorter inflorescences (3.5–12.2 cm long), with fewer flowers (9–27), fewer stamens (7–9), and shorter styles (1.7–2.0 mm), whereas *P. ochreata* has inflorescences 8.1–17.4 cm long with 21–49 flowers, 9–15 stamens, and 2.1–2.6 mm long styles. Additionally, *P. loxensis* occurs in southern Ecuadorean Andes, whereas *P. ochreata* is distributed in northern Ecuador from Carchi to Bolívar.

Polyplepis ochreata (Wedd.) Bitter (1911: 597–598) ≡ *Acaena ochreata* Weddell (1855: 240). Lectotype (designated by Simpsom 1979):—ECUADOR. Pichincha, W slopes of Cerro Pichincha, 3600 m, May 1856, Jameson 73 (lectotype P![P-01819251], isolectotype A!, G!, GH!, US!; F! [F-0360600F], US! [US-00107827])

= *Polyplepis ochreata* var. *integra* Bitter (1911: 598). Type:—ECUADOR. Imbabura, Volcán Mojanda, March 1901, Sodiro s.n. (holotype FI; isotype GOET!).

= *Polyplepis subintegra* Benoist (1934: 326). Type:—ECUADOR. Pichincha, W slopes of Cerro Pichincha, Taurichupa, 4000 m, 28 November 1930, Benoist 3356 (holotype P![P-01819252]).

Trees 2–10 m tall. **Leaves** strongly congested at the branch tips, imparipinnate with 4–7 pairs of lateral leaflets, obtrullate in outline, (3.9–)4.4–7.0 × 2.9–4.7 cm; rachises glabrous to densely sericeous, points of leaflet attachment with a tuft of long, straight whitish hairs; stipular sheaths apically acute, glabrous to sparsely sericeous (adult) or densely sericeous (juvenile) in the upper surface; leaflets narrowly elliptic in outline, second pair from the terminal leaflet the largest, one of this pair 1.6–3.0 × 0.5–0.7 cm; margins entire to slightly serrate with 4–6 teeth, coriaceous, apically emarginate, basally unequally cordate; upper leaflet surfaces glabrous; lower leaflet surfaces densely sericeous with whitish silky hairs 1.3–2.0 mm long in juvenile plants and 0.3–0.5 mm long in adult plants. **Inflorescences** pendant, 8.1–15.5(–17.4) cm long, bearing (21)26–49 flowers; floral bracts 5.9–12.8 mm long, narrowly triangular, densely sericeous on the outer surface; rachises sericeous. **Flowers** 6.6–9.0 mm diam.; sepals 4, ovate, green, densely sericeous outside; stamens 9–13, anthers orbicular, with a dense tuft of straight white hairs on the upper half; styles fimbriate, 2.1–2.6 mm long. **Fruits** turbinate, with variable numbers and placement of flattened spines, densely sericeous; 4.7–7.5 × 6.1–7.9 mm including spines.

Distribution, habitat and ecology:—*Polyplepis ochreata* is distributed from southern Colombia (Nariño) to northern Ecuador (Carchi to Bolívar). It grows in humid montane forest at 2950–4350 m elevation. It co-occurs with *P. pauta* in Mojanda (Pichincha) where both species hybridize extensively (Romoleroux 1996), and with *P. longipilosa* in Tulcán (Carchi) (Fig. 2).

Conservation status:—The estimated EOO for *Polyplepis ochreata* is 7,525 km² and the AOO is 112 km². It is known from sixteen locations. It is protected in Ecuador within El Angel Ecological Reserve (Carchi) and Yanacocha Reserve (Pichincha), where is subject to reforestation activities. We asses *P. ochreata* as Vulnerable (VU B1a+B2a, C1).

Additional specimens examined:—ECUADOR. Bolívar: Guaranda, Parroquia Salinas, recorrido entre los Arrayanes y Pambabuela, 01°22'06"S, 079°03'47"W, 3615 m, 10 February 2005, Vargas López 4696 (AAU!, K, MO!, QCNE, US!). Carchi: Cumbal, 00°48'19"N, 077°53'03"W, 3500 m, Bensman 418 (MO!, WIS); Km 31 west of Tulcán on road to Maldonado, 00°52'N, 077°55'W, 3900 m, 21 June 1984, Todzia 2485 (MO!). La Libertad (Alizo), 00°45'N, 077°59'W, Asplund 17037 (S); Páramos de El Angel S of Volcán Chiles, 00°45'N, 077°58'W, 3850 m, 14 March 1985, Eriksen 59086 (AAU!, MO!). Maldonado, Volcán Los Chiles, along road 9 km W of Tufiño, 00°49'N, 077°57'W, 3500 m, 10 March 1992, Lægaard 101661 (AAU!, GOET, QCA!); Tufiño, Road Tulcán-Maldonado, near Volcán Chiles, 00°48'N, 077°56'W, 3850–4000 m, 16 August 1985, Lægaard 54966 (AAU!, MO!, QCA!); S slopes of Volcán Chiles, 14–16 km W of Tufiño on road to Maldonado, 0–1 km S of the road, 00°47'N, 077°57'W, 3850–3900 m, 18 January 1988, Molau 2536 (AAU!, GB, MO!, QCA!); a 33 km de Tulcán, 00°48'N, 077°54'W, 3900 m, Romoleroux 173 (AAU!, QCA!); Carretera Tulcán-Tufiño-Maldonado, 00°47'N, 077°57'W, 3800–3900 m, 12 October 1986, Romoleroux 189 (AAU!, QCA!); Tulcán, 33.4 km W of Tulcán on road to Maldonado, Páramo de Chilos on Colombia border, 00°48'19"N, 077°53'03"W, 3900 m, 22 September 1979, Gentry 26342 (AAU!, MO!, QCA!).

Cotopaxi: Toacaso, Quebrada Faldiguera, 00°41'S, 078°45'W, 3750 m, 16 February 1991, *Jørgensen* 93000 (AAU!, MO!, QCA!). Imbabura: González Suárez, Laguna Mojanda, camino, forêt d'altitude, 00°08'N, 078°15'W, 2500 m, 01 February 1996, *Billiet* 6762 (BR, MO!). La Merced de Buenos Aires: at road Chauasqui-Merced de Buenos Aires, km 20, near pass, 00°33'N, 078°17'W, 3700–3850 m, 10 December 1984, *Lægaard* 53475 (AAU!, MO!, QCA!). Otaval: forested path to Laguna Mojanda (La via antigua a Mojanda por el cementerio), 00°10'00"N, 078°15'00"W, 3800 m, 31 December 2000, *Clark* 5820 (QCA!, US). San Rafael, W slopes of Volcán Cayambe, 00°10'00"N, 078°15'00"W, 3700–3900 m, 27 July 1967, *Sparre* 17789 (AAU!, S). Pichincha: N-side of Volcán Pichincha above Hacienda Yanacocha, 00°07'S, 078°34'W, 3950–4050 m, 02 June 1985, *Lægaard* 54457 (AAU!, MO!, QCA!); along, Northern slopes of Cerro Corazón, 2–4 km W along on the road to Hacienda El Pongo, 00°28'S, 078°36'W, 3100–3200 m, 13 May 1979, *Holm-Nielsen* 18007 (AAU!, MO!); Corazón, 00°31'53"S, 078°39'36"W, 3260 m, *Sodiro s.n.* (AAU!); Lloa, Volcán Atacazo, W slope, 17 km from San Juan, 00°20'S, 078°38'W, 2850 m, 25 August 1980, *Holm-Nielsen* 25115 (AAU!); 25148 (AAU!); Volcán Atacazo, SW slope, km 19 from San Juan, 00°21'S, 078°39'W, 2900 m, 25 August 1980, *Holm-Nielsen* 25169 (AAU!); West-side of Volcán Atacazo, along drinkwater-canal, 00°20'S, 078°38'W, 3700–3750 m, 11 August 1984, *Lægaard* 52639 (AAU!, MO!, QCA!); 52641 (AAU!); along drinkwater-canal on W-side of Atacazo, c. 5 km S of Campamento, 00°20'S, 078°38'W, 3700–3800 m, 24 October 1984, *Lægaard* 53256 (AAU!); along drinkwater-canal on W-side of Atacazo, c. 5 km S of Campamento, 00°20'S, 078°38'W, 3750 m, 28 October 1984, *Lægaard* 53259 (AAU!); 53260 (AAU!); along drinkwater-canal on W-side of Volcán Atacazo, 00°20'S, 078°38'W, 3200 m, 24 November 1985, *Lægaard* 55665 (AAU!, GOET, MO!, QCA!); Volcán Atacazo, 00°20'S, 078°37'W, 3500 m, *Mille* 364 (US); carretera Quito-San Juan-San José de la Victoria, 00°17'53"S, 078°38'20"W, 2900–3400 m, 24 December 1987, *Zak* 3265 (AAU!, GB, MO!); Nono, Camino Yanacocha NW of Volcán Pichincha, 00°05'S, 078°33'W, 3200–3800 m, 03 October 1981, *Balslev* 2049 (AAU!, MO!, NY, QCA!); 28 November 1930, *Benoist* 3356 (P); Yanacocha, faldas noroccidentales, 00°07'S, 078°35'W, 22 March 1987, *Jaramillo Asanza* 9573 (AAU!, NY, QCA!); 9588 (AAU!, QCA!); N-side of Volcán Pichincha above Hacienda Yanacocha, 00°07'S, 078°34'W, 3800 m, 04 June 1985, *Lægaard* 54458 (AAU!, MO!); 54459 (AAU!); 54462 (AAU!, QCA!); 54463 (AAU!, MO!); 54467 (AAU!, MO!); 54474 (AAU!, MO!, QCA!); 54476 (AAU!, MO!, QCA!); 54477 (AAU!, MO!, QCA!); Carretera Quito-Nanegalito-Santa Ana del Tablón, desvío Hda Yanacocha km 1–10 desde el desvío, 00°07'S, 078°34'W, 3500–3600 m, 06 December 1992, *Romoleroux* 1495A (AAU!); Yanacocha, 3617 m, 28 November 2008, *Romoleroux* 5342 (QCA!); Yanacocha, sector La Despensa, 00°07'52"S, 078°35'06"W, 3837 m, 14 Febrero 2009, *Romoleroux* 5413 (MO!, QCA!); Reserva Yanacocha, Trocha "Inca" 1–600 m, 00°06'44"S, 078°34'24"W, 3536 m, 11 June 2011, *Ulloa Ulloa* 2171 (MO!, QCA!); carretera Quito-Nono-Tandayapa, desviación a Yanacocha en la localidad de Guanto-Pugro, en la hacienda "Alto Perú", estribaciones N.O. del Volcán Pichincha, 00°05'S, 078°35'W, 3200–3300 m, 17 November 1987, *Zak* 2946 (AAU!, GB, MO!); Quito, SW-slopes of Volcán Atacazo, 00°20'S, 078°35'W, 3650 m, 11 October 1984, *Brandbyge* 42817 (AAU!, MO!, QCA!); SW-slopes of Volcán Atacazo, 00°20'S, 078°35'W, 3700–3800 m, 28 October 1984, *Brandbyge* 42837 (AAU!, MO!, QCA!); Volcán Pichincha, N slopes, road to Hda. Yanacocha from pass on Quito-Nono road, km 7–11.2, 00°07'S, 078°33'W, 3600–3500 m, 12 October 1991, *Øllgaard* 99187 (AAU!); Carretera a San Juan-Atacazo, km 1–12, 00°20'S, 078°35'W, 3700–4000 m, 02 September 1990, *Romoleroux* 1060 (AAU!, QCA!); Tocachi, 00°08'N, 078°16'W, 3260 m, *Asplund* 17103 (S); 00°08'N, 078°16'W, *Benoist* 4549 (S); NW side of Pichincha, 00°08'N, 078°16'W, *Fagerlind s.n.* (S); 00°08'N, 078°16'W, *Holmgren* 664 (S); 00°08'N, 078°16'W, *Jameson s.n.* (MO!); Páramo de Mojanda, at Laguna Negra and S-side of Laguna Grande, 00°08'N, 078°16'W, 3800 m, 14 May 1985, *Lægaard* 54316A (AAU!, QCA!); 00°08'N, 078°16'W, *Romoleroux* 1495 (AAU!, QCA!); 243 (QCA!); 245 (NY, QCA!); 305 (QCA!); 00°08'N, 078°16'W, 3700 m, *Romoleroux* 350 (QCA!).

Notes:—The taxonomy of this species and *P. pauta* has long been confused (Simpson 1979, Romoleroux 1996). Boza *et al.* (2019) described this species as having sparse sericeous hairs 0.9–1.2 mm long. Upon examination of a larger series of specimens, we here revise this description to state that the indument of the lower leaflet surfaces is a very dense layer of sericeous hairs only 0.3–0.5 mm long. As we have now confirmed during our field work, this discrepancy stems from the fact that juvenile individuals of this species have long hairs, whereas mature plants have short hairs. Accordingly, in many herbaria, specimens were not divided by species, but rather separated the juvenile and adult plants. Although all species of *Polylepis* show some degree of morphological differentiation between juvenile and adult leaves, just *P. ochreata* and *P. pauta* share the character of having extremely different juvenile and mature leaves. The juvenile leaflets have crenate margins with the upper and lower surfaces densely sericeous with longer hairs, whereas adult leaflets have entire or lightly serrate margins with the upper surfaces glabrous and lower surfaces densely sericeous with whitish silky short hairs 0.3–0.5 mm in *P. ochreata*, and upper leaflets with crenate margins with upper surfaces glabrous or sparsely sericeous with few hairs on the mid veins, and lower surfaces sparsely sericeous with whitish hairs 0.4–0.9 mm in *P. pauta*.

Polylepis pauta Hieronymus (1895: 313). Neotype (designated here):—ECUADOR. Pichincha, 2 km al E de la cumbre de la carretera Pifo-Papallacta (La Virgen), 3900 m, 00°20'S 078°15'W, 28 November 1987, Neil 8018 (neotype QCA!, isoneotype AAU!, GB, MO!, QCNE)

= *Polylepis annulatipilosa* Bitter (1911:596). Lectotype (designated by Simpson 1979):—ECUADOR. Pichincha, Andes of Quito, date? Jameson 16 (lectotype W, isolectotypes G, GH; F! [27497], MO! [MO-1610335], US!).

= *Polylepis stuebelii* Hieronymus (1896:313). Neotype (designated here):—ECUADOR. Pichincha-Napo: base del Volcan Antisana, entrada por Pintag hacia laguna Michacocha, campamento EMAP, 4000–4100 m, 00°27'S 078°10'W, 9 October 1990, Romoleroux 1117 (neotype QCA!, isoneotype AAU!).

Trees 2–12 m tall. **Leaves** strongly congested at the branch tips, imparipinnate with 4–5(–6) pairs of lateral leaflets, obtrullate in outline, 3.2–4.9 × 2.2–3.0 cm; rachises sparsely sericeous, points of leaflet attachment with a tuft of long, straight whitish hairs; stipular sheaths apically acute with spurs, glabrous to sparsely sericeous (adult) or densely sericeous (juvenile) in the upper surface; leaflets elliptic in outline, second pair from the terminal leaflet the largest, one of this pair (1.1–)1.4–1.6 × 0.5–0.6 cm; margins crenate with 4–6 teeth, subcoriaceous, apically emarginate, basally unequally cordate; upper leaflet surfaces glabrous or sparsely sericeous with few hairs on the mid veins; lower leaflet surfaces sparsely sericeous with whitish hairs 0.4–0.9 mm long. **Inflorescences** pendant, (8.1–)12.6–14.3(–19.3) cm long, bearing 9–15(–21) flowers; floral bracts (9.1–)10.0–12.2 mm long, narrowly triangular, densely sericeous on the outer surface; rachises densely villous. **Flowers** 6.0–7.4(–9.2) mm diam.; sepals 4, ovate, green, densely sericeous outside; stamens 9–15, anthers orbicular, with a dense tuft of straight white hairs on the upper half; styles fimbriate, 2.2–3.0 mm long. **Fruits** turbinate, with variable numbers and placement of flattened spines, densely sericeous; (2.6–)3.4–5.5 × 3.3–6.0(–8.2) mm including spines.

Distribution, habitat and ecology:—*Polylepis pauta* is distributed in the northern Cordillera Oriental of Ecuador. This species occurs in high Andean forest at 2600–4200 m elevation, often in mixed forest with *Gynoxys acostae* Cuatrec., *Solanum stenophyllum* Humb. & Bonpl. ex Dunal and *Hesperomeles obtusifolia* (Pers.) Lindl. (Cjerjaks *et al.* 2007a, 2008, Romoleroux 2016) (Fig. 2).

Conservation status:—The estimated EOO for *Polylepis pauta* is 1,590 km² and the AOO is 132 km². It is known from fourteen locations. It is protected within Cayambe-Coca National Park and Antisana Ecological Reserve. We assess *P. pauta* as Vulnerable (VU A1, B1a+B2a, C1).

Additional specimens examined:—ECUADOR. Pichincha: Pifo, 2 km S of Paso de la Virgen on road Quito-Baeza, 00°20'S, 078°13'W, 3850 m, 16 May 1984, Lægaard 52133 (AAU!, QCA!). Imbabura: Atahualpa (Habaspamba), Páramo de Mojanda, on the SW slope of the peak Nudo de Mojanda, 4130 m, 06 November 2007, Sklenář 10746 (QCA!). Gonzalez Suarez, Lagunas de Mojanda, Laguna Negra, 00°08'N, 078°15'W, 3700 m, 22 September 1990, Ollgaard 98194 (AAU!); Vía hacia la laguna de Mojanda, 00°08'N, 078°15'W, 3500 m, 02 November 1987, Romoleroux 475 (AAU!, QCA!); Otavalo, road from Otavalo to lagunas Mojanda, ca 3 km before the lakes, 00°10'N, 078°17'W, 3500 m, 23 October 1983, Balslev 4450 (AAU!, QCA!); Quiroga, Cotacachi, Reserva Ecológica Cotacachi-Cayapas, alrededores de la Laguna de Cuicocha, Quebrada Chumabí, 00°18'N, 078°22'W, 3300 m, 02 March 1992, Peñafiel 1091 (MO!); Tocachi, Laguna Grande de Mojanda, 15 km S of Otavalo, 00°08'N, 078°16'W, 3750 m, 14 May 1985, Eriksen 59359 (AAU!); Laguna Grande de Mojanda, 15 km S of Otavalo, 00°08'N, 078°16'W, 3750 m, 14 May 1985, Eriksen 59374 (AAU!). Napo: Archidona, crescit prope Bambasacha in declibus orientalibus mentis Quilindañia sitis, 3700 m, Stübel 204 (F, MO!, NY, US); Cangahua, 8 kms de la población de Oyacachi, siguiendo el sendero hacia Cochapamba, 3500 m, 12 March 1991, Gavilánez 462 (QCA!); Reserva Ecológica Oyacachi, 3917 m, 14 March 2009, Romoleroux 5475 (QCA!); Oyacachi, 0°12"S, 78°8"W, 3680 m, 08 April 2012, Homeier 4948 (QCA!); N of Volcán Los Puntos, 3850 m, Lægaard 54756 (QCA!); N of Volcán Los Puntos, 00°12'S, 078°10'W, 4200 m, 27 July 1985, Lægaard 54756A (AAU!); N of Volcán Los Puntos, 00°12'S, 078°10'W, 3850 m, 28 July 1985, Lægaard 54756B (AAU!); 54756C (AAU!); 54756D (AAU!); 54756E (AAU!); 54756F (AAU!); 54757 (QCA!); 54758 (QCA!); 54759 (QCA!); 54761 (AAU!, MO!); Oyacachi, Yarupaccha; restos de bosque frente a la entrada del tunel, 3620 m, 16 January 1996, Navarrete 1449 (QCA!); Reserva Ecológica Oyacachi, 3895 m, 23 February 2007, Romoleroux 4340 (QCA!); Reserva Ecológica Oyachachi, 3465 m, 08 March 2008, Romoleroux 4751 (QCA!); Reserva Ecológica Oyachachi, 3929 m, 13 September 2008, Romoleroux 5167 (QCA!); Reserva Ecológica Oyachachi, 3681 m, 13 September 2008, Romoleroux 5168 (QCA!); Reserva Ecologica Oyacachi, bordes de la parte N del parche, 00°13'49"S, 078°08'44"W, 3915 m, 16 Diciembre 2008, Romoleroux 5346 (MO!, QCA!); Reserva Ecologica Oyacachi, Parche 6, 3880 m, 16 May 2009, Romoleroux 5489 (QCA!); Páramo de la Virgen, camino antiguo, 3904 m, 29 September 2004, Salgado 1 (QCA!); about 3 km W of Oyacachi, 3550 m, 27 March 1996, Ståhl 2278 (QCA!); Papallacta, Carretera

Quito-Tena via Baeza km 52, 3820 m, 03 August 1984, *Dodson* 14832 (MO!); Oyacachi, 00°18'6"S, 78°8'28"W, 3970 m, 10 June 2009, *Homeier* 4191 (QCA!); Paramo de Papallacta, 00°20'S, 078°10'W, 12 January 2015, *Kessler* s.n. (Z!); Pifo-Papallacta, 3–5 km E of Paso de La Virgen, 00°21'S, 078°11'W, 3700 m, 09 June 1992, *Lægaard* 103115 (AAU!, GOET!, QCA!); 3 km E of Paso de la Virgen on road Pifo-Papallacta, 00°20'S, 078°11'W, 3950 m, 02 June 1985, *Lægaard* 54442 (AAU!, QCA!); 54443 (AAU!); 54444 (AAU!, MO!); 54446 (AAU!); 54447 (AAU!, MO!, QCA!); 54448 (AAU!, MO!, QCA!); 54449 (AAU!, QCA!); 54450 (AAU!, MO!); 54451 (AAU!, MO!); 54452 (AAU!, MO!); 3 km E of Paso de la Virgen on road Pifo-Papallacta, 3951 m, 06 February 1985, *Lægaard* 54452 (QCA!); along road Pifo-Papallacta, E of Paso de la Virgen, 00°21'S, 078°11'W, 3750 m, 21 June 1985, *Lægaard* 54558 (QCA!); 54558B (AAU!); 54558C (AAU!); 54558D (AAU!); 54559 (AAU!, MO!, QCA!); 54560 (AAU!, MO!); 54560 (QCA!); 54561 (AAU!); Road Quito-Baeza, 7–8 km NW of Laguna de Papallacta (Páramo de Guamaní), 00°19'S, 078°08'W, 3800 m, 20 July 1976, *Øllgaard* 8156 (AAU!, MO!, NY); Reserva Ecológica Oyacachi., 3940 m, 28 January 2007, *Romoleroux* 4282 (QCA!); 4297 (QCA!); Páramo de Guamaní, alrededores de la laguna de Papallacta, 3900 m, 06 December 1987, *Romoleroux* 491 (AAU!, NY, QCA!); Reserva Ecologica Oyacachi, 00°17'46"S, 078°08'49"W, 3927 m, 20 Septiembre 2008, *Romoleroux* 5194 (MO!, QCA!); Reserva ecológica Oyacachi, 3560 m, 23 February 2007, *Romoleroux* A4321 (QCA!); Carretera Quito-Baeza, paramo above Papallacta, 00°21'S, 078°10'W, 3400 m, 28 May 1987, *van der Werff* 9638 (AAU!, GB, MO!); Pifo, Carretera Oyacachi-Papallacta, colecciones a 11 km de la Laguna de Loreto, 3800 m, 27 March 1998, *Guerrón* 343 (QCA!); Páramo de Guamaní, road Quito Papallacta, 4000 m, 04 March 1979, *Kieft* 228 (QCA!). Pintag, Paso de Guamaní, quebrada, about +4 km E Paso de Guamaní, on road to Papallacta, 00°20'S, 078°20'W, 3900 m, 26 March 1967, *Sparre* 15029 (AAU!, S); Quijos, Parroquia Papallacta, 00°21'S, 078°11'W, 3700 m, 28 May 1990, *Cerón Martínez* 10054 (MO!); Reserva Ecológica Antisana, carretera Pifo-Baeza, Páramo de la Virgen, 00°20'S, 078°12'W, 3960 m, 23 Noviembre 1998, *Freire* 2852 (AAU!, ILLS, MO!, QCNE); Reserva Ecológica Antisana, carretera Pifo-Baeza. Páramo de la Virgen, 00°23'S, 078°12'W, 3730 m, 24 Noviembre 1998, *Freire* 2870 (ILLSS, MO!, QCNE); Reserva Ecológica Antisana. Páamo de Guamaní; carretera Pifo-Papallacta, La Virgen, 00°20'S, 078°12'W, 4140 m, 24 Julio 1998, *Vargas* 1946 (AAU!, ILLS, MO!, QCNE). Pichincha: Cayambe, Carretera Cayambe-Hda. Piamonte-Patapamba, 00°02'S, 078°04'W, 3700 m, 04 December 1993, *Freire* 2606 (AAU!, QCA!). Papallacta, along road Pifo-Papallacta, E of Paso de la Virgen, 00°21'S, 078°11'W, 4200 m, 20 June 1985, *Lægaard* 54558A (AAU!); Pichincha-Napo, base del Volcán Antisana, entrada por Pintag hacia laguna Micacocha, campamento de EMAP, 00°27'S, 078°10'W, 4000 m, 09 October 1990, *Romoleroux* 1117 (AAU!, QCA!); 1118 (AAU!, QCA!); Páramo de la Virgen. Camino antiguo, 00°20'S, 78°12'W, 3938 m, 20 September 2004, *Salgado* 3A (QCA!). Pifo, 3700 m, *Asplund* 18244 (S); Mount Guamaní, 00°20'S, 78°33'W, 3600 m, 15 September 1939, *Asplund* 8767 (QCA!); 2 km west of La Virgin on the road from Pifo to Papallacta, 00°17'S, 078°12'W, 3950 m, 20 May 1984, *Brandbyge* 42638 (AAU!, MO!); The pass on Quito-Papallacta road, 3800 m, 06 April 1991, *Kessler* 2749 (GOET!, MO!); 2750 (GOET!, MO!); 2753 (GOET!, MO!); 2754 (GOET!, LPB, MO!); Pifo-Papallacta (new road) app. 1 km W of Paso de la Virgen, 00°19'S, 078°13'W, 3700 m, 16 April 1992, *Lægaard* 102327 (AAU!, GOET!); 2 km S of Paso de la Virgen on road Quito-Baeza, 00°20'S, 078°13'W, 4000 m, 19 May 1984–20 May 1984, *Lægaard* 52134 (AAU!); 52135 (AAU!); 52138 (AAU!, MO!); 52162 (AAU!); 52176 (AAU!, QCA!); Road Pifo-Papallacta, near Paso de la Virgen, 00°19'S, 078°13'W, 4000 m, 13 March 1985, *Lægaard* 53849 (AAU!, MO!, QCA!); Road Pifo-Papallacta, 3 km W of Paso de la Vrgen, 00°18'S, 078°14'W, 3700 m, 07 August 1985, *Lægaard* 54901A (AAU!); 54901B (AAU!); 54901C (AAU!); 54901D (AAU!); 54902AA (AAU!); 54902K (AAU!); 54902M (AAU!); 54902P (AAU!); 54902S (AAU!); 54902U (AAU!); 54902W (AAU!); 54902Y (AAU!); at Paso de la Virgen, 00°18'S, 078°12'W, 4000 m, 28 November 1985, *Lægaard* 55729 (AAU!, GOET!, MO!); Páramo de la Virgen, 3100 m, 01 November 2006, *Muñoz* 4 (QCA!); Carretera Quito-Papallacta, 1 km al este de la cumbre (La Virgen), 00°20'S, 078°15'W, 3800 m, 06 October 1986, *Neill* 7378A (AAU!, MO!, QCA!); 2 km al E de la cumbre de la carretera Pifo-Papallacta (La Virgen), 00°20'S, 078°15'W, 3900 m, 28 November 1987, *Neill* 8018 (AAU!, GB, MO!, QCA!, QCNE); Vía Baeza, 1 km antes del cruce de la Virgen, 00°18'S, 078°12'W, 3950 m, 01 March 1989, *Palacios* 3994 (AAU!, MO!); Carretera Quito-Papallacta km 40–53, 00°16'S, 078°15'W, 3300 m, 27 December 1992, *Romoleroux* 1507 (AAU!, QCA!); 00°21'S, 078°13'W, *Romoleroux* 353 (QCA!); Páramo de Guamaní, on the left side of the road Quito-Papallacta, 00°19'S, 78°12'W, 4000 m, 28 June 1997, *Sklenář* 2019 (QCA!); Quito, Parroquia Pifo, carretera Quito-Baeza, Páramo de la Virgen, 00°14'S, 078°20'W, 3500 m, 25 April 1992, *Cerón Martínez* 18792 (MO!); Road from Quito via Pifo to Papallacta, 00°34'S, 078°19'W, 3950 m, 04 July 2014, *Kessler* 14602 (Z!); 14603 (Z!); 14604 (Z!); 14605 (Z!); Páramo de Guamani, carretera Pifo-Papallacta, Km 27, 00°19'S, 078°12'W, 3960 m, 13 June 1990, *León* 1149 (QCA!); Baeza-Quito km 53, 00°20'S, 078°12'W, 4200 m, 08 July 2002, *Schmidt-Lebuhn* 378 (GOET!, QCA!). Tabacundo, at highest pass on road Mojanda-Tabacundo, 00°07'N, 078°15'W, 4030 m, 08 April 2001, *Lægaard* 21538A (AAU!); 21538B (AAU!); Laguna grande de Mojanda-Cajas, 3800 m, 19 September 2011, *Pérez* 5117 (QCA!).

Tocachi, 3960 m, 27 February 1999, *Jaramillo* 20986 (QCA!); Páramo de Mojanda, at Laguna Negra and S-side of Laguna Grande, 00°08'N, 078°16'W, 3800 m, 14 May 1985, *Lægaard* 54316B (AAU!, MO!, QCA!); 54330 (AAU!, MO!); 54333 (AAU!, MO!, QCA!); 54336 (AAU!); 54346 (AAU!, MO!, QCA!). TABACUNDO: Lagunas Mojanda, 00°07'N, 078°16'W, 3800 m, 30 July 1992–31 July 1992, *Palacios* 10210 (AAU!, MO!); 10239 (AAU!, MO!); Lagunas de Mojanda, ca. Laguna Grande, 00°08'N, 078°16'W, 3700 m, 01 June 1988, *Romoleroux* 654 (AAU!, QCA!).

Notes:—An outstanding feature of *P. pauta* are the differences in leaflet number, shape, and indument between young and adult plants. On young plants, leaves look very similar to those of *P. longipilosa*, whereas as the plants mature, the leaves become almost glabrous and have only 4–5 lateral leaflet pairs. Sometimes, specimens of *P. pauta* resemble those of *P. ochreata* in number of lateral leaflets pairs, but leaflet margins are entire to slightly serrate in *P. ochreata* and crenate in *P. pauta*.

Alphons Stübel made numerous collections mainly in the Andes of Colombia and Ecuador (Jørgensen & León-Yáñez 1999), and Hieronymus (1895) described his new species. Unfortunately, most of Stübel collections were lost in Berlin (B), including the types of both *Polylepis pauta* and *P. stuebelii* that were only deposited at B. Hieronymus (1985) did not cite any additional specimens of these taxa. There is a fragment of a Stübel collection of *P. pauta* (Stübel 232a) at F (F 6477882), but this fragment belongs to a juvenile leaf which differs markedly from the adult leaves of this species and does not fit the protologue, which is based on adult material. This fragment thus cannot be used as type material (Botanical Code Art. 9.14). Therefore, no type or other original material is preserved, which prompts us to select a neotype for both *Polylepis pauta* and *P. stuebelii*. During the herbarium survey, we successfully found some flowering specimens of *Polylepis pauta* and *P. stuebelii*. Considering that (i) the plants generally agree with the morphological characters of both *P. pauta* and *P. stuebelii* protologue and (ii) the plants were collected around their type locality.

We consider *P. stuebelii* to be a junior synonym of *P. pauta* because both share the important characters of having 4–5 pairs of apically emarginate and basally unequally cordate lateral leaflet pairs with crenate margins with 4–6 teeth per side, and long, multiflowered inflorescences. There are no significant differences mentioned in the protogues nor visible on the photographs of the type specimens. Further, the type material of both species was collected in the same general geographical area, where multiple collections and our own field work show that only one, somewhat variable species occurs.

Hybrids

Polylepis ochreata (Wedd.) Bitter × *Polylepis pauta* Hieronymus

Specimens examined:—**ECUADOR.** Pichincha: Mojanda, alrededores de la laguna grande, 00°08'N 078°16'W, 3700–3800 m, 24 May 1987, K. *Romoleroux* 339 (QCA!); camino hacia laguna Mojanda, 00°08'N 078°16'W, 3000–3500 m, 2 November 1987, K. *Romoleroux* et al. 476 (AAU!, QCA!); Laguna grande de Mojanda, 00°08'N 078°16'W, 3725–3750 m, 30 June 1988, K. *Romoleroux* & S. *Laegaard* 657 (AAU!, QCA!), 658 (AAU!, QCA!), 659(QCA!); camino a Mojanda desde Otavalo, km 15, 00°09'16"N 078°16'48"W, 3659 m, 24 August 2016, K. *Romoleroux* et al. 6099 (QCA!); Páramo de Mojanda at Laguna Negra and S-side of Laguna Grande, 00°08'20"N 078°15'12"W, 3800 m, 14 May 1985, S. *Laegaard* 54331 (AAU!, MO!, QCA!), 54334 (AAU!, MO!, QCA!), 54335 (AAU!, MO!, QCA!), 54343 (AAU!, MO!, QCA!); Laguna Mojanda en los alrededores de la orilla, 00°08'20"N 078°15'12"W, 3770 m, 21 September 2000, J. *Lizarzaburu* 21 (QCA!).

Notes:—At Laguna de Mojanda, almost half of the herbarium collections show characters that are intermediate between those of *P. ochreata* (of which we have only seen a single collection from this area) and *P. pauta* (which accounts for about 60% of all collections). Despite their abundance, we assign these intermediate plants as hybrids rather than as a distinct taxon because both putative parent species are present and because the presumed hybrids are highly variable, showing a wide range of character combinations of the parent species, suggesting that this is a hybrid swarm with backcrossing. This hybrid swarm was already recognized by Romoleroux (1996) and was confirmed by us during recent field work. In addition to the two species already mentioned, this hybrid swarm also includes influence of *P. incana*.

Unplaced specimens

There are three distinctive collections of the *P. pauta/sericea* complexes that we have been unable to assign to species. A single collection from the province of Loja (*J. Jaramillo 7312B*, Cerro Chinchilla “Parroquia Celén”, 3500–3780 m, 19 Sep 1984, AAU!, QCA!) resembles *P. longipilosa* but has different leaflet shape (ovate vs obovate) with serrate margins (vs. entire to slightly crenate), longer lower leaflet surface hairs (1.5–1.8 mm vs 1.1–1.6 mm), and longer styles (2.7–3.0 mm vs. 1.6–2.0 mm). Also, two collections from Laguna Mojanda (*Brandbyge 42200*, AAU!, MO!, NY, QCA!; and *Molau 2294*, AAU!, GB, QCA!) are similar but have lower leaflet surface hairs 1.5–1.6 mm long and styles 2.8–2.9 mm long. These specimens cannot be assigned to any of the five species we recognize here, but we refrain from treating them as a distinct species because despite targeted field work at both collecting localities, we have been unable to study this form in field. In any case, considering the notable geographical distance, it is uncertain whether the specimens from Mojanda belong to the same form as the one from Loja. Those at Mojanda were collected in a well-known hybrid zone and although they are not simply intermediate between the potential parent species (*P. incana*, *P. ochreata*, *P. pauta*) so that we cannot simply interpret them as hybrids, it is possible that some unique gene combinations in hybrids might lead to morphotypes that fall outside of the morphological range of the parent taxa. In Loja, the situation is somewhat different, because the only species present there is *P. loxensis*, so that a hybrid origin is less likely, although in a wind-pollinated genus such as *Polylepis* pollen dispersal might conceivably take place over long distances. Considering these uncertainties, we are unable to taxonomically place these specimens. However, should they belong to a separate species, then on present knowledge this species would be very rare or even on the verge of extinction. We strongly urge trying to locate populations of this form to assess its taxonomic and conservation status.

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