

**CASTILLEJA ISIDOROII (OROBANCHACEAE) — A NEW SPECIES FROM
NORTHWESTERN PERÚ,
RANGE EXTENSIONS FOR *C. ALPICOLA*,
AND A GUIDE TO THE SPECIES OF *CASTILLEJA* SUBG. *COLACUS*
IN ANDEAN SOUTH AMERICA**

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ABSTRACT

Castilleja isidoroii J.M. Egger, Montesinos, & Dasher **sp. nov.**, is described from the Andes Mountains in the Departments of Amazonas and Cajamarca of northern Perú. The new species is most similar morphologically to *C. vadosa* Chuang & Heckard and to *C. peruviana* Chuang & Heckard, also of that region. The new species differs primarily in bract coloration, structure and coloration of the corollas, and growth form. The new species is a rarely collected and apparently range-limited endemic, and its conservation status deserves attention. An annotated list and field images of the species of *Castilleja* subg. *Colacus* in South American are provided, as well as a key to their identification. Significant range extensions are documented for *C. alpicola* Chuang & Heckard, as well as new distributional records for each species.

RESUMEN

Se describe *Castilleja isidoroii* J.M. Egger, Montesinos & Dasher, **sp. nov.**, procedente de la cordillera de los Andes en el norte de Perú, en los departamentos de Amazonas y Cajamarca. La nueva especie presenta una mayor similitud morfológica con *C. vadosa* Chuang & Heckard y con *C. peruviana* Chuang & Heckard, también propias de esa región. La nueva especie se distingue principalmente por la coloración de las brácteas de las flores, la estructura y coloración de las corolas, y su forma de crecimiento. La nueva especie es un endemismo raramente colectado y aparentemente de distribución limitada, y su estado de conservación merece atención. Se proporciona una lista comentada e imágenes de campo de las especies de *Castilleja* subg. *Colacus* en Sudamérica, así como una clave para su identificación. Se documentan ampliaciones significativas del área de distribución de *C. alpicola* Chuang & Heckard, así como nuevos registros distribucionales para cada especie.

In their landmark paper describing four new annual, bee-pollinated species of *Castilleja* subg. *Colacus* from the Andes Mountains of Perú, Chuang and Heckard (1992) brought needed attention to a unique assemblage of such species with seemingly close affinities to a similar assemblage at low to moderate elevations in southwestern North America, almost entirely within the California floristic region. The new species and their close relatives were fully treated, with line drawings, range maps, citation of specimens, and estimates of phenology, elevation ranges, and ecological information. They also provided valuable chromosome counts for several of the species, with most proving to be tetraploid or higher polyploids.

A second significant contribution to the documentation and understanding of *Castilleja* subg. *Colacus* in South America was provided by Tank and Olmstead (2009). The authors employed

phylogenetic analyses to determine both the relatedness and the origins of the Andean species, including the likelihood that there have been three long-distance dispersal events from the California floristic region at various times in the past, as well as two and possibly three allopolyploid speciation events since then, that have contributed to the diversity of species in subg. *Colacus* in Andean South America. Their results suggest that one of the allopolyploid species, *C. cerroana* Edwin, and possibly the similar *C. laciniata* Hook. & Arn., both with lateral calyx lobes distinctly shorter than the abaxial and adaxial clefts, were possibly derived from hybridization between an annual and a perennial species outside of subg. *Colacus*. They found strong support for such an origin in the case of *C. cerroana*, though not for *C. laciniata*. While *C. laciniata* was treated as an annual and placed in subg. *Colacus*, sect. *Oncorhynchus* by Chuang and Heckard (1992), they tentatively considered *C. cerroana* to be perennial and placed it in their sect. *Pallescentes*. However, Tank and Olmstead observed that *C. cerroana* is “most likely annual” and is more likely a part of sect. *Oncorhynchus*, along with *C. laciniata* and the other South American members of subg. *Colacus*. We agree with Tank and Olmstead’s conclusions about *C. cerroana* and its placement, as we have never observed a specimen of that species to have roots appearing to be anything other than annual, including the type collection. They also suggested that the polyploid species, *C. profunda* T.I. Chuang & Heckard, likely arose by allopolyploid speciation through hybridization between two of the annual species already established in Perú.

Following the publication of Chuang and Heckard’s paper, Egger began a review of specimens from numerous herbaria, including the relevant type collections, both to provide updated annotations and to better understand the proposed new species. During this review, a handful of collections stood out as distinct and not easily placed in any of the existing species. Most were originally determined as *Castilleja* sp. or *Orthocarpus* sp., and some had subsequent annotations as one of the recently described species, *Castilleja vadosa* Chuang & Heckard, though in a 1999 annotation of a specimen at F (*Sagastegui et al. 14012*), N. Hensold observed that the collection was “similar to *C. vadosa* but flowers very large.” In 2005, Egger joined Dave Tank in planning and conducting *Castilleja* field research in northern Perú and together examined specimens at the HUT and HAO herbaria in Trujillo and CPUN in Cajamarca. At the latter institution, we met with Dr. Isidoro Sánchez-Vega, who graciously showed us the *Castilleja* collections. Sadly, just a few years after our visit, the HAO Museum burned, with the loss of all plant collections, including duplicates of our collections from 2005. During our field work, we visited one site, Pozo Kuan, near Contumazá, Dept. Cajamarca, particularly to look for a population of the anomalous plants. While we found several *Castilleja* species in the vicinity, we failed to locate any that resembled the earlier collections in question.

The mystery plants remained unverified until December 2023, when Montesinos posted photos of plants he and his associates, including Cameron Dasher, collected several months earlier in the Chachapoyas region of Dept. Amazonas, Perú. It soon became evident that the plants Montesinos collected and photographed are of the same species Egger had been intrigued by years earlier. Egger subsequently contacted Dr. Juan Montoya Quino, present curator of the CPUN Herbarium, regarding the new findings, and Montoya sent photos of a plant he had only recently collected of what appeared to be the same species, confirmed following further examination of the photos and images of the collection made therefrom and now deposited at CPUN. The unique traits of both the early collections and the two recent collections support the description of the new species within subg. *Colacus*, sect. *Oncorhynchus* described below.

CASTILLEJA ISIDOROI J.M. Egger, Montesinos, & Dasher **sp. nov.** **TYPE:** Perú. **Cajamarca.** Cajamarca Province: SAIS José Carlos Mariátegui, Km 20–40 on Sunchubamba–San Juan road [approximate inferred location: -7.371167, -78.571278]. Jalca with small patches of Ceja de Selva in rocky area between 3300 and 3500 m. Bunches 10–50 cm diameter, bracts scarlet, flowers scarlet, lip yellow green with black spots, 5 Jun 1984, *D.N. Smith and I. Sánchez-Vega* 7565 (holotype: MO; isotypes: F, WTU). Figures 1–4; Maps 1–2.

Differs from *Castilleja vadosa* Chuang & Heckard in its relatively large and conspicuous, deep scarlet to violet-red corollas with beaks at least twice to often three times the length of the lower lip, the latter contrastingly colored pale greenish with conspicuous medial black splotches proximal to the whitish, distinctly triangular distal teeth; bracts inconspicuously colored dull pale green proximally, gradually becoming tan to dull, pale reddish-brown, or dull, pale violet-red distally; and growth form often profusely branched.

Plants Annuals (0.5–)1–3 dm tall in flower, with a short (2–5 cm), slender to $\pm$ stout taproot. **Stems** almost always branched, often profusely and compoundly so throughout and thus with a $\pm$ bushy growth form, 10–50+ cm in diameter, sometimes few-branched from near the base, occasionally solitary; branches ascending-erect to proximally spreading, becoming ascending distally, 5–25 cm tall, dull reddish to dull reddish brown, pubescence whitish, moderately to densely pilose to hispid, eglandular, but usually mixed with at least some shorter, stipitate-glandular hairs. **Leaves** 1–4(–5) cm long, proximal-most sometimes entire but usually deeply pinnately divided into 3–7 lobes, the blades and lobes mostly linear; lobes 0.5–20 mm long, distal lobes ascending, medial and proximal lobes spreading-ascending to divaricate-spreading, apices acute to narrowly obtuse; entirely pale green, entirely or distally pale tan, or entirely or distally dull reddish; pubescence densely hispidulous to pilosulous with whitish, eglandular hairs mixed with $\pm$ shorter, stipitate-glandular ones. **Inflorescences** spicate, 3–10 cm long in flower, with few to more often many, sessile to short-pedicellate flowers, pedicels 0–3 mm. **Bracts** very weakly differentiated from the leaves, (5–)7–11 lobed, the blade narrowly linear-lanceolate, the lobes narrowly linear, ascending to spreading, the apices acute to narrowly obtuse or rounded or the distal portion of the central lobe sometimes very narrowly spatulate; usually very pale greenish proximally, gradually becoming tan, dull, pale reddish-brown, or dull, pale violet-red distally; pubescent as in leaves, though often less densely so. **Calyces** 12–20 mm long, cleft subequally 40–50% of the calyx length, lobes narrowly lanceolate, apices acute to narrowly obtuse; variably dull colored, as in bracts; pubescent as in leaves and bracts but tube more sparsely so. **Corollas** conspicuous, 25–40 mm long, with the beak and at least part of the lower lip and sometimes the distal portion of the tube exerted from the calyces at full anthesis; beak conspicuous, 13–20 mm in length and exceeding the lower lip by 5–7(–10) mm, deep scarlet to violet-red throughout, densely puberulent on the adaxial surface with a mix of stipitate-glandular and eglandular hairs of equal length and usually colored as in the beak surfaces; lower lip prominent but only weakly inflated, 5–7 mm long, proximally colored as in the beak but abruptly transitioning distally to white mixed with varying amounts and shades of green, this portion interrupted medially with large splotches or often a continuous band of near-black, divided into 3 equal, slightly incurved lobes, fused proximally, distally forming 3 teeth, these 1.5–3 mm in length, distinctly triangular, and acute-tipped; stigma capitate and inconspicuous, ca. 0.5 mm in diameter, usually exerted 2–5 mm from the tip of the beak, anthers included, narrowly elongate, ca. 3 mm x 0.5 mm, stramineous, pollen grains ca. 0.1 mm in diameter. **Capsules** 10–15 mm x 4–7 mm, oblong with acuminate apices, outer surfaces muriculate; seeds numerous, ca. 70–100 per capsule, seeds wedge-shaped, 1.0–1.5 mm x 0.5–0.75 mm; seed coats translucent, loose-fitting, shallowly reticulate, cells narrowly rectangular to oblong, radial walls shallow and smooth, inner tangential walls fully ruptured at maturity; inner seed blackish. **Chromosome number** unknown.



Figure 1. Holotype of *Castilleja isidoroï*, Prov. Cajamarca, Dept. Cajamarca, Perú. Smith & Sánchez-Vega 7565, MO.

Etymology. The new species is named in honor of Dr. Isidoro Sánchez-Vega, former Curator of the CPUN Herbarium and Professor at the University of Cajamarca, Perú and “Padre de la Jalca” in honor of his dedicated work supporting the study and conservation of the Andean flora of Perú.

Recommended Common Names: We suggest the English common name, Isidoro’s Paintbrush for the new species, as well as the Spanish common name, El Pincel de Isidoro.

Additional specimens examined. Perú. Dept. Amazonas. Prov. Chachapoyas: Leymebamba, Atuén, Camino Laguna Rio Atuén a Laguna Yanacocha, 6°53’59”S, 77°45’47”W, 3790 m, 24 July 2023, *Montesinos 9708, Dasher, and Chávez* (WTU), Figures 5–9. **Dept. Cajamarca. Prov. Contumazá:** Alrededores del Pozo Kuán, ladera, 3600–3800 m, 13 Jun 1981, *Segástegui et al. 10061* (HUT, MO), Figures 17–18; Jalca del Pozo Kuán, 4000 m, 27 Jun 1983, *Sagástegui et al. 10766* (HUT, MO), Figures 13–14; Pozo Chuño, Jalca húmido, *Sagástegui et al. 14012*, 30 May 1988 (F, HUT), Figures 15–16; **Prov. Cajamarca:** Dist. San Juan. Carretera al Sureste de la Hacienda Hucraruco, área de afloramiento rocoso, 7°21’22.65”S, 78°24’6.54”W, 3992 m, 21 Mar 2026, *Montoya 2579* and *Dávila* (CPUN), Figures 10–12.



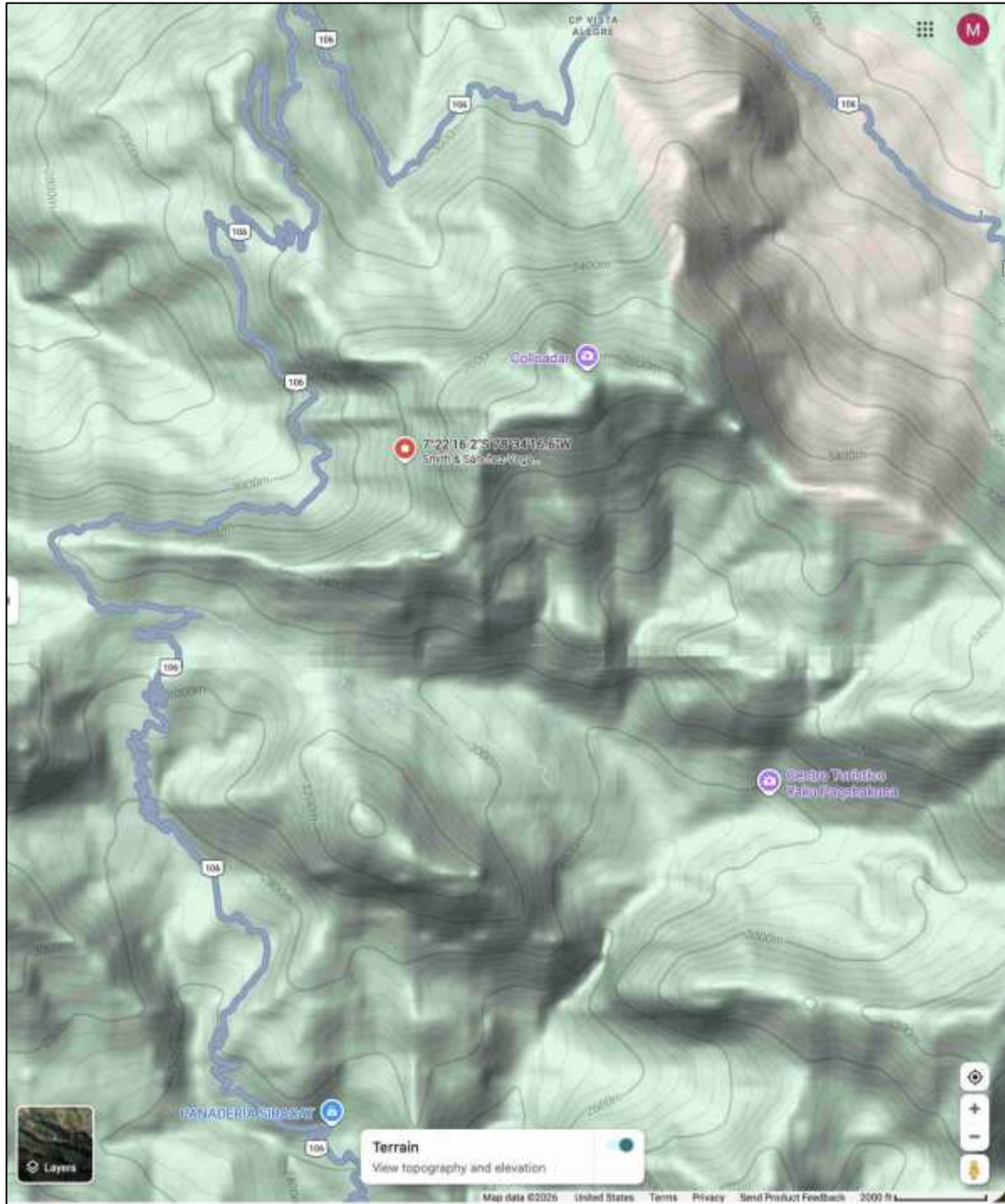
Figure 2. Holotype of *Castilleja isidoroï*, Prov. Cajamarca, Dept. Cajamarca, Perú. *D.N. Smith & I. Sánchez-Vega 7565*, MO. Close up image of typical profuse-branched specimen.



Figure 3. Isotype of *Castilleja isidoroï*, Prov. Cajamarca, Dept. Cajamarca, Perú. D.N. Smith & I. Sánchez-Vega 7565, F.



Figure 4. Isotype fragments of *Castilleja isidoroï*, Prov. Cajamarca, Dept. Cajamarca, Perú. D.N. Smith & I. Sánchez-Vega 7565, WTU.



Map 1. An approximation of the location (red circle) of the type locality of *Castilleja isidoro* based on the estimated location and elevation data provided on the label of the holotype sheet at MO.



Figure 5. *Castilleja isidoroï*, Prov. Chachapoyas, Dept. Amazonas, Perú, 24 July 2023. Collection site for Montesinos *et al.* 9708, WTU. Photo by Montesinos.



Figure 6. *Castilleja isidoroï*, Prov. Chachapoyas, Dept. Amazonas, Perú, 24 July 2023. Collection site for Montesinos *et al.* 9708, WTU. Photo by Montesinos.



Figure 7. *Castilleja isidoroï*, Prov. Chachapoyas, Dept. Amazonas, Perú, 24 July 2023. Collection site for Montesinos *et al.* 9708, WTU. Note the distinctive corolla structure and coloration patterns, the relatively less conspicuously colored and deeply lobed bracts with 5–9 linear lobes, and the subequally cleft calyces. Photo by Montesinos.



Figure 8. *Castilleja isidoroï*, Prov. Chachapoyas, Dept. Amazonas, Perú, 24 July 2023. Collection site for Montesinos *et al.* 9708, WTU. Note the subequal calyx clefts, corolla beak nearly three times in length of the lower lip, mixed pubescence of longer, eglandular hairs and shorter, stipitate-glandular hairs, and exserted stigma and anthers. Photo by Montesinos.

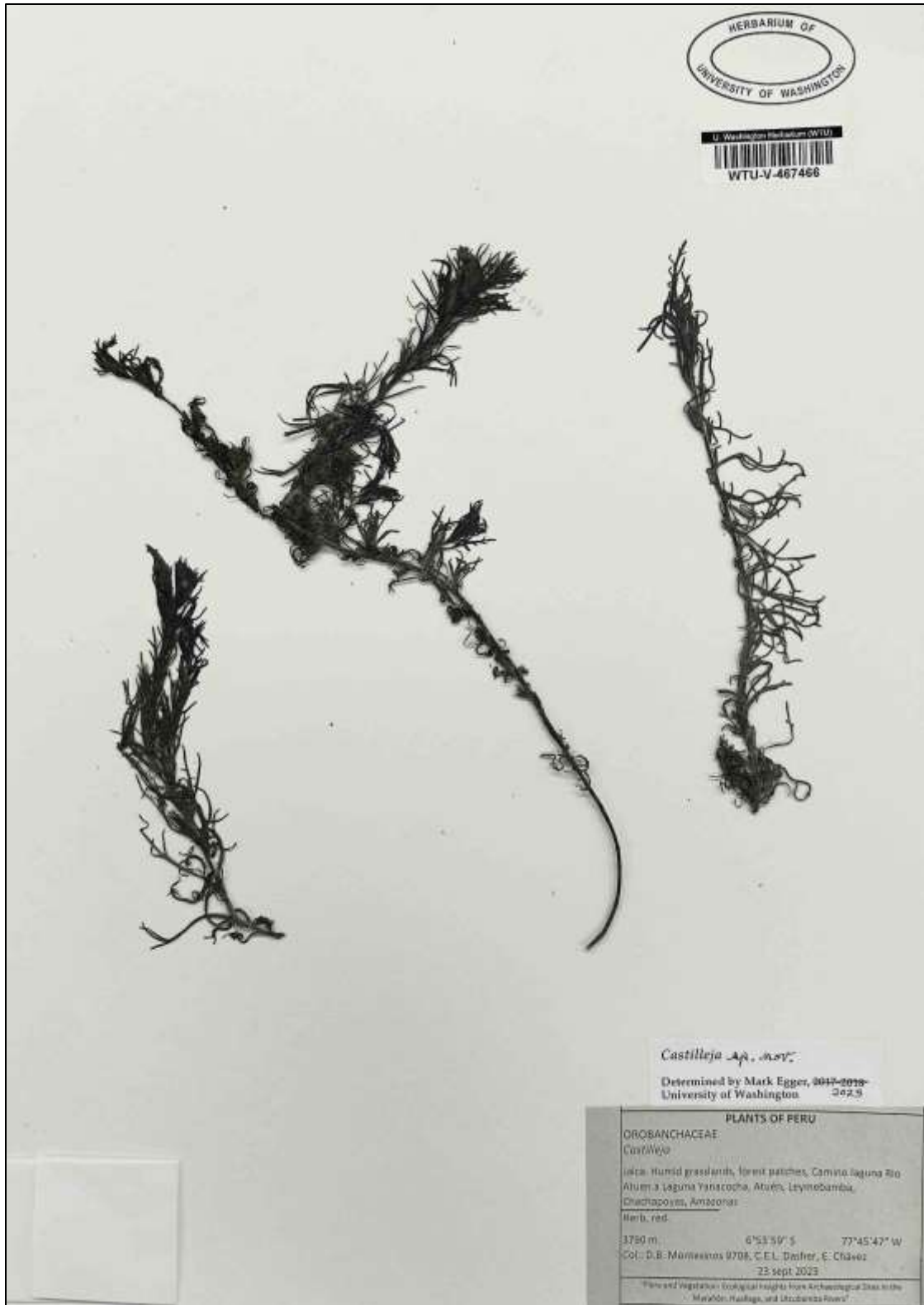


Figure 9. *Castilleja isidoroï*, Prov. Chachapoyas, Dept. Amazonas, Perú. Montesinos *et al.* 9708, WTU. While this unicate collection is not adequate for a type collection, it serves as a voucher for the best set of field photos we have of this rare species. The collection date was 24 July 2023, now corrected on the sheet at WTU.



Figure 10. *Castilleja isidoroï*, plant just starting to flower, Prov. Cajamarca, Dept. Cajamarca, Perú, Montoya 2579 & Dávila, CPUN. A recent collection not far from the type locality.



Figure 11. *Castilleja isidoroi*, young but vigorous plant just beginning to flower, Prov. Cajamarca, Dept. Cajamarca, Perú, Montoya 2579 & Dávila, CPUN. Field photo of collected plant. Photo by Montoya.



Figure 12. *Castilleja isidoroi*, young but vigorous plant just beginning to flower, Prov. Cajamarca, Dept. Cajamarca, Perú, Montoya 2579 & Dávila, CPUN. Field photo of collected plant. Note that the beak and lower lip of the corolla from this young inflorescence have not yet fully expanded. Photo by Montoya.



Figure 13. *Castilleja isidoroï*, Prov. Contumazá, Dept. Cajamarca, Perú, Sagastegui et al. 10766, MO.



Figure 14. *Castilleja isidoroï*, Prov. Contumazá, Dept. Cajamarca, Perú, Sagastegui et al. 10766, HUT.



Figure 15. *Castilleja isidoroï*, Prov. Contumazá, Dept. Cajamarca, Perú, Sagastegui et al. 14012, HUT.



Figure 16. *Castilleja isidoroï*, Prov. Contumazá, Dept. Cajamarca, Perú, *Sagastegui et al.* 14012, F. Note the unsigned handwritten annotation, “Similar to *C. vadosa*, but flowers huge.”



Figure 17. *Castilleja isidoroï*, Prov. Contumazá, Dept. Cajamarca, Perú, Sagastegui et al. 10061, HUT.

Figure 18. *Castilleja isidoroï*, Prov. Contumazá, Dept. Cajamarca, Perú, Sagastegui et al. 10061, MO.

Phenology, ecology, and associated species. *Castilleja isidoro* has been collected in flower from 21 March to 23 September. The only detailed ecological notes we have are those recorded by Montesinos and Dasher at the population site near Atuén, Leymebamba district, in the Dept. Amazonas (Figures 19–21). Ecology: Jalca grassland, forest patches, with rocky outcrops, disturbed by cattle grazing and occasional fires. Soil substrate: Thin, rocky, acidic soil over sandstone bedrock, poorly drained. Closely associated species include *Salvia lanicaulis*, *Gynoxys hutchisonii*, *Arcytophyllum leynebambense*, *Arenaria mallquii* sp. nov., ined., and several grasses (*Festuca* spp.). Of these, the first two appeared to be potential hosts to the *Castilleja*. Other taxa observed in the vicinity include *Ascidogyne wurdackii*, *Bomarea superba*, *Dendrophorbium chopinii*, *Elaphoglossum paleaceum*, *Greigia raporum*, *Isolepis inundata*, *Lysipomia sphagnophila*, *Miconia latifolia*, *Passiflora parvifolia*, *Peperomia hartwegiana*, *Salvia squalens*, *Siphocampylus jelskii*, *Stellaria utcubambensis*, and *Thalictrum decipiens*. In addition, Montoya (personal communication, 2026) noted the following species in the vicinity of his collection of *C. isidoro* in Dept. Cajamarca: *Acaulimalva sulphurea*, *Gamochaeta purpurea*, *Stachys aperta*, *Bartsia patens*, *Cheilanthes scariosa*, *Gnaphalium dombeyanum*, *Monnina conferta*, and *Stachys aperta*.

No pollinating organisms have been directly observed visiting *Castilleja isidoro*, but, in line with other species of subg. *Colacus*, it is likely pollinated by small native bees, possible of Family Halictidae, individuals of which were observed in the vicinity by Montesinos. No cases of herbivory on *C. isidoro* have been recorded, though it is highly likely that both insect larvae and a variety of mammalian herbivores feed on this species at least occasionally, as has been noted for many *Castilleja* species (Egger et al. 2019).



Figure 19. La Jalca Perúana and Ceja de Selva (humid grassland to cloud forest) interface, habitat of *Castilleja isidoro* in the vicinity of the collection site of Montesinos 9708. Photo by Montesinos.

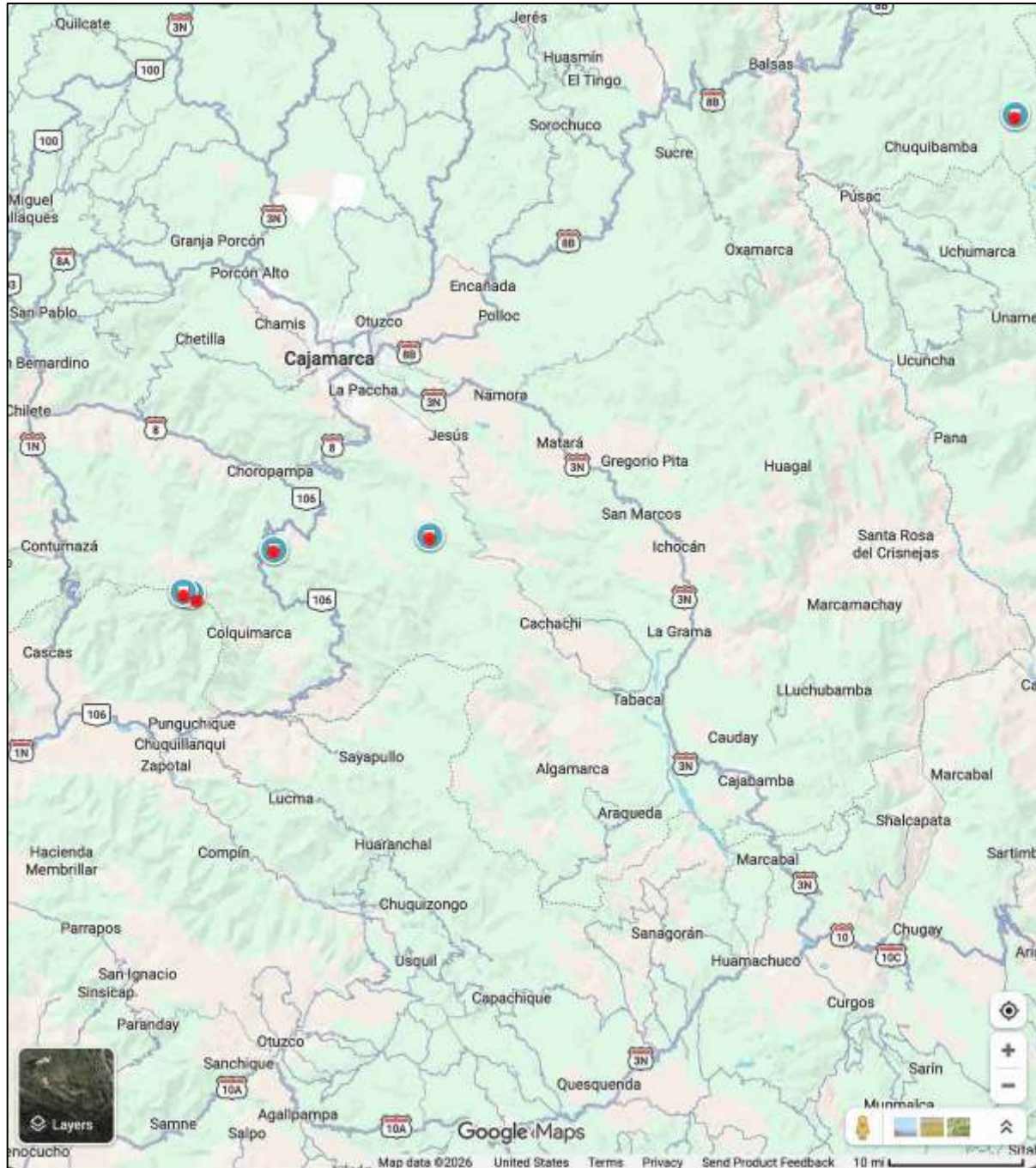


Figure 20. La Jalca Perúana and Ceja de Selva (humid grassland to cloud forest) interface, habitat of *Castilleja isidoroï* in the vicinity of the collection site of *Montesinos 9708*. Photo by Montesinos.



Figure 21. La Jalca Perúana and Ceja de Selva (humid grassland to cloud forest) interface, habitat of *Castilleja isidoroï* in the vicinity of the collection site of *Montesinos* 9708. Photo by Montesinos.

Range and Distribution. *Castilleja isidoro* is known to occur at elevations between 3,300–4,000 m and is entirely endemic to the Andes Mountains in northwestern Perú, with known populations in Dept. Amazonas in Prov. Chachapoyas and in Dept. Cajamarca in provinces Cajamarca and Contumazá (Maps 2–3). In Contumazá Province, it occurs close to the border of Dept. La Libertad, and the new species may well occur therein.



Map 2. Locations of known populations (light blue circles with red centers) of *Castilleja isidoro* in Dept. Cajamarca (left-center) and Dept. Amazonas (upper right) in northwestern Perú. Note: the left-most two tags are partially overlapping, as the locations (Pozo Kuan and Pozo Chuño) are too close to be resolved on the map, and there are two collections from the vicinity of Pozo Kuan.

Conservation status. *Castilleja isidoro* is presently known from only six populations. Most collection labels provide no information on the size of the local population. The population in the vicinity of Montesinos *et al.* 9708 consisted of approximately 15–20 plants in a 50 m² area, and in the vicinity of the most recent collection (Montoya 2579 & Dávila), “It was not possible to estimate the total population size of the species due to the small number of individuals and their scattered distribution within the study area, with only a few isolated individuals recorded” (Montoya, personal communication, 2026). On this basis, *C. isidoro* should be considered a candidate for listing as globally endangered, due to both small numbers of populations and small population sizes, with a suggested NatureServe rank of G1 or G2. Livestock grazing, human population growth, and global warming are all potential threats to this species.

Taxonomic relationships and identification. The genus *Castilleja* consists of about 200 species of the western hemisphere and arctic-boreal Asia (Egger *et al.* 2019), with about 20 species known from South America, at least 13 of which occur in Perú. South of Perú and east of the Andes Mountains, the number of species drops off dramatically. All but three of the *Castilleja* species in South America are endemic to the continent, and all but one, *C. arvensis* Schltdl. & Cham., are limited within the continent to the northern two-thirds of the Andean Cordillera. A comprehensive modern treatment of the genus in South America has yet to be written, though country-based treatments were provided by Pennell (1953) for Venezuela and by Holmgren (1984) for Ecuador. Edwin (1970, 1971) described several new species and listed nine species of *Castilleja* for Perú, though four of these proved to be synonymous with previously described species. He included a tenth species, *C. laciniata* Hook. & Arn., but he listed it as *Orthocarpus laciniatus* (Hook. & Arn.) Keck. Of the Peruvian species now included in *Castilleja* subg. *Colacus*, only *C. cerroana* and *C. laciniata* were recognized by Edwin. More recent papers have added new species to and clarified taxonomic issues within *Castilleja* in South America, including Egger (2009, 2017, 2018), González and Pabón-Mora (2013), and Muñoz *et al.* (2026).

In the two departments of northern Perú in which *Castilleja isidoro* is found, there are three other species of subg. *Colacus*, *C. cerroana*, *C. peruviana*, and *C. vadosa* (reports of *C. profunda* from near Celendín in Dept. Cajamarca have proved inconclusive). Of these, the new species appears to be morphologically most like *C. peruviana* (in the markings of the lower corolla lip) and especially *C. vadosa*, the species with which it is most often confused on herbarium annotations. *Castilleja isidoro* is like *C. vadosa* in its general growth form, frequently with many stems from the base and these often branched above, and the architecture of the leaves and bracts are similar. However, the new species is well differentiated from both species in the characters outlined in the diagnosis and in the key below. In the field, *C. isidoro* is quite distinctive, with it mostly pale-colored bracts and relatively large, distinctively colored corollas with long beaks and prominent lower lips with three well developed and boldly spotted triangular teeth (Figure 22). However, when field collections are pressed and dried, the specimens often lose their colors, and the general vegetative features become more easily confused with those of *C. vadosa*.



Figure 22. Comparison of the inflorescences of the four species of *Castilleja* subg. *Colacus* known from Depts. Cajamarca and Amazonas in northern Perú: Upper left, *C. cerroana*; upper right, *C. peruviana*; lower left, *C. vadosa*; lower right, *C. isidoroï*. Photos by Egger and Montesinos.

Annotated List of the Species of *Castilleja* subg. *Colacus* in Perú and Adjacent Countries

The species of *Castilleja* subg. *Colacus* in South America are found only in the Andean portions of Ecuador (1 species), Perú (6 species), and Chile (3 species). To promote awareness and conservation of the flora of the central Andes Mountains region, we present below an updated key to the species of *Castilleja* subg. *Colacus* known to occur there, along with nomenclatural notes and synonymies, photos of living plants in habitat to aid in field identification, and brief commentaries concerning our current understanding of the status and distribution of each species in the form of an annotated list. This section is intended as supplementary to, rather than a revision of, the work presented by Chuang and Heckard (1992), which included thorough descriptions, specimen citations, and range maps for all the relevant species except *C. isidoro*. It should be noted that posts on the iNaturalist and the integrated Naturalista website (iNaturalist 2026), reviewed and partially annotated by the authors, have significantly expanded our knowledge of the distribution of many of the species, and new records are cited for *C. alpicola* in particular, a species previously known only from the type locality. Range maps provided in this section show the locations of verified iNaturalist posts and can be compared to the specimen-based maps provided by Chuang and Heckard for a more complete view of the range of each species. A full citation of specimens and iNaturalist images is provided only for *C. alpicola* due to the significant expansion of its range based on very recent observations. Finally, Egger's research on the location of type material for all species of *Castilleja* has revealed the presence of a few isotypes not cited by Chuang and Heckard, and these are included as well.

KEY *CASTILLEJA* SUBG. *COLACUS* IN SOUTH AMERICA

1. Bract tips white, rarely pale pink; plants of lower elevations on the Pacific slope of central Chile ***Castilleja attenuata***
1. Bract tips rarely if ever white; plants of Dept. Loja, Ecuador, Perú, and the northern half of western Chile, usually at moderate to high elevations in the Andes Mountains, sometimes to near sea level.
 2. Abaxial and adaxial calyx clefts about 1/2 of calyx length, lateral clefts conspicuously shorter, 1/5–1/4(–1/3) of the calyx length; corolla beaks straight, not hooked at the tip; adaxial surface of corolla beaks densely covered with shaggy, white to cream-white hairs.
 3. Pubescence hirsute to hirsute-hispid, eglandular; seed coats ± deeply reticulate; coloration of bracts pink to pink-purple, at least distally; plants annual; limited to the Cuzco region of southern Perú and disjunct at lower elevation in west-central Chile ***Castilleja laciniata***
 3. Pubescence pilose mixed with short, stipitate-glandular hairs; seed coats shallowly reticulate; coloration of bracts variable, dull pale-orange, dull red-orange, dark reddish-brown, dull reddish, or dull reddish-purple, at least distally; plants annual or short-lived perennials; limited to northwestern Perú and adjacent southern Ecuador ***Castilleja cerroana***
 2. Calyx clefts subequal, about 1/2 of calyx length, or laterals inconspicuously shorter, > 1/3 of the calyx length; corolla beaks slightly hooked at the tip or straight; adaxial surface of corolla beaks variously pubescent but not usually with white to cream-white hairs.
 4. Plants 3–7 cm tall, stems prostrate with only the inflorescence ascending; inflorescences compact, 1.5–4.5 cm long; corollas, at least the distal half, typically deep red throughout except for a small green to yellow-green patch on the distal portion of each lobe of the lower lip ***Castilleja alpicola***
 4. Plants 10–45 cm tall, stems erect-ascending to widely spreading but not prostrate; inflorescences gradually elongating, 5–25 cm long; corollas variously colored but never as above.
 5. Pubescence of stems, leaves and inflorescences hirsute or hirsute-hispid, eglandular; seed coats very deeply reticulate; lower lip of corollas moderately inflated, with the sacs usually bright yellow with few markings except at the base of the teeth; corolla beaks narrowing and weakly decurved at the tip ***Castilleja profunda***

5. Pubescence of stems, leaves and inflorescences pilose to villous or glandular-viscid and mixed with shorter, stipitate-glandular hairs; seed coats shallowly reticulate; lower lip of corollas weakly to moderately inflated, with the sacs either not at all yellow or yellow only in the distal-most portion and often with dark-colored dots or splotches in the medial portion of the sacs and/or at the base of the teeth; corolla beaks not at all to slightly decurved at the tip.

6. Corollas relatively large, 25–40 mm long, and conspicuously colored, the beaks 2–3 times the length of the lower lip; bracts inconspicuously colored pale tan to pale brownish-red or pale greenish; plants often highly branched throughout, the branches ascending-erect to often spreading-ascending **Castilleja isidoro**

6. Corollas smaller, 18–25 mm long, and less conspicuously colored, the beaks < 2 times the length of the lower lip, often only slightly so; bracts conspicuously colored red to pink-purple or red-violet; plants unbranched to highly branched, the branches erect to ascending-erect.

7. Bracts at least distally pink-purple to sometimes red-violet; stems often well-branched; corolla beaks shaggy-pubescent and 2–4 mm longer than the lower lips; stigmas usually exserted at a horizontal angle **Castilleja vadosa**

7. Bracts at least distally red to reddish-purple; stems simple to few-branched; corolla beak adaxially puberulent and only 1–2 mm longer than the lower lip; stigma included or only slightly exserted **Castilleja peruviana**

1. CASTILLEJA ALPICOLA T.I. Chuang & Heckard, Syst. Bot. 17: 420. 1992. **TYPE:** Perú. **Dept. La Libertad.** Prov. Santiago de Chuco, Jalca de Coipín, jalca, alt. 4000 m, 16 Jun 1984, A. Sagástegui A., J. Mostacero L. & M. Diestra Q. 11,969 (holotype: GB; isotypes: HUT, MO). Figure 26.

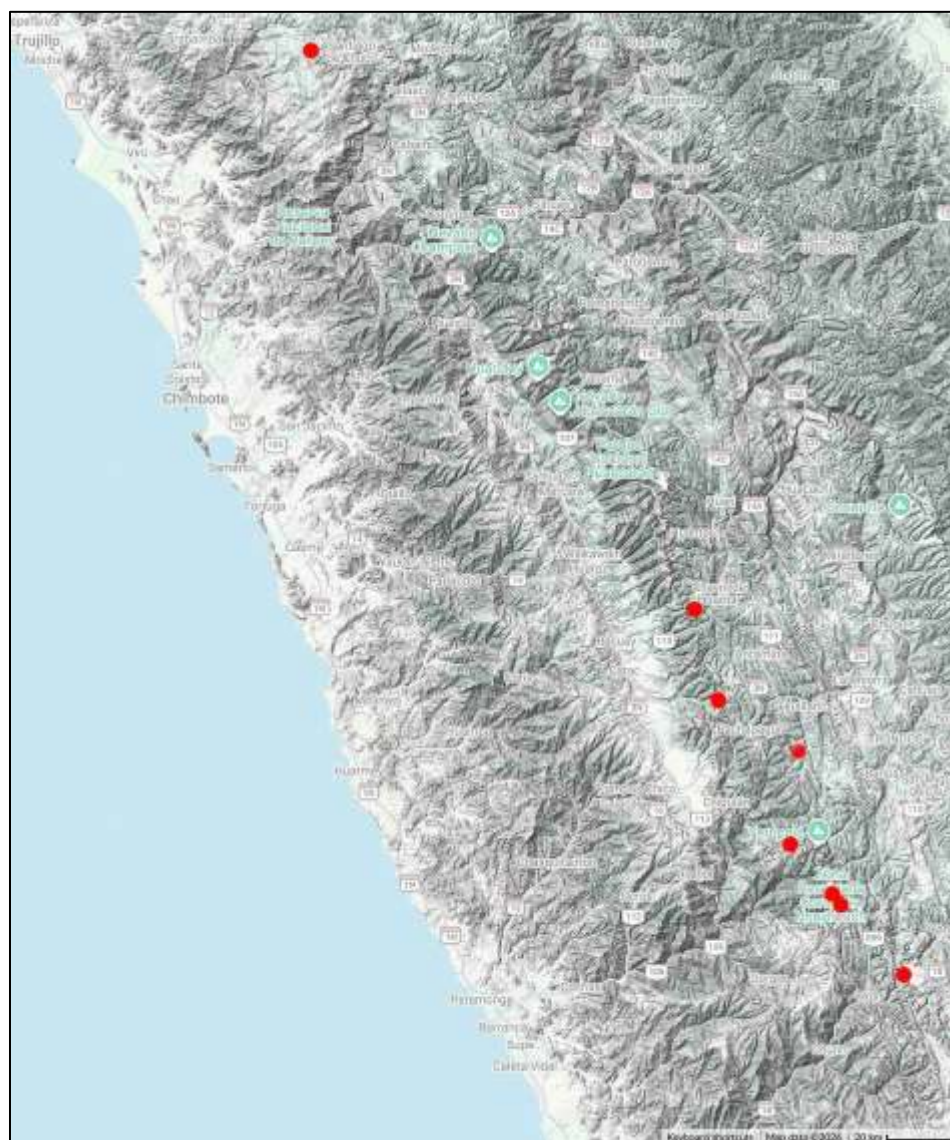
Other specimens examined. Perú. **Dept. La Libertad.** Prov. Santiago de Chuco, Jalca de Coipín, 4200 m, 17 April 1984, *Tank 2005-33 and Egger* (Egger field number 1336) (F, WTU). Figures 24–27. Note: a collection of plants of similar aspect from the same region and labeled as “*Castilleja cf. alpicola*” is a collection of the dwarfed high elevation morph of *C. peruviana*: Huerco Grande (Arriba de Quiruvilca), 4120 m, 23 March 1994, *Leiva and Leiva 1050* (F, HUT). Also see Figure 55.

iNaturalist observations: Perú. **Dept. Ancash.** Bolognesi Prov., -9.86915, -77.17905, [Huascarán], 4720 m, L. Flint, 6 June 2018, <https://www.inaturalist.org/observations/13200638>; -10.26783, -76.97812, [Cordillera Huayhuash], ca. 4800 m, A. Deberdt, 13 June 2025, <<https://www.inaturalist.org/observations/293170982>> (Figures 30–31); -10.01849, -76.96928, ca. 4510 m, L. Vilca Bustamonte, 18 July 2026, <https://www.inaturalist.org/observations/385483411>. Huari Prov., ca. -9.62572, -77.25448, [just below highest pass on trail from Recuay to Chavin de Huantar], ca. 4600 m, L. Malek, 24 July 2004, <<https://www.inaturalist.org/observations/19519443>> (Figure 32). **Dept. Lima.** Prov. Catatambo, -10.41131, -76.85524 [near Laguna Viconga de Uramasa], ca. 4460 m, G. Galice, 13 June 2025, <<https://www.inaturalist.org/observations/289547665>>; -10.38904, -76.88213, [Cordillera Huayhuash], ca. 4800 m, Chauncy, 20 Jun 2023, <<https://www.inaturalist.org/observations/177379835>>. Prov. Oyon, -10.60368, -76.68322 [N of Hwy. 18], 4660 m, L. Vilca Bustamante, 8 Feb 2026, <<https://www.inaturalist.org/observations/90145417>>.

When this species was described in 1992, it was known only from the type collection from Dept. La Libertad. Egger and Tank visited the site in 2005 with the assistance of botanists from HAO, and we obtained a second collection (Figures 24–26) and the first photos of living plants (Figures 27–28). Since that time, observers posting photos on iNaturalist have documented seven additional populations, three from Dept. Lima and four from Dept. Ancash (Map 3). Apparently, there are still only two physical collections of this species, both from the type locality. It is entirely endemic to Perú.

Castilleja alpicola is a high elevation species of open, rocky and gravelly slopes and ridges, and rock crevices, with all known populations occurring between 4100–4800 m elevation (Figures 29). It is apparently very rare, but it has a low growth form and is relatively inconspicuous in the jalca grasses and rock crevices and may be often overlooked. It is also uncommon even in habitat and occurs in scattered clusters of small numbers of individuals. It has been observed in flower from February to July, with four of eight records in June.

Morphologically, the plants show little or no geographical variations and vary little from the original description. One exception is a population in the Cordillera Huayhuash in Bolognesi Province, Department Ancash. While some individuals in that populations are typical, others are striking in their corolla coloration, which is primarily yellow with blushes of very pale red, primarily on the tube and lower lip (Figure 30). This variant form has not been recorded elsewhere.



Map 3. Map of northwestern Perú showing the known range of *Castilleja alpicola*. Red circles indicate the locations of verified populations. The type locality is the northernmost circle, in Dept. La Libertad. The other sites are all at least about 150 km to the southeast, but all populations follow the main axis of the highest portions of the central Andes Mountains.



Figure 23. Holotype of *Castilleja alpicola*, GB. Isotypes are found at HUT and MO.



Figure 24. *Castilleja alpicola*, topotype, Tank 2005-33 and Egger (Egger field number 1336), WTU.



Figure 25. *Castilleja alpicola*, topotype, crop showing two plants and dissected flowers, Tank 2005-33 and Egger (Egger field number 1336), WTU.



Figure 26. *Castilleja alpicola*, topotype, Tank 2005-33 and Egger (Egger field number 1336), F.



Figure 27. *Castilleja alpicola* from the type locality, part of Tank 2005-33 and Egger (Egger field number 1336), F, WTU. Jalca de Coipín, Dept. La Libertad, Perú, 17 April 2005. Photos by Egger.



Figure 28. *Castilleja alpicola* from the type locality, Jalca de Coipín, Dept. La Libertad, Perú, 17 April 2005. Photo by Egger.



Figure 29. Two views of the type locality of *Castilleja alpicola*, Jalca de Coipín, Dept. La Libertad, Perú, 17 April 2005. The plants grow on the rocky slopes, not on the marshy flats around the Laguna de Coipín. Photos by Egger.



Figure 30. *Castilleja alpicola*, rare color form, Cordillera Huayhuash, Dept. Ancash, Perú, 13 June 2025. More typically colored plants were also documented in this population. Photo by A.J. DeBerdt.



Figure 31. Habitat of *Castilleja alpicola* at ca. 4800 m elevation, Cordillera Huayhuash, Dept. Ancash, Perú, 13 June 2025. Photo by A.J. DeBerd.



Figure 32. *Castilleja alpicola* and habitat, near Punta Yanashallash, Huari Prov., Dept. Ancash, Perú, 24 July 2004. Some corollas appear unusually long due to the viewing angle. Photo by Lada Malek.

2. **CASTILLEJA ATTENUATA** (A. Gray) T.I. Chuang & Heckard, Syst. Bot. 16: 656. 1991. **BASIONYM:** *Orthocarpus attenuatus* A. Gray, Pacific Rail. Rept. 4: 121, 1856. **TYPE:** **USA. California.** Marin Co., Corte Madera, (16 Apr) 1854, J.M. Bigelow s.n. (holotype: GH; isotype: NY). Figure 33.

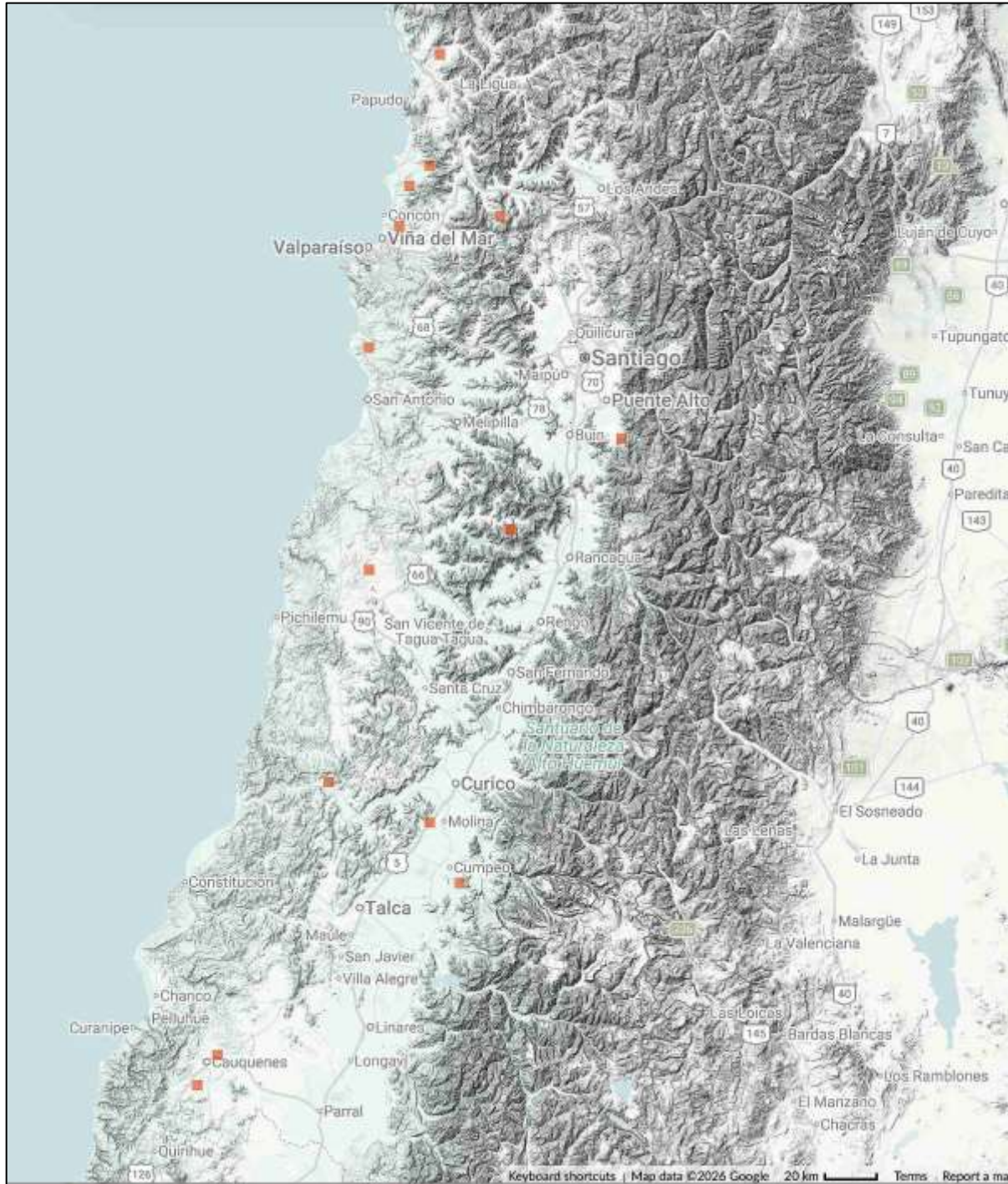
Chuang and Heckard recorded the first report of *Castilleja attenuata* in South America as a collection obtained in 1889 from the coastal region of central Chile. However, Muñoz-Schick et al. (2026) documented an earlier collection by R.A. Philippi in Quilpué, Valparaíso Region, in September 1871 (SGO 104129). This species is almost certainly a recent introduction to Chile, either human-mediated or by long-distance dispersal by migratory birds. The Chilean plants exhibit no morphological divergence from the plants in North America, and their occurrence in South America remains limited to the region in which the species was first located, occurring at elevations below 1000 m elevation. Another case of the recent introduction of *C. attenuata* is its naturalization in the state of Victoria in southern Australia (VicFlora 2026).

Combining herbarium specimens cited by Chuang and Heckard (1992) with confirmed records on iNaturalist (Map 4) as of July 2026, *Castilleja attenuata* is known in South America from the following Provinces in central Chile: Cachapoal, Calquenes, Cardinal Caro, Chacabuco, Colchagua, Cordillera, Curicó, Petorca, San Antonio, Santiago, Talca, and Valparaíso.

Castilleja attenuata is apparently very common and somewhat weedy where it occurs in Chile, very much like its occurrences in western North America. Examination of specimens and photographs of the Chilean plants show them to be virtually indistinguishable from the plants in North America, even to the occurrence on both continents of similar minor variations in size and corolla markings (Figure 33). This fact strongly supports previous suggestions of its recent introduction to Chile. It occurs in the same region of the country as some populations of *C. laciniata*, but *C. attenuata* appears to be much more common there, with *C. laciniata* known only from a relatively few specimens and no verified observations reported on iNaturalist as of July 2026. The two can be easily distinguished by calyx incisions and coloration of the inflorescences. *C. attenuata* has subequally cleft calyces and white (rarely pale pink) bract tips, while *C. laciniata* has calyces with much more shallow lateral calyx clefts and pink-purple bract tips. The latter appears to be far more common in the Cusco region of southern Perú than in Chile.



Figure 33. *Castilleja attenuata*, holotype of the basionym, *Orthocarpus attenuatus* A. Gray (GH), left hand stem only, though all specimens on this sheet are of the same species.



Map 4. Verified iNaturalist reports of *Castilleja attenuata* (red squares) in central Chile as of July 2026.



Figure 34. *Castilleja attenuata*, typical variants seen in populations in both western North America and in west-central Chile. The pale pink form is rarely seen in either country. Photos by Egger.

3. **CASTILLEJA CERROANA** Edwin, Phytologia 19: 403. 1970. **TYPE: Perú. Dept. Ancash.** Cordillera Blanca, (central Perú), alt. 4400 m, 12 Aug 1954, *W. Rauh & G. Hirsch P-2096* (holotype F). Figure 35.

Though described in 1970, this species is one of the more common and widespread members of subg. *Colacus* in South America, ranging from Dept. Loja in southern Ecuador, where it is apparently rare and known only from a single collection (S slopes of Cerro Villonaco, W of Loja, *Harling 25346*, GB, NY, UC), south to the Dept. Huancavelica in central Perú. Combining herbarium specimens cited by Chuang and Heckard (1992) with confirmed records on iNaturalist (Map 5) as of July 2026, *Castilleja cerroana* is now known from the following departments and provinces: **Ecuador.** Dept. Loja. **Perú. Dept. Ancash.** Prov. Bolognesi, Prov. Carhuaz, Prov. Huaráz, Prov. Huari, Prov. Huaylas, Prov. Yungay. **Dept. Cajamarca.** Prov. Cajamarca, Prov. Celendín, Prov. Chachapoyas, Prov. Contumazá, Prov. Gran Chimú, Prov. Hualgayoc. **Dept. Huancavelica.** Prov. Huancavelica, Prov. Tayacaja. **Dept. Huánuco.** Prov. Huamalís, Prov. Huánuco. **Dept. Junín.** Prov. Chupaca, Prov. Concepción, Prov. Huancayo, Prov. Jauja, Prov. Tarma. **Dept. La Libertad.** Prov. Huamachuco, Prov. Santiago de Chuco. **Dept. Lima.** Prov. Canta, Prov. Oyon.

Castilleja cerroana is in many ways similar morphologically to *C. laciniata*. It shares several traits with that species, including the shallow lateral calyx clefts, the mostly straight corolla beaks with prominently white-pubescent adaxial surfaces, and similarly structured lower lips. They also apparently share an annual habit. While Chuang and Heckard (1992) assumed *C. cerroana* was a perennial, there is little evidence to support that assumption, and Tank and Olmstead (2009) rightfully called this into question. However, the two are generally separable, especially in the field, and their ranges are disjunct, with *C. laciniata* limited to the Cusco region of southern Perú, with another, apparently rare, population system in west-central Chile. Reasonably consistent traits to distinguishing *C. cerroana* from *C. laciniata* include the generally reddish-brown to dull reddish coloration of the bracts and calyces (vs. usually pink-purple), the mixed pubescence including stipitate-glandular hairs (vs. entirely eglandular hairs), and the shallowly reticulate seed coats (vs. deeply reticulate). The flowering stems of *C. cerroana* also tend to be relatively narrower on average, though there is overlap in this trait. Most records are from 3500–4500 m, though it has been found as low as 2500–2600 m in Ecuador.

Fairly typical plants of *Castilleja cerroana*, as well as some unusual variations, are shown in Figures 36–41 below.



Figure 35. Holotype of *Castilleja cerroana* (F). The type collection is apparently unicate.

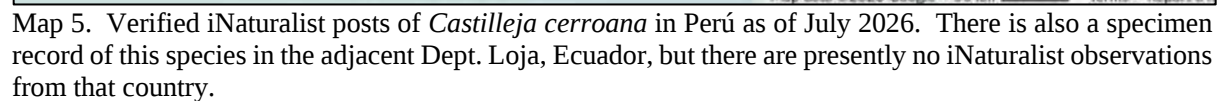




Figure 36. *Castilleja cerroana*, Abra Gran Chimú, E of Cajamarca, Dept. Cajamarca, Perú, 12 April 2005. Photo by Egger.



Figure 37. *Castilleja cerroana*, Abra Gran Chimu, E of Cajamarca, Dept. Cajamarca, Perú, 12 April 2005. Photo by Egger.



Figure 38. *Castilleja cerroana*, showing atypical coloration and unusually wide calyces and lobes, near Laguna Pozo Kuan, above Contumaza, Dept. Cajamarca, Perú, 14 April 2005. Photo by Egger.



Figure 39. *Castilleja cerroana*, Monte Viudo, Chachapoyas, Dept. Amazonas, Perú, 25 July 2024. Photo by Montesinos.



Figure 40. *Castilleja cerroana*, atypical color form with entirely greenish bracts and calyces, Yarowilca archeological site, Dept. Huánuco, Perú, 16 May 2017. Photo by Montesinos.



Figure 41. *Castilleja cerroana*, form with atypical coloration and markings on the lower corolla lip, Hwy. 3N, N of Yanashallash, Bolognesi Prov., Dept. Ancash, Perú, 7 May 2016. Photo by Ruth Ripley.

4. **CASTILLEJA ISIDOROÏ** J.M. Egger, Montesinos & Dasher (see pages 1–28, Figures 1–22, and Maps 1–2 above.)
5. **CASTILLEJA LACINIATA** Hook. & Arn., Bot. Beechey's Voyage: 40. 1830. *Bartsia laciniata* (Hook. & Arn.) Ruíz & Pávon ex A. López, Anal. Inst. Bot. Cavanilles 17: 444. 1859. *Orthocarpus laciniatus* (Hook. & Arn.) D.D. Keck, Proc. Calif. Acad. Sci., Ser. 4, 16: 548. 1927. *Orthocarpus australis* Benth. in DC., Prodr. 10: 537. 1846. The latter name is illegitimate and superfluous because it is based in part of Hooker and Arnott's type. **TYPE: Chile.** Concepcion [= Concepción], (9-20 Oct 1825), G.T. Lay & A. Collie s.n. (holotype: K-HOOK). Figure 42. The holotype collection consists of one plant mounted in the upper left portion of the same sheet that also contains specimens of the other two listed syntypes of the illegitimate name, *Orthocarpus australis* Benth. (Figure 42). In addition, the annotation label placed below Lay and Collie's type collection from the Beechey Voyage adds some confusion, as it contains the collection number "Cuming 327", as well as a sketch of a magnified seed. This sketch and collection number appear to come from a different collection of *C. laciniata* not mounted on this sheet. Cuming 327 may be associated with the type collection of another synonym, *Oncorhynchus tenellus* Fischer & Meyer (see below). In addition, in making his new combination, Keck (1927) confused one of other syntypes of *Orthocarpus australis* Benth. (Matthews 460) with the single holotype of *C. laciniata*. Keck also erred in listing the collection number for that syntype as "Mathews 4601", an incorrect transcription of Matthews 460. It should also be noted that Matthews 460 was collected in Huamantanga District (cited as "Huamontongo"), east of Lima, Perú and is a collection of *C. profunda*, not *C. laciniata*.
***Castilleja pseudopallescens* Edwin**, Phytologia 19: 404. 1970. **TYPE:** Perú. Dept. Apurímac: Prov. Grau, cuesta Quellipata, stony slopes, alt. 1700 m (8700 ft), 9 Mar 1946, C. Vargas C. 5800 (holotype: F!) Figure 43.
***Oncorhynchus pinnatifidus* Lehm.**, in D.F.L. Schlechtendal, Linnaea 8, Litt. 5. 1833 or 1834. ***Oncorhynchus pinnatifidus* Lehm.**, Sem. Hort. Bot. Hamburg. 1832, nomen nudum. **TYPE:** Chile. J.G.C. Lehmann s.n. (holotype: HBG?).
***Oncorhynchus tenellus* Fischer & Meyer**, Ind. Sem. Hort. Petrop. 1: 35, 1835. **TYPE:** Chile, [cultivated 1834 and 1835], H. Cuming s.n. (holotype: LE). [Note: this taxon may be based on H. Cuming 327, Chile. Chuquiragua, prope Valpariso, (Cordillera of Chile), 1831, E[2], CGE, K-HOOK, K-BENTH, PH, photo: UC, which is one of the three syntypes of *Orthocarpus australis* Benth. However, the synonymy of these collections has yet to be conclusively established.

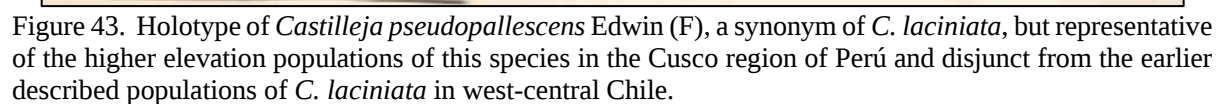
Castilleja laciniata is by far the earliest and for many years the sole member of subg. *Colacus* known to occur in South America, first described from a collection by Lay and Collie from the historic Beechey Voyage and described by Hooker and Arnott in 1830. Many older herbarium sheets of species later described as separate species bear earlier annotations as either *C. laciniata* or the synonymous *Orthocarpus australis*. Despite the long history, this species remains incompletely understood and has a complex nomenclatural history outlined above. According to Chuang and Heckard (1992), the distribution of this species has two disjunct components, the first represented by the type collection in central Chile and the other based in the Andes Mountains near Cuzco, in southern Perú. The Peruvian plants were proposed as a separate species, *Castilleja pseudopallescens* Edwin in 1970, but Chuang and Heckard reduced it to synonymy under *C. laciniata*, a decision with which we tentatively agree, though the populations in Chile remain relatively little known and deserve further study and documentation. In Peru, this species is known to occur from 1700–3600 m, while in Chile it is known from near sea level to about 560 m elevation.

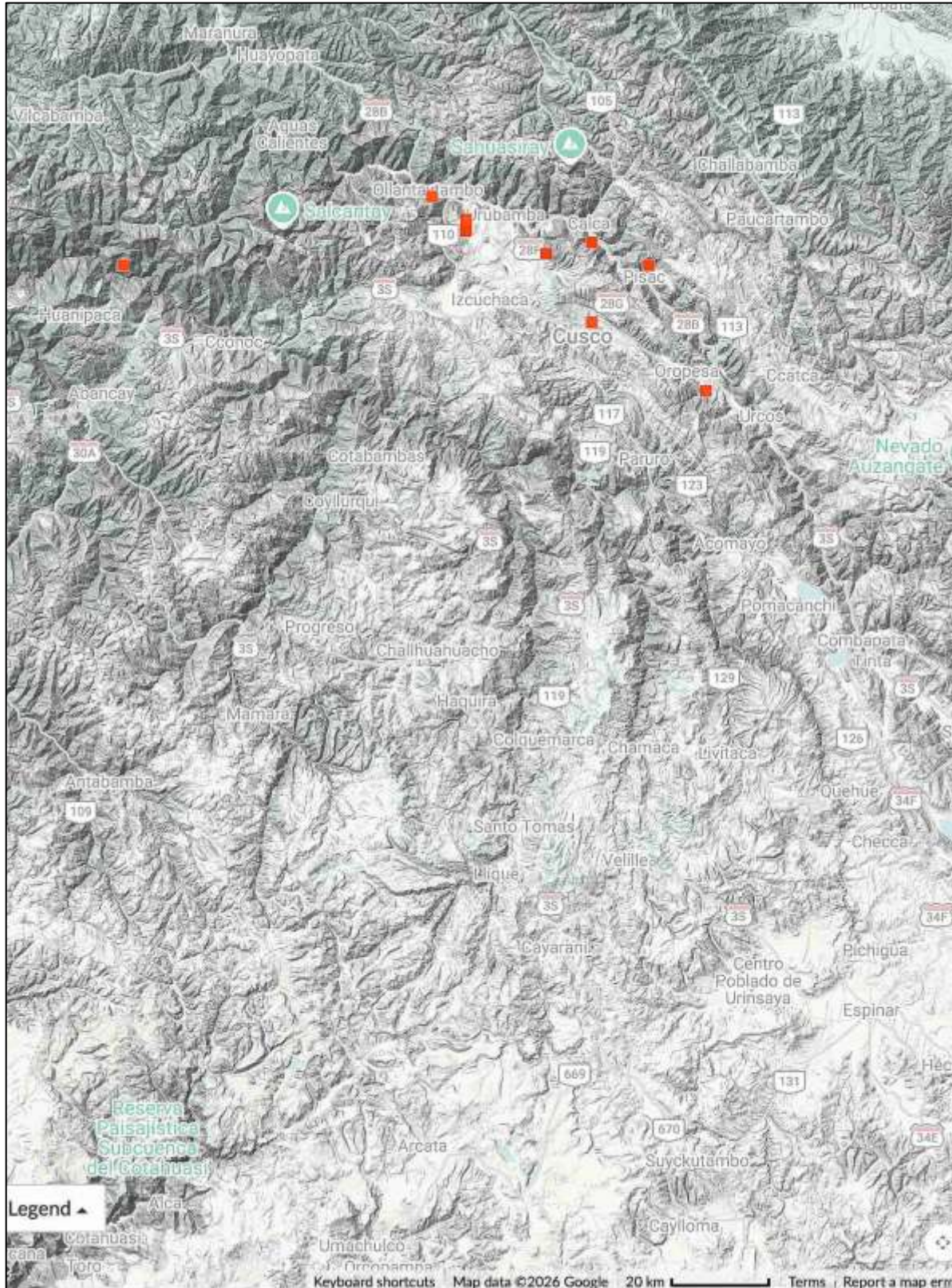
Castilleja laciniata is also known from surprisingly few correctly identified physical collections. Heckard and Chuang cited only six collections from Chile and four from Perú, and, although there are 13 verified posts on iNaturalist from the Cuzco region of Perú, there are no plants of

this species posted from Chile. Combining herbarium specimens cited by Chuang and Heckard (1992) with confirmed records on iNaturalist (Map 6) as of July 2026, *Castilleja laciniata* is known from the following departments and provinces: **Chile.** Prov. Coquimbo, Prov. Concepción, Prov. Maule, Prov. Santiago, Prov. Valparaíso. **Perú.** **Dept. Apurímac.** Prov. Grau (also where the type of the synonymous *C. pseudopallescens* was collected). **Dept. Cusco.** Prov. Anta, Prov. Calca, Prov. Cusco, Prov. La Convención, Prov. Paucartambo, Prov. Quispicanchi, Prov. Urubamba.



Figure 42. Holotype of *Castilleja laciniata* (upper left), Lay and Collie s.n., K. This sheet was also intended by Bentham to represent the four syntypes of his superfluous *Orthocarpus australis*. Cuming 327 and Bridges s.n. are also *C. laciniata*, but Matthews 460, upper right, is a collection of *C. profunda* from near Lima, Perú. Heckard's incorrect annotation of that specimen as holotype of *C. australis* is likely based on his initial (in 1985) interpretation of Keck's (1927) erroneous citation.





Map 6. Verified iNaturalist posts of *Castilleja laciniata* (red dots) in Perú as of July 2026. While this species is known to occur in central Chile, from near Santiago south to about Concepción, no verified reports of *C. laciniata* from Chile are recorded on iNaturalist to date.



Figure 44. *Castilleja laciniata*, Zona Arqueologica Moray, Prov. Urubamba, Dept. Cusco, Perú, 28 March 2024. Photo by Tom Bentley.



Figure 45. *Castilleja laciniata*, Mirador del Valle de Urquillos, Prov. Urubamba, Dept. Cusco, Perú, 15 March 2025. Note the relatively shallow lateral calyx clefts. Photo by Daniel Kennedy.



Figure 46. *Castilleja laciniata*, Zona Arqueologica Moray, Prov. Urubamba, Dept. Cusco, Perú, 18 March 2025. Photo by Anders Hastings.



Figure 47. *Castilleja laciniata*, Zona Arqueologica Moray, Prov. Urubamba, Dept. Cusco, Perú, 18 March 2025. Photo by Anders Hastings.



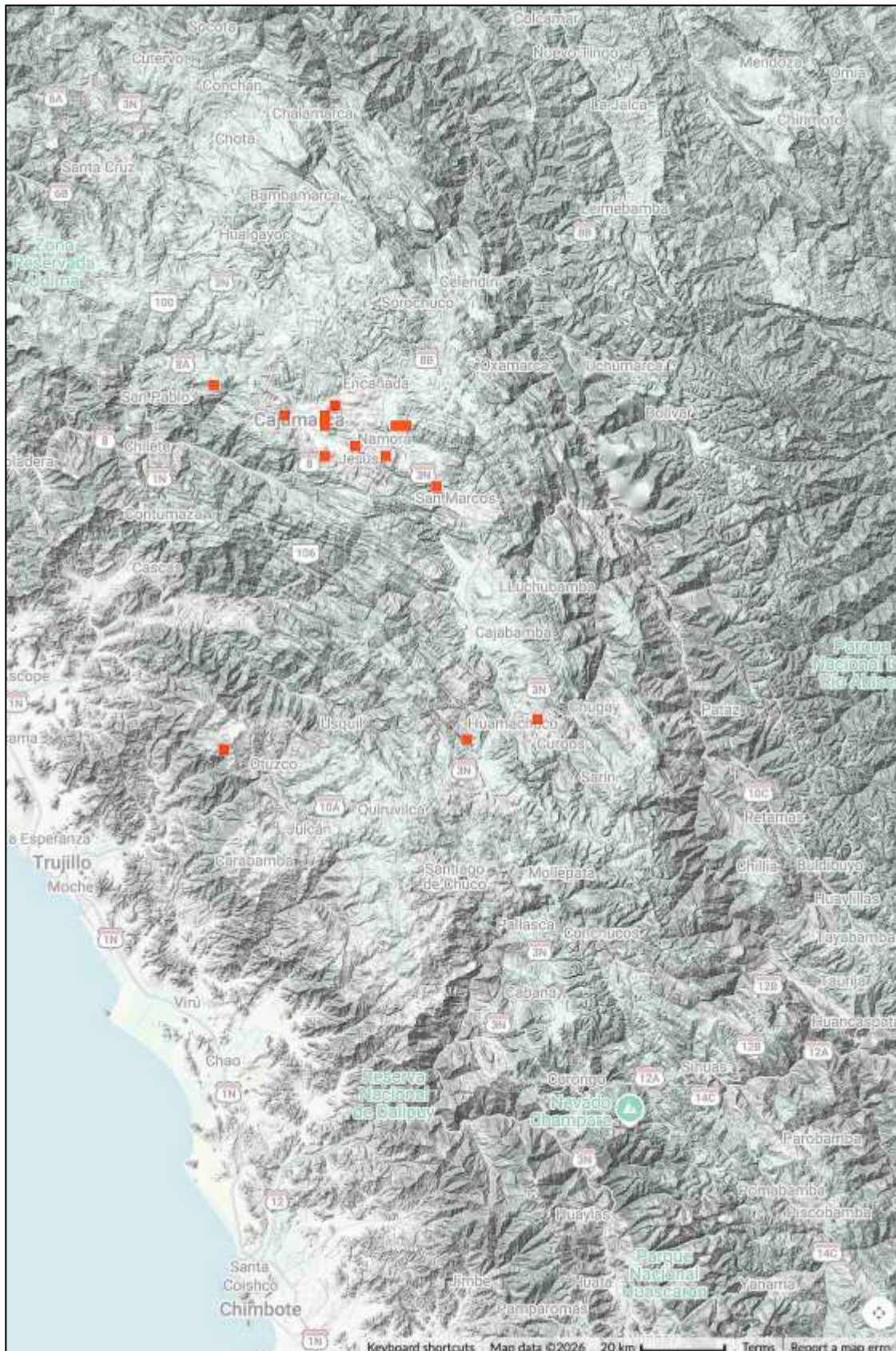
Figure 48. *Castilleja laciniata*, with entirely green lower corolla lip, Prov. Urubamba, Dept. Cusco, Perú, 23 March 2005. Photo by Rhonda Ridley.

6. **CASTILLEJA PERUVIANA** T.I. Chuang & Heckard, Syst. Bot. 17: 426. 1992. **TYPE: Perú. Dept. La Libertad.** Prov. Otuzco, along road to Huamachuco near km 105, ca. 15 km from Shorey beyond Agallpampa, elev. 3150 m, 20 Jun 1981, *T. Duncan 2846* (holotype: UC; isotypes: F, GH, K, MO, NY, UC, US, USM). Figure 49.

Among the species of subg. *Colacus* in South America, *Castilleja peruviana* is of relatively limited distribution and is common only in the provinces of Cajamarca and La Libertad. It is distinctive in its unbranched to weakly branched growth form, decidedly reddish to reddish-purple bract coloration, highly glandular pubescence, short corolla beaks, scarcely exceeding the lower lip by 1-2 mm, and the white to pale green or yellow-green coloration of the lower corolla lip, with small blackish spots at the base of each distal tooth. Typical plants are seen in Figures 50–53. Most records of this species are from 2500–3500 m, though there are a few records of dwarfed high elevation forms of this species known from above 4,200 m near Abra Quiruvilca in Dept. La Libertad (Figure 54). This form has been confused with *C. alpicola*, but the two are easily separable on close inspection and are contrasted in Figure 55. There is some morphological evidence of hybridization between *C. peruviana* and *C. vadosa* (see below under the latter species).

Combining herbarium specimens cited by Chuang and Heckard (1992) with confirmed records on iNaturalist (Map 7) as of July 2026, *Castilleja peruviana* is known from the following departments and provinces in northern Perú, to which it is endemic: **Dept. Amazonas.** Prov. Chachapoyas. **Dept. Cajamarca.** Prov. Cajamarca, Prov. Cutervo, Prov. Celendín, Prov. San Marcos. **Dept. La Libertad.** Prov. Huamachuco, Prov. Otuzco, Prov. Sánchez Carrión, Prov. Santiago de Chuco.

Figure 49. Holotype of *Castilleja peruviana*, Duncan 2846 (UC).



Map 7. Verified iNaturalist posts of *Castilleja peruviana* (red squares) in northern Perú as of July 2026.



Figure 50. *Castilleja peruviana*, Abra Gavilan, Dept. Cajamarca, Perú, 10 April 2005. Photo by Egger.



Figure 51. *Castilleja peruviana*, Abra Gavilan, Dept. Cajamarca, Perú, 10 April 2005. Note the deep lateral calyx clefts, only slightly less deep than the abaxial-adaxial clefts. Photo by Egger.



Figure 52. *Castilleja peruviana*, between Celendín and Río Marañón, Dept. Cajamarca, Perú, 12 April 2005. Photo by Egger.



Figure 53. *Castilleja peruviana*, E of Agallpampa on road to Quiruvilca, Dept. La Libertad, Perú, 16 Apr 2005.



Figure 54. *Castilleja peruviana*, dwarfed form at 4270 m elevation, ca. 1 km E of Abra Quiruvilca, Dept. La Libertad, Perú, 16 Apr 2005. Plants in habitat and single plant closeup. Photos by Egger.



Figure 55. Comparison of typical plants of *Castilleja alpicola* (top) from the type locality and the very rare, dwarfed, high elevation form of *C. peruviana*, known only from the vicinity of Abra Quiruvilca. Both photos from ca. 4200 m in Dept. La Libertad, Perú, April 2005. Note the differences in pubescence and in the lower lips of the corollas. Typical plants of the two species are easily separable by growth form and stature, as well as other traits. Photos by Egger.

7. **CASTILLEJA PROFUNDA** T.I. Chuang & Heckard, Syst. Bot. 17: 427. 1992. **TYPE: Perú. Dept. Arequipa.** Mollendo, sandy slope, desert hills, (after Oct. rains), 17 Nov 1923, A. S. Hitchcock 22404 (holotype: US). Figures 56–57.

Castilleja profunda is distinguished from related species by the combination of entirely eglandular pubescence, pink-purple bract tips, corollas with bright yellow lower lips and beaks with pink-purple pubescence and narrowed, distinctly decurved tips, and very deeply (“profoundly”) reticulate seed coats. The latter trait is that from which the specific name was derived (Chuang & Heckard 1992). Typical plants of this species are shown in Figures 58–60.

This species is apparently uncommon and is known from scattered localities from Dept. Ancash southward in Perú, mostly at middle elevations (870–3760 m) in the western ranges of the Andes Mountains, though the type specimen was collected in coastal lomas near sea level. It is apparently most common in Dept. Lima, though this may be an artifact of its vicinity to a major population center. Combining herbarium specimens cited by Chuang and Heckard (1992) with confirmed records on iNaturalist (Map 8) as of July 2026 and data from Heim and Pauca-Tanco (2026) for Dept. Arequipa, *Castilleja profunda* is known from the following departments and provinces in western Perú, to which it is mostly endemic: **Dept. Ancash.** Prov. Bolognesi. **Dept. Arequipa.** Prov. Caylloma, Prov. Condesuyos, Prov. Islay, Prov. La Unión. **Dept. Ayacucho.** Prov. Lucanas. **Dept. Huancavalica.** Prov. Castrovirreyna. **Dept. Lima.** Prov. Canta, Prov. Huarochirí, Prov. Lima. **Dept. Moquegua.** Prov. Mariscal Nieto.

Examination of a collection cited by Chuang and Heckard (1992) of *Castilleja profunda* from Dept. Cajamarca, Prov. Celendín (above Balsas on road to Celendín, Hutchison & Wright 5267, F, UC) shows it to be more likely *C. vadosa*. This conclusion is also supported by the location of this site far to the north and east of other reports of *C. profunda*, and there have been no subsequent collections or iNaturalist reports of the species from that region. In 2005 Egger and Tank searched for *C. profunda* in the vicinity of the Hutchison and Wright collection site and found only populations of *C. vadosa* and *C. peruviana*, with specimens of the former strongly resembling the cited collection (see Figure 64).

In addition to the reports cited above for Perú, a recent, well-documented study in Chile has revealed the not unexpected presence of several populations of *Castilleja profunda* in the near-coastal, far northwestern portion of that country, adjacent to Perú (Muñoz et al. 2026). The authors reported three recent collections of *C. profunda* from the foothills of Arica Province and an overlooked collection (Muñoz 2889, SGO) from coastal Antofagasta Province in 1941. These specimens confirm the presence of *C. profunda* in Chile suggested by a single iNaturalist post from the same part of Arica Province in 2023 (see Map 8). The occurrence of populations of *C. profunda* in coastal northwestern Chile in lomas and lomas-like habitats also gives more eco-geographical context to the otherwise somewhat anomalous location of the type gathering of the species near Mollendo, near sea level in adjacent far southwestern coastal Perú. This elevational disjunction between higher elevation Andean populations and low elevation, near-coastal populations, both within species and between closely related taxa, occurs in a variety of species groups, as documented in Ibáñez et al. (2022) and likely includes *C. profunda* (Muñoz et al. 2026). A similar explanation may account for the disjunct ranges of *C. laciniata* in Andean Perú and near-coastal central Chile noted under that species.

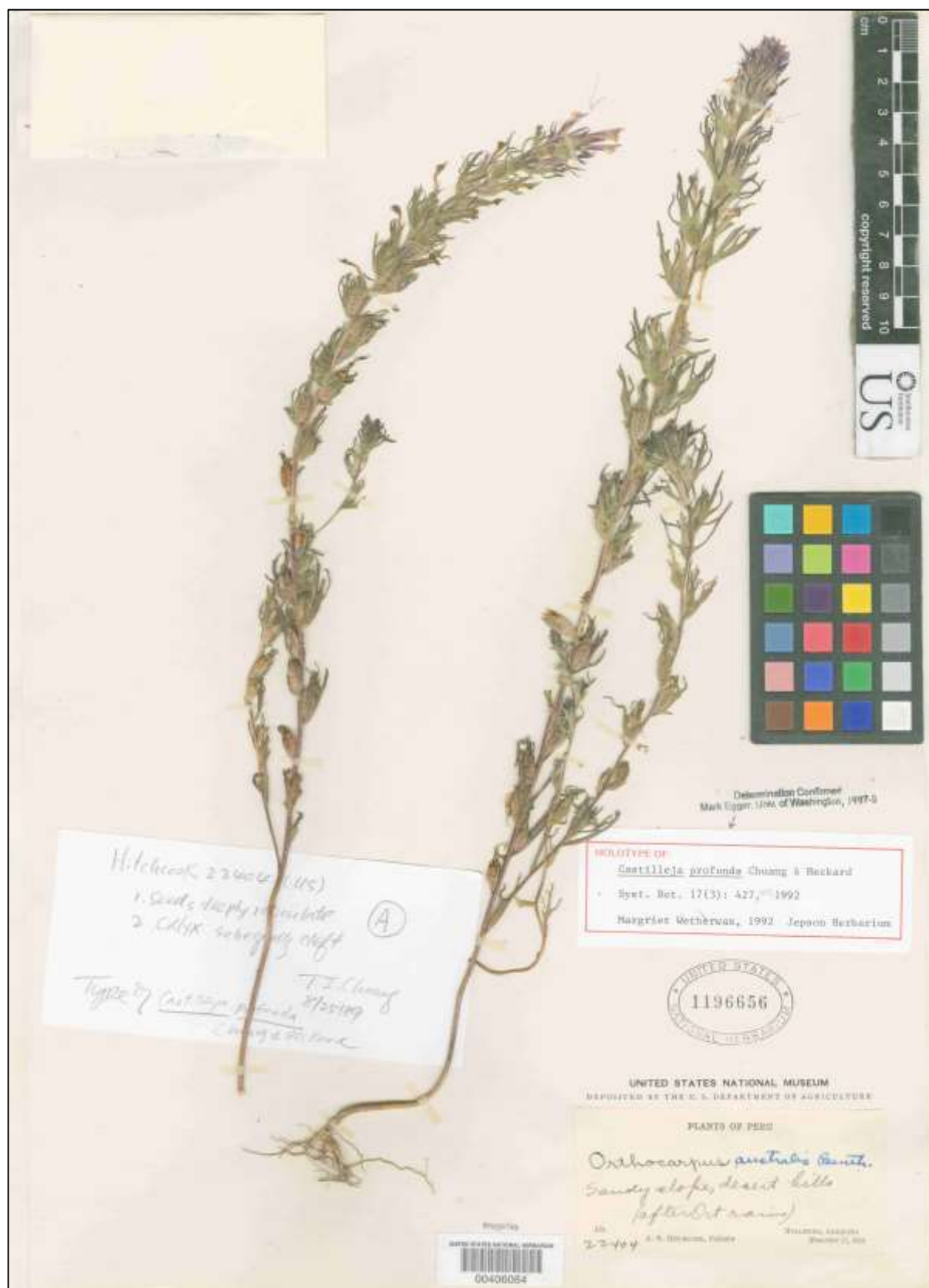
Figure 56. Holotype of *Castilleja profunda*, Hitchcock 22404 (US).



Figure 57. Holotype of *Castilleja profunda* Hitchcock 22404 (US), cropped to show details of the inflorescences.



Map 8. Verified iNaturalist posts of *Castilleja profunda* (red squares) in Perú and northern Chile as of July 2026. The red circle indicates the approximate position of several recent collections (all within a 10 km radius) of *C. profunda* from Arica Prov., Chile. The blue circle represents the location of the type collection of *C. profunda*. While Chuang and Heckard (1992) reported a collection from Dept. Cajamarca in northern Perú, we believe that collection is of *C. vadosa*, and we have seen no clear evidence of its presence north of southern Dept. Ancash, from which there are two specimens cited by Chuang and Heckard from Prov. Bolognesi.



Figure 58. *Castilleja profunda*, Hwy. 100 near Lolegon, Dept. Moquegua, Perú, 8 April 2019. Photo by Kent J. Chicalla-Rios.



Figure 59. *Castilleja profunda*, near Cabanaconde, Dept. Arequipa, Perú, 11 May 2024. Note the yellow lower corolla lip and eglandular pubescence. Photo by Jacek Pietruszewski.



Figure 60. *Castilleja profunda*, near Hwy. 119, Pachacamac District, Dept. Lima, Perú, 23 May 2009. Photo by Dan Lane.

8. **CASTILLEJA VADOSA** T.I. Chuang & Heckard, Syst. Bot. 17: 429. 1992. **TYPE: Perú. Dept. La Libertad.** Prov. Huamachuco, Río Marañón canyon, summit above Huamachuco, (limestone area), alt. 3970 m, 10 Aug 1964, P. C. Hutchison, J. K. Wright, & R. M. Straw 6266 (holotype: UC; isotypes: F, K, MO, NY, UC[2], US, USM). Figure 61.

Castilleja vadosa is one of the more widespread and common species of subg. *Colacus* in South America, at least in the northern half of Perú, the region in which it is endemic. Most records are from 2500–4100 m, though it may occur higher in a dwarfed form (see below and Figure 72). It is also among the most variable morphologically, with several slightly differing, population-level forms. A few of these are distinctive enough to warrant further studies in the field and at the genetic level to determine if they deserve nomenclatural recognition.

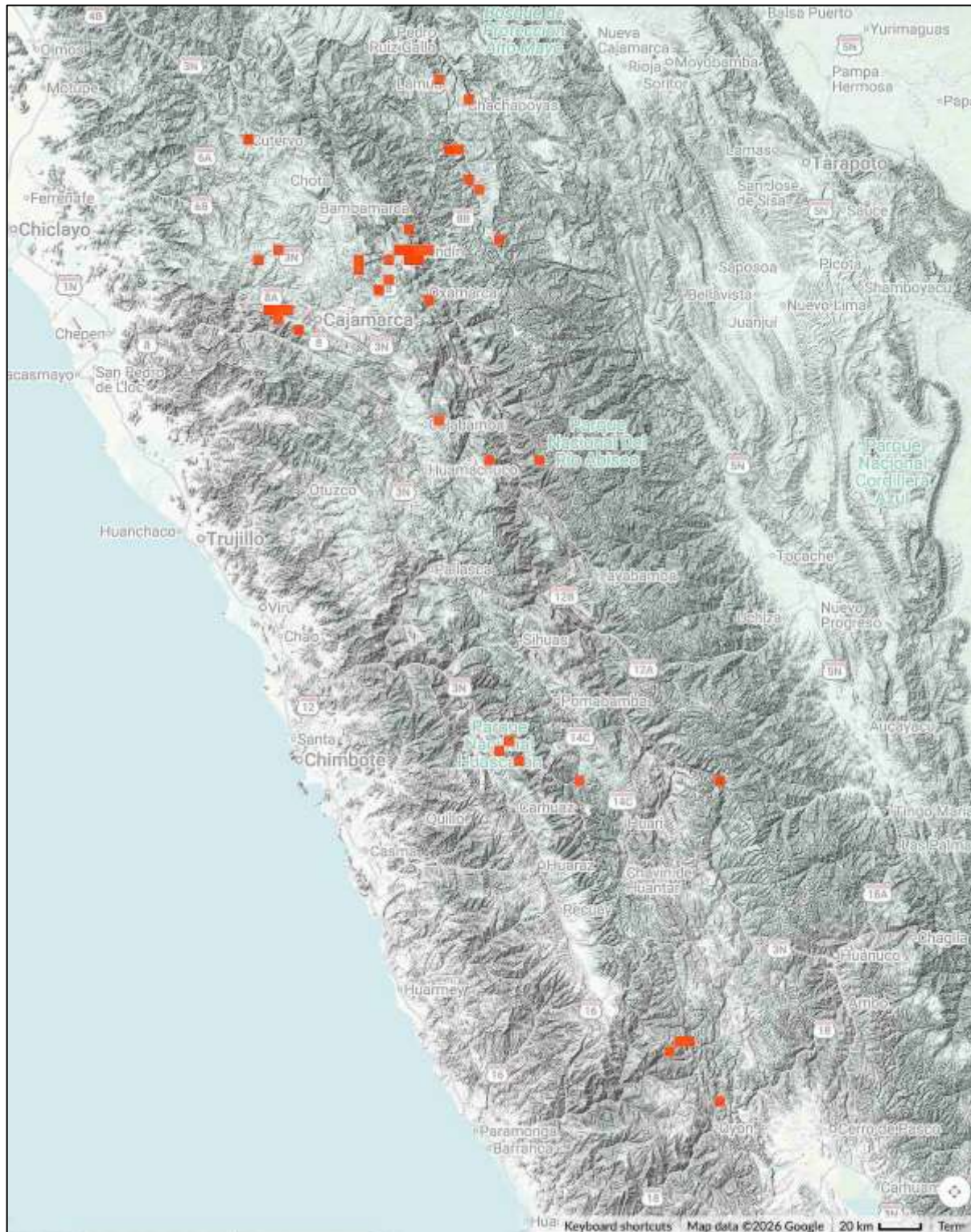
The images presented below in Figures 62–65 show minor variations between a few populations of what can be characterized as the typical form of *C. vadosa* from different parts of its range. These are followed by images of two of the more distinctive forms. The first of these is referred to as the “Cascabamba form” for the remote area in which it occurs east of Contumazá in the southern part of Dept. Cajamarca. As seen in Figures 66–68, this form is distinctive in the very intense pigmentation of the bracts, calyces, and all but the distal-most portion of the lower corolla lip, which is yellowish with white to pale pinkish teeth. A second distinctive form, pictured in Figures 69–70, is located northeast of the city of Cajamarca on the highway to Celendín, near the small community of Micuypampana and is referred to as the “Micuypampana form.” It is vegetatively typical of *C. vadosa*, but the corollas are differently colored and marked, reminiscent of the corollas of *C. peruviana*. It is possible that this form represents past introgression from that species or remnants of a common ancestry. While it is premature to do more than note these variants without additional studies and a more comprehensive understanding of variation within *C. vadosa*, we believe that such studies are justified. Like *C. peruviana*, *C. vadosa* also includes dwarfed growth forms that occur at high elevations (Figure 72).

Apart from *Castilleja attenuata*, *C. vadosa* is the one species among the Andean representatives of *Castilleja* subg. *Colacus* which bears a significant morphological resemblance to one of the North American species and suggests the ancestry of the two may be directly related. That species is *C. exserta* (A. Heller) T.I. Chuang & Heckard, a morphological complex species with three presently recognized varieties and several other distinctive, geographically limited forms currently under review by Egger. It occurs in a wide range of habitats at low to moderate elevations throughout much of California except the northern tier and ranges eastward in the Sonoran Desert into extreme eastern New Mexico and south into northern Baja California, and it often occurs in large, colorful displays in favorable years. *Castilleja exserta* and *C. vadosa* typically have similar inflorescence coloration, shaggy pubescence of the adaxial surface of the corolla beaks, beaks with hooked tips (though more so in *C. exserta*), with horizontally exserted stigmas, and deeply divided leaves and bracts, usually with many lobes. However, *C. exserta* differs from *C. vadosa* in having bract lobes that slightly widen distally, more deeply inflated lower corolla lips, more robustly and densely flowered inflorescences, and adaptation to lower elevation, temperate grasslands. Typical inflorescences of these two species can be compared in Figure 71.

Unlike the case of *Castilleja attenuata*, which is likely a recent addition to South America and has not diverged morphologically from its North American counterparts, *C. vadosa* has presumably had a much longer and likely more complicated history in South America and has evolved its own characteristic traits in isolation, while retaining some morphological traces of its North American ancestry. Hybridization and polyploidy may have played some role in the evolutionary history of *C. vadosa*, as the two chromosome counts provided by Chuang and Heckard (1992) for that species are of $n = 36$, while their earlier counts of *C. exserta* yielded only counts of $n = 12$ (Chuang and Heckard 1982).

[illegible]

Figure 61. Holotype of *Castilleja vadosa*, Hutchison et al. 6266 (UC).



Map 9. Verified iNaturalist posts of *Castilleja vadosa* (red squares) in Perú as of July 2026.



Figure 62. *Castilleja vadosa*, primitive road from Cascabamba to Pozo Kuan, above Contumazá, Dept. Cajamarca, Perú, 14 April 2005. Photo by Egger.



Figure 63. *Castilleja vadosa*, S of Contumazá on road to Cascas, ca. 5 km S of Contumaza, Dept. Cajamarca, Perú, 15 April 2005. Photo by Egger.



Figure 64. *Castilleja vadosa*, E of Celendín on road to Balsas, E of the pass and on the upper slopes of the canyon W of the Rio Marañón, Dept. Cajamarca, Perú, 12 April 2005. Note the mixed pubescence, including stipitate-glandular hairs. Photo by Egger.



Figure 65. *Castilleja vadosa*, road from Contumazá to Cascabamba, Dept. Cajamarca, Perú, 15 April 2005. Photo by Egger.



Figure 66. *Castilleja vadosa*, "Cascabamba form", narrow ridge along road from Contumazá to Cascabamba and Pozo Kuan, Dept. Cajamarca, Perú, 14 April 2005. Photo by Egger.



Figure 67. *Castilleja vadosa*, "Cascabamba form", narrow ridge along road from Contumazá to Cascabamba and Pozo Kuan, Dept. Cajamarca, Perú, 14 April 2005. Photo by Egger.



Figure 68. *Castilleja vadosa*, "Cascabamba form", narrow ridge along road from Contumazá to Cascabamba and Pozo Kuan, Dept. Cajamarca, Perú, 14 April 2005. Photo by Egger.



Figure 69. *Castilleja vadosa*, "Micuyampana form", vicinity of Micuypampa, along road from Cajamarca to Celendín, Dept. Cajamarca, Perú, 11 April 2005. This form may be of hybrid origin between *C. vadosa* and *C. peruviana*. Photo by Egger.



Figure 70. *Castilleja vadosa*, "Micuyampana form", vicinity of Micuypampa, along road from Cajamarca to Celendín, Dept. Cajamarca, Perú, 11 April 2005. This form may be of hybrid origin between *C. vadosa* and *C. peruviana*. Photo by Egger.



Figure 71. Comparison of the inflorescences of *Castilleja exserta* var. *exserta* (left), adjacent to California Hwy. 198 in vicinity of Priest Valley, Monterey County, California, USA, 17 April 2019, and *C. vadosa* (right), E of Celendín on road to Balsas, E of the pass and on the upper slopes of the canyon of the Rio Marañón, Cajamarca, Perú, 12 April 2005. Photos by Egger.



Figure 72. *Castilleja vadosa*, dwarfed high elevation form from the Cordillera Huayhuash in Prov. Cajatambo, Dept. Lima, Perú, 31 May 2025. Unfortunately, we could not verify the precise location of this observation nor the elevation, although it was found on a high mountain trek. Photo by Taylor Barron.

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