

**CASTILLEJA SALAISOLAVEAE (OROBANCHACEAE):
A REMARKABLE NEW SPECIES
AND A GUIDE TO THE CASTILLEJA SPECIES OF NUEVO LEÓN, MÉXICO**

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ABSTRACT

Castilleja salaisolaveae J.M. Egger, C.G. Velazco-Macías, & Huereca, **sp. nov.**, is described from limestone mountains in the Sierra Madre Oriental from the municipalities of Santa Catarina and Monterrey, Nuevo León, México. The new species is most similar morphologically to *Castilleja saltensis* Eastw. of western Durango but differs from that species in several characters. The new species is a rare and apparently highly range-limited endemic, and its conservation status deserves immediate attention. An annotated list and field images of the 13 *Castilleja* taxa of Nuevo León, as well as a key to their identification, are provided.

The iNaturalist and the integrated Naturalista websites provide a unique opportunity for biologists and naturalists to share observations and often learn substantially, as well as to establish new forms of long-distance collaboration (e.g., Egger & Sánchez-Velázquez 2018; Egger & Excoffier 2021). The discovery and description of a new and distinctive species of *Castilleja* from Nuevo León serves as an elegant example.

While conducting fieldwork for the project "Lichens and Associated Fungi of Northeastern México" in late February 2018, Alejandro Huereca-Delgado and associates visited the vicinity of "El Jonuco," a small community located in a canyon in the northern portion of the Gran Sierra Plegada, a physiographic subprovince of the Sierra Madre Oriental, west of the city of Monterrey, Nuevo León. This canyon is characterized by its rocky limestone substrate and vegetation, which transitions from piedmont-scrub to pine-oak forest. During this visit, the plants described here were first observed in the pine-oak forest zone by Daniela Salais-Olave, but no photographs or specimens were obtained at that time.

On 29 April 2019, Huereca, accompanied by Héctor Orozco-Montemayor and D. Alejandro Cuevas-Aguilar, visited El Jonuco again, during the City Nature Challenge 2019, and photographed the unknown *Castilleja* species without knowing how rare it was. Over the next days (30 April-4 May), Huereca posted sets of photographs of these plants on the Naturalista and associated iNaturalist

websites from three subpopulations, where they were observed by Egger, who recognized through his specialization on *Castilleja* that the plants in question likely represented an undescribed species. Voucher specimens were not collected, however, until two years later, when Huereca and Carlos Velazco-Macías visited the area on 17 April 2021 to secure specimens in flower and fruit for a type collection and to gather additional photographs and more complete information on the habitat and ecology of the new species. In addition, while curating *Castilleja* posts from Nuevo León on the Naturalista website, we discovered the existence of a second population of the new species, this one on Cerro de las Mitras, an isolated sky island situated in the metropolitan city of Monterrey. This population was documented by Oswaldo Zurita-Zaragoza with a series of excellent photos obtained in February 2021 and March 2022. (Figs. 15-17).

CASTILLEJA SALAISOLAVEAE J.M. Egger, C.G. Velazco-Macías, & Huereca, **sp. nov.** **Type:** **México. Nuevo León.** Mpio. Santa Catarina: El Jonuco, verada camino a La Calle, 25.640746, -100.634981, 2250 m, 17 Apr 2021, A. Huereca and C.G. Velazco-Macías s.n. (holotype: WTU; isotypes: MEXU, US). Figures 1-8.

Similar to *Castilleja saltensis* Eastw. in its divided leaves and bracts and the general structure of the corollas and calyces but differing from that species in its strongly rhizomatous-stoloniferous habit, lack of a persistent basal rosette of leaves, longer and differently colored calyces, often twice pinnately divided leaves and bracts, strongly decurved distal portion of the style, and habitat on rocky, calcareous, forested slopes.

Plants herbaceous perennials from a slender woody caudex, with a slender, sometimes branching taproot. **Stems** 1-several, unbranched, upright-ascending or proximally prostrate and white-rhizomatous to sometimes stoloniferous, becoming distally ascending-erect, the above ground portion 5–30 cm tall, dull greenish brown to deep reddish purple, densely short-pilose with a mix of fine, silky, non-glandular hairs and an understory of shorter, stipitate-glandular hairs; rhizomes puberulent and bearing scattered vestigial, scale-like leaves 1-2 mm in length. **Leaves** 1.5–4 cm, sometimes as wide as long, with (1-)3-7 primary, pinnate lobes, these often again pinnate, often irregularly so; blades and lobes mostly linear, lobes 0.5–20 mm long, distal lobes ascending, medial and proximal lobes divaricate-spreading, apices acute to more often obtuse to rounded; pubescent as in stems but often less densely so; entirely green or the distal-most entirely to partially deep purplish red. **Inflorescences** spicate, 3–10 cm long, with few to many, sessile to pedicellate flowers, pedicels 0-7 mm. **Bracts** gradually differentiated from leaves, (3-)5-7 lobed, the lobes ascending to spreading and often bearing short secondary lobes, apices often slightly widened, acute to obtuse or rounded, pubescent as in stems though less densely on the adaxial surfaces, the margins stipitate-glandular; proximal-most bracts entirely greenish, entirely deep reddish purple, or greenish to deep reddish purple proximally, becoming red to red-orange distally; medial and distal bracts dull greenish proximally, becoming red-orange to orange distally or red-orange to orange throughout. **Calyces** 20–30 mm long, elongating to 38-40 mm in fruit, abaxial and adaxial clefts subequal and 30-40% of the calyx length, lateral clefts emarginate to shallow, 0.5-3(-5) mm deep, lobes rounded to short-apiculate; pale greenish to cream-colored near the base, becoming pale, dull purplish red to dull salmon medially, and gradually becoming pale orange to reddish orange distally; pilose, especially along veins, with a mix of glandular and non-glandular hairs, becoming sparsely puberulent distally and between the veins. **Corollas** 30-37 mm long, with the beak, lower lip and stigma exerted from the calyces at full anthesis; beak 8-12 mm, greenish to greenish yellow on the adaxial surface and whitish to pale orange or reddish orange on the moderately wide margins, densely puberulent on the adaxial surface with a mix of stipitate-glandular and eglandular hairs of equal length; lower lip dark green to greenish-yellow, ca. 2 mm, reduced and thickened, divided into 3 subequal, strongly incurved lobes,



Figure 1. Holotype of *Castilleja salaisolaveae*, Huereca and Velazco s.n., WTU.

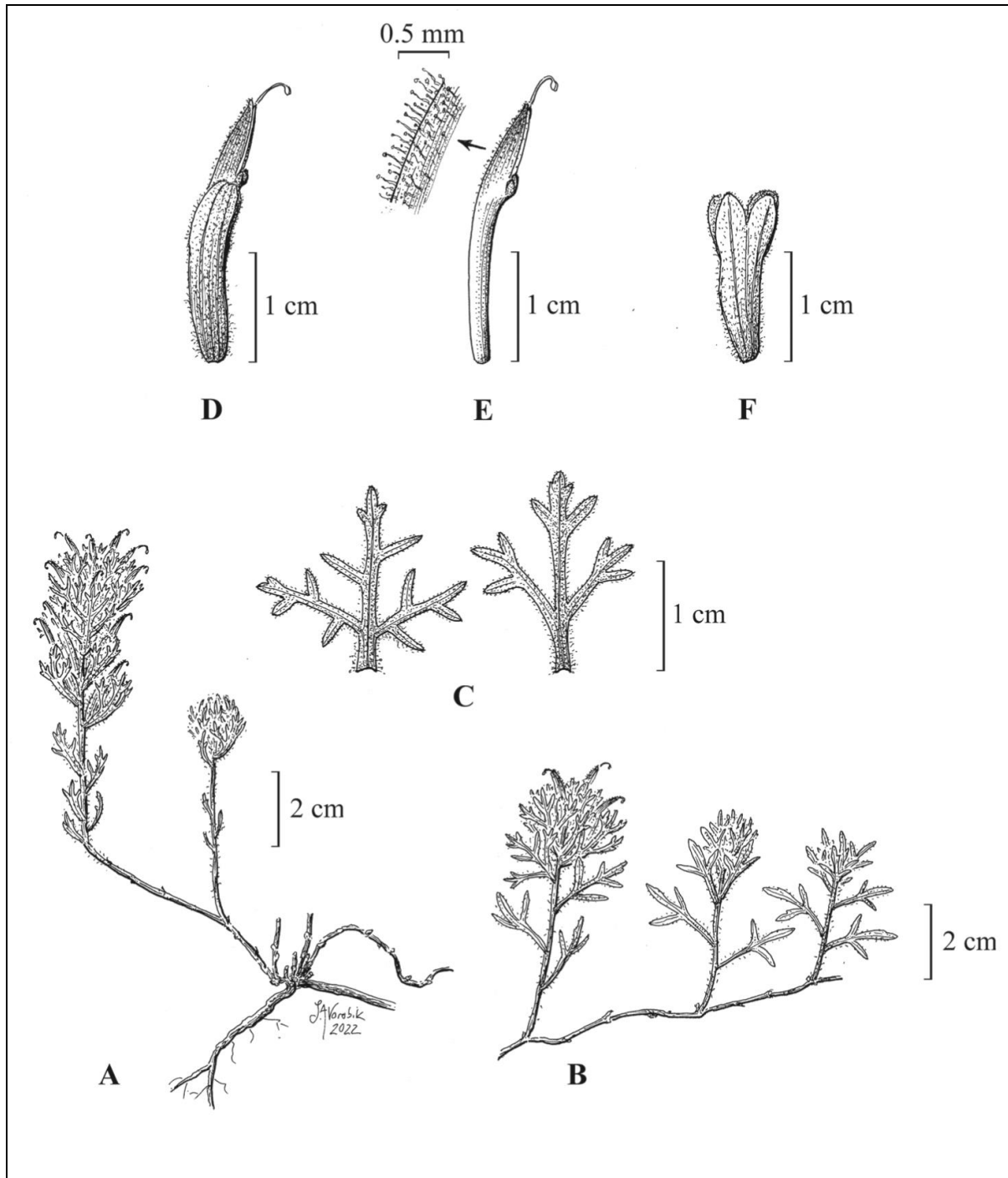


Figure 2. Illustration of *Castilleja salaisolaveae*, based on the type gathering, *Huereca and Velazco s.n.*, 17 April 2021. Illustration by Linda Ann Vorobik, October 2022. A, B. Habit and rhizomatous growth form. C. Floral bracts, abaxial view. D. Flower, showing typical calyx morphology with greatly reduced lateral cleft. E. Corolla with closeup of vestiture on beak. F. Calyx variant with slightly deeper lateral cleft.

with the teeth of each reduced to a short, acute, greenish apiculation; distal portion of style exerted and decurved, often strongly so, stigma entire, slightly expanded to capitate; filaments ca. 20 mm long, anthers included, narrowly elongate, ca. 3 mm x 0.5 mm, sometimes apparently fused at anthesis. **Capsules** 10-12 mm x 4-5 mm, oblong with acuminate apices; seeds numerous, ca. 70-100 per capsule, seeds wedge-shaped, 1.5-2.0 mm x 0.5-0.75 mm, pale brownish; seed coats tight-fitting, shallowly reticulate, cells narrowly rectangular to oblong, radial walls shallow and smooth to obscurely horizontally striate, inner tangential walls smooth and unruptured at maturity. Chromosome number unknown.

Additional images examined. While herbarium specimens of *Castilleja salaisolaveae* are presently limited to the type gathering, additional photos from both known localities are presented on the Naturalista and iNaturalist websites. **Nuevo León. Mpio. Santa Catarina:** 25.643518, -100.639243, 29 Apr 2019, D.A. Cuevas-Aguilar, (<https://www.naturalista.mx/observations/24541204>); ahuerca, (= Huereca) 25.643518, -100.639243, (<https://www.naturalista.mx/observations/24260271>); ahuerca, 25.643518, -100.639243, (<https://www.naturalista.mx/observations/24299848>). **Mpio. Monterrey:** Cerro de Las Mitras, 28 Feb 2021, cucuchuchu (= Oswaldo Zurita-Zaragoza), 25.712247, -100.420074, (<https://www.naturalista.mx/observations/70347821>).

Etymology. The new species is named in honor of Daniela Salais-Olave, who first spotted this unique species while assisting with one of many lichenological surveys in northeastern México.

Recommended common names. We suggest the English common name "Daniela's Paintbrush" for the new species, as well as the Spanish common name, "Pincel de Daniela," in accordance with nomenclatural usage in northern México.

Phenology, ecology, and associated species. *Castilleja salaisolaveae* is known to flower from February through at least early May. It is likely that the typical flowering season for this species occurs over longer periods of time, depending on rainfall, perhaps by several months, and the phenology of this species is not yet fully documented. The type population is restricted to north facing mountain slopes, and the plants are found adjacent to trails under the forest canopy in shaded and humid locations (Figs. 9-13). In this area, plants are dispersed in two small subpopulations within two kilometers of each other. No particularly close associations with other plant species were noted as potential hosts for the presumably hemiparasitic *Castilleja salaisolaveae*. The soil-covering moss species *Pleurochaete luteola* (Besch.) Ther. (Pottiaceae) is common at the collection site, often covering large patches of the ground. The underlying soil is rocky and calcareous-derived and is rich in decaying organic matter, Phaeozem type (IUSS, 2015).

The vegetation around the type locality is mixed temperate forest with *Pinus greggii*, *Arbutus xalapensis*, *Pseudotsuga menziesii* var. *glauca*, *Purshia plicata*, *Juniperus flaccida*, *Rhus virens*, *R. muelleri* and *Quercus* sp. Other herbaceous plants in the area include: *Chrysactinia mexicana*, *Salvia greggii*, *Bouvardia ternifolia*, *Packera montereyana*, *Ipomopsis aggregata*, *Castilleja tenuiflora* var. *xylorrhiza*, and *Castilleja lanata*.

The population found on Cerro de las Mitras was at first known only from images of a single plant photographed by Oswaldo Zurita-Zaragoza on 28 February 2021, (Figs. 15-16). This mature plant in full flower was observed growing in a rock crevice, in soil stabilized by mosses and other plants, on a steep calcareous slope at 1800 m elevation. It was growing alongside *Pinguicula gracilis* Zamudio, another regionally endemic species of similar microhabitats (Zamudio 1988). Zurita revisited the plant's location on 6 March 2022, and it was still extant, though not in flower. On the latter date, new growth was visible from the plant documented the previous year, and one or possibly two apparent seedlings were observed near the older plant, indicating at least some recruitment (Fig. 17). The Cerro de las Mitras population, though also on a north-facing exposure and at similar

elevation to the type locality, is different in its more exposed, less shaded placement in a crevice in a rock wall. In addition to *Pinguicula gracilis*, other closely associated species include *Dasyllirion berlandieri*, *Selaginella novoleonensis*, *S. pilifera*, *Myriopteris alabamensis*, and moss species. Species of the adjacent open, mixed oak forest association include *Agave bracteosa*, *Quercus canbyi*, *Q. laceyi*, *Q. polymorpha*, *Decatropis bicolor*, *Cercocarpus* sp., *Arracacia atropurpurea*, *Chaptalia texana*, *Valeriana scandens*, *Phanerophlebia umbonata*, and *Llavea cordifolia*.

While the regional climate type is mid-latitude steppe and desert climate (BSH), the micro-climate of the habitat in which the species occurs seems to best fit a semi-cold, semi-humid type with a longer and more humid summer (Cwb) (Peel et al. 2007).

The photographs by Huereca from 2019 (Fig. 14) show all plants infested with a species of white flies (Homoptera: Aleyrodidae). These sucking insects may be attempting to extract nutrients from the *Castilleja* plants, but at least some of the insects appear to have become ensnared in the partially stipitate-glandular pubescence, perhaps limiting the deleterious effects of their predation. The photos by Velazco and Huereca in 2021 show no evidence of similar infestation of plants near the type locality and within 12 days of the same date from 2019. No additional signs of herbivory or other plant-animal interactions involving *C. salaisolaveae* were observed during visits to the two known populations. No potential pollinators were observed, though red to orange *Castilleja* species are frequently pollinated by both hummingbirds and bees (Egger et al. 2019).

Distribution and range. *Castilleja salaisolaveae* is currently known for two populations, one near El Jonuco, in Mpio. Santa Catarina, and the other on the upper north slope of Pico Perico, a high point along the summit ridge of Cerro de las Mitras, Mpio. Monterrey, Nuevo León. These two sites are separated by a straight-line distance of about 23 kilometers. The species is restricted to limestone-derived mountain slopes at the northern portion of the Gran Sierra Plegada, a physiographic subprovince of the Sierra Madre Oriental in central-eastern Nuevo León, within an elevational range of 1750–2250 m. Near the type locality, plants were observed sporadically within a distance of less than two kilometers. The Cerro de las Mitras population is known only from a single rock crevice.

Despite its limited distribution and restricted ecology, *Castilleja salaisolaveae* should be searched for in other locations in the adjacent mountains of Nuevo León and Coahuila, since similar habitats and limestone substrates, supporting similar plant communities, are not uncommon in the region. Attention should be given to the nearby Cerro de Chipinque, a private nature reserve.

Conservation status. Since *Castilleja salaisolaveae* is a narrow endemic presently known from only two numerically and spatially small populations and a restricted elevational range, we recommend that it be treated as globally and regionally endangered, at least until nearby areas of similar habitat can be thoroughly surveyed and protected. Under IUCN (2022) Red List criteria, *C. salaisolaveae* presently qualifies as Endangered (EN) or possibly Critically Endangered (CR), based on extent of occurrence and area of occupancy, both estimated to be less than 2 km², as well as on the number of populations (two) and very small and restricted numbers of individual plants (<25 individuals). The Cerro de las Mitras population consists of only a single, multi-stemmed, rhizomatous individual and one or two apparent seedlings immediately adjacent. However, similar habitat on steep slopes and nearly vertical rock crevices with a calcareous substrate in temperate mixed forest exists in this region, and the new species may prove to be more common than is known at present.

Climate change related to global warming may be a significant threat to this species of rhizomatous growth form, dependent on the leaf litter and the moss mats through which the rhizomes penetrate, from the drying effects of increasingly severe periods of drought and higher temperatures.

Recurrent and recently intensifying regional drought and associated wildfires (Yocom et al. 2010, Zúñiga-Vásquez et al. 2019) represent the most immediate threat to *Castilleja salaisolaveae*, especially to the El Jonuco population.

While both populations are located within or near the Monterrey metropolitan area, the new species does have some protection, since its known range is within the boundaries of the Parque Nacional Cumbres de Monterrey, in the case of the El Jonuco population, while the second population is on steep slopes within the Reserva Natural Estatal Sierra Las Mitras. While the former location is in an area of limited development, the latter is within a popular area for hiking and rock climbing directly adjacent to the city center of Monterrey, and recreational and related activities may lead to localized habitat degradation. The single occurrence in that area is immediately adjacent to a popular recreational trail.

The Sierra Madre Oriental is known for its high rates of endemism and species diversity, harboring around 13% of endemic plant species of México (Salinas-Rodríguez et al. 2017, 2018), and the new species adds a highly distinctive element to this diversity of endemic forms.

Taxonomic relationships and identification. Due to the structure of the long calyces, with subequal abaxial and adaxial clefts and shallow to emarginate lateral clefts, and the corollas, with long tubes to match the calyces, and comparatively much shorter beaks and lower lips, *Castilleja salaisolaveae* is easily assigned to sect. *Euchroma* (Nutt.) Benth. (sensu Eastwood 1909), an assemblage reaching its greatest species diversity in México. In the last three decades, many new species have been described from this group, including several uncommon to rare and range-restricted forms (Nesom 1992b, 1992c, 1992d, 1995; Egger 2002; Medina & Carranza 2017). The rhizomatous growth form of *C. salaisolaveae* is uncommon in the genus but is like that of *Castilleja rhizomata* N.H. Holmgren and *Castilleja linifolia* N.H. Holmgren, both endemics of the Sierra Madre Occidental, as well as *Castilleja filiflora* Nesom, a rare endemic of eastern Chiapas (Nesom 1992e), and *Castilleja exigua* Egger a similarly rare endemic of moist paramo in the Andes Mountains of Venezuela (Egger 2009), but that group of species is otherwise very different from *C. salaisolaveae* and belongs to sect. *Castilleja*, characterized by strongly irregular primary calyx clefts, with the longer-beaked corollas often pendently exerted. This convergence in rhizomatous growth form in *C. salaisolaveae* is possibly related to its occurrence in forested understories with substantial accumulations of leaf litter and mosses, as with both *C. linifolia* and *C. rhizomata*. The vast majority of *Castilleja* species occur in more open, less forested habitats, and the few other rhizomatous species, such as *C. gracillima* Rydb., are usually limited to very moist substrates.

While twice-pinnate bracts and leaves are occasionally observed in other *Castilleja* species, such as *C. rupicola* Piper, *C. chambersii* Egger & Meinke, and some of the still incompletely known entities surrounding *C. fissifolia* L.f. in northern South America, this trait is common in *C. salaisolaveae*, much more so than in any other species in the genus. This trait, combined with the similarly uncommon rhizomatous habit, make the new species one of the more unique and distinctive in *Castilleja*.

Castilleja salaisolaveae is most closely similar morphologically to *Castilleja saltensis* Eastw. (Fig. 18), an endemic of the central Sierra Madre Occidental in western Durango. In addition to their widely disjunct distributions, the two are easily distinguished by the following couplet.

1. Plants compact, with a persistent basal rosette of leaves, and not at all rhizomatous; bracts sparsely pubescent, mainly along the veins, +/- palmately to pinnately 3-5 lobed, secondary lobes absent, lobes ascending-erect to spreading-ascending; calyces 18-22 mm, usually greenish proximally and abruptly becoming red to reddish orange only on the apices; distal portion of the style not decurved;

plants flowering late June through September (early November) in wet meadows and flats, often while partially submerged ***Castilleja saltensis***

1. Plants creeping and strongly rhizomatous-stoloniferous, without a persistent basal rosette of leaves; bracts more densely and uniformly pubescent, pinnately (3-)5-7 lobed and these often with regular to irregular secondary lobes, lobes divaricate-spreading to ascending; calyces 20-30(-40) mm, pale greenish to cream-colored near the base, becoming pale, dull purplish-red to dull salmon medially, and gradually becoming pale orange to reddish-orange distally; distal portion of the styles slightly to more often strongly decurved; plants flowering at least late February through early May on rocky, calcareous, forested slopes ***Castilleja salaisolaveae***

Annotated List of the *Castilleja* species of Nuevo León, México

The genus *Castilleja* consists of about 200 species of the western hemisphere and arctic-boreal Asia (Egger et. al. 2019), over 80 of which occur in México (Villaseñor 2016; Egger, unpublished data). The only comprehensive treatment of the Mexican species remains that of Eastwood (1909), though Nesom (1992e) provided a taxonomic overview of the Mexican and Guatemalan species of sect. *Castilleja*. Various floristic lists enumerate the *Castilleja* species of México (e.g., Méndez-Larios & Villaseñor 2001; Villaseñor 2016), while others include lists specific to the flora of Nuevo León or the Sierra Madre Oriental (e.g.: Hinton & Hinton 1995; Villarreal & Estrada 2008; Velazco 2009; Alanís-Flores et al. 2011; Salinas-Rodríguez et al. 2017, 2018, 2021). In addition, a recent account of the flora of the Parque Nacional Cumbres de Monterrey (Estrada et al. 2013) listed only four species of *Castilleja*, though that study only covered the region of the park in seven municipalities, mostly in the northern and central portions of the Sierra Madre Oriental of Nuevo León.

Our survey of herbarium records, field work, and recently published taxonomic evaluations cited elsewhere in this paper reveal the presence of 12 accepted *Castilleja* species in the state, though some are uncommon to rare and/or of limited distribution. Almost all records of the genus in Nuevo León are limited the southern and western half of the state, although some areas remain sparsely sampled. To promote awareness and conservation, we present a key to the *Castilleja* species of the state, as well as field photos and brief commentaries concerning the status, ecology, and distribution of each species in the form of an annotated list.

1. *CASTILLEJA ARVENSIS* Schltdl. & Cham. var. *ARVENSIS* (Fig. 19)

While common in much of southern and central México, often in ruderal habitats, this species is absent from most of the northern tier states. It is apparently uncommon and peripheral in Nuevo León, reaching its northeastern limit just north of Monterrey. In this state it has been recorded at moderate elevations, between 560-1800 m. It occurs in a wide range of habitats but almost always in disturbed areas such as pastures, agricultural fields, roadsides, and rural towns. Verified from the municipalities of Aramberri, General Escabedo, Monterrey, and Santiago.

2. *CASTILLEJA BELLA* Standl. (Fig. 20)

This regional endemic is limited to a few stony alpine summits and subalpine meadows in the high mountains of the Gran Sierra Plegada in extreme eastern Coahuila, Nuevo León, and closely adjacent Tamaulipas (MacDonald 1990; Nesom 1992b). In Nuevo León, *C. bella* occurs only near and above timberline on Cerro El Potosí and on Picacho de San Onofre and the adjacent Cerro de Peña Nevada, at 3000-3700 m, mostly above 3300 m. While highly restricted in habitat and range, it can be locally abundant. This species occasionally intergrades with *C. scorzonrifolia* around timberline (Nesom 1992b; Egger, pers. obs. 1999). Verified from the municipalities of Galeana and General Zaragoza.

3. CASTILLEJA GALEHINTONIAE G.L. Nesom (Figs. 21-22)

This recently described species is found in open, mid-elevation sites with a gypsum substrate in matorral, grasslands, cedar savannas, and open pine woods at moderate elevations (1300-2480 m) in central-western Nuevo León (Nesom 1992b). Originally thought to be endemic to the state, this uncommon but distinctive species was recently documented in adjacent parts of Coahuila and San Luis Potosí, as well as in an apparently disjunct record from Guanajuato (Egger, unpublished data). Verified from the municipalities of Aramberri and Galeana.

4. CASTILLEJA INTEGR A. Gray (Fig. 23)

This species is a frequent element of the arid hills and lower mountains of northwestern México, in northeastern Sonora and northern Chihuahua and Coahuila, but it is apparently rare and peripheral in Nuevo León, known only from a small number of collections from open pine woodlands with an understory of *Juniperus* and *Yucca* species between 2050-2430 m elevation in Mpio. Galeana, between San Marcos and Entronque San Roberto.

5. CASTILLEJA INTEGRIFOLIA L.f. (Figs. 24-25)

The distribution of this species in the Sierra Madre Oriental is still incompletely known, but in Nuevo León it is apparently limited to forest openings and rocky slopes in the middle and upper elevations of the western portion of the range, between 2150-3400 m. In this area, where the species reaches its northern limit, most plants have a striking and distinctive pattern of coloration, with the orange to yellow or greenish calyces contrasting with the prominent reddish apical tuft of sterile bracts. This species ranges from the northern Andes Cordillera of South America in Colombia and Venezuela northward through the mountainous regions of Central America and southern and eastern México. There are many regional variations throughout the range, and the entire complex needs study and a comprehensive revision (Egger, in preparation). Verified from the municipalities of Aramberri, Galeana, General Zaragoza, Mier y Noriega, Montemorelos, Reyones, and Santiago. The images presented below represent two forms of *C. integrifolia* that occur in Nuevo León.

6. CASTILLEJA LANATA A. Gray (Fig. 26)

A relatively common species of calcareous hillsides and flats between 700-2200 m elevation in the Sierra Madre Oriental and adjacent arid lands to the west and north, often in piedmont scrub and other chaparral-like vegetation in open cedar and pine-oak woods. Verified from the municipalities of Aramberri, Bustamante, Doctor Arroyo, Galeana, Lampazos, Mina, Monterrey, Nuevo León, Parás, Reyones, Sabinas Hidalgo, Santa Catarina, Santiago, and Villadama.

7. CASTILLEJA MEXICANA (Hemsl.) A. Gray (Figs. 27-28)

This distinctive species consists of two regional forms that somewhat overlap in range and sometimes intergrade, with distinctly white corollas being common in the eastern portion of its range, in northeastern México, while in the northwestern portion of interior northern México, as well as in southwestern Texas, the yellow-flowered form predominates. Intermediates have also been observed in some locations, though they are few in both number and location. The yellow-flowered form has been described as *Castilleja tortifolia* Pennell, though Nesom (1992a) reduced it to synonymy under *C. mexicana*, and this treatment was tentatively followed by Egger et al. (2019). Given the apparent separation of the ranges of the two forms, it may be appropriate to resurrect *C. tortifolia* at some level, though this is complicated by the ambiguity of assigning the lectotype of *C. mexicana* (Coulter 1355, K-HOOK) to one of the forms, due to its collection locality in Zacatecas, a state in which both forms are known to occur, while the corolla coloration of the type material has faded and is uncertain. In Nuevo León, where the species is limited to the western half of the state, it occurs between 1150-2200 m elevation on slopes and flats on limestone and gypsum substrates in open pine and scrub habitats. While the white-flowered form is far more commonly encountered than the yellow-flowered form in the state, a few herbarium records of the latter exist as well, based on the label descriptions.

Verified from the municipalities of Doctor Arroyo, Galeana, García, General Zaragoza, Monterrey, and Santa Catarina.

8. *CASTILLEJA RIGIDA* Eastw. (Fig. 29)

In Nuevo León, this species is relatively common in the arid regions of the western tier, mostly west and north of the Sierra Madre Oriental, between 1650-2100 m elevation. It is almost always found in close association with and likely parasitic on *Agave* species, especially *A. lecheguilla* Torr. but also *A. bracteosa* S. Wats. ex Engelm. Verified from the municipalities of Doctor Arroyo, Galeana, García, Hidalgo, Mina, Monterrey, Santa Catarina, and Santiago.

9. *CASTILLEJA SALAISOLAVEAE* Egger, Velazco-Macias, & Huereca (Figs. 1-17)

See pages 1-7 of this paper. Verified from the municipalities of Monterrey and Santa Catarina.

10. *CASTILLEJA SCORZONERIFOLIA* Kunth (Figs. 30-31)

This is a common to uncommon species throughout much of eastern and central México south to Oaxaca, and it is endemic to the country. It is a relatively common species of middle to upper elevations (1140-3360 m) throughout the Sierra Madre Oriental, to which it is apparently limited in the state. Within these mountains, it occurs in a wide range of habitats and vegetation types, though most commonly in open forests and meadowy forest edges. Nuevo León is also the northern terminus of the main range of this species, though a disjunct population was found recently to the northwest, near Monclova, Coahuila. Verified from the municipalities of Aramberri, Bustamante, Doctor Arroyo, Galeana, General Zaragoza, Monterrey, Reyes, and Santiago.

11. *CASTILLEJA SESSILIFLORA* Pursh (Fig. 32)

Apparently rare and peripheral in the state and known only from a few scattered sites west or north of the Sierra Madre Oriental. All records from the state are of the form with pink to purplish or dull reddish bracts and calyx lobes, described as f. *purpurina* Pennell (Pennell 1935, p. 525), which extends eastward and northward into Coahuila and southwest Texas. It is found in dry limestone scrublands from 1600-2120 m elevation. Verified from the municipalities of Doctor Arroyo, Galeana, Mina, and Monterrey.

12. *CASTILLEJA TENUIFLORA* Benth. var. *TENUIFLORA* (Fig. 33)

In his review of the ranges of the varieties of the widespread *Castilleja tenuiflora*, Nesom (1992e) did not include Nuevo León in the range of var. *tenuiflora*, with all mapped occurrences in the state assigned to var. *xylorrhiza*. However, Hinton & Hinton (1995), Villareal & Estrada (2008), and Salinas-Rodríguez et al. (2021) have included both varieties as part of the flora of the state. In their floristic lists, the latter authors likely followed the Hinton's documentation of their own collections in the state. We have verified three collections of var. *tenuiflora* in Nuevo León, including the two cited by the Hinton's, one each from the municipalities of Galeana, Aramberri, and General Zaragoza. However, the vast majority of herbarium and field records from Nuevo León examined for this study are of var. *xylorrhiza*. The two varieties are very similar morphologically, but the typical form is distinguished by its red to orange-red inflorescences (on bracts and calyces). Both varieties occur in similar habitats (see below), with the known populations of var. *tenuiflora* occurring between 1750-3300 m elevation.

13. *CASTILLEJA TENUIFLORA* Benth. var. *XYLORRHIZA* (Eastw.) G.L. Nesom (Figs. 34-36)

A relatively widely distributed and locally common form of open, rocky habitats and open forests, most commonly in piedmont scrub and pine-oak forests at lower to moderately high elevations (800-3300 m) in the Sierra Madre Oriental. Inflorescences of var. *xylorrhiza* are yellow to yellow-orange on bracts and calyces, and the plants often become subshrubs on favorable sites. Intermediate morphs are occasionally observed between this and the typical variety (Fig. 37).

Verified from the municipalities of Galeana, García, Guadalupe, Iturbide, Mier y Noriega, Montemorelos, Monterrey, Nuevo León, San Pedro Garza García, and Santiago.

Excluded names. Villaseñor (2016) listed *Castilleja nervata* Eastw. and *C. lithospermoides* Kunth as species occurring in Nuevo León. While *C. nervata* is a currently accepted species, it does not occur in the Sierra Madre Oriental or anywhere in northeastern México. Reports from Nuevo León are likely referable to the morphologically similar *C. rigida* and/or *C. arvensis*. *Castilleja lithospermoides* is now known to be synonymous with *C. scorzonrifolia* (Nesom 1992b; Egger 2017). It has also been confused with *C. arvensis*, and reports of *C. lithospermoides* in the state are referable to one or the other of these two species. A more thorough discussion of these entities is provided by Egger (2017).

A key to the *Castilleja* species of Nuevo León

1. Abaxial calyx clefts at least twice as deep as adaxials.
 2. Inflorescences with a prominent apical tuft of apparently sterile, non-floriferous, +/- spatulate bracts; floral pedicels 10-20 mm at anthesis; corolla beaks conspicuously pilose-bearded; leaf bases attenuate and not at all clasping ***Castilleja integrifolia***
 2. Inflorescences floriferous throughout, mostly lacking an apical tuft of sterile bracts; floral pedicels 0-6 mm at anthesis; corolla beaks puberulent; leaf bases ampliate and sub-clasping.
 3. Calyces and distal bracts red to orange-red, at least on the distal portions ***Castilleja tenuiflora* var. *tenuiflora***
 3. Calyces and distal bracts yellow to pale yellow-orange), at least on the distal portions ***Castilleja tenuiflora* var. *xylorrhiza***
1. Abaxial and adaxial calyx clefts subequal to much less than twice as deeply cut in either direction.
 4. Corollas distally falcate, with the beak, lower lip, and distal portion of the tube well exerted from the calyces and the lower lip teeth petaloid and divaricately spreading from the tube.
 5. Lateral calyx clefts 1.5-6 mm; stem pubescence hispid, mixed with shorter, stipitate-glandular hairs; bracts greenish throughout; plants annuals or short-lived perennials; leaf margins often crisped ***Castilleja mexicana***
 5. Lateral calyx clefts 5-15 mm; stem pubescence lanulose, non-glandular; bracts green to purplish throughout, sometimes reddish brown, or pinkish throughout, or distally white or pale yellow, sometimes distally dull pink, salmon, orangish, buff, or cream; perennials; leaf margins not crisped ***Castilleja sessiliflora***
 4. Corolla tubes straight to somewhat declined but not falcate.
 6. Plants annual; corollas included in the calyces; calyces green with a distal band of dark green ***Castilleja arvensis* var. *arvensis***
 6. Plants perennial; at least the distal portion of the corolla exerted from the calyces; calyces uniformly greenish to more often greenish with the distal portion contrastingly colored with shades of red, orange or yellow.
 7. Stem pubescence lanate to lanulose-tomentose.
 8. Bracts usually entire to less often with one pair of short, lanceolate lateral lobes, these almost always originating from the middle of the blade or above; secondary calyx clefts 4-14 (-16) mm; stem pubescence tomentose ***Castilleja integra***

8. Bracts usually deeply divided with one pair of much longer, narrowly oblanceolate to less often lanceolate to linear-lanceolate lobes, usually originating from well below the middle of the blade; secondary calyx clefts 0-5 mm; stem pubescence lanate.
9. Stems 20-100 cm tall; bracts and calyces distally bright red to red-orange; lanate pubescence of the bracts proximal, usually not extending to the bract tips; corollas 22-37 mm **Castilleja lanata**
9. Stems 5-25 cm tall; bracts and calyces distally pale yellow to less commonly pale orange or pale reddish on the bract apices; pubescence of the bracts entirely covering them and extending to the tips; corollas 15-20 mm **Castilleja galehintoniae**
7. Stem pubescence various but not lanate to lanulose-tomentose.
10. Upper leaves and bracts deeply divided; low growing, caespitous plants of the alpine and subalpine, or rhizomatous plants of mixed forest understories.
11. Plants low growing, caespitous, and entirely limited to the rocky alpine to subalpine zone; bracts 3-5-lobed, the lateral lobes ascending and narrower than the central lobe; pubescence of stems and leaves sparsely pilose and eglandular **Castilleja bella**
11. Plants rhizomatous, with proximally prostrate stems becoming ascending distally, and occurring in the understory of mixed forests at moderate elevations; pubescence of stems and leaves moderately densely pilose with a mixture of fine, eglandular hairs and much shorter, stipitate-glandular hairs **Castilleja salaisolaveae**
10. Leaves and bracts mostly entire; plants with ascending-erect stems and of open habitats in the foothills and mountains, but almost never alpine.
12. Leaf bases attenuate and not clasping; stems very often slightly zigzag near the nodes; pubescence of the calyces uniformly puberulent; almost always closely associated with and very likely parasitic on *Agave* species **Castilleja rigida**
12. Leaf bases expanded and clasping to subclasping; stems straight to sometimes zigzag; pubescence of the calyces sparsely puberulent on the distal 1/4, becoming abruptly villous below, corresponding with the border between the brightly colored apices and the greenish proximal portions; plants not associated with *Agave* species **Castilleja scorzonifolia**

ACKNOWLEDGEMENTS

We thank Carol I. Miles and Julian Shepherd, both of SUNY-Binghamton, for assistance with insect identification and the personnel of the UNL and WTU herbaria for assistance with loans and the processing of specimens, especially Crystal Shin (WTU) for the image of the holotype sheet. We also thank Linda Ann Vorobik for her fine illustration of the new species and Kanchi Gandhi for consultation on the construction of the Latin name. We also thank Oswaldo Zurita-Zaragoza for the use of his photos of the Cerro de las Mitras population. AH is deeply thankful to Adrian González-Garza and Marielena Bueno-Huereca for supporting this study and helping with fieldwork logistics in the El Jonuco community, as well to the board of the community for their kindness. Also, AH is deeply grateful to Alejandro Aguilar and Héctor Orozco for their support and assistance in the field in conducting the lichen flora project. Finally, JME thanks Guy Nesom for his correspondence and editorial assistance and advice over the last three decades.

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Figure 3. Inflorescence of *Castilleja salaisolaveae* from type gathering, Huereca and Velazco s.n., 17 Apr 2021. Photo by Huereca.



Figure 4. Inflorescence of *Castilleja salaisolaveae* from type gathering, Huereca and Velazco s.n., 17 Apr 2021. Photo by Velazco.



Figure 5. Rhizomatous growth form of *Castilleja salaisolaveae* from type gathering, Huereca and Velazco s.n., 17 Apr 2021. Photo by Velazco.



Figure 6. Rhizomatous growth form of *Castilleja salaisolaveae* from type gathering, Huereca and Velazco s.n., 17 Apr 2021. Photo by Velazco.



Figure 7. Stem of *Castilleja salaisolaveae* from type gathering, Huereca and Velazco s.n., 17 Apr 2021. Note long calyces, lengthening in fruit, and the twice pinnate lower bracts. Photo by Velazco.



Figure 8. Stem of *Castilleja salaisolaveae* from type gathering, Huereca and Velazco s.n., 17 Apr 2021. Note apparently stoloniferous proximal stem, unlike the typical rhizomes, and the twice-pinnate lobes of the upper leaves and the lower bracts. Photo by Velazco.



Figure 9. *In situ* plant *Castilleja salaisolaveae* from type locality, 17 Apr 2021. Note the relatively deep adaxial calyx cleft, the exerted and strongly decurved distal portion of the style, the distinctive pubescence, and the twice-pinnate lobes of the upper leaves and the lower bracts. Photo by Velazco.



Figure 10. *In situ* plant and rocky, calcareous habitat of *Castilleja salaisolaveae* from type locality, 17 Apr 2021. Also note the rhizomatous spreading of the stems of this single plant and the associated moss species, *Pleurochaete luteola*. Photo by Velazco.



Figure 11. *In situ* plant and forest floor habitat of *Castilleja salaisolaveae* from type locality, 17 Apr 2021. Also note the rhizomatous spreading of the stems of this single plant and the associated moss species, *Pleurochaete luteola*. Photo by Velazco.



Figure 12. *In situ* plant and forest floor habitat of *Castilleja salaisolaveae* from type locality, 17 Apr 2021. Also note the rhizomatous spreading of the stems of this single plant. Photos by Velazco.



Figure 13. Mixed forest mountain side habitat of *Castilleja salaisolaveae* from type locality, 17 Apr 2021. This site is on the far northern fringes of the Sierra Madre Oriental. Photos by Velazco.



Figure 14. Plant of *Castilleja salaisolaveae* infested white flies (Homoptera: Aleyrodidae) and other small insects, some of which are apparently trapped on the stipitate-glandular pubescence of the plant. Also note the twice-pinnate bract lobes and the emarginate calyx lobes. Vicinity of the type locality, 29 Apr 2019. Photo by Huereca.



Figure 15. *In situ* plant *Castilleja salaisolaveae* from the second know population, near the crest of Cerro de las Mitras, Mpio. Monterrey, 28 February 2021. Note the strongly decurved distal portion of the style and the habitat in a crevice of a steep limestone rock wall. A young plant of *Dasyllirion berlandieri* is seen in the background. Photo by Oswaldo Zurita-Zaragoza.



Figure 16. *In situ* plant of *Castilleja salaisolaveae* from the second know population, near the crest of Cerro de las Mitras, Mpio. Monterrey 28 February 2021. Note the strongly decurved distal portion of the style, the distinctive pubescence, and the often twice-pinnate leaves. Photo by Oswaldo Zurita-Zaragoza.



Figure 17. *In situ* plants of *Castilleja salaisolaveae* from the second know population, near the crest of Cerro de las Mitras, Mpio. Monterrey, 6 March 2022. In the center and on the right are fresh growth from the plant observed in 2021, while on the lower left one and possible two seedlings can be seen, though these may simply be rhizomatous extensions of a single individual. Associated species seen here include a young plant of *Dasyllirion berlandieri*, *Pinguicula gracilis*, and *Selaginella* sp. Photo by Oswaldo Zurita-Zaragoza.

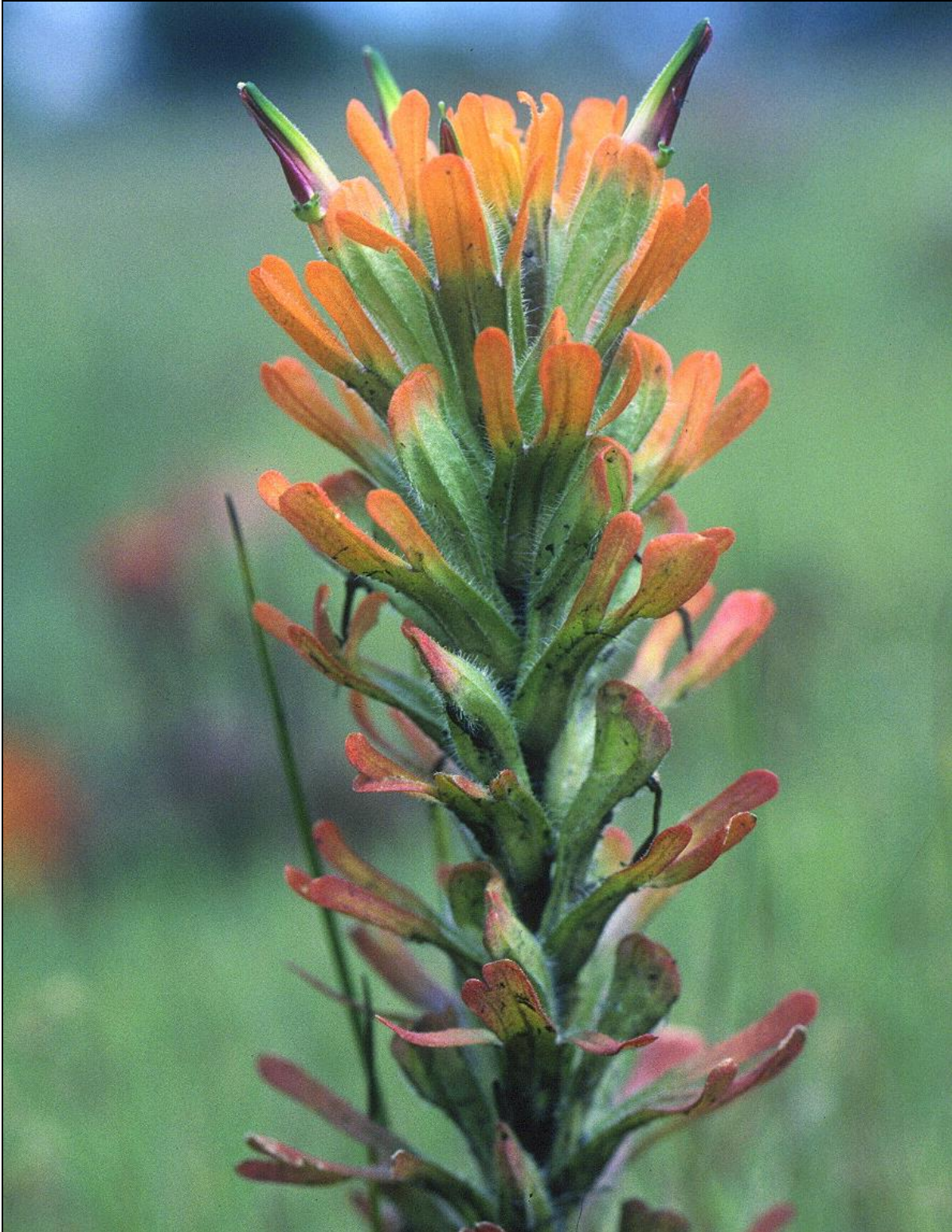


Figure 18. *Castilleja saltensis*, a morphological similar species to *C. salaisolaveae* but lacking the rhizomatous growth form and twice-pinnate leaves of that species. Plants of *C. saltensis* also form distinct basal rosettes of leaves in the dry season. That trait has not been recorded in the new species. *Castilleja saltensis* is endemic to the Sierra Madre Occidental in west-central Durango. Near La Rumarosa, SW of El Salto, Durango, 2 Sep 1997. Photo by Egger.



Figure 19. *Castilleja arvensis* var. *arvensis* in a field of corn, on which it is often parasitic but not at all obligately so, growing with a wide variety of plant hosts, Mpio. Aramberri, Nuevo León, Nov 2019. Photo by Huereca.



Figure 20. *Castilleja bella*, summit ridge of Cerro El Potosí, Mpio. Galeana, Nuevo León, 2 Aug 1999. Photos by Egger.



Figure 21. *Castilleja galehintoniae*, NW of Galeana, Mpio. Galeana, Nuevo León, 1 Aug 1999. Photo by Egger.



Figure 22. *Castilleja galehintoniae*, NW of Galeana, Mpio. Galeana, Nuevo León, 1 Aug 1999. Photo by Egger.



Figure 23. *Castilleja integra*, near Elizabethtown, NE of Sangre de Cristo Range, Colfax County, New Mexico, 31 Jul 2001. Photo by Egger.



Figure 24. Distinctive form of *Castilleja integrifolia* with orange calyces found in the Sierra Madre Oriental, especially in Nuevo León. Upper north flanks of Cerro El Potosí, Mpio. Galeana, Nuevo León, 24 Aug 2013. Photo by Velazco.



Figure 25. Distinctive form of *Castilleja integrifolia* with yellowish calyces found in the Sierra Madre Oriental, especially in Nuevo León. Middle northeast flanks of Cerro El Potosí, Mpio. Galeana, Nuevo León, 1 Aug 1999. Photo by Egger.



Figure 26. *Castilleja lanata*, color forms, Pecos Co., Texas, 19 Apr 1997. Photos by Egger. While this species varies somewhat in color, the reddish form is by far the most common one.



Figure 27. *Castilleja mexicana*, white-flowered form, Camino a La Esmeralda, Mpio. Galeana, Nuevo León, 6 Jul 2014. This is the color form most frequently observed in Nuevo León. Photo by Velazco.



Figure 28. *Castilleja mexicana*, yellow-flowered "*C. tortifolia*" form, southwest of La Junta, Chihuahua, México, 18 Aug 1998. This form is apparently rare in Nuevo León. Photo by Egger.



Figure 29. *Castilleja rigida* with its frequent host, *Agave lecheguilla*, Brewster Co., Texas, 18 Aug 1991. Note the slightly zigzag stems, characteristic of this species. Photo by Egger.



Figure 30. *Castilleja scorzonerifolia*, lower-middle slopes on NE side of Cerro El Potosí, Nuevo León, México, 1 Aug 1999. With the lovely *Penstemon leonensis* Straw. Photo by Egger.



Figure 31. *Castilleja scorzonerifolia*, lower-middle slopes on NE side of Cerro El Potosí, Mpio. Galeana, Nuevo León, México, 1 Aug 1999. Note clasping leaves and conspicuously villous calyces. Photo by Egger.



Figure 32. *Castilleja sessiliflora* f. *purpurina*, Mpio. Galeana, Nuevo León, 23 Aug 2020, upper photo, by Huereca; Crockett County, Texas, 19 Apr 1997, lower photo, by Egger.



Figure 33. *Castilleja tenuiflora* var. *tenuiflora*, SE of Pachuca, Hidalgo, México, 16 Aug 2000. Almost all populations of *C. tenuiflora* in Nuevo León belong to var. *xylorrhiza*, but a few specimen records exist of the typical form as well, especially in the far southern tier, as well as a few apparently intermediate forms (see Fig. 37). *Castilleja tenuiflora* is by far the most common and widespread *Castilleja* species in México. Photo by Egger.



Figure 34. *Castilleja tenuiflora* var. *xylorrhiza*, inflorescence (above) and habit (below), east of Iturbide, Mpio. Iturbide, Nuevo León, 1 Aug 1999. Photos by Egger.



Figure 35. *Castilleja tenuiflora* var. *xylorrhiza*, east of Iturbide, Mpio. Iturbide, Nuevo León, México, 1 Aug 1999. Uncommon color morph growing within a large population of plants with entirely yellow calyces and bracts. Photo by Egger.



Figure 36. *Castilleja tenuiflora* var. *xylorrhiza*, east of Iturbide, Mpio. Iturbide, Nuevo León, México, 1 Aug 1999. Typical color morph. Photo by Egger.



Figure 37. *Castilleja tenuiflora*, likely intermediate between the typical expression and var. *xylorrhiza*, south of General Zaragoza, Mpio. General Zaragoza, Nuevo León, México, 26 Jul 2019. Photo by Huereca.