

**NOMENCLATURAL CHANGES AND SELECTED
LECTOTYPIFICATIONS IN *CASTILLEJA*
(OROBANCHACEAE)**

J. Mark Egger

Herbarium, Burke Museum of Natural History and Culture, Box
355325, University of Washington, Seattle, WA 98195-5325, U.S.A
m.egger@comcast.net

ABSTRACT

The following nomenclatural novelties are established in the genus *Castilleja*: *C. affinis* var. *neglecta* (Zeile) J.M. Egger, *C. ambigua* var. *humboldtiensis* (D.D. Keck) J.M. Egger, *C. ambigua* var. *insalutata* (Jeps.) J.M. Egger, *C. bryantii* var. *socorrensis* (Moran) J.M. Egger, *C. campestris* var. *succulenta* (Hoover) J.M. Egger, *C. ctenodonta* var. *altorum* (Standl. & Steyerl.) J.M. Egger, *C. densiflora* var. *gracilis* (Benth.) J.M. Egger, *C. densiflora* var. *obispoënsis* (D.D. Keck) J.M. Egger, *C. exserta* var. *latifolia* (S. Watson) J.M. Egger, *C. exserta* var. *venusta* (A. Heller) J.M. Egger, *C. integrifolia* var. *chiapensis* (Brandege) J.M. Egger, *C. integrifolia* var. *longibracteata* (M. Martens & Galeotti) J.M. Egger, *C. miniata* var. *fulva* (Pennell) J.M. Egger, *C. minor* var. *exilis* (A. Nelson) J.M. Egger, *C. minor* var. *stenantha* (A. Gray) J.M. Egger, *C. minor* var. *spiralis* (Jeps.) J.M. Egger, *C. moranensis* var. *cinerascens* (Eastw.) J.M. Egger, *C. pallida* var. *hyparctica* (Rebrist.) J.M. Egger, *C. pallida* var. *lapponica* (Rebrist.) J.M. Egger, *C. pallida* var. *saccata* (Pennell) J. M. Egger, *C. pallida* var. *yukonis* (Pennell) J.M. Egger, *C. pectinata* var. *purpusii* (Brandege) J.M. Egger, *C. rubicundula* var. *lithospermoides* (Benth.) J.M. Egger, *C. subinclusa* var. *jepsonii* (Bacig. & Heckard) J.M. Egger, and *C. tenuiflora* var. *tancitaroana* (G.L. Nesom) J.M. Egger. Lectotypifications are proposed for the following names: *C. longibracteata* M. Martens & Galeotti and *C. spiralis* Jeps. Complete synonymies are provided for all treated taxa.

KEY WORDS: *Castilleja*, Lectotypification, nomenclature, Orobanchaceae, *Orthocarpus*, Scrophulariaceae.

This paper proposes a number of nomenclatural changes, along with relevant lectotypifications and synonymies within the genus *Castilleja* Mutis ex L.f., formerly placed in Scrophulariaceae but now included within Orobanchaceae (Olmstead et al. 2001). Some of the *Castilleja* taxa treated here were previously placed in the genus *Orthocarpus* but were later transferred to *Castilleja* (Chuang and Heckard 1991). These changes are proposed in preparation for the upcoming treatment of *Castilleja* in the Flora of North America series and in other forthcoming regional treatments of the genus.

The nomenclatural novelties are proposed in an effort to standardize the usage of infraspecific taxa within *Castilleja* with the rank of variety, following the suggestions of Holmgren (1994), Turner and Nesom (2000) and others, and to provide a consistent nomenclatural basis for my own on-going work in the genus. Historically, such taxa in *Castilleja* have almost always been treated as either varieties or subspecies, and in only one work were both ranks employed for classification, strictly within a single species (Boivin 1952). There is no indication in the major treatments of *Castilleja* in the botanical literature that those authors treated varieties and subspecies as other than essentially of equivalent biological/evolutionary standing.

Roughly two-thirds of the major historic treatments and revisions of taxa now included in *Castilleja* in which infraspecific taxa have been assigned utilized only the rank of variety. These include the works of G. Bentham (e.g. 1846), H. A. Weddell (1857), A. Gray (e.g. 1880), A. Eastwood (e.g. 1909), D. D. Keck (e.g. 1927), M. Ownbey (e.g. 1959), N. H. Holmgren (e.g. 1984a), and G. L. Nesom (e.g. 1992). Weddell (1857) was unique in also employing the rank of subvariety in *Castilleja*. Major treatments employing the rank of subspecies include those of F. W. Pennell (e.g. 1934) and T. I. Chuang and L. R. Heckard (e.g. 1991, 1992). P. A. Munz applied subspecies in some publications (e.g. 1958), while using varieties in others (e.g. 1932). With the exception of Pennell's work, most treatments using subspecies have applied primarily to the California flora.

Among the authors of significant taxonomic treatments of *Castilleja*, only Holmgren (1971, p.26) provided an explicit description of the species concept employed in his classification, "based primarily

on morphological distinctiveness among natural populations” wherein, in most cases, “morphological continuity is correlated with geographic discontinuity.” Further, “The populations within a species are all closely related and have been exchanging genes at least in recent times.” I follow Holmgren’s work, both in terms of species concept and in his use of variety as the basis for infraspecific groupings in this genus. Through 24 years of intensive field work involving all North American taxa and most of those in Latin America, as well as herbarium study of approximately 22,000 sheets, including almost all know type collections, my studies in the genus have, with only a few minor exceptions, confirmed Holmgren’s revisionary treatments of *Castilleja* across a number of regional floras (Holmgren 1970, 1973, 1978, 1984a, 1984b,) and species groups (Holmgren 1971, 1976).

My own application of the rank of variety as the fundamental unit of infraspecific classification in *Castilleja* is essentially both functional, in defining patterns of natural variation in a consistent and meaningful manner, and biological, in reflecting and defining evolutionary trends in natural populations and establishing hypotheses upon which to base future phylogenetic investigation. I define varieties as diverging systems of natural populations within a presumed progenitor species and characterized by relatively minor but reasonably consistent patterns of morphological divergence, combined with varying degrees and combinations of ecological and/or geographical partitioning. While some overlap in the defining characteristics is allowed, as one would expect in infraspecific groupings, any such overlaps should be limited in extent and non-clinal, and the taxa involved should still be generally separable through the examination of suites of characters.

The following new combinations and changes of status are here established. Full synonymies and locations of verified type specimens are provided for each name, and relevant lectotypifications are proposed where needed. Type collection citations are extracted from the protologues and amended where possible with additional documentation from the original herbarium labels. Any such label information is enclosed in parentheses. Additional technical notes regarding the type collections gleaned from my own research are enclosed in brackets. I have included exclamation points following the abbreviations of institutions housing type collections of *Castilleja* I

have seen and verified. Other locations without exclamation points are from published sources and need verification, though some have been certified in recent decades by competent taxonomists. Institutional abbreviations followed by a question mark represent those listed in the protologues or in secondary sources as locations at which type material was deposited but which could not be relocated during the research for this study. Abbreviations followed by a question mark enclosed in parentheses are hypotheses as to where type material may be located for those taxa for which neither a location was listed in the protologue nor any specimens found during this study.

Though not so arranged in the treatments below, the proposed nomenclatural changes can be divided into three categories. The first category, consisting of 12 novelties, provides varietal status to taxa previously treated as subspecies within the same species in order to standardize nomenclature in *Castilleja*. My conception of the identities and circumscriptions of the taxa included in this first group are essentially identical to that of the authors of the subspecies names, so little further comment is necessary. The second category, consisting of 12 novelties, includes names previously used only at the species level or as subspecies of different taxa but which my research indicates are better treated as varieties of the names indicated below. The third category includes a single new combination, reassigning a named variety of a parent taxon that is now known to be synonymous with an earlier-published name. Further explanatory comments are provided below for each taxon in the second and third groups of new combinations. Finally, I propose two lectotypifications necessary to provide an unequivocal basis for the identity of the taxa treated in this paper. Additional lectotypifications are needed in *Castilleja* and will be addressed in future publications. The accepted taxa are presented in alphabetical order, and their arrangement is of no taxonomic significance. Keys to all of the treated taxa and their relatives will be presented in later publications, including the Flora of North America and the Flora Mesoamericana.

Castilleja affinis Hook. & Arn. var. *neglecta* (Zeile) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja neglecta* Zeile in W. L. Jepson, Man. Fl. Pl. Calif.: 936, 1925. *Castilleja affinis* subsp. *neglecta* (Zeile) T.I. Chuang & Heckard, Novon 2: 185, 1992.

TYPE: United States. California: Marin Co., hillsides, Tiburon, (7 Jul 1907), *Brandegee s.n.* (holotype: JEPS!; isotype: CAS!). [Note: while the collection of *Brandegee s.n.* at CAS is annotated as the "type collection" by A. Eastwood, it is unclear if this sheet contains valid type material. While it was collected in the same location as the holotype, the date on Brandegee's label for the CAS sheet is "May 1909." Unless this date is incorrect, then the CAS sheet is merely a topotype.]

Castilleja ambigua (Hook. & Arn.) T.I. Chuang & Heckard var. *humboldtiensis* (D.D. Keck) J.M. Egger, **comb. nov.** BASIONYM: *Orthocarpus castillejoides* Benth. var. *humboldtiensis* D.D. Keck, Proc. Calif. Acad. Sci., Ser. 4, 16: 536, 1927. *Castilleja ambigua* subsp. *humboldtiensis* (D.D. Keck) T.I. Chuang & Heckard, Syst. Bot. 16: 655, 1991. TYPE: United States. California: Humboldt Co., Eureka, (partly dry) saline flats, 20 Jun 1925, *Munz 9890* (holotype: RSA-POM!; isotypes: DS!, GH!).

Castilleja ambigua (Hook. & Arn.) T.I. Chuang & Heckard var. *insalutata* (Jeps.) J.M. Egger, **comb. nov.** BASIONYM: *Orthocarpus castillejoides* Benth. var. *insalutatus* Jeps., Man. Fl. Plants of Calif.: 944, 1925. *Castilleja ambigua* subsp. *insalutata* (Jeps.) T.I. Chuang & Heckard, Syst. Bot. 16: 656, 1991. TYPE: United States. California: Monterey Co., Pacific Grove, 8 Aug 1896, *Jepson 21110* (holotype: JEPS!).

Castilleja bryantii Brandegee var. *socorrensis* (Moran) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja soccorensis* Moran, Mem. San Diego Nat. Hist. Soc. 16: 52, 1989. TYPE: México. Baja California: Isla Socorro, fairly common in low vegetation, east slope of Cerro Evermann at 980 m, near 18°46.5'N, 110°57.5'W, 4 Apr 1981, *Moran 29505* (holotype: SD!; isotypes: ARIZ!, BISH!, CAS!, ENCB, F!, MEXU, MICH!, MO!, NY!, RSA!, TEX!, UC!, US!).

Comments: Moran distinguished *C. soccorensis* from *C. bryantii* on the basis of overall stem height, calyx length, and corolla measurements. Of these, only the corolla lengths appear to be non-overlapping. While the corolla size differences do appear to be

consistent, such limited variation in a single character in *Castilleja* typically distinguishes varieties rather than full species.

Castilleja campestris (Benth.) T.I. Chuang & Heckard var. *succulenta* (Hoover) J.M. Egger, **comb. nov.** BASIONYM: *Orthocarpus campestris* Benth. var. *succulentus* Hoover, Leafl. W. Bot. 1: 228, 1936. *Orthocarpus succulentus* (Hoover) Hoover, Four Seasons 2(4): 14, 1968. *Castilleja campestris* subsp. *succulenta* (Hoover) T.I. Chuang & Heckard, Syst. Bot. 16: 656, 1991. TYPE: United States. California: Merced Co., Ryer, 1 May 1936, *Hoover 1076* (holotype: CAS!; isotypes: GH!, JEPS[2]!, PH[2]!, UC!, US!).

Castilleja ctenodonta Eastw. var. *altorum* (Standl. & Steyermark) J. M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja altorum* Standl. & Steyermark, Field Mus. Publ. Bot. 23: 85, 1943. TYPE: Guatemala. Huehuetenango: Open alpine meadows, top of Cerro Chemalito, Sierra de los Cuchumatanes, 3.5 miles west of Santa Eulalia, alt. 3,100-3,150 meters, 2 Aug 1942, *Steyermark 49908* (holotype: F!).

Comments: In describing *C. altorum*, its authors did not distinguish it from the earlier *C. ctenodonta* and were probably unaware of the close similarity of the Guatemalan material to that of Eastwood's species, an apparently very rare taxon known only from the type collection and that of a companion of Pringle at the time he made the type collection (*Smith 539*, NY[2]!, UC!). I visited the vicinity of the type locality in August 2001 but was unable to find any plants of this distinctive species. The Guatemalan form is distinguished primarily by its generally wider leaves with less deeply denticulate margins. While the two apparently disjunct populations may eventually prove to be synonymous, I prefer to maintain them as separate varieties pending additional fieldwork.

Castilleja densiflora (Benth.) T.I. Chuang & Heckard var. *gracilis* (Benth.) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Orthocarpus gracilis* Benth., Scroph. Ind.: 12, 1835. *Orthocarpus densiflorus* Benth. var. *gracilis* (Benth.) D.D. Keck, Proc. Calif. Acad. Sci., Ser. 4, 16: 538, 1927. *Castilleja densiflora* subsp. *gracilis* (Benth.) T.I. Chuang & Heckard, Syst. Bot. 16: 656, 1991. TYPE: United States. (Nova) California: [central coastal region,

probably in southern Monterey Co.], (1833) [1831, 1832 or possibly Nov 1833], *Douglas s.n.* (holotype: K-BENTH!; isotypes: BM!, CGE!, GH!, NY!). [Note: the Kew Herbarium labels on some of the type sheets indicate the collection date as 1833, but this is probably incorrect, as Douglas was only in California from 4-28 November of that year, during which time it is very unlikely that this Spring annual would be in full bloom. It is also possible that 1833 indicates when Bentham actually received the specimens at Kew. The isotype sheet at BM contains two stems of the type collection on the upper portion, with two unrelated collections elsewhere. According to Keck (1951), the type collection was obtained “doubtless (in the) Santa Lucia Mountains.”]

Orthocarpus parishii A. Gray, Proc. Amer. Acad. Arts 17: 229, 1882. TYPE: United States. California: San Diego Co., San Jacinto Mountain, Jul 1880, *Parish & Parish 482* (holotype: GH!). [Note: some confusion exists in the literature with regard to the type collection. While A. Gray’s protologue matches the collection label on the holotype sheet, Parish (1901) corrected this, stating that “The type station of this species, erroneously given as ‘San Jacinto Mts.’, should be: Meadows near Stonewall Mine, in the Cuyamaca Mts.” Parish’s correction is further supported by the fact that the San Jacinto Mountains are in Riverside Co., while the Cuyamaca Mountains are in San Diego Co., the latter county matching that given in the protologue. Compounding the confusion in the literature is reference to an apparent isotype sheet at PH(!). This sheet, incorrectly annotated as belonging to the type collection, is actually from a different collection. Its label reads: “San Jacinto Mts., Aug 1880, *Parish & Parish 408*.” Confusion between this latter collection and the true type may well be the source of the original and erroneous labeling of *Parish & Parish 482*.]

Castilleja densiflora (Benth.) T.I. Chuang & Heckard var. *obispoënsis* (D.D. Keck) J.M. Egger, **comb. nov.** BASIONYM: *Orthocarpus densiflorus* Benth. var. *obispoënsis* D.D. Keck, Proc. Calif. Acad. Sci., Ser. 4, 16: 539, 1927. *Castilleja densiflora* subsp. *obispoënsis* (D.D. Keck) T.I. Chuang & Heckard, Syst. Bot. 16: 656, 1991. TYPE: United States. California: San Luis Obispo Co., 1 mi N of Morro, (grassy slope in view of the ocean, alt. 150 ft.), 8 Apr 1926, *Munz & Keck 10242* (holotype: RSA-POM!; isotypes: GH!, RM!).

Castilleja exserta (A. Heller) T.I. Chuang & Heckard var. *latifolia* (S. Watson) J.M. Egger, **comb. nov.** BASIONYM: *Orthocarpus purpurascens* Benth. var. *latifolius* S. Watson, Bot. King's Exped.: 458, 1871. *Castilleja exserta* subsp. *latifolia* (S. Watson) T.I. Chuang & Heckard, Syst. Bot. 16: 657, 1991. TYPE: United States. California: Mendocino Co., seacoast at Noyo, *Bolander* 6538 (holotype: GH!; isotypes: UC[2]!).

Orthocarpus purpurascens Benth. var. *multicaulis* Jeps., Man. Fl. Plants of Calif.: 944, 1925. TYPE: United States. California: Mendocino Co., Ft. Bragg, 1914, *Mathews s.n.* (holotype: JEPS!).

Castilleja exserta (A. Heller) T.I. Chuang & Heckard var. *venusta* (A. Heller) J.M. Egger, **comb. nov.** BASIONYM: *Orthocarpus venustus* A. Heller, Muhlenbergia 2: 141, 1906. *Orthocarpus purpurascens* Benth. var. *venustus* (A. Heller) D.D. Keck. Proc. Calif. Acad. Sci., Ser. 4, 16: 542, 1927. *Castilleja exserta* subsp. *venusta* (A. Heller) T.I. Chuang & Heckard, Syst. Bot. 16: 657, 1991. TYPE: United States. California: San Bernardino Co., Kramer, in the Mojave Desert in sand, 13 Apr 1905, A. A. Heller 7677 (holotype: BKL!; isotypes: BM!, CAS!, F!, GH!, K!, MO, MSC!, NY!, PH!, UC!, US!).

Orthocarpus purpurascens Benth. var. *ornatus* Jeps., Man. Fl. Plants of Calif.: 944, 1925. *Orthocarpus ornatus* A. Heller ex Jeps., Man. Fl. Plants of Calif.: 944, 1925, nomen subnudum. TYPE: United States. California: San Bernardino Co., (sandy wash), Calico Wash, Barstow, central Mojave Desert, (2,500 ft.), 28 Apr 1914, *Jepson* 5819 (holotype: JEPS!). [Note: as far as I can determine, Heller never published this name directly.]

Castilleja integrifolia L.f. var. *chiapensis* (Brandege) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja chiapensis* Brandege, Univ. Calif. Publ. Bot. 6: 62, 1914. TYPE: México. Chiapas: in the highest region of Cerro del Boqueron, Aug 1913, *Purpus* 6884 (holotype: UC!; isotypes: F!, GH!, NY!, US!).

Comments: The widespread and complex *C. integrifolia* consists of a widely distributed nominate variety, extending from the northern Andes of South America northward into the Sierras of northeastern Mexico, and a number of distinctive, narrowly distributed endemic

forms, particularly in southwestern México and northern Central America. Some of these localized offshoots, such as the recently described *Castilleja albobarbata* H.H. Iltis & G. L. Nesom (Iltis et al. 2003), may well have diverged sufficiently to be regarded as full species, though most will require further study before unequivocal determination of rank. However, two forms are now well enough known to confirm them as valid taxa but not so fully divergent from the nominate form as to warrant full species rank. The first of these is var. *chiapensis*, based on its highly distinctive, densely villous, golden-yellow pubescence and its limited but well-defined distribution as an endemic of the Sierra Madre de Chiapas of southern Chiapas, México. Nesom (1992) mentions apical lobes or teeth on the terminal bracts as also characteristic of this form, but my studies show this to be occasional and sporadic in var. *chiapensis*, unlike the case with the following variety.

Castilleja integrifolia L.f. var. *longibracteata* (M. Martens & Galeotti) J.M. Egger, **comb. & stat. nov.** BASIONYM: *Castilleja longibracteata* M. Martens & Galeotti, Bull. Acad. Roy. Soc. Bruxelles 12(2): 28, 1845. **LECTOTYPE**, designated here: México. Oaxaca: dans les bois de Juquila del Sur (cote pacifique d'Oaxaca), 5000 pieds, Sep 1840, *Galeotti* 988, in part (hololectotype: BR!; isolectotypes: BR[2]!, G! K?, P!). [Note: while a second location is mentioned in the protologue ("a Talea et dans le Rincon, cordill. orientale d'Oaxaca"), all three sheets of *Galeotti* 988 at BR mention only the first locality listed above, and it is clear that collection was intended by the authors to serve as the type. I could not locate any sheets bearing a label for the second location mentioned in the protologue. The isolectotype sheet at G, while bearing the type number, appears to be a specimen of *Castilleja tenuiflora* Benth., and it lists somewhat different location information, "Bois de Cote, de la Mer Pacifique, 5500 pieds." It seems likely that this specimen was incorrectly numbered and should not be regarded as authentic material from the type collection.]

Comments: Though first described in 1845, this poorly understood taxon was overlooked until recent field work revealed it to be a morphologically-consistent and fairly common endemic in the Sierras surrounding the valley of Oaxaca in southern Mexico. Its

range apparently extends from the Sierra Madre del Sur south of Miahuatlan, near which it was first collected, northward to the Sierra Juarez, north of the city of Oaxaca. The plants are unique in their distinctively broad and strongly fimbriate terminal bracts, clearly displayed in the specimens of the type collection, and unusually long, prominently colored corollas, but they are otherwise like the nominate variety. A key to some of the taxa associated with *C. integrifolia* will be presented in the forthcoming treatment of the genus in the Flora Mesoamericana.

Castilleja miniata Douglas ex Hook. var. *fulva* (Pennell) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja fulva* Pennell, Proc. Acad. Nat. Sci. Phila. 86: 540, 1934. TYPE: Canada. British Columbia: North slopes of Peace R. Valley, high bluffs at Hudson Hope, (NW of the town, about 56°2'N, 121°55'W, alt. 2000 feet), 16 Jun 1932, *Raup & Abbe 3602* (holotype: PH!; isotypes: CAN!, F!, GH[2]!, NY!, S!, US!). [Note: some isotype sheets list the elevation as "2100 ft".]

Comments: This little-known form is fairly common only in a limited area near the type locality but extending eastward into adjacent central-western Alberta. It is distinguished by its usually yellowish to apricot-orange and densely villous inflorescence.

Castilleja minor (A. Gray) A. Gray var. *exilis* (A. Nelson) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja exilis* A. Nelson, Proc. Biol. Soc. Wash. 17: 100, 1904. *Castilleja stricta* Rydb., Mem. N.Y. Bot. Gard. 1: 354, 1900, later homonym, not Benth., 1846. TYPE: United States. Nevada: [Elko Co.], Ruby Valley, 6000 ft., Aug 1868, *Watson 809* (holotype: NY!; isotypes: US!, YU!). [Note: Nelson's name is simply a renaming of Rydberg's later homonym.]

Euchroma lanceolata Nutt. ex A. Gray, Amer. J. Sci. Arts 84: 336, 1862, nomen subnudum. TYPE: United States. (Lewis River), [in 1834], *Nuttall s.n.* (holotype: PH!). [Note: this name was listed by Gray as a synonym of *Castilleja affinis* Hook. & Arn. var. *minor* A. Gray. The type collection is represented by a single stem mounted in the center of the same sheet as that containing the type of *Euchroma simplex* Nutt. ex A. Gray (see below). Apparently, these two specimens were collected at or near the same location, as

the labels are identical except for the names assigned to them by Nuttall.]

Euchroma simplex Nutt. ex A. Gray, Amer. J. Sci. Arts 84: 336, 1862, nomen subnudum. TYPE: United States. (Oregon) [Territory]: (Lewis River), [1834], *Nuttall s.n.* (holotype: PH!; isotype: K-HOOK!). [Note: this name was listed by A. Gray as a synonym of *Castilleja affinis* Hook. & Arn. var. *minor* A. Gray. The type collection is represented by a single stem mounted on the left side of the same sheet as that containing the type of *Euchroma lanceolata* Nutt. ex A. Gray.]

Comments: *Castilleja minor* is a complex species that has been treated at various times as either four separate species or as two subspecies distinguished by the length of the corolla beak. My conclusion after review of hundreds of specimens and scores of populations from throughout the range of the species is that this complex is best treated as a single polymorphic species consisting of four essentially parapatric varieties distinguished by relatively minor but reasonably consistent characters. A key to these varieties will be presented in the treatment of *Castilleja* in the Flora of North America.

Castilleja minor (A. Gray) A. Gray var. *stenantha* (A. Gray) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja stenantha* A. Gray, Syn. Fl. N. Amer. 2: 295, 1878. *Castilleja stenante* (A. Gray) L. Abrams, Fl. Los Angeles: 369, 1904 [transcriptional error of A. Gray's original name]. TYPE: United States. California: [Monterey Co.?], moist grounds ...from Monterey to San Diego and through the southern part of the Sierra Nevada, (moist, shady places, Carmel River, 1848), *Hartweg 1897 (134)* (= *Pl. Hartweg. 329*, "in part") (holotype: GH!; isotypes: BM!, K-BENTH!, K-HOOK!, NY!). [Note: on the holotype sheet, only the second stem from the left is material from *Hartweg 1897*. The sheet also contains two collections of the present taxon obtained by others. The isotype sheet at K-BENTH contains one stem of the type collection mounted on the right side with an unrelated collection of the left, while the sheet at K-HOOK contains one stem on the left side along with two unrelated collections elsewhere. The isotype sheet at BM contains a single stem of the type collection, mounted on the far left, along with two stems from a different collection

found elsewhere on the sheet. Pennell (1951) lists the type locality as the "vicinity of Fort Tejon", which is located in southwestern Kern Co., CA, an assertion for which there is little evidence, especially considering the fact that the holotype sheet specifies "Carmel River" as the location of Hartweg's collection. The holotype sheet is the only label to associate the added (field number?) 134 to Hartweg's collection number.]

Castilleja minor (A. Gray) A. Gray var. ***spiralis*** (Jeps.) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja spiralis* Jeps., Fl. W. Mid. Calif. 412, 1901. *Castilleja stenantha* A. Gray subsp. *spiralis* (Jeps.) Munz, Aliso 4: 98, 1958. *Castilleja minor* subsp. *spiralis* (Jeps.) T.I. Chuang & Heckard, Novon 2: 188, 1992. **LECTOTYPE**, designated here: United States. California: Napa Co., moist rivulets, Butt's Canyon, (Pope Valley to Coyote Valley), northern Napa Co., 13 Jul 1897, *Jepson 21113, sheet 2 of 2* (hololectotype: JEPS!; isolectotype: JEPS!). [Note: the lectotypification is necessary because the two sheets of the type collection at JEPS have never been distinguished in the literature. The hololectotype sheet is JEPS #2513, labeled "sheet 2 of 2", and the isolectotype is JEPS #2514, labeled "sheet 1 of 2." The sheet chosen as the hololectotype bears flowering stems, while the other sheet contains only younger, non-flowering stems.]

Castilleja moranensis Kunth var. ***cinerascens*** (Eastw.) J.M. Egger, **comb. nov.** BASIONYM: *Castilleja schaffneri* Hemsl. var. *cinerascens* Eastw., Proc. Amer. Acad. Arts 44: 573, 1909. TYPE: México. Puebla: dry hills about Chalchicomula [= Ciudad Serdan], alt. 2592 m (8,500 ft.), 27 Jul 1901, *Pringle 8545* [= field number 187] (holotype: GH!; isotypes: BKL!, CM!, ENCB!, K!, LYBON[2]! MEXU!, MO!, MSC!, NY!, P!, PH[2]!, S!, UC!, US!, WIS[2]!). [Note: according to Pringle's diaries, the type collection was made "a little to the west of town" (of Chalchicomula).]

Comments: This long-overlooked taxon, known primarily from the ample type collection and a few smaller collections from near the type locality, was originally described as a variety of *Castilleja schaffneri* Hemsl. Recent examination of relevant types makes it clear that the latter name is synonymous with the earlier *C. moranensis* Kunth, necessitating the new combination. Apparently,

this form has not been collected in decades, and a search of the vicinity of the type locality in 2000 failed to locate any plants. Until new populations can be located, this taxon should be considered as very rare or possibly extinct.

Castilleja pallida (L.) Spreng. var. *hyparctica* (Rebrist.) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja hyparctica* Rebrist., Nov. Syst. Pl. Vasc. 1 (Leningrad): 289, 1964. *Castilleja pallida* subsp. *hyparctica* (Rebrist.) A. Löve & D. Löve, Bot. Notiser 128: 518, 1976. TYPE: [Russia.] Ad Kolymam inferiorem, prope pagum Penteleicha, 12 Jul 1950, *Nepli s.n.* (holotype: LE).

Castilleja pallida (L.) Spreng. var. *lapponica* (Gand. ex Rebrist.) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja lapponica* Gand. ex Rebrist., Nov. Syst. Pl. Vasc. 1 (Leningrad): 293, 1964. *Castilleja lapponica* Gand., Fl. Europ. 18: 25, 1889, nomen nudum. *Castilleja pallida* subsp. *lapponica* (Gand. ex Rebrist.) A. Löve & D. Löve, Bot. Notiser 128: 518, 1976. TYPE: Russia. Lapponia rossica. Ad Svjatoines, 12 Aug 1880, *Enwald & Knabe s.n.* (holotype: LY-GAN!; isotype: S!, TUR!). [Note: the labels on the apparent isotypes are identical to that of the holotype, except that the date on the former sheet is listed as 10 Aug 1880. While this name was originally listed by Gandoger, Rebristaya was the first to provide a proper diagnosis.]

Castilleja angustifolia Gand., Fl. Europ. 18: 25, 1889, nomen nudum and later homonym, not (Nutt.) G. Don, 1838. TYPE: Russia. Lapponia rossica. Hab. Svjatoines, 12 Aug 1880, *Enwald s.n.* (holotype: LY-GAN!). [Note: the type of *Castilleja angustifolia* Gand. was collected on the same date and by the same primary collector as the type of *Castilleja lapponica* Gand. ex Rebrist., and the two may well be different sheets of the same collection, with slightly different label information. The two appear to be no more than minor variants of the same taxon.]

Castilleja pallida (L.) Spreng. var. *borealis* Pohle ex Rebrist., Arktich. Fl. SSSR 8: 284, 1980, nomen subnudum. TYPE: not cited or located for this study (holotype: LE[?]). [Note: this name is based on an unknown herbarium sheet, presumably at LE, and is listed by O. V. Rebristaya as a synonym of *Castilleja lapponica*

Gand. ex Rebrist. Apparently, the present varietal name was never published by R. R. Pohle.]

Castilleja schrenkii Rebrist. Nov. Syst. Pl. Vasc. 1 (Leningrad): 293, 1964. TYPE: Russia. Lapponia rossica, 1838, *Schrenk s.n.* (holotype: LE; isotype: LY-GAN!).

Castilleja pallida (L.) Spreng. var. *saccata* (Pennell) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja pallida* (L.) Spreng. subsp. *saccata* Pennell, Proc. Acad. Nat. Sci. Phila. 86: 523, 1934. TYPE: Russia. River banks, 20 mi. S of Ustj-Kamchatka, Kamchatka, Jul 1925, *Eyerdam 53* (holotype: PH!).

Castilleja olgae A.P. Khokhr. Biol. Rast. i Fl. Sev. Dal'n Vostok 16, 1981. TYPE: Russia. Chamchatka [= Kamchatka], in vicinity of Petropavlovsk, Tri Brata, 19 Sep 1978, *Mazurenko & Khokhrjakov s.n.* (holotype: MW!).

Castilleja pavlovii Rebrist. Nov. Syst. Pl. Vasc. 1 (Leningrad): 294, 1964. *Castilleja pallida* (L.) Spreng. subsp. *pavlovii* (Rebrist.) A. Löve & D. Löve, Bot. Notiser 128: 518, 1976. TYPE: Russia. Kamczatka [= Kamchatka], in pratis secus alveum fl. Leyvi Abgin sub monticulo Opalskaja, 27 Aug 1935, *Pavlov s.n.* (holotype: LE, isotype: MW!).

Castilleja pallida (L.) Spreng. var. *yukonis* (Pennell) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja yukonis* Pennell, Not. Nat. Acad. Nat. Sci. Phila. 86: 531, 1934. *Castilleja tristis* W. Wight ex Standl. var. *pubens* W. Wight ex Standl. in J.B. Mertie, U.S. Dept. Inter. Geol. Surv. Bull. 810: 108, 1929, nomen nudum and superfluous. TYPE: Canada. Yukon: dry gravelly slopes and hillsides, Lewes River, (60°23'N, 134°49'W), 24 Jun 1899, *Gorman 1056* (holotype: CAN!; isotypes: NY!, PH!, S!, U, US!). [Note: the listing of the name *C. tristis* var. *pubens* in synonymy here is based on an annotation as "Type" of the sheet at US which later became an isotype of the properly published *C. yukonis*. Pennell also annotated the isotype sheet of *C. yukonis* at PH as the type collection of "*C. tristis* var. *pubens* Wight, ined." In addition, Hultén (1949) states, "In using this name Wight alludes to the plant which is here called *C. yukonis*," but he does not explain upon what evidence his statement is based. Hultén did not cite a lectotype for this name. Standley's publication of this name without

type or comment was likely intended simply to identify collections supplied to him by Mertie and was not intended by Standley as a typification. Apparently, Wight never published the name *C. tristis* var. *pubens*.]

Castilleja muelleri Pennell. Not. Nat. Acad. Nat. Sci. Phila. 86: 533, 1934. TYPE: Canada. Yukon: Lake Kluane to Donjek (Don Jek) River, 11-27 Aug 1920, *Müller s.n.* (holotype: PH!; isotype: PH!).

Comments: The *C. pallida* complex is perhaps the most widespread and taxonomically confusing group in *Castilleja*. Extending across virtually all the Palearctic region (except for Scandinavia) and most of the western and central Nearctic, it is characterized by numerous little known and recently evolved regional and polyploid forms. Rebristaya (1964) is the only author thus far to attempt a comprehensive revision of these plants. While her treatments are extensive, detailed, and highly valuable as a preliminary assessment of the diversity present in *Castilleja* across this broad area, they lack the perspective provided by knowledge of the patterns of species diversity and variation throughout the primary range of the genus in sub-arctic North America and the montane regions of the Neotropics. Pennell (1934) made much the same sort of study of *Castilleja* in the western Nearctic, but with more limited material and lacking a full understanding of the Palearctic forms. While many unanswered questions remain in the analysis of *C. pallida* and its near relatives, some conclusions regarding the entire complex are now within reach, such as the synonymies presented in this and the three preceding new combinations. My research indicates that *C. pallida* is best viewed as a complex of largely parapatric varieties. While full explication of those occurring in the Palearctic awaits future field studies and examination of type specimens not easily accessible to me, I believe that *C. pallida* is represented in the Nearctic by three variable forms, the nominate variety, var. *caudata* (Pennell) B. Boivin, and var. *yukonis*. The latter two forms were treated as separate species by Pennell (1934). Neither of these is strongly divergent from the nominate variety, which appears to have a wide range across much of northern-central and northeastern Eurasia. Pennell believed that the nominate form also occurs in coastal northwestern Alaska. My examination of herbarium sheets supports this assertion, especially with collections from the general

vicinity of Nome, Alaska. However, further fieldwork in that region will be needed to clarify the status and distribution of var. *pallida* in North America.

Among the additional Nearctic taxa treated by Pennell (1934) and Hultén (1949) as part of the *Castilleja pallida* complex, I regard *C. annua* Pennell as synonymous with *C. pallida* var. *caudata*. The type collection of *C. annua* represents an inconstant morph with small flowers and branching stems found sporadically throughout much of the range of var. *caudata* and usually grading into the more typical morphs within populations and local areas.

The closely related taxa *Castilleja elegans* Malte and *C. raupii* Pennell are more strongly differentiated from *C. pallida* and deserve recognition as full species.

Castilleja pectinata M. Martens & Galeotti var. ***purpusii*** (Brandege) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja purpusii* Brandege, Zoe 5: 181, 1904. TYPE: México. Est. de México: on rocky slopes above the timber line of [Volcán] Iztaccihuatl [= Iztaccihuatl], Mar-Jul 1903, *Purpus 320* (holotype: UC!; isotypes: GH!, MO!, RSA-POM!, US!).

Comments: The taxon described as *Castilleja purpusii* is very similar to the earlier *C. pectinata*, but the vegetative characters originally used to distinguish the two are consistent in the plants found on the subalpine slopes of the Volcán Iztaccihuatl-Volcán Popocatepetl massif, to which var. *purpusii* appears to be endemic.

Castilleja rubicundula (Jeps.) T.I. Chuang & Heckard var. ***lithospermoides*** (Benth.) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Orthocarpus lithospermoides* Benth., Scroph. Ind.: 13, 1835. *Castilleja rubicundula* subsp. *lithospermoides* (Benth.) T.I. Chuang & Heckard, Syst. Bot. 16: 658, 1991. TYPE: United States. (Nova) California: [probably in San Francisco Bay region or southwestern portion of Sacramento Valley], (1833) [1831,1832 or possibly Nov 1833], *Douglas s.n.* (holotype: K-BENTH!; isotypes: BM!, CGE!, GH!, PH!). [Note: the Kew Herbarium labels on some of the type sheets indicate the collection date as 1833, but this is probably incorrect, as Douglas was only in California from 4-28 November of that year, during which time it is very unlikely that this Spring annual would be in full bloom. It is

also possible that 1833 indicates when Bentham actually received the specimens at Kew. The isotype sheet at PH contains two different collections of this taxon, with the type collection represented only by a single stem mounted on the left side of the sheet, with a specimen from another collector on the right. The GH isotype sheet contains only a single stem of type material mounted on the far right portion of the sheet, along with stems from three other collections of the same species obtained by others mounted elsewhere.]

Castilleja subinclusa Greene var. *jepsonii* (Bacig. & Heckard) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja jepsonii* Bacig. & Heckard, Leafl. W. Bot. 10: 282, 1966. TYPE: United States. California: San Benito Co., north-facing slope of side-cañon, among shrubs of *Haplopappus linearifolius*, just north of “Syncline Divide”, in narrow valley of Vallecitos Creek, along road to New Idria, about 10.5 miles south of Panoche, elevation about 2000 feet, 14 May 1958, *Bacigalupi 6343*, with *Robbins & Hutchison* (holotype: JEPS!; isotypes: BM!, CAS!, F!, GH!, JEPS!, MICH!, NY!, OSC!, RSA!, US!, WTU!).

Castilleja exserta Eastw. ex C.F. Baker, W. Amer. Pl. 3: 4, 1904, nomen nudum. TYPE: United States. California: Tulare Co., S. Fork Kaweah River, Summer 1904, *Culbertson s.n.*, distributed as *Baker 4300* (holotype: CAS?; isotypes: K!, MO!, ND-G!). [Note: this name is spelled “*exerta*” by Eastwood on the isotype sheets.]

Comments: Although *Castilleja jepsonii* was subsumed within *C. subinclusa* by Chuang & Heckard (1993), the characters used by Bacigalupi & Heckard to first distinguish it from *C. subinclusa* at the species level appear to be consistent and sufficient to warrant recognition at the varietal level. In addition, var. *jepsonii* occurs in more open, brushy, and xeric habitats than does the uncommon nominate variety, which is limited to openings and borders in oak woodlands of the central-western foothills of the Sierra Nevada.

Castilleja tenuiflora Benth. var. *tancitaroana* (G.L. Nesom) J.M. Egger, **comb. et stat. nov.** BASIONYM: *Castilleja tancitaroana* G.L. Nesom, Phytologia 73: 401, 1992. TYPE: México. Michoacán: Mpio. Ziracuaretiro, 12 km NE of Uruapan, in San Andres Coru, pine-oak woods, “someros” soils in malpais, 1710 m,

24 May 1980, *Soto N. 2211* (holotype: TEX!; isotype: MEXU!).

Comments: This recently described taxon from central Mexico is distinguished by relatively minor but reasonably consistent features from typical *C. tenuiflora*. However, my field work across most parts of the described range indicates that the differences are not as extensive or consistent as portrayed in the protologue, and I believe that this form is better viewed as a morphological variant of *C. tenuiflora*. However, because it occurs in fairly uniform populations, with a definable center of distribution in Michoacán, I favor maintaining it at the varietal level. The two varieties are almost inseparable in the field, but the odd, mostly sunken glandularity of the foliage in var. *tancitaroana* is striking under magnification and unusual in the genus as a whole.

ACKNOWLEDGEMENTS

I wish to thank the curatorial staff of the following herbaria for timely and valuable assistance with loans of specimens, digital photography of type specimens, and other herbarium-related matters: ALA, ARIZ, ASC, ASU, BKL, BM, BR, BRIT, CM, CAN, CAS, CGE, CIIDIR, COLO, CPUN, DES, DS, ENCB, F, G, GH, HAL, HAO, HU, HUT, IEB, K, KANU, LIV, LY-BON, LY-GAN, LINN, MICH, MIN, MO, MEXU, MSC, MT, MW, NA, ND, ND-G, NMC, NO, NY, OKLA, OSC, OSC-ORE, OSC-WILLU, P, PH, RENO, RM, RSA, RSA-POM, S, SD, SJNM, TEX/LL, TUR, UC/JEPS, U, UBC, UCR, UNM, US, UT, UTC, UVSC, V, UVIC, VT, WIS, WS, WTU, Z, and ZEA. I also thank especially David Giblin (Collections Manager) and Richard Olmstead (Curator) of WTU for their continuing logistical support of my work on *Castilleja* and related genera and to Noel Holmgren (NY), Guy Nesom (BRIT) and Dave Tank (Y) for their critiques of the manuscript.

LITERATURE CITED

- Bentham, G. 1846. Scrophulariaceae, p. 186-586 in: DeCandolle, A. P., *Prodromus systematis naturalis regni vegetabilis*, Vol. 10. Treuttle & Würtz, Paris.
- Boivin, B. 1952. Subordination des variations de *Castilleja pallida* (Linné) Sprengel. *Nat. Canad.* 79: 320-321.

- Eastwood, A. 1909. Synopsis of the Mexican and Central American species of *Castilleja*. Proc. Amer. Acad. Arts 44: 565-591.
- Chuang, T.I. and L.R. Heckard. 1991. Generic realignment and synopsis of subtribe Castillejinae (Scrophulariaceae – Tribe Pedicularieae). Syst. Bot. 16: 644-666.
- Chuang, T.I. and L.R. Heckard. 1992. Nomenclatural changes of some Californian *Castilleja* (Scrophulariaceae). Novon 2: 185-189.
- Chuang, T.I. and L.R. Heckard. 1993. *Castilleja*. P. 1016-1024 in: J. C. Hickman, ed. The Jepson Manual. Higher Pl. of Calif. Univ. of Calif. Press. Berkeley, CA.
- Gray, A. 1880. Revision of the genus *Castilleja*. Amer. J. Sci. Arts, Ser. 2, 34: 335-339.
- Holmgren, N.H. 1970. *Castilleja*. P. 1439-1442 in: D. S. Correll and M. C. Johnston. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, TX.
- Holmgren, N.H. 1971. A taxonomic revision of the *Castilleja viscidula* group. Mem. N. Y. Bot. Gard. 21: 1-63.
- Holmgren, N.H. 1973. *Castilleja*. P. 416-422 in: C. L. Hitchcock and A. Cronquist, eds. Flora of the Pacific Northwest. Univ. of Washington Press, Seattle, WA.
- Holmgren, N.H. 1976. Four new species of Mexican *Castilleja* (subgenus *Castilleja*, Scrophulariaceae) and their relatives. Brittonia 28: 195-208.
- Holmgren, N.H. 1978. *Castilleja* (Scrophulariaceae) of Costa Rica and Panama. Brittonia 30: 182-194.
- Holmgren, N.H. 1984a. Scrophulariaceae. P. 344-506 in: A. Cronquist, A. H. Holmgren, N. H. Holmgren, and J. L. Reveal, eds., Intermountain flora, Vol. 4. New York Bot. Gard., NY.
- Holmgren, N.H. 1994. Redefinition of *Dodecatheon dentatum* (Primulaceae) and rationale for use of varietal rank. Brittonia 46: 87-94.
- Holmgren, N.H. 1984b. *Castilleja*. P. 174-184 in: G. Harling and B. Sparre, eds. Flora of Ecuador, Vol. 21. Publ. House Swedish Research Councils, Stockholm, Sweden.
- Hultén, O.E.G. 1949. Fl. of Alaska and Yukon. Lunds Universitets Årsskrift N.F., Avd. 2, 45: 1386-1397.
- Iltis, H.H., G.L. Nesom, and J.M. Egger. 2003. *Castilleja albobarbata* sp. nov. (Orobanchaceae) from Sierras Manantlán and Cacoma, Jalisco, Mexico. Sida 20: 1343-1350.

- Keck, D.D. 1927. A revision of the genus *Orthocarpus*. Proc. Calif. Acad. Sci. IV, 16(17): 517-571.
- Keck, D.D. 1951. *Orthocarpus*. P. 810-819 in: L. Abrams, ed., Illust. fl. of the Pacific States, Vol. 3, Stanford Univ. Press, Palo Alto, CA.
- Munz, P.A. 1932. Southern California plant notes 4. Bull. S. Calif. Acad. Sci. 31: 61-70.
- Munz, P.A. 1958. California miscellany 4. Aliso 4: 87-100.
- Nesom, G.L. 1992. Taxonomy of the *Castilleja tenuiflora* group (Scrophulariaceae) in México, with an overview of sect. *Castilleja*. Phytologia 73: 389-415.
- Olmstead, R.G., C.W. dePamphilis, A.D. Wolfe, N.D. Young, W.J. Elisons, and P.A. Reeves. 2001. Disintegration of the Scrophulariaceae. Amer. J. Bot. 88: 348-361.
- Ownbey, M. 1959. *Castilleja*. P. 295-326, in: C. L. Hitchcock, A. Cronquist, and M. Ownbey, eds. Vasc. pl. of the Pacific Northwest, Part 4: Ericaceae through Campanulaceae. Univ. of Wash. Press, Seattle and London.
- Parish, S.B. 1901. Errors in the reported stations of some southern California plants. Zoe 5: 109-120.
- Pennell, F.W. 1934. *Castilleja* in Alaska and northwestern Canada. Proc. Acad. Nat. Sci. Phila. 86: 517-540.
- Pennell, F.W. 1951. *Castilleja*. P. 819-846 in: L. Abrams, ed., Illust. fl. of the Pacific States, Vol. 3, Stanford Univ. Press, Palo Alto, CA.
- Rebristaya, O.V. 1964. Genus *Castilleja* Mutis in Eurasia. Nov. Syst. Pl. Vasc. 1964: 283-311.
- Turner, B.L. and G.L. Nesom. 2000. Use of variety and subspecies and new varietal combinations for *Styrax plantifolius* (Styraceae). Sida 19: 257-262.
- Weddell, H.A. 1857. Chloris Andina, Vol. 2. Chez P. Bertrand, Paris.