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PECTOCARYA ANISOCARPA, A NEW SPECIES OF BORAGINACEAE, AND A REVISED KEY FOR THE GENUS IN WESTERN NORTH AMERICA

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ABSTRACT

Pectocarya is a genus of 13 currently accepted taxa in Boraginaceae, subtribe Cryptanthinae. The genus has an amphitropical distribution in the New World, with eight taxa in western North America, seven in South America, and two occurring in both continents. Members of *Pectocarya* are distinctive in having a bilaterally or radially symmetrical fruit of four strongly divergent nutlets. Taxa within the genus are distinguished largely by the morphology of the nutlets, including shape, size, margin, posture, and variability both within a fruit and/or within a plant. *Pectocarya* "anisocarpa" (Boraginaceae) was previously named and described, but not validly published. Along with taxon-specific nutlet ornamentation, *P.* "anisocarpa" has fruits within a plant that are monomorphic and nutlets within a fruit that are heteromorphic. It is common throughout its range, which in the United States includes the southern half of California, Arizona, and southern Utah to the east. The species' southernmost extent is in northwestern Baja California, Mexico. It is often encountered in mixed populations with congeners, and has been confused historically with *P. penicillata* and *P. linearis* var. *ferocula* in California and Baja California and *P. heterocarpa* in Arizona and Utah. Here we validly publish the name **P. anisocarpa**, as well as provide illustrations, an image of the holotype specimen, and a range map of the new taxon. A revised taxonomic key and photographs of the fruits of the North American *Pectocarya* taxa are also included.

Key words: Biogeography, Boraginaceae, Cryptanthinae, *Gruvelia*, *Pectocarya*, *Pectocarya anisocarpa*.

Pectocarya DC. ex Meisn. is a genus of diminutive annual herbs in Boraginaceae, tribe Cynoglosseae (Långström and Chase 2002; Schwarzer 2007; Weigend 2010; Nazaire and Hufford 2012), subtribe Cryptanthinae (Hasenstab-Lehman and Simpson 2012). The genus is characterized by a bilaterally or radially symmetrical fruit of four strongly divergent nutlets. The currently recognized *Pectocarya* taxa have been placed in sect. *Gruvelia* I.M.Johnst. [= subgenus *Gruvelia* Gray] and sect. *Pectocarya* [as *Eupectocarya* = subgenus *Knetospermum* Gray] (Johnston 1924). Section *Gruvelia* includes only *P. pusilla* and *P. setosa* both with opposite basal leaves, radially symmetrical calyces, and calyx lobes that exceed the nutlets at maturity (Fig. 1–6). Members of sect. *Pectocarya* have alternate basal leaves, bilaterally symmetrical calyces, and calyx lobes that are shorter than the nutlets at maturity. *Pectocarya* is amphitropically distributed between North America and South America, with two species (*P. linearis* and *P. pusilla*) shared between these regions; the remainder of the species are endemic to either North America or South America (Table 1).

Several morphological features have been used to circumscribe taxa in *Pectocarya*, and fruit features have been among the most important historically. The three-dimensional shape of the fruit is variable in the genus, with some taxa bearing fruits comprising nutlets in one plane (e.g., *P. linearis* var. *ferocula*; Fig. 7–12), and others bearing fruits of nutlets not in one plane (e.g., *P. recurvata*; Fig. 13–15). Nutlets of *Pectocarya*, as we are describing them, consist of a central *body*, with or without marginal *wings* (thin, membranous tissue that is confluent along nutlet margin), *teeth* (where membranous tissue forms discrete, incised lobes), and/or *hairs* or *bristles*. *Ornamentation* refers to the morphology of any marginal wings, teeth, or hairs/bristles. Within a fruit, the shape of the nutlet body is taxonomically important, with nutlet body shapes ranging from linear to obovate. Nutlet margins in *Pectocarya* are generally diversely ornamented with teeth, hairs, uncinate bristles, or expanded wings of tissue; combinations of these features are common. However, these taxonomically important features—fruit planarity, nutlet shape, and nutlet margin ornamentation—can vary weakly to strongly within a species. Subtle variation in these features sometimes occurs within a single plant; in many taxa of *Pectocarya*, nutlets exhibit a very slight and gradual change in size and ornamentation from the base to the apex of the plant. However, in other taxa there is a strong and discontinuous variation in nutlet morphology within a plant, either between nutlets within a single fruit or between nutlets at the base versus apex of the plant (or both). These latter aspects of nutlet variation are of significant taxonomic importance.

Morphological variability among fruits within an individual is termed here fruit *dimorphism*. Strong fruit dimorphism, marked by large and discontinuous morphological differences between fruits at the base of the plant and those along the inflorescences, is found in *P. heterocarpa* and *P. peninsularis* of North America, and *P. dimorpha* of South America.

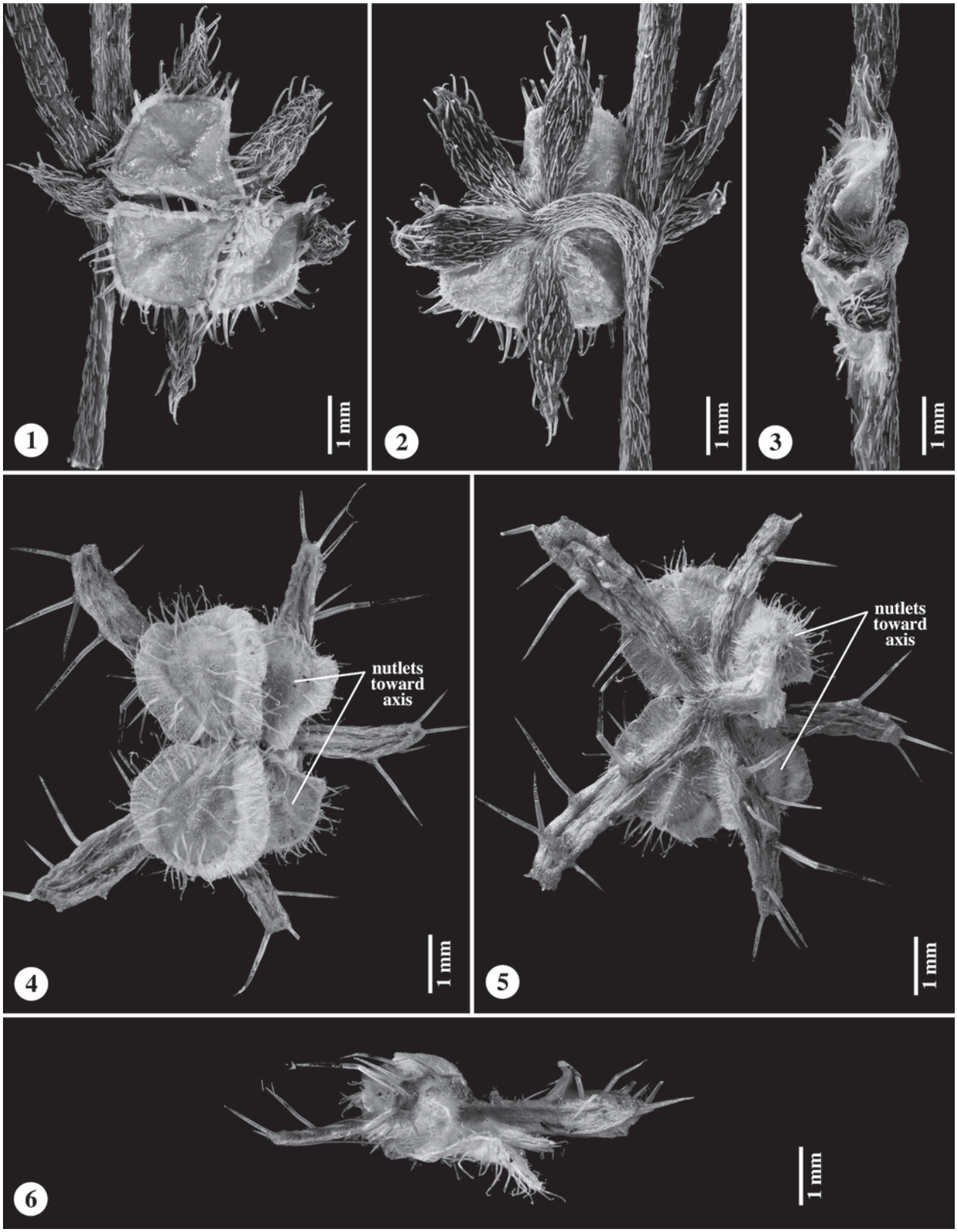

Fig. 1–6. *Pectocarya* sect. *Gruvelia*.—1–3. *Pectocarya pusilla* (*Guilliams 995*), in face (1), back (2), and side (3) views. Note that one nutlet is missing in this material.—4–6. *Pectocarya setosa* (*Simpson 2372*, SDSU 17305), in face (4), back (5), and side (6) views. Scale bar = 1 mm. All nutlet images were obtained using a Visionary Digital BK Plus Lab System.

Table 1. Currently recognized *Pectocarya* taxa, with information on distribution. Asterisks (**) denote a taxon present in both North America and South America.

Pectocarya of North America	Distribution
Pectocarya anisocarpa Veno (this paper)	Mexico: Baja California; USA: AZ, CA, UT
Pectocarya heterocarpa (I.M.Johnst.) I.M.Johnst.	Mexico: Baja California, Sonora; USA: AZ, CA, NM, NV, TX, UT
Pectocarya linearis (Ruiz & Pav.) DC. var. *ferocula* I.M.Johnst.**	Mexico: Baja California, Baja California Sur; USA: CA
Pectocarya penicillata (Hook. & Arn.) A.DC.	Canada: British Columbia; Mexico: Baja California; USA: AZ, CA, ID, NV, OR, WA, WY
Pectocarya peninsularis I.M.Johnst.	Mexico: Baja California, Baja California Sur; USA: CA
Pectocarya platycarpa (Munz & I.M.Johnst.) Munz & I.M.Johnst.	Mexico: Baja California, Sonora; USA: AZ, CA, NM, NV, TX, UT
Pectocarya pusilla (A.DC.) A.Gray**	USA: CA, OR, WA
Pectocarya recurvata I.M.Johnst.	Mexico: Baja California, Sonora; USA: AZ, CA, NM, NV
Pectocarya setosa A.Gray	Mexico: Baja California; USA: AZ, CA, ID, NM, NV, OR, UT, WA
Pectocarya of South America	Distribution
Pectocarya anomala I.M.Johnst.	Chile; Peru
Pectocarya boliviana (I.M.Johnst.) I.M.Johnst.	Bolivia
Pectocarya dimorpha (I.M.Johnst.) I.M.Johnst.	Chile
Pectocarya lateriflora (Lam.) DC.	Argentina; Bolivia; Peru
Pectocarya linearis (Ruiz & Pav.) DC. var. *ferocula* I.M.Johnst.**	Argentina; Chile
Pectocarya linearis (Ruiz & Pav.) DC. var. *linearis*	Argentina; Chile
Pectocarya pusilla (A.DC.) A.Gray**	Chile

Figures 16–19 show basal and cauline fruits of *P. heterocarpa*. Note the reduced marginal ornamentation of the nutlets in the basal fruits relative to the nutlets in cauline fruits, the common pattern when fruits are dimorphic. Interestingly, this pattern of strongly dissimilar basal and cauline fruits appears to be associated with flowers being either cleistogamous or chasmogamous, respectively (Veno 1979). Basal fruits derived from cleistogamous flowers are often found buried beneath the soil surface and are easily overlooked. For the majority of *Pectocarya* taxa, however, fruit monomorphism is the common condition.

Where nutlets within an individual fruit differ, the nutlets are termed *heteromorphic*. Nutlets that are all alike within a fruit are termed homomorphic. In *Pectocarya*, when nutlets within a fruit vary, it is generally the lower nutlet closest to the inflorescence axis that differs from the remaining three nutlets. Occasionally, both nutlets toward the inflorescence axis will be less or differently ornamented and smaller, often due in part to a reduced marginal wing. Prior to Veno (1979), six species were known to possess heteromorphic nutlets: *P. heterocarpa*, *P. peninsularis*, *P. platycarpa*, and *P. setosa* from North America, and *P. dimorpha* and *P. lateriflora* from South America. Figures 20–22 show cauline fruits of *P. peninsularis* with markedly heteromorphic nutlets. Note that *P. platycarpa* (Fig. 23–25) was originally described as possessing heteromorphic nutlets (Johnston 1928), but almost all subsequent state and regional treatments describe it as homomorphic. All other North American *Pectocarya* taxa, including *P. linearis* var. *ferocula*, *P. penicillata*, and *P. recurvata*, were described as possessing equal to subequal nutlets, meaning that nutlets are homomorphic (Johnston 1932; Abrams 1951; Kearney and Peebles 1960; Munz 1973, 1974).

During her dissertation studies, Veno (1979) discovered an undescribed *Pectocarya* species from central and southern California, Arizona, southwestern Utah, and Baja California, Mexico. This new taxon, which she referred to as *P.* ''anisocarpa'', was determined in that study to be tetraploid ($n = 24$) and to have diagnostic nutlet ornamentation, monomorphic fruits, and heteromorphic nutlets. The name *P.* ''anisocarpa'' was never validly published. In preparation for writing the taxonomic treatment for *Pectocarya* (Boraginaceae) for the Flora of North America North of Mexico, Kelley and Guilliams began evaluating this unpublished species to determine if it warranted taxonomic recognition. After studying Veno's work (1979), herbarium specimens annotated as *P.* ''anisocarpa'' by Veno, herbarium records of all *Pectocarya* taxa at CAS, DS, JEPS, UC, and UCR, and plants in the field (by Kelley in 2012), it is clear that *P.* ''anisocarpa'' is morphologically distinct. Here we provide a valid publication of *P.* ''anisocarpa'', which includes a formal description, an illustration, an image of the holotype specimen, photographs of fruits, a range map, and discussion of morphologically similar congeners. We conclude with a revised taxonomic key for members of the genus in North America.

Pectocarya anisocarpa Veno, sp. nov. (Fig. 26–32).—TYPE: USA. California, Kern County: gravel wash approximately 300 ft W of California State Highway 14, 0.25 mi S of Red Rock Canyon, 21.5 mi NE of Mojave, 3000 ft, 20 Mar 1977, *Veno 357* (holotype CAS; isotypes RSA, SD).

Description.—[Note: means and ± one standard deviation are listed in brackets]. Plant an annual herb, branched from the base. Stems slender, prostrate to decumbent, cinereous-strigose appressed, 4.0–30.0 cm [11.3 ± 5.7 cm] long. Leaves narrow, linear, cinereous-strigose appressed to setulose, 1.0–7.0 cm [3.8 ± 0.6 cm] long, 0.25–1.0 mm [0.4 ± 0.1 mm] wide. Flowers chasmogamous; pedicels in flower 0.25–0.5 mm [0.4 ± 0.1 mm] long; calyces in flower setulose, lobes five, lanceolate, 0.75–1.4 mm [1.0 ± 0.2 mm] long; corollas funnelform, lobes five, 0.5–2.25 mm [1.4 ± 0.3 mm] long, limb 0.5–1.0 (1.5) mm in diameter, fornices five, yellow. Pedicels in fruit free, ascending (to recurved), 1.25–2.75 mm [2.0 ± 0.2 mm] long. Calyces in

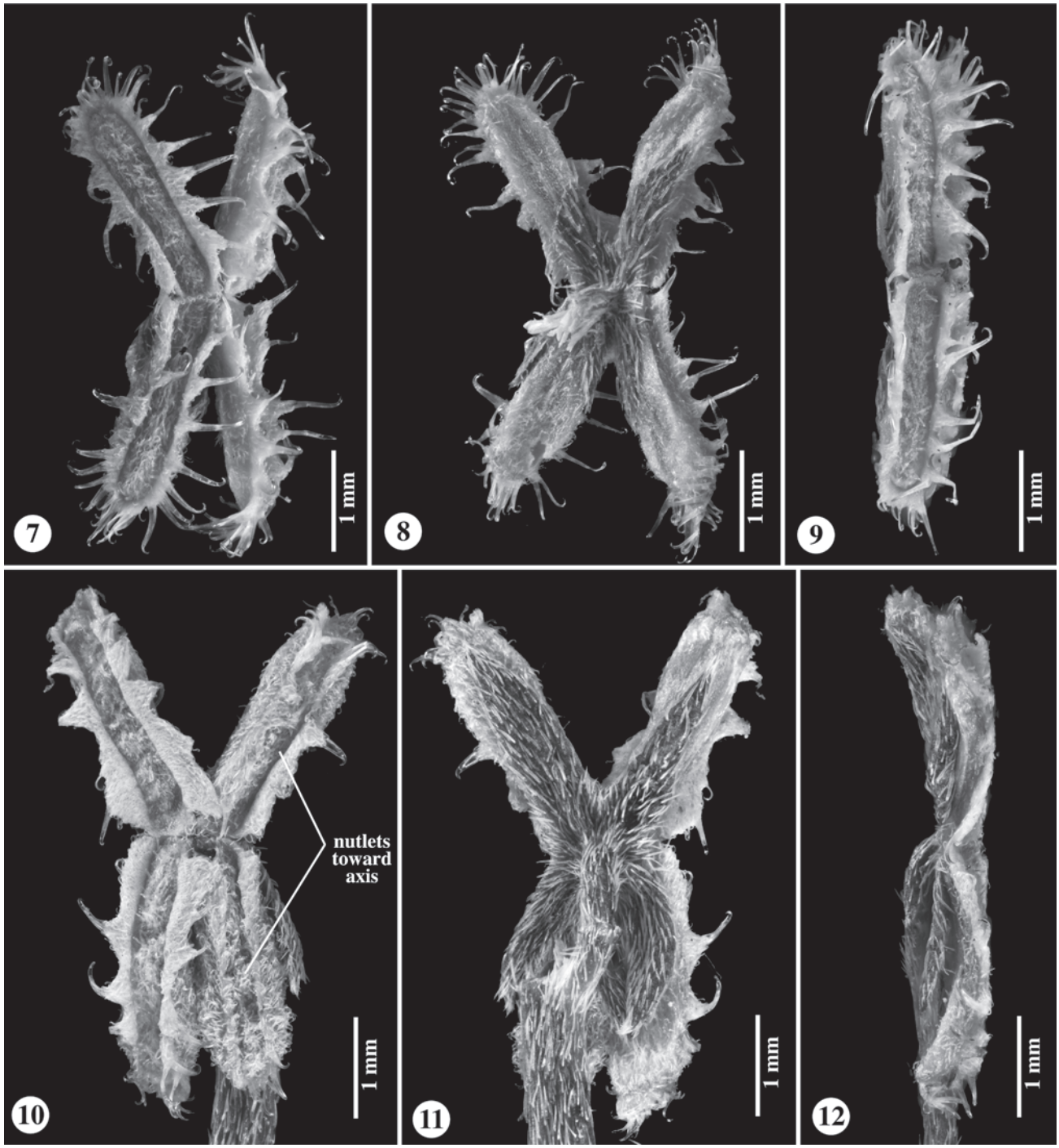

Fig. 7–12. *Pectocarya linearis* var. *ferocula*.—7–9. Fruit of homomorphic nutlets (*Simpson 25IV96B*, SDSU 12126), in face (7), back (8), and side (9) views.—10–12. Fruit of heteromorphic nutlets (*Kelley 1974*), in face (10), back (11), and side (12) views. Side view shows nutlets in one plane. Note slightly reduced wings of nutlets toward inflorescence axis. Scale bar = 1 mm.

fruit bilaterally symmetrical, lobes divaricate, 2.6–3.9 mm [3.3 ± 0.3 mm] long, shorter than the nutlets. Fruits monomorphic; nutlets generally four per fruit, arranged in two pairs, heteromorphic; nutlet bodies oblanceolate, 1.5–2.5 mm [2.0 ± 0.2 mm] long, 0.4–0.75 mm [0.6 ± 0.1 mm] broad; nutlet outline oblance-ovate to oblong; nutlets winged; wings ascending to erect (to rarely subinvolute); wings on nutlets toward the inflorescence axis, especially lower, narrow, 0.05–0.25 mm [0.15 ± 0.05 mm] wide, margin bearing few, irregularly spaced bristles; wings on nutlets away from the inflorescence axis 0.3–0.75 mm [0.5 ± 0.1 mm] wide, margin undulate to shallowly and broadly dentate, generally with uncinate bristles; all nutlets with a distal pectinate fringe of uncinate bristles; gynobase broad-pyramidal. Chromosome number $n = 24$ (Veno 1979).

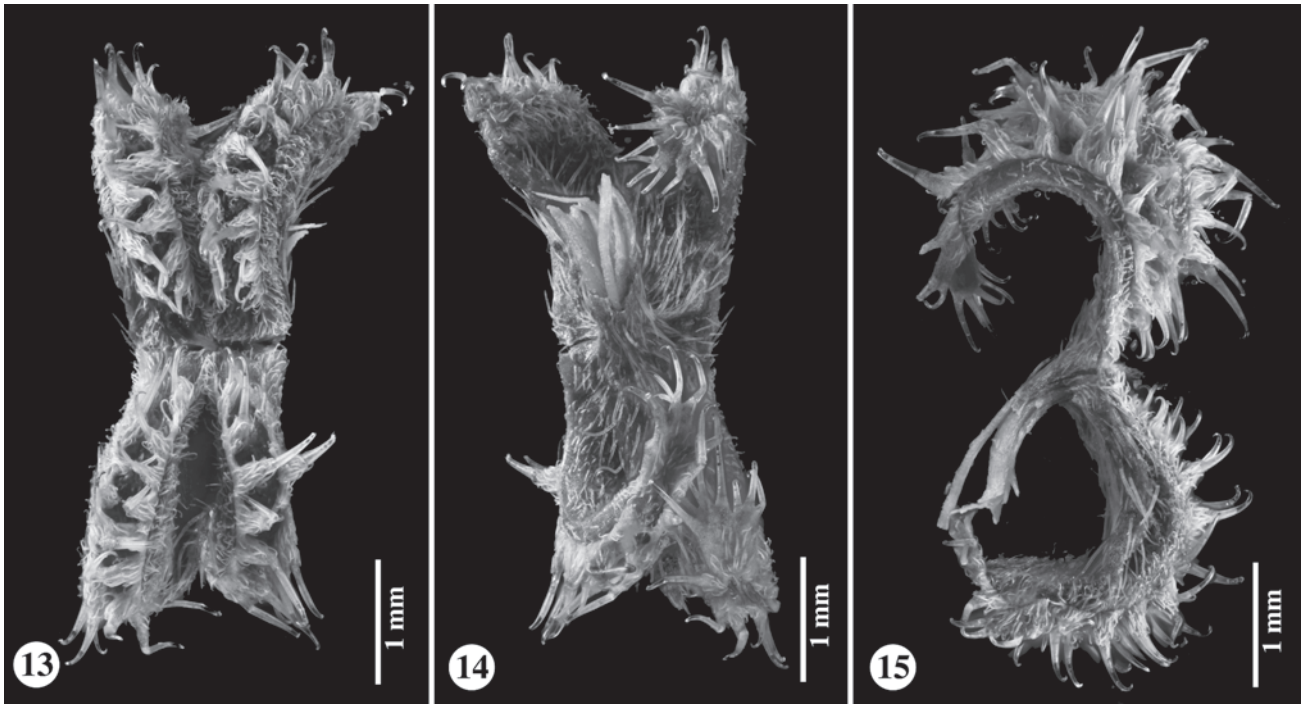

Fig. 13–15. *Pectocarya recurvata* (*Young 12*, SDSU 12802), in face (13), back (14), and side (15) views. Side view shows nutlets not in one plane. Scale bar = 1 mm.

Phenology.—*Pectocarya anisocarpa* usually sprouts with early winter rains in October or November and dies mid-May, with maximal flowering from mid-March through mid-April.

Distribution and ecology.—*Pectocarya anisocarpa* is common in shrub-grassland ecotonal regions of west central to southern California, and extends somewhat disjunctly into southwestern Utah, western and southern Arizona, and northwestern Baja California, Mexico (Fig. 31). It is most commonly found in disturbed habitats, desert shrub associations, grasslands, chaparral openings, oak woodlands, roadsides, and washes. It occurs from the relatively mesic inner central California Coast Ranges and western San Joaquin Valley southward to the Mojave and, less commonly, Sonoran deserts at elevations of 90 m (300 ft) to 1500 m (5000 ft). A list of all *P. anisocarpa* specimens examined, arranged by region, is given in Appendix 1.

Etymology.—The specific epithet *anisocarpa*, meaning unequal fruits, refers to the heteromorphic nutlets.

DISCUSSION

Pectocarya anisocarpa is a widespread, morphologically distinctive taxon that is most common in central and southern California. Based on a search of herbarium records, it appears to have been first collected in Fallbrook, San Diego County, California, by Marcus E. Jones on 28 Mar 1882. Since then, it has been routinely mistaken for *P. penicillata*, *P. heterocarpa*, *P. peninsularis*, and occasionally *P. linearis* var. *ferocula*, and mixed collections of *P. anisocarpa* and these taxa are common. It was not until taxonomic and cytological analysis of the genus by Veno (1979) that *P. anisocarpa* was recognized as a distinct taxonomic entity. It was first afforded published recognition in Volume 4 of the Intermountain Flora as "*Pectocarya* sp." (Cronquist et al. 1984).

Pectocarya anisocarpa is a member of the *Pectocarya penicillata* Group (sensu Veno 1979), which also includes *P. heterocarpa*, *P. penicillata*, and *P. peninsularis*. It can be distinguished from these congeners using a combination of morphological features. *Pectocarya anisocarpa* is morphologically and ecologically most similar to *P. penicillata*, so not surprisingly, it is this taxon with which *P. anisocarpa* has been most often confused. Both species have nutlets with a dense, pectinate fringe of uncinate bristles distally (Fig. 33–35). *Pectocarya anisocarpa* differs in having heteromorphic nutlets, while *P. penicillata* possesses homomorphic nutlets. In addition, the nutlet wings of *P. penicillata* are bilobed and generally without teeth or bristles proximally. In contrast, in *P. anisocarpa* the nutlet wings on the pair of nutlets away from the inflorescence axis generally have an undulate margin with regularly spaced uncinate bristles proximally. Nutlets of *P. anisocarpa* towards the inflorescence axis have a reduced nutlet wing and fewer bristles and may bear a resemblance to the nutlets of *P. penicillata*.

In parts of its range, *P. anisocarpa* has been confused with *P. heterocarpa* and less frequently with *P. peninsularis*. It appears that all herbarium records of *P. heterocarpa* from the inner central California Coast Range region are misidentifications of *P. anisocarpa*. These three species may be confused, as all have cauline fruits with heteromorphic nutlets. *Pectocarya heterocarpa*, however, is easily distinguished from all congeners, including *P. anisocarpa*, by the presence of three unique features of the cauline fruits: biplanar pairs of nutlets, partial adnation of the pedicel to the lower nutlet toward the inflorescence axis, and resulting deformation of the lower

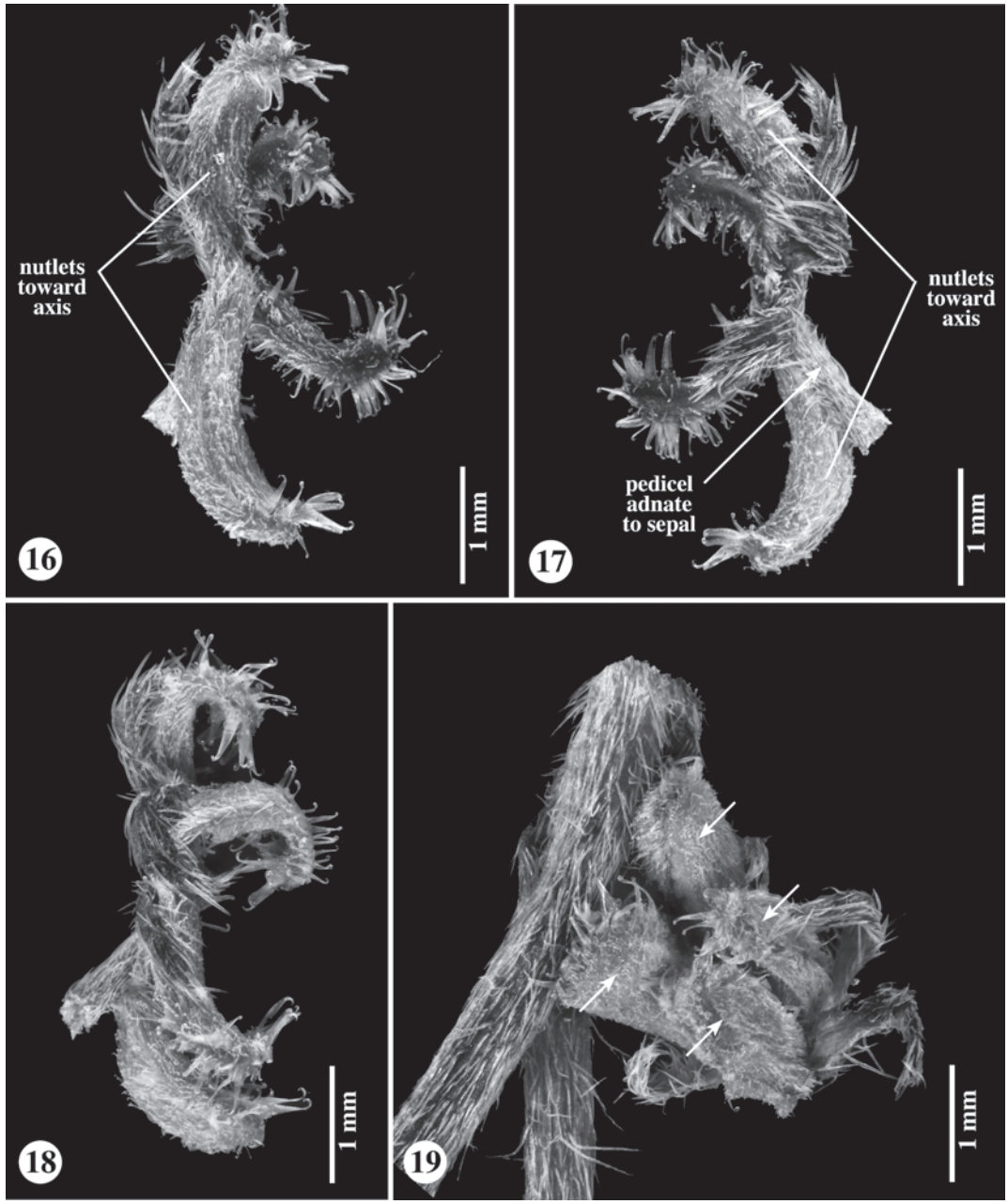

Fig. 16–19. *Pectocarya heterocarpa*.—16–18. Cauline fruit in face (16), back (17, both *Wedberg 1158*), and side (18, *Kelley 1987*) views. Note reduced wing of nutlets toward inflorescence axis.—19. Basal fruit (*Kelley 1987*), in face view; nutlets indicated by arrows. Note the irregular nutlet arrangement and the lack of nutlet ornamentation. Scale bar = 1 mm.

three calyx lobes (Johnston 1939; Fig. 16–19). *Pectocarya peninsularis* differs in possessing the largest corolla diameter of any *Pectocarya* species, 3–3.5 mm early in anthesis diminishing to 1.5 mm at the end of the period, while the remaining congeners, including *P. anisocarpa*, have corolla diameters from 1 to 1.5 mm diminishing to 0.5 mm. Additionally, both *P. heterocarpa* and *P. peninsularis* have dimorphic fruits, while *P. anisocarpa* has monomorphic fruits.

Pectocarya anisocarpa has been also misidentified as *P. linearis* var. *ferocula*, a member of the *Pectocarya recurvata* Group (sensu Veno 1979). Their ranges overlap considerably in California and they are often found growing together. *Pectocarya anisocarpa* can readily be distinguished from *P. linearis* var. *ferocula*, however, as nutlets of the former are broadly winged, with the wing margin subentire to undulate. Nutlets of *P. linearis* var. *ferocula* bear obvious teeth, arising directly from the nutlet body or from a narrow wing (Fig. 7–12). Note that Johnston (1932) originally described *P. linearis* var. *ferocula* as having homomorphic nutlets, a view that was adopted in all subsequent taxonomic treatments. Veno (1979) observed that nutlets of *P. linearis* var. *ferocula* may be slightly heteromorphic, but did not include this character state in her

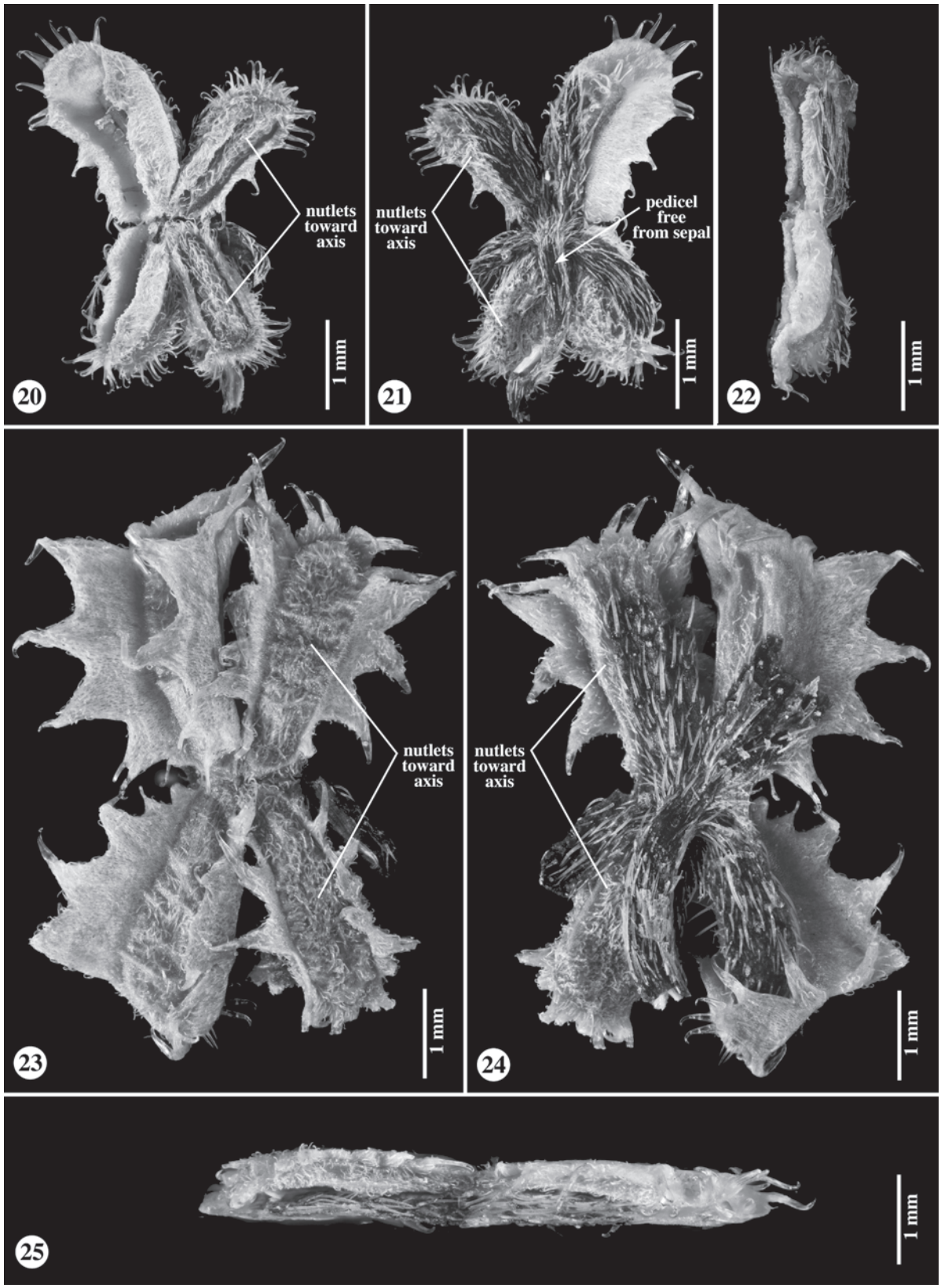

Fig. 20–25. *Pectocarya peninsularis* and *P. platycarpa*.—20–22. *Pectocarya peninsularis* cauline fruits (*Barth 135*, SDSU 17619), in face (20), back (21), and side (22) views. Note reduced wing of upper and lower nutlets toward inflorescence axis.—23–25. *Pectocarya platycarpa* (*Howe 3182*, SDSU 4020), in face (23), back (24), and side (25) views. Note reduced wing of nutlets toward inflorescence axis. Scale bar = 1 mm.

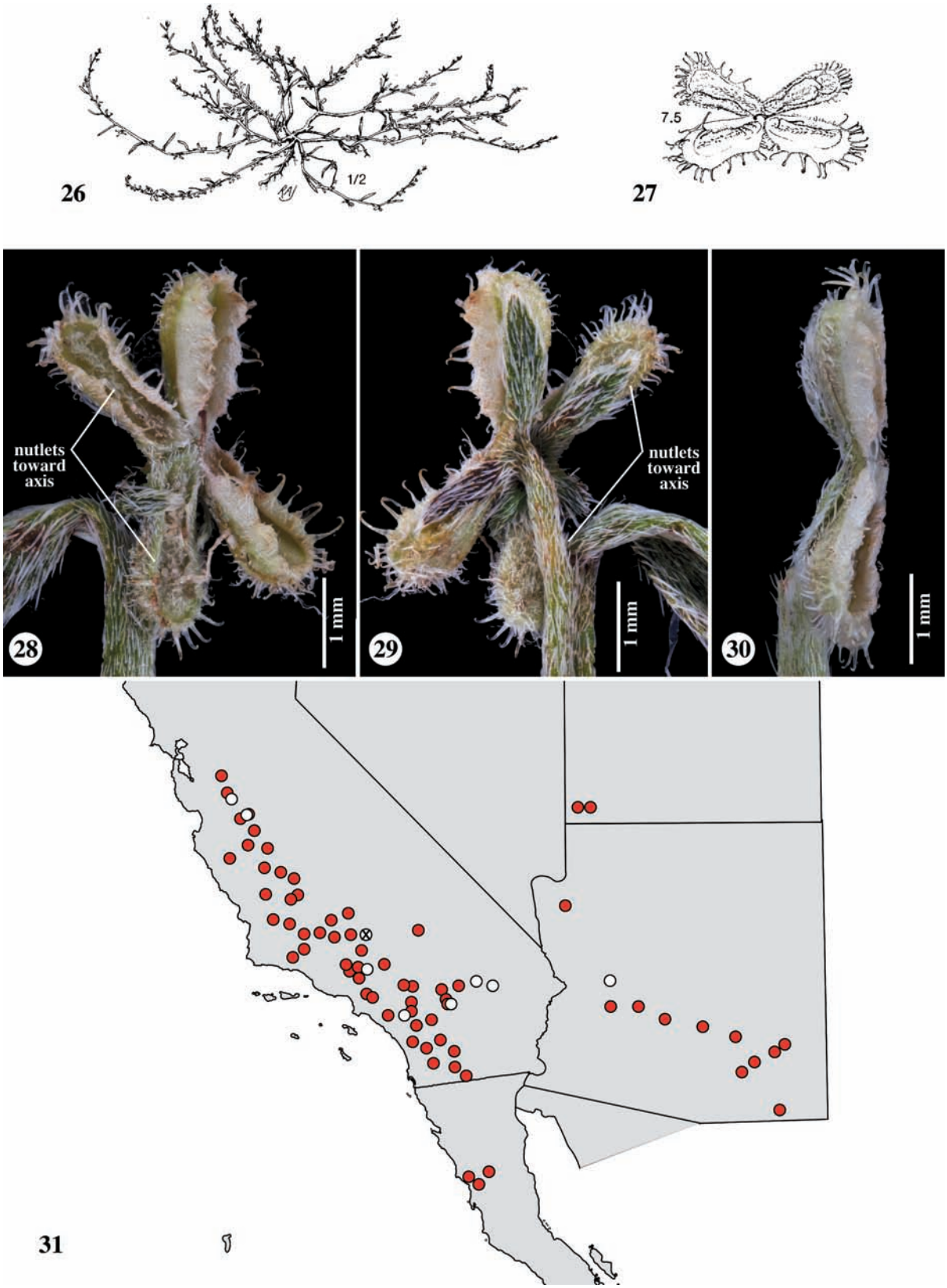

Fig. 26–31. *Pectocarya anisocarpa.*—26–27. Illustration from Cronquist 1984, page 289 (cited as *Pectocarya* sp.), courtesy of the New York Botanical Garden.—28–30. Nutlet images (*Kelley 1960*), in face (28), back (29), and side (30) views. Note reduced wing of nutlets toward inflorescence axis. Scale bar = 1 mm.—31. Map showing range of *Pectocarya anisocarpa* in western North America; open circles denote chromosome count voucher populations; open circle with "x" denotes the type locality.

Fig. 32. Scan of holotype of *Pectocarya anisocarpa*, *Veno 357* (CAS barcode 0214946).

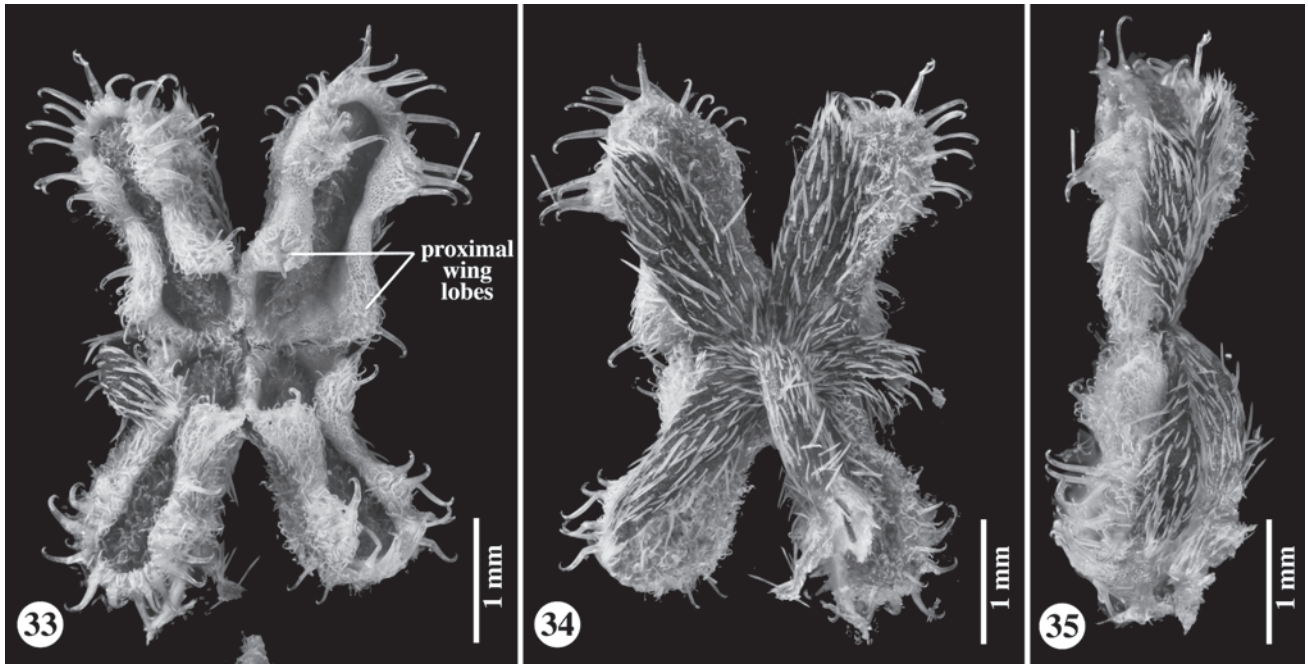

Fig. 33–35. *Pectocarya penicillata* nutlet images (*Guilliams 1066*), in face (33), back (34), and side (35) views. Scale bar = 1 mm.

key. Heteromorphic nutlets in *P. linearis* var. *ferocula* were often observed by Kelley during fieldwork, and Guilliams has occasionally observed this fruit feature during herbarium study. When nutlets are heteromorphic, it is often because the teeth (and narrow wing, if present) on the nutlets toward the inflorescence axis are angled inward, obscuring the central region of the nutlet body, while the teeth (and narrow wing, if present) on the nutlets away from the inflorescence axis are angled outward. This previously unreported nutlet heteromorphism may be the source of confusion for these two sympatric taxa. Our revised key (below) incorporates the observations that both *P. linearis* var. *ferocula* and *P. platycarpa* may have heteromorphic or homomorphic nutlets.

An investigation of chromosome numbers in *Pectocarya* by Veno (1979) showed that *P. anisocarpa* is a tetraploid, $n = 24$. Based upon geographic range and morphological intermediacy, Veno (1979) hypothesized that *P. anisocarpa* may be an allopolyploid derived from hybridization between the ancestors of the diploids *P. penicillata* and *P. heterocarpa* (followed by genome duplication). A molecular phylogenetic study is underway to evaluate this hypothesis (Guilliams et al., in prep).

TAXONOMIC KEY FOR *PECTOCARYA* IN NORTH AMERICA

Below is a revised taxonomic key for *Pectocarya* in North America reflecting the addition of *P. anisocarpa* and recent changes in our understanding of the genus. This key has been adapted from the treatment of the genus in the second edition of the Jepson Manual (Kelley 2012) and Veno's dissertation (1979).

1. Calyx radially symmetric, lobes > nutlets; nutlet body ± circular to obovate or ± rhomboid angular; lower cauline leaves opposite, fused at base (sect. *Gruvelia*)
   2. Nutlets homomorphic, equally divergent, nutlet body ± rhomboid angular; calyx lobe tip with slender, uncinate hairs; stem not branched or branched near base, sparsely strigose; pedicel in fruit 1–2.3 mm . . . . . *P. pusilla*
   2′ Nutlets heteromorphic, divergent in pairs, nutlet body ± circular to obovate; calyx lobe tip with pungent, straight bristles; stem branched above, ± hispid; pedicel in fruit ± 0.5 mm . . . . . *P. setosa*

1′ Calyx not radially symmetric, ± bilateral or irregular, lobes ≤ nutlets; nutlet body linear or oblanceolate to oblong or ovate-elliptic; lower cauline leaves generally alternate, not fused at base (sect. *Pectocarya*)
   3. Nutlets of cauline fruits homomorphic, all nutlets similar in size and/or degree of ornamentation
      4. Nutlets conspicuously winged, the wing margin often bearing bristles or teeth, wing ≥ teeth or bristles
         5. Nutlet wing ± lobed on both sides proximally, with uncinate hairs or bristles distally, not toothed . . . . . *P. penicillata*
         5′ Nutlet wing not appearing lobed, hairs and bristles absent, toothed the length of the nutlet, teeth stout . . . . . *P. platycarpa* (2)
      4′ Nutlets not conspicuously winged, nutlet body appearing to bear bristles or teeth ± directly, wing wanting or << teeth or bristles
         6. Stems ascending to erect; fruit not flat; nutlets strongly recurved to coiled . . . . . *P. recurvata*

6′ Stems prostrate to decumbent; fruit ± flat; nutlets straight or slightly recurved at tip . . . . . *P. linearis* var. *ferocula* (2)

3′ Nutlets of cauline fruits heteromorphic, the lower nutlet or both lower and upper nutlets toward inflorescence axis differing from nutlets away from inflorescence axis in size and/or degree of ornamentation

7. Cauline and basal fruits ± similar in shape and margin ornamentation (fruits monomorphic)

8. Nutlets away from inflorescence axis winged, wing margins ± undulate, not or barely toothed, not lacerate . . . . . *P. anisocarpa*

8′ Nutlets away from inflorescence axis winged or not, if winged, wing margin not entire to undulate, toothed to lacerate along ± length of nutlet

9. Stems ascending to erect; nutlet wing broad, tooth width at base ± = length, nutlet body ± oblong . . . . . *P. platycarpa* (2)

9′ Stems prostrate to decumbent; nutlet wing, if present, narrow, tooth width at base generally << length, nutlet body ± linear . . . . . *P. linearis* var. *ferocula* (2)

7′ Cauline and basal fruits strongly dissimilar (fruits dimorphic); basal fruit nutlets ± homomorphic, and having nutlets ± without marginal ornamentation, cauline fruit nutlets heteromorphic and with obvious nutlet ornamentation

10. Nutlets of cauline fruits in 2 planes; pair away from inflorescence axis incurved, nutlet wing laceratetoothed; pair toward inflorescence axis spreading to deflexed; pedicel in fruit partially adnate to lower nutlet toward inflorescence axis; corolla limb diameter 0.5–1 (1.5) mm . . . . . *P. heterocarpa*

10′ Nutlets of cauline fruits all in 1 plane; pair away from inflorescence axis flat, nutlet wing generally entire with uncinate bristles; pair toward inflorescence axis flat; pedicel in fruit free from nutlets; corolla limb diameter 1.5–3.5 mm . . . . . *P. peninsularis*

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APPENDIX 1.

Pectocarya anisocarpa specimens examined

ARIZONA. Cochise County. Valley near Camp Lowell, 6 May 1883, *Pringle s.n.* (F); mesas, Camp Lowell, Apr 1881, *Pringle s.n.* (US); mesas near Camp Lowell, 16 Apr 1881, *Pringle s.n.* (MO). Gila County. 10 mi W of Coolidge Dam, *Maguire, Richards, & Moeller 10469* (F, MO, UC, US); Six Shooter Canyon, *Pase 1798* (ASU). Graham County. Pinaleno Mts, *Bingham 1096* (ASU); 10 mi S of Safford, *Maguire, Richards, & Moeller 10140* (GH, MO, US); 14 mi S of Pima, *Maguire, Richards, & Moeller 10568* (GH). Maricopa County. Aguila, 3 Apr 1930, *M.E. Jones s.n.* (BM, MO); Wickenburg, 3 Apr 1921, *W.W. Jones s.n.* (K, MO); Peoria, 29 Apr 1896, *Orcutt s.n.* (UC); Wickenburg, *Peebles 8478* (F, UC). Mohave County. 14 mi SW of Hackberry, *Wiegand 1976* (GH). Pima County. 14 mi E of Tucson, *Brass 14189* (GH, MO, NY); Reddington, March–April 1913, *Kilgour s.n.* (ARIZ); Rillito, 9 Mar 1902, *Thornbur s.n.* (ARIZ). Pinal County. 6 mi N of Apache Junction, *Abrams 12943* (CAS-DS). Yavapai

County. US 93, 1.1 mi N of Santa Maria River bridge, *Pinkava et al. 11380b* (ASU); progeny of *Pinkava et al. 11380b*, 1.1 mi N of Santa Maria River bridge, University of California, Los Angeles, *Veno 485* (CAS). Unspecified County. Arizona, *Palmer 380* (US).—CALIFORNIA. Fresno County. 0.1 mi E of Fresno-San Benito County line, *Chisaki & Ray 2266* (ARIZ, BM, UC); Coalinga, *Eastwood 13438* (CAS); 1 mi E of Fresno County line, *Gould 231* (ARIZ); between Mendota and Coalinga, *Hoover 427* (CAS, UC); 9 mi E of Coalinga, *Hoover 2908* (UC); between Arroyo Hondo and Cantua Creek, *Hoover 3292* (GH, UC); Kettleman Hills, *Hoover 4250* (CAS, GH, UC); Coalinga, *Jepson 15354* (UC); W of Hayes Station, *Jepson 16979a* (UC); SE of Coalinga, *Jepson 17014* (UC); Coalinga, *Jepson 17018* (UC); Waltham Creek, *Keck 2152* (CAS-DS); Jacalitos Hills, *J.H. Thomas 12558* (CAS-DS). Imperial County. Jacumba Natural Area, In-Ko-Pah Mts, *J.P. Rebman 7122* (UCR). Inyo County. Pleasant Canyon, Panamint Mts, *J. Hirshberg 372* (UCR); Panamint Mts, *S.D. White 3277* (UCR). Kern County. Between Mojave and Calico, *Abrams 11817* (CAS-DS); Kern River Canyon, 7 Apr 1900, *Abrams s.n.* (CAS-DS); US Route 6, 16 mi N of Mojave, *Alava, Bacigalupi, & Tyron 1730* (UC); Mt. Breckenridge Road, *Benson 3081* (US); Rose Station, 28 Mar 1930, *S. Benson s.n.* (UC); Mojave Desert, *Bright 9209* (US); Bakersfield, *Davy 1726* (UC); Tehachapi Grade, *Ferris 4062* (CAS-DS); Owens Peak Eastern Watershed, saddle between Short Canyon and Five Fingers, *N. Fraga 328* (UCR); 2 mi NE of Caliente, *Higgins 8380* (NY); Maricopa Hills, *Hoover 3104* (ARIZ, GH, UC, US); 3 mi S of Blackwell's Corner, *J.T. Howell 5896* (CAS); Sand Canyon, *Howell & True 49131* (CAS); 12 mi E of Maricopa, *Keck 5868* (CAS-DS); Taft High School, *Keck & Clausen 3115* (CAS-DS, GH); Tejon Ranch, *Keck & Clausen 3170* (CAS-DS, GH); 3 mi SE of McKittrick, *Johannsen 1474* (UC); 5 mi S of Muroc, *Mason 6888* (GH, UC); Caliente Creek, *Munz 13658* (GH, UC); E side of Barren Ridge, *M. Provance 2004* (UCR); Wheeler Ridge, *Rose 37053* (UC); Mojave Desert, sand dunes on the S side of Koehn Dry Lake, *A.C. Sanders 7709* (SD); 5 mi NNE of California City on Randsburg-Mojave Road, May–June 1979, *T. Shields s.n.* (UCR); ¼ mi NW of Poso Mine, *C.N. Smith 47* (UC); Adobe Canyon, *C.N. Smith 1172* (UC); North Lost Hills, *Twisselmann 870* (CAS); Annette Road, Antelope Valley, *Twisselmann 920* (CAS); Middlewater Plain, *Twisselmann 973* (CAS-DS); Poso Creek Road, *Twisselmann 4199* (CAS); Silver Queen Road, *Twisselmann 6839* (CAS); E of Ridgecrest, *Twisselmann 11839* (CAS); Hwy 14, 0.25 mi S of Red Rock Canyon, *Veno 445* (CAS); San Joaquin Valley, *Wolf 6327* (ARIZ, W); Mojave, 13 Mar 1913, *Wooton s.n.* (US). King County. Hwy 41, 10 mi SW of Kettleman City, *Brenckle 51206* (UC); Kettleman City, *Hoover 2915* (CAS, UC); Kettleman Hills, *Hoover 2929* (GH, UC, US). Los Angeles County. Santa Susanna Mts, *Brewer 210* (GH, US); Soledad Pass, Kentucky Springs, *D. Charlton 3032B* (UCR); San Francisquito Canyon, *Clokey & Templeton 4674* (NY, UC in part); Padua Park, *D.S. Cooper 411-1* (UCR); Santa Clarita Valley, *M.A. Elvin 2449* (UCR); Bullrush Ridge, Santa Catalina Island, *F.R. Fosberg S-4655* (UCR); Pueblo de Los Angeles, 7 Mar 1884, *Gamble s.n.* (GH); Pasadena, *Grant 914* (UC); W of Lancaster, 24 Mar 1962, *Griesel s.n.* (CAS-DS); Verdugo Mts, *L. Gross 756* (UCR); Neenach School, Antelope Valley, E of California Poppy Preserve, *S.R. Hill 33343A* (UCR); *Jepson 19236* (UC); Lovejoy Buttes, *Kamb 801c* (UC); Soledad Canyon, *B.G. Pitzer 3729* (UCR); Whittier Hills, *T.S. Ross 4312* (UCR); W of Castaic Lake on ridge dividing Marple Canyon from Grasshopper Canyon, *T.S. Ross 8350* (UCR); Texas Canyon, *T.S. Ross 8463A* (UCR); NE end of Santa Susana Mts, Newhall Ranch, *A.C. Sanders 25702* (UCR); NE end of Santa Susana Mts, Newhall Ranch, *A.C. Sanders 25713* (UCR); NE end of Santa Susana Mts, Newhall Ranch, *A.C. Sanders 25955* (UCR); Newhall Ranch, S of Magic Mountain theme park, *A.C. Sanders 26015* (SD); Santa Clarita area, lower Mint Canyon, *A.C. Sanders 29442* (UCR); Santa Clarita Area, Cruzan Mesa, *A.C. Sanders 29914* (UCR); Santa Clarita area, Plum Canyon, *A.C. Sanders 30172* (UCR); Verdugo Mts, *V. Soza 1168* (UCR); South Hills, *R.G. Swinney1534* (UCR); San Dimas Experimental Forest, *R.G. Swinney 8638* (UCR); Bob's Gap, 3.2 mi S of Hwy 138, *R.G. Swinney 10246* (UCR); Littlerock Creek, *R.G. Swinney 10459A* (UCR); Carr Canyon, *R.G. Swinney 10581B* (UCR); Colton, *Vasey 331* (BM); Hwy N2, 1.5 mi NW of Palmdale, *Veno 150* (CAS); Hwy N2, 1.5 mi NW of Palmdale, *Veno 154* (CAS); Limekiln Canyon, *L.C. Wheeler 9249* (UCR); Liebre Mts, *L.C. Wheeler 9351* (UCR); Liebre Mts, *L.C. Wheeler 9352* (UCR); Liebre Mts, Tapia Canyon, *S.D. White 9210* (UCR). Merced County. N of Ortigalita Creek, *Hoover 4298* (CAS, GH, UC, US); Laguna Seca Hills, *Lyon 1627* (CAS). Monterey County. San Lorenzo Creek, *J.T. Howell 39236* (CAS); Old Metz Road, *Howitt 1456* (CAS). Orange County. Santiago Creek, 27 Mar 1902, *Geis s.n.* in part (CAS-DS). Riverside County. Winchester, *Amstall 398* (UC); Double Buttes, *Bacigalupi & Heckard 8418* (UC); Hemet, *C.F. Baker 4139* (CAS-DS, UC); San Jacinto Wildlife Area, *J. Greene 1320* (UCR); Riverside, *Hall 2943* (CAS-DS, UC); Riverside, *Hall 2964* (UC, US); Big Morongo Canyon, 3–3.5 mi below the caretaker's house at Big Morongo Preserve, *G.K. Helmkamp D-29* (UCR); 2.5 mi NW of Perris, *A.C. Sanders 1432* (UCR); Coachella Valley, *A.C. Sanders 16116* (UCR); Box Springs Mts, *A.C. Sanders 19754* (UCR); Coachella Valley, Garnet, *A.C. Sanders 23852* (UCR); Hemet, *A.C. Sanders 24117* (UCR); Perris-Aguanga Basin, *A.C. Sanders 24235* (UCR); Perris-Aguanga Basin region, *A.C. Sanders 26575* (UCR); Temescal Canyon at Alberhill, *A.C. Sanders 37701* (UCR); Alberhill, S foot of Gavilan Hills, *A.C. Sanders 37728* (UCR); southeastern Gavilan Hills N of Alberhill, *A.C. Sanders 37862* (UCR); Menifee Hills, *A.C. Sanders 38000* (UCR); Temescal Canyon, *A.C. Sanders 40088* (UCR); Whitewater, *Shreve 8156* (ARIZ); 6.5 mi SE of Banning, *J.H. Thomas 50* (CAS-DS); Hwy 71, 11 mi SE of Corona, *Veno 147* (CAS); Indian Avenue, *Veno 218* (CAS); Indian Avenue, *Veno 257* (CAS); 11 mi SE of Corona, *Veno 398* (CAS); Hwy 71, 11 mi SE of Corona, *Veno 458* (CAS); 5 mi S of Winchester, 30 Mar 1947, *Vestal s.n.* (CAS-DS); Lakeview Mts, *S.D. White 2740* (UCR). San Benito County. 25 mi S of Dos Palos, *Ferris 6956* (CAS-DS); 3 mi from Panoche, *Ferris 6979* (CAS-DS, NY); Mendota-Panoche Road, *Ferris 9737* (CAS-DS, GH); Panoche Valley, *Jepson 18123* (UC); Griswold Hills, *Quibell 903* (CAS-DS). San Bernardino County. Hackberry Mt, *Ferris 7267* (CAS-DS); 20.5 mi NW of Barstow and 1.5 mi W of Opal Mt, *J. Hendrickson 16678* (UCR); ca. 4 mi WNW of Flamingo Heights, 2.6 mi SW of Ruby Mt, *M. Honer 3003B* (UCR); Morongo Valley, *J.T. Howell 3405* in part (CAS); Saltdale, *Jepson 19513a* (UC); San Bernardino Valley, *Parish 41* (CAS-DS, NY, US); San Bernardino, May 1888, *Parish s.n.* (F); Lytle Creek Wash, just S of Glen Helen Parkway, *B.G. Pitzer 2945* (UCR); Jurupa Hills at Jurupa Hills Regional Park, *A.C. Sanders 16518* (UCR); 1.4 mi below the community of Blue Cut, *A.C. Sanders 17960* (UCR); Colton Dunes, N of Santa Ana Avenue and E of Riverside Avenue, *A.C. Sanders 25810* (SD); San Bernardino Mts, Wye Peak at Cajon Junction, NE of Hwy 215/Hwy 138 intersection, *Swinney 8560* (SD); San Bernardino County, *Vasey 696* (K, NY, US); 5 mi SW of Yucca Valley, *Veno 125* (CAS); Twentynine Palms, *Veno 142* (CAS); 6 mi NE of Morongo Valley, *Veno 249* (CAS); 6 mi NE of Morongo Valley, *Veno 259* (CAS); 6 mi SW of Yucca Valley, *Veno 425* (CAS). San Diego County. Ramona, April 1899, *T.S. Brandegee s.n.* (UC); San Diego, 1884, *Cleveland s.n.* (SD); Fallbrook, *M.E. Jones 3123* (CAS, US); Mountain Springs Grade, *Orcutt 236* (UC); Mason Valley, *Purer 6322* (GH, SD); Mason Valley, *Purer 6976* (SD); Crestridge Ecological Reserve, *J.P. Rebman 10906* in part (UCR); Lilac Road, 7 mi SE of Pauma Valley, *Veno 118* (CAS); 0.6 mi NW of Lake Jean, *Veno 149* (CAS); 4.3 mi E of Banner, *Wiggins 14098* (CAS-DS). San Joaquin County. Corral Hollow, *Eastwood & Howell 2103* (CAS); Corral Hollow, *Ferris 9398* (CAS-DS, GH, NY, UC); Corral Hollow, *Hoover 6078* (UC). San Luis Obispo County. Carrizo Plain, *Breedlove 2087* (CAS-DS); San Luis Obispo County, *Clokey 5829* (ARIZ, BM, CAS-DS, F, G, GH, MO, NY, SD, UC, US, W); Cuyama Valley, 13 Apr 1935, *Essau s.n.* (CAS); 1 mi N of Spanish Ranch, *French 878* (UC); Cottonwood Pass, *Hoover 6883* (CAS, UC); San Juan River, *Hoover*

7463 (CAS); Panorama Hills, *Hoover 9776* (CAS); Temblor Range, *Hoover 10306* (CAS); Carrizo Plain, *Jepson 16216a* (UC); Elkhorn Plain, *Robbins & Bacigalupi 3450* (UC); 11.5 mi S of Shandon, *Twisselmann 1767* (CAS). Santa Barbara County. Santa Barbara, *Nuttall s.n.* (K); Ballinger Canyon, *Twisselmann 1815* (CAS). Stanislaus County. S of Del Puerto Canyon, *Hoover 4291* (UC); Crow Creek Canyon, *Hoover 4312* (CAS, GH, UC, US); 12 mi W of Patterson, grown at Stanford from *Breedlove 4859* (CAS-DS), *Raven 18752* (CAS-DS, US). Tulare County. Pixley Natural Area, 25 Mar 1967, *McClintock s.n.* (CAS). Unspecified county. Southern California, *Coulter 516* (EDH, GH).—UTAH. Washington County. 5.7 mi S of Gunlock, *Gould 1597* (GH, NY, WS); Diamond Valley, *Gould 1701* (ARIZ, CAS-DS, GH, NY, UC, US).—MEXICO. Baja California. Sierra Juárez; 1.0 km SE of Jacumé, *Moran 26991* (SD); San Rafael Ranch, 14 May 1886, *Orcutt s.n.* (UC); 3.0 mi E of Los Héroes de la Independencia, on road from Ensenada to San Felipe, *Reeder 7199* (SD); Valle Trinidad, *Wiggins 16055* (CAS, DS, US).