MADROÑO, Vol. 63, No. 3, pp. 283–291, 2016

TWO NEW SUBSPECIES OF *ARCTOSTAPHYLOS* (ERICACEAE) FROM CALIFORNIA AND IMPLICATIONS FOR UNDERSTANDING DIVERSIFICATION IN THIS GENUS

V. THOMAS PARKER
Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132
parker@sfsu.edu

MICHAEL C. VASEY
Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132, and San Francisco Bay National Estuarine Research Reserve, 3152 Paradise Drive, Tiburon, CA 94920

ABSTRACT

We describe two new subspecies of the widespread shrub *Arctostaphylos*. One subspecies is a southern extension of *A. purissima*; ***A. purissima*** subsp. ***globosa*** V.T. Parker and M.C. Vasey. It differs from the nominate species in several ways, but principally in having glandular hairs on the young stems and inflorescences and having a globose fruit typically with fused nutlets. We also describe a new subspecies of *A. patula*; ***A. patula*** subsp. ***gankinii*** M.C. Vasey and V.T. Parker. *Arctostaphylos patula* subsp. *gankinii* is a distinctive variant of the montane greenleaf manzanita that occurs widely at various localities in the Sierra Nevada extending into the inner North Coast, Klamath, and Siskiyou ranges of California and southern Oregon. This new subspecies appears to have been identified incorrectly as *A. manzanita* subsp. *roofii* and subspecies of *A. mewukka* in herbarium collections. The patterns of diversity for both species and their subspecies illustrate common taxonomic issues in the genus, representing potential inter-population hybrid introgression and intra-population morphological diversification, a potentially common mode of speciation in this genus.

Key Words: Endemism, fog influence, hybrid speciation, subspecies.

Most taxa in *Arctostaphylos* occupy a wide diversity of habitats that differ largely or subtly by climate or soil characteristics distributed in many different geographic settings. Diversification in *Arctostaphylos* appears to be driven by a number of processes involving fire regimes, soils, and climates (Vasey and Parker 2014). Additionally, climate fluctuations (Raven and Axelrod 1978), evolution of the obligate seeder life history (Wells 1969; Keeley and Zedler 1978; Parker and Kelley 1989; Parker 2015), and hybridization between species are factors likely to have played significant roles (Parker and Vasey 2004; Keeley et al. 2007; Parker et al. 2007; Vasey and Parker 2014). Frequently, parsing these different modes of diversification is difficult, although new molecular techniques may provide better insight.

In this paper we recognize two additional *Arctostaphylos* subspecies from California, one limited in geographic range to coastal western Santa Barbara County, and the other more widespread in montane habitats in the central and northern Sierra Nevada as well as inner coast range mountains of northern California and southern Oregon.

Concentrations of diversity of *Arctostaphylos* taxa between the two regions from which we describe these taxa differ considerably. The Sierra Nevada contains several wide-ranging species and few endemics, perhaps reflecting less soil diversity and a more continental climate with winter extremes. In contrast, the California outer coast ranges host the largest number of taxa in *Arctostaphylos* (Cody 1986; Keeley 1992; Vasey and Parker 2014) including numerous local endemics, probably reflecting greater edaphic diversity and a strong environmental gradient generated by a summer fog-moderated climate near the coast rapidly changing to a more interior continental climate in relatively short distances (Richerson and Lum 1980; O'Brien 1998; Francis and Currie 2003). This climatic gradient contributes to more favorable water relations for *Arctostaphylos* shrubs along the coast in contrast to more interior sites, permitting physiological diversification along a moisture water potential gradient (Vasey et al. 2012, 2014). The climatic distinctions between these two regions appear to underlie the origin of the subspecies we describe below.

THE GLOBOSE LA PURISIMA MANZANITA

This taxon was brought to our attention by several botanical consultants who were concerned that they could not confidently identify it. The first was from a site adjacent to Hwy 246 between Lompoc and Buellton, whereas the next two were from Hollister Ranch on the south slopes of the Santa Ynez Mountains to the west of Hwy 101, all from Santa Barbara County. A search of the California Consortium of Herbaria (2007) and visits to the Santa Barbara (SBBG) and Rancho Santa Ana botanic

TABLE 1. Key trait differences among *A. purissima* subspecies and two taxa to the east along the Santa Ynez Mountains.

	A. purissima subsp. *purissima*	*A. purissima* subsp. *globosa*	*A. refugioensis*	*A. glauca*
Twig pubescence	densely non-glandular short-hairy, non-glandular long-hairy	densely non-glandular short-hairy, glandular long-hairy	densely non-glandular short-hairy, glandular long-hairy	glabrous (rarely short hairs, or sparsely glandular)
Leaf length (cm)	1–2.5	2–3	3–4.5	2.5–5
Leaf width (cm)	1–2.5	1–2.5	2–3	2–4
Leaf color	green	green	glaucous-green	white glaucous
Inflorescence	raceme	raceme	5–10 branched panicle	4–8 branched panicle
Bracts/Rachis	non-glandular short-hairy (sparsely with long hair)	glandular short-hairy (sparsely with long glandular hair)	glandular short-hairy (sparsely with long glandular hair)	glabrous
Fruit diameter (mm)	4–8	4–8	10–15	10–15
Fruit shape	depressed globose	globose	globose	globose
Nutlets	separable, rugose exterior	frequently fused, rugose exterior	fused, smooth exterior	fused, smooth exterior

garden (RSA) herbaria yielded other collections that were south of Lompoc. All of these samples were glandular-hairy on their twigs and inflorescences, a condition that differs from the non-glandular nominate species located in Vandenberg Air Force Base, Burton Mesa, La Purisima Mission, and sites slightly farther north. Collections south of the Burton Mesa and Vandenberg Air Force Base differ in characteristics from the nominate species. For example, a series of collections along Jalama Road, south and west of Lompoc, all demonstrate glandular hairs on young stems and inflorescences (e.g., RSA635895, RSA635910, RSA635915, RSA635916, RSA635939) as well as a site 3.9 km west of Hwy 101 (Vasey 1468, Vasey and Parker 1489). Recently, we were able to collect this taxon in fruit from a large population at the Albolado Ranch in Santa Barbara County (34°30.727N, 120°16.052W) and discovered that, not only are stems and inflorescences covered with glandular hairs, but fruits are principally globose as well. Collections of fruit from the new subspecies in both May and July 2015 indicated that the typical fruit is globose, about 7 mm in diameter, with about half to over two-thirds of the fruit having rugose nutlets fused together. Typical *A. purissima* subsp. *purissima* have non-glandular branchlets with depressed-globose fruits and separable stones (e.g., UC1361241) (Wells 1968).

TAXONOMIC TREATMENT

Arctostaphylos purissima subsp. **globosa** V.T. Parker & M.C. Vasey, subsp. nov.—Type: USA, California, Santa Barbara Co., western Santa Ynez Mountains, mostly Matilija sandstone outcrops; 34°30′43.62″N, 120°16′03.96″W, 379 m, 24 May 2015, Parker & Vasey 1495 (holotype UCB; isotypes CAS, SFSU).

Differs from nominate species in having glandular hairs on stems and in inflorescence, fruit being globose rather than depressed globose, and frequently having fused nutlets.

Erect to spreading shrub, 2–7 m high; *stems* with burl absent; bark red-brown, smooth; *branchlets* covered in short, dense, non-glandular hairs with long, usually gland-tipped hairs; *leaves* green, isofacial, stomata equally dense on both surfaces, leaf surfaces sparsely short pubescent to glabrous with short glandular hairs along the edges, midrib, and along the petiole; blade ca. 2–3 cm long, 1.4–2.2 cm wide, oblong in shape, tips abruptly acute, base auriculate and clasping the stem; petioles < 2 mm long; *immature inflorescence* raceme supporting buds subtended by leaf-like bracts 4–5 mm long; *bracts* usually densely ciliate with some gland-tipped hairs; *flowers* conical-urceolate, whitish-pink supported by pubescent pedicels; *ovary* glabrate; *fruit* usually globose, reddish-tan, 4–8 mm wide, nutlets fused, weakly or partially fused, or sometimes separable.

Distribution and ecology. Maritime chaparral, associates include *A. glandulosa* subsp. *glandulosa*, *Pickeringia montana*, *Vaccinium ovatum*, *and Quercus agrifolia*; individuals are often adjacent to or intermixed with coastal sage scrub or oak woodland.

Etymology. The specific epithet refers to the distinct shape of the fruit compared to the nominate species, *A. purissima* subspecies *purissima*.

Taxonomic relationships. This glandular taxon suggests a zone of genetic introgressive hybrid exchange across the western portion of the Santa Ynez Mountains (Table 1). A sequence grade of taxa appears to occur from non-glandular *A. purissima* subsp. *purissima* to the north and west, then south to glandular *A. purissima* subsp. *globosa*, then to the glandular endemic *A. refugioensis* to the east, and finally to the widespread *A. glauca* farther east along the Santa Ynez Mountains and elsewhere. The typically glabrous *A. glauca* individuals in the Santa Ynez Mtns may sometimes present sparse pubes-

cence. The mosaic of characters in Table 1 suggests a few hypotheses. One is that *A. refugioensis* is of hybrid origin from a cross between an auriculate-leaved species with the large, globose-fruited *A. glauca* characterized by fused stones (Gankin 1967). The newly described subspecies of *A. purissima* with the fused globose fruit could represent introgression between *A. purissima* subsp. *purissima* and *A. refugioensis* along the northern edge of the range of the latter species.

Alternatively, historically, *A. purissima* and *A. glauca* may have dispersed into one another's populations during climatic fluctuations, even within the last 10,000 years, yielding a sequence of populations better adapted to shifts in microclimate or soils. This alternative would suggest that *A. purissima* subsp. *globosa* is of hybrid origin that sorted back toward the auriculate parent with introgression, while *A. refugioensis* is from a similar cross that sorted back toward *A. glauca* but retained auriculate leaves and other traits. An examination of the pubescence patterns support this latter hypothesis (Figs. 1, 2). Both *A. purissima* subspecies display long stiff hairs over a matrix of generally dense shorter hair; the difference is that the longer hairs in subsp. *globosa* are glandular-tipped with small clear-to-orange or amber glands (Fig. 1). The pattern of pubescence appears to be identical between *A. purissima* subsp. *globosa* and *A. refugioensis* (Fig. 2). In addition to the character sequence, the distribution of these four taxa range from foggy maritime to sunny hot and dry interior chaparral in a similar gradient fashion, suggesting the taxa may represent an ecological adaptive sequence.

Key to *Arctostaphylos* species of western Santa Barbara County and nearby areas

1. Plants with burl at base of main stems, resprouting after fire
   2. Leaves with stomata only on lower leaf surface . . . . . *A. crustacea* subsp. *eastwoodiana*
   2. Leaves with stomata on both surfaces
      3. Main stems with gray, rough, and shreddy bark . . . . . *A. rudis*[1]
      3. Main stems with smooth reddish bark . . . . . *A. glandulosa*
1. Plants lacking burl at base of main stems, not resprouting after fire
   4. Main stems with gray, rough, and shreddy bark . . . . . *A. rudis*[2]
   4. Main stems with smooth reddish bark
      5. Leaves lobed, rounded, or slightly cuneate at base, leaves glaucous white. . . . . *A. glauca*
      5. Leaves with an auriculate base, leaf color various shades of green or gray-green
         6. Stems, immature inflorescence lacking glandular hairs
            7. Leaf blade 2–5 cm L; fruit 8–12 mm wide; stones generally fused . . . . . *A. pechoensis*
            7 Leaf blade 1–2.5 cm L; fruit 5–8 mm wide; stones free . . . . . *A. purissima* subsp. *purissima*
         6. Stems, immature inflorescence with glandular hairs present
            8. Leaf blade 3–4.5 cm L; leaves glaucous or dull; fruit 12–15 mm wide. . . . . *A. refugioensis*
            8. Leaf blade 1–2.5 cm L; leaves green; fruit 5–8 mm wide . . . . . *A. purissima* subsp. *globosa*

The Gankin Manzanita

The greenleaf manzanita (*Arctostaphylos patula* Greene) is one of the most widespread species in the genus. It is a common understory shrub in open montane yellow pine forest, white fir forest, and red fir forest and is a canopy dominant in montane chaparral, ranging along the Pacific Coast from the Cascade range of southern Washington through Oregon and the California North Coast range as far as Mt. Hull in Lake County and on both slopes of the Sierra Nevada Range, including western Nevada, then disjunct to the San Gabriel, San Bernardino, and San Jacinto Mountains of southern California, and again disjunct farther south into the Sierra San Pedro Martir in northern Baja California, Mexico. It also ranges east with a few reported occurrences in Montana and then into the Rocky Mountains from the Wasatch range, Utah through the Umcompahgre Plateau of Colorado south to the canyon lands of southern Utah and northern Arizona, and west into uplands of the Basin and Range Province of eastern Nevada.

Throughout most of this extensive range, *A. patula* presents shiny green glabrous leaves and twigs and inflorescence axes covered with dense hairs capped by distinctive stipitate golden glands (e.g., NDG37621, NDG37622, NDG37623) (Greene 1891). Whereas other species of manzanitas have glandular hairs, none have the same distinctive pattern as *A. patula*. Consequently, although its growth form varies greatly from low mounding to spreading erect shrubs, and post-fire resprouting varies geographically, the presence of these dense golden glands on twigs and inflorescence axes is generally a reliable key character to distinguish this species wherever it occurs.

However, in the upper-elevation mountain ranges of the Sierra Nevada of California, particularly in the central and northern regions, and in the inner North Coast, Siskiyou, and Klamath ranges of California and southern Oregon, individuals of *A. patula* can be found that lack these distinctive golden glands. These otherwise typical greenleaf manzanitas that lack golden glands instead present a non-glandular, short canescent tomentum on twigs and inflorescence axes. Non-glandular, canescent individuals of *A. patula*

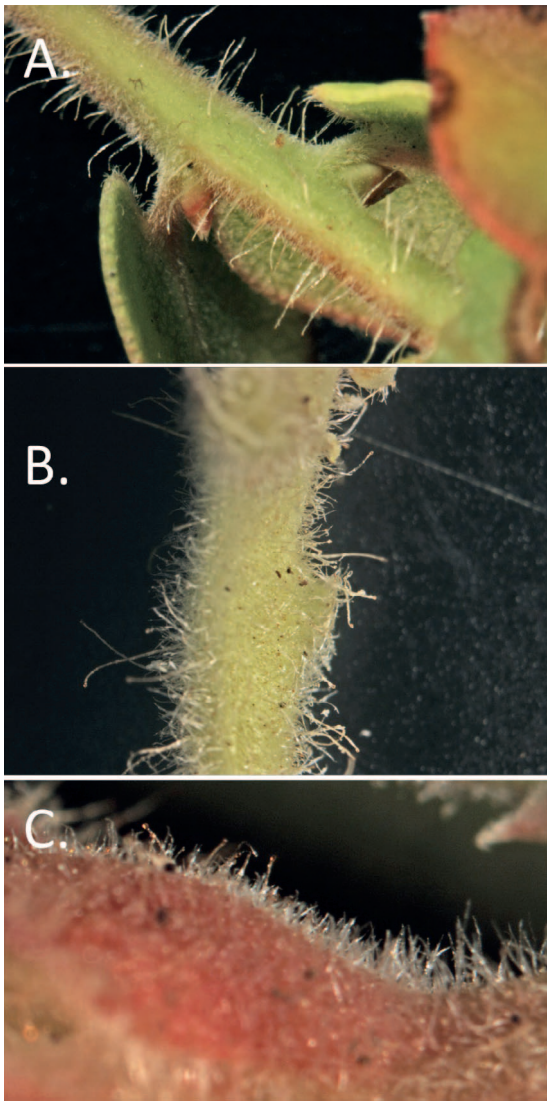

FIG. 1. *Arctostaphylos purissima* subspecies showing pubescence differences. A) stem of subsp. *purissima* showing the multi-layered pubescence; note the lack of glands at the tips of the longer hairs; B) stem hairs on *A. purissima* subsp. *globosa* illustrating the small orange glands at the tips of the longer hairs, and sometimes on the shorter hairs; C) small glands on the tips of hairs along the bracts of *A. purissima* subsp. *globosa*.

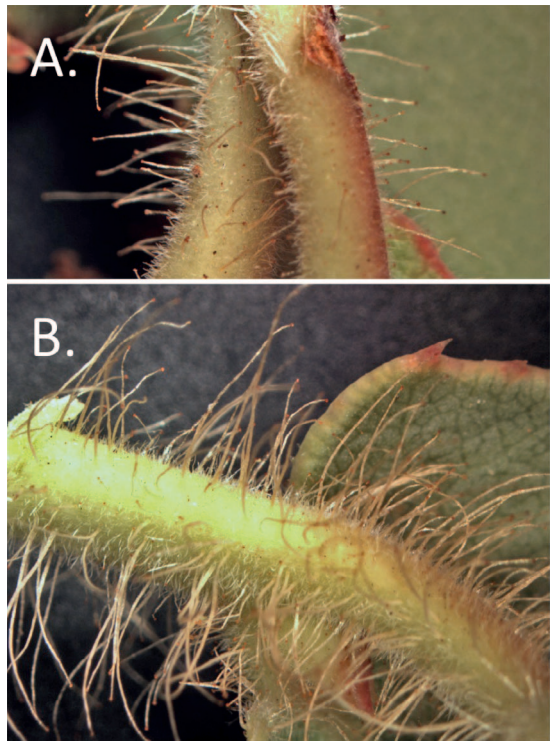

FIG. 2. Pubescence on *Arctostaphylos refugioensis*. A) pubescence at the stem-rachis transition, note the small orange glands at the tips of the longer hairs; B) pubescence along the stem with the bi-layer of hairs, glandular on the longer stiff hairs.

often occur in stands inter-mixed with typical *A. patula* and, consequently, collectors have often overlooked non-glandular *A. patula*. Accessions of non-glandular *A. patula* date back at least to a collection by W. R. Dudley in 1897 (CAS18246). Examination of herbarium specimens of *A. patula* at CAS and UC revealed approximately fifty collections of canescent, non-glandular *A. patula* by well-known botanists such as Jepson (UC38822), Eastwood (CAS202040), Abrams (CAS27374), McMinn (UC1281165), Heller (CAS38928), Raven (CAS410293), Jepson (UC38822), Adams (UC549428), True (CAS911822), J.T. Howell (CAS863126), and others throughout the twentieth century. Although some botanists noted the undescribed canescent, non-glandular 'form', it was Roman Gankin in a 1988 collection from Highway 49 near Bassetts Station, Sierra County, CA, (CAS976495) who wrote an extensive note calling for formal recognition of this entity. Gankin, an experienced manzanita expert, mentioned that we should keep an eye out for greenleaf manzanitas that lack golden glands. We had also previously observed the canescent, non-glandular *A. patula* in 1993 along Old Highway 50 below Echo Summit, El Dorado County and along Bailey Road in Calaveras County in 1995 (e.g., Vasey 0245; Vasey 0770).

We subsequently made several visits to various stands of montane chaparral in the vicinity of the Sierra Buttes and the Gold Lakes region of Sierra and Plumas Counties and encountered large numbers of the non-glandular greenleaf manzanita, often in mixed populations with the typical glandular greenleaf manzanita. In this region, the non-glandular individuals can dominate these stands, as was demonstrated in a random survey of montane

FIG. 3. Differences of stem and rachis pubescence of *Arctostaphylos patula* subspecies. A) *A. patula* subsp. *gankinii* illustrating short canescent hair on leaves, petiole and stem; B) close-up of rachis and bracts on *A. patula* subsp. *gankinii*; C) *A. patula* subsp. *patula* rachis and bracts showing the short golden glandular hairs characteristic of the species.

chaparral stands along Tamarack Trail above Upper Sardine Lake near the type locality (39°37′10″N, 120°37′35″W; 1900 m). In eight random samples, the non-glandular morph ranged from 22% to 78% of the stand. Overall, 58% of all 397 individuals sampled in this population were non-glandular.

As pointed out in the 1988 note by Gankin, the recognition of non-glandular, canescent *A. patula* mixed with typical *A. patula* was actually recorded earlier by Adams (1940) and McMinn (1939). Adams remarked "there occurs infrequently with the typical form in the Sierra Nevada a form in which the glandular puberulence of inflorescence axes and peduncles is replaced by a light, simple pubescence. These are in complete agreement with the typical form in all other respects, including the presence of an enlarged root-crown." (Adams 1940, p. 26). Adams noted several specimens from the UC Herbarium with this character from "Modoc Co., Lassen Co., Glenn Co., Eldorado Co., Tuolumne Co., Mono Co., and Ormsby Co., Nevada." (Adams 1940, p. 26). Ormsby Co. is no longer existent and is situated within Carson City, NV. McMinn (1939) stated that the two forms "are often found associated in the same colonies (Alpine Highway from Jackson to Silver Lake)." (McMinn 1939, p. 401) (El Dorado, Co.: UC1281165, UC1281167).

Clearly, large numbers of non-glandular *A. patula* are widespread in pure or mixed populations with glandular *A. patula* over a substantial range of the Sierra Nevada, particularly the central and northern regions, as well as the inner North Coast, Siskiyou, and Klamath ranges. In at least some places, such as in the vicinity of the Sierra Buttes, non-glandular *A. patula* individuals dominate stands. This situation has created some understandable confusion with other *Arctostaphylos* taxa that have similar morphology but occur in different ecological settings, namely *A. manzanita* subsp. *roofii* (Gankin) Wells and *A. mewukka* Merriam. *Arctostaphylos manzanita* subsp. *roofii* and *A. mewukka* are also burl forming, scale-bracted, paniculate manzanitas. In *A. manzanita* subsp. *roofii*, twigs and inflorescence axes are also covered in short, canescent hairs. In *A. mewukka*, twigs and inflorescences are typically glabrous and leaves are more glaucous.

Arctostaphylos manzanita subsp. *roofii* is typically found in the inner North Coast range of Glenn and Mendocino cos.; however, it also has a disjunct occurrence in the Sierra Nevada foothills along Cohasset Road at about 500 m elevation in Butte Co. Most *A. manzanita* subsp. *roofii* collections are generally found at lower elevations (400–800 m) in chaparral and foothill woodland. However, several herbarium collections (e.g., Butte Co.: CHSC23443, UCD52219; Calaveras Co.: UCD52220; Plumas Co.:UCD52221) have been attributed to *A. manzanita* subsp. *roofii* from localities at much higher elevations (1400–1800 m) with more typical montane associates (e.g. *A. patula*, *A. nevadensis, Pinus ponderosa* P. Lawson and C. Lawson, *Abies magnifica* A. Murray bis, and *Calocedrus decurrens* [Torr.] Florin). Most *A. mewukka* populations occur at higher elevations than *A. manzanita* subsp. *roofii* (~1000 m); however, they typically are found below *A. patula* subsp. *patula* and *A. patula* subsp. *gankinii*. We have found collections labeled as *A. mewukka* that better match this newly described subspecies of *A. patula* in elevation, associates, and locality (e.g., *A. mewukka*, Plumas Co.: UC1408974, and *A. mewukka*, Sierra Co.: SJSU12015). Examination of

these specimens of *A. manzanita* subsp. *roofii* and *A. mewukka*, as well as their presence in high montane habitats with associates typical of *A. patula*, indicates that they most likely represent the proposed *A. patula* subsp. *gankinii*. Thus, part of our motivation in naming this subspecies is to help to provide relief from this taxonomic confusion.

Taxonomic Treatment

Arctostaphylos patula subsp. **gankinii** M.C. Vasey & V.T. Parker, subsp. nov.—Type: USA, CA, Sierra Co., south facing slope above Upper Sardine Lake near east end of lake, Tahoe National Forest, 1760 m, Sierra Nevada Mountains, 39°37′12.77″N, 120°37′02.22″W, 3 September 2006, M. Vasey1132 (holotype: UCB; isotypes: CAS, SFSU).

Differs from nominate species by having stems and inflorescence with densely short-canescent, non-glandular pubescence.

Erect to spreading shrub, 1–3 m high, *stems* with burl present, prominent to obscure; bark red-brown, smooth; *branchlets* covered in short, dense, non-glandular hairs; *leaves* erect, shiny green hue, isofacial, stomata equally dense on both surfaces; blade ca. 2.5–6 cm long, 1.5–4 cm wide, widely ovate to round, flat margins, tip abruptly soft-pointed, base rounded or truncate; petioles 0.5–1 cm long; *immature inflorescence* 2–8 branched panicle with pendent branches, axis 1.5–3 cm; *bracts* scale-like, deltate acuminate; *flowers* conical-urceolate, whitish or pink, pedicels glabrous; *ovary* glabrous or white, non-glandular hairy; *fruit* usually depressed-globose, reddish-tan, 7–10 mm wide, glabrous, nutlets typically separable.

Paratypes. USA, CA, Calaveras Co., Dorrington, 26 June 1978, J. T. Howell (CAS911722); El Dorado Co., Baily Road, 7 October 1995, Vasey 0770; El Dorado Co., Highway 50 below Echo Summit, 13 June 1993, Vasey 0245; Plumas Co., mouth of Butterfly Creek, 10 July 1967, J.T. Howell (CAS863255); Sierra Co., montane chaparral along Highway 49 near Bassetts, 25 August 1988; R. Gankin (CAS976495).

Distribution and ecology. Occurs in mixed stands with subsp. *patula* in montane chaparral and open conifer forest between 1400–2000 m. Widespread and occasionally common in the central and northern Sierra Nevada, less common in the southern Sierra, and also found in the North Coast, Klamath, and Siskiyou ranges extending into southern Oregon. Associates include *A. nevadensis*, *Quercus vaccinifolia*, *Garrya fremontii*, *Ceanothus cordulatus*, *Prunus emarginata*, *Sorbus californicus*, *Spiraea densiflora*, *Pinus ponderosa, Pinus jeffreyi, Abies magnifica, and Abies concolor*.

Etymology. This subspecies is named in honor of Roman Gankin acknowledging his keen eye for manzanitas and his many contributions to understanding *Arctostaphylos* systematics.

Key to resprouting *Arctostaphylos* of mid-to-high elevation mountains in the western United States and northern Baja California

1. Leaves dull or shiny, light green to bright green in hue
   2. Plants typically prostrate, spreading or low mounding, immature inflorescence typically a short raceme (northern California to southern Oregon) . . . . . *A. nevadensis* subsp. *knightii*
   2. Plants mounding to erect, immature inflorescence a wide-spreading panicle
      3. Fruits depressed-globose, stones separable or rarely fully fused
         4. Immature inflorescence bracts scale-like or awl-shaped
            5. Branchlets and immature inflorescence with dense, stipitate golden glands (mountains and high desert forests and woodland usually above snow line in western USA and northern Baja) . . . . . *A. patula* subsp. *patula*
            5. Branchlets and immature inflorescence canescent, lacking stipitate golden glands
               6. Bracts awl-shaped, high elevation sites, generally above winter snowline (Sierra Nevada, North Coast, Klamath, Siskiyou mountains, California and southern Oregon) . . . . . *A. patula* subsp. *gankinii*
               6. Bracts scale-like with marcescent tips, middle elevation sites, generally below winter snowline (inner central North Coast and Sierra mountains). . . . *A. manzanita* subsp. *roofii*
         4. Immature inflorescence bracts typically leaf-like, at least in part, especially towards the base of the rachis
            8. Stones of fruit separable or only partially fused
               9. Branchlets and immature inflorescence densely glandular (widespread, coast range from southern Oregon to northern Baja) . . . . . *A glandulosa* subsp. *glandulosa*
               9. Branchlets and immature inflorescence canescent or with long, non-glandular hairs
                  10. Branchlets and immature inflorescence canescent, lacking long non-glandular hairs (widespread, coast range in southern Oregon to northern Baja) . . . . . *A. glandulosa* subsp. *cushingiana*
                  10. Branchlets and immature inflorescence both canescent and w long, non-glandular hairs (Transverse Range, California) . . . . . *A. glandulosa* subsp. *mollis*
            8. Stones of fruit fully fused (Western Transverse Range) . . . . . *A. glandulosa* subsp. *gabrielensis*

3. Fruits globose, stones typically fused
   11. Panicle multiple-branched, wide-spreading, branches and immature inflorescence sparsely glandular (southern California, Peninsular Range) . . . . . *A. rainbowensis*
   11. Panicle few branched, compact, branches and immature inflorescence canescent, not glandular (Eastern Transverse Range) . . . . . *A. parryana* subsp. *tumescens*

1. Leaves typically glaucous-white or gray in hue
   12. Branchlets and immature inflorescence densely glandular hairy (southern California and northern Baja) . . . . . *A. glandulosa* subsp. *leucophylla*
   12. Branchlets and immature inflorescence typically non-glandular, hairy or glabrous
      13. Branchlets and immature inflorescences short hairy or canescent
         14. Fruit depressed-globose with separable stones (southern California and northern Baja) . . . . . *A. glandulosa* subsp. *adamsii*
         14. Fruit typically globose with fused stones (southern California to northern Baja) . . . . . *A. parryana* subsp. *desertica*
      13. Branchlets and immature inflorescence glabrous
         15. Fruit depressed-globose with separate stones
            16. Fruit 6–10 mm wide, reddish (northern Baja). . . . . *A. incognita*
            16. Fruit 10–16 mm wide, dark chocolate brown (Sierra Nevada California) . . . . . *A. mewukka* subsp. *mewukka*
         15. Fruit typically with fused stones (northern Baja) . . . . . *A. peninsularis* subsp. *peninsularis*

Discussion

We recognize two new Californian subspecies in *Arctostaphylos*: *A. purissima* subsp. *globosa*, a rare, narrow endemic of maritime chaparral, mostly on Matilija sandstone outcrops in western Santa Barbara County in the Santa Ynez Mountains; and *A. patula* subsp. *gankinii*, an overlooked widespread and distinctive variant of the greenleaf manzanita, *A. patula*, that co-occurs with typical *A. patula* in the high mountains of the Sierra Nevada and inner coastal mountains of the North Coast, Klamath, and Siskiyou ranges of California and southern Oregon. This latter taxon is frequently confused with other taxa with similar morphology and, whereas we consider this taxon worthy of recognition on its own merits, we hope that its recognition as a subspecies will help eliminate this problem.

These two new subspecies each reflect a pattern of morphological variation found in other infra-specific taxa recognized within *Arctostaphylos*. In both cases, a distinct pattern of tomentum differs between the two taxa. In *A. purissima* subsp. *globosa*, individuals within populations are consistently glandular pubescent and also display globose fruits with typically fused stones, both in contrast to *A. purissima*. *Arctostaphylos patula* subsp. *gankinii* also exhibits a substantially different pubescent pattern from the much more broadly distributed *A. patula* subsp. *patula,* but with no other obvious morphological differences over a widespread distribution constrained to high mountains in northern California and southern Oregon.

For *A. patula* subsp. *gankinii*, the subspecies has a distinct geographic pattern that is nested within the more broadly distributed nominate species. This situation is not unique within *Arctostaphylos* and this entity historically might have been named as a variety; however, the distinction between infra-specific treatment of subspecies and varieties is now regarded as largely unimportant by most botanists (Hamilton and Reichard 1992) and editors of floras stress a consistent treatment of one or the other infra-specific rank versus mixing the two ranks within the same genus. Other intra-population variants within *Arctostaphylos* are recognized as subspecies; e.g., the glandular *A. glandulosa* subsp. *glandulosa* versus canescent *A. glandulosa* subsp. *cushingiana* and non-glandular *A. canescens* subsp. *canescens* versus glandular *A. canescens* subsp. *sonomensis*. As we are in a time of change regarding species concepts (e.g., Soltis and Soltis 2009; Hausdorf 2011; Soltis 2013), we feel it is important to clarify the existence of this taxon. Should we choose to ignore the distinctive non-glandular variant of *A. patula*, however, its lack of recognition in floras will most likely continue the unfortunate current taxonomic confusion within the botanical community, as illustrated by *A. patula* individuals lacking golden glands that likely have been misidentified in several herbaria.

The origin of *A. patula* subsp. *gankinii* is not clear. This widespread canescent, non-glandular morph of *A. patula* has a pubescence pattern similar to populations of other manzanitas, such as *A. canescens* and *A. nissenana*, that do not co-occur with *A. patula*. The geographic movements of these other montane species since the last glacial epoch or before are not well understood and the origins of subspecies *gankinii* lie somewhere in a past we cannot yet tease apart.

Arctostaphylos purissima subsp. *globosa*, an unrecognized geographically bounded local infra-specific endemic of maritime chaparral, in contrast, morphologically suggests several possible origins. The grade of characters between *A. purissima* subsp. *purissima* to *A. glauca* (Table 1) may well represent a case of introgression between the more widespread interior *A. glauca* and *A. purissima*, with the possibility that *A. refugioensis* may also be a parent

in the mix with *A. purissima*. The putative role of homoploid hybrid origin for a taxon in a region lying between the warm, dry interior and cool, foggy coast is likely a relatively common phenomenon and other species seem to fit a similar geographic, climatic pattern, e.g., *A. gabilanensis* (Parker and Vasey 2004), and hybridization is a generally common process stimulating speciation in plants (Rieseberg 1995).

In a genus as diverse as *Arctostaphylos*, multiple pathways are likely in the origin of both species and infra-specific taxa. Bringing taxonomic coherence to the treatment of this genus requires recognizing significant entities and later research will hopefully test for different modes of origin.

Special Status Consideration

Arctostaphylos patula subsp. *gankinii* is a widespread and relatively common taxon, most frequently found on National Forest Service lands. This taxon does not seem to require special status. *Arctostaphylos purissima* subsp. *globosa*, on the other hand, is principally found on private property. Most of the land is under traditional ranching and as such is not directly threatening the chaparral stands with subsp. *globosa*. On the other hand, on the south-facing slopes of the Santa Ynez Mtns are sites associated with development, such as the former Hollister Ranch. Due to the limited geographic extent of this taxon and its patchy distribution, we consider this subspecies in need of special status consideration for CNPS Category 1b.

Acknowledgments

We thank Larry Ballard and Liz Gaspar for their enthusiasm and help locating stands of *A. purissima* subsp. *globosa*, Finally, we again acknowledge Roman Gankin's encouragement of our efforts to study *Arctostaphylos* and to further evaluate the non-glandular variant of *Arctostaphylos patula* that we name in his honor.

Literature Cited

Adams, J. E. 1940. A systematic study of the genus *Arctostaphylos* Adans. Journal of the Elisha Mitchell Scientific Society 56:1–62.

Cody, M. L. 1986. Diversity, rarity and conservation in Mediterranean-climate regions. pp. 122–152 in M.E. Soulé (ed.), Conservation biology: the science of scarcity and diversity. Sinauer Association, Sunderland, MA.

Consortium Of California Herbaria (CCH). Data provided by the participants of the Consortium of California Herbaria. Regents of the University of California 2015. Website http://ucjeps.berkeley.edu/consortium/ (14 April 2007).

Francis, A. P. and D. J. Currie. 2003. A globally consistent richness-climate relationship for angiosperms. American Naturalist 161:523–536.

Gankin, R. 1967. A new species of *Arctostaphylos* from Santa Barbara County, California. The Four Seasons 2(2):13–14.

Greene, E. L. 1891. *Arctostaphylos patula*. Pittonia 2(10):171.

Hamilton, C. W. and S. H. Reichard. 1992. Current practice in the use of subspecies, variety, and forma in the classification of wild plants. Taxon 41:485–498.

Hausdorf, B. 2011. Progress toward a general species concept. Evolution 65:923–932.

Keeley, J. E. 1992. A Californian's view of fynbos. pp. 372–378 in R. M. Cowling (ed.), The ecology of fynbos: nutrients, fire, and diversity. Oxford University Press, Capetown, South Africa.

——— and P. H. Zedler. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. American Midland Naturalist 99:142–161.

———, M. C. Vasey, and V. T. Parker. 2007. Subspecific variation in the widespread burl-forming *Arctostaphylos glandulosa*. Madroño 54:42–62.

McMinn, H. E. 1939. An illustrated manual of California shrubs. University of California Press, Berkeley.

O'Brien, E. M. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. Journal of Biogeography 25:379–398.

Parker, V. T. 2015. Dispersal mutualism incorporated into large-scale, infrequent disturbances. PLoS ONE 10(7): e0132625. doi: 10.1371/journal.pone.0132625

——— and M. C. Vasey. 2004. *Arctostaphylos gabilanensis*, a newly described auriculate-leaved manzanita from the Gabilan Mountains, California. Madroño 51:322–325.

——— and V. R. Kelly. 1989. Seed banks in California chaparral and other Mediterranean climate shrublands. Pp. 231–255 in M.A. Leck, V.T. Parker, and R.L. Simpson (eds.), Ecology of soil seed banks. Academic Press, New York, NY.

———, M. C. Vasey, and J. E. Keeley. 2007. Taxonomic revisions in the genus *Arctostaphylos* (Ericaceae). Madroño 54:148–155.

Raven, P. H. and D. I. Axelrod. 1978. Origin and relationships of the California flora. University of California Publications in Botany 72:1–134.

Richerson, P. J. and K. L. Lum. 1980. Patterns of plant species diversity in California: relation to weather and topography. American Naturalist 116:504–536.

Rieseberg, L. H. 1995. The role of hybridization in evolution: old wine in new skins. American Journal of Botany 82:953–944.

Soltis, P. S. 2013. Hybridization, speciation and novelty. Journal of Evolutionary Biology 26:291–293.

——— and D. E. Soltis. 2009. The role of hybridization in plant speciation. Annual Review of Plant Biology 60:561–588.

Stebbins, G. L. and J. Major. 1965. Endemism and speciation in the California flora. Ecological Monographs 35:1–35.

Vasey, M. C. and V. T Parker. 2014. Drivers of diversity in woody plant lineages experiencing canopy fire regimes in Mediterranean type climates. Pp. 179–200 in N. Rajakaruna, R. S. Boyd, and T. B. Harris (eds.), Plant ecology and evolution in harsh environments. Nova Publishers.

———, M. E. Loik, and V. T. Parker. 2012. Influence of summer marine fog and low cloud stratus on water relations of evergreen woody shrubs (*Arctostaphylos*, Ericaceae) in the chaparral of central California. Oecologia 170:325–337.

———, V. T. PARKER, K. D. HOLL, M. E. LOIK, AND S. HIATT. 2014. Maritime climate influence on chaparral composition and diversity in the coast range of Central California. Ecology and Evolution 4(18):3662–3674.

WELLS, P. V. 1968. New taxa, combinations and chromosome numbers in Arctostaphylos (Ericaceae). Madroño 19:193–210.

———. 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23:264–267.