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Monograph of Artemisia Subgenus Tridentatae (Asteraceae–Anthemideae)

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ABSTRACT. *Artemisia* subgenus *Tridentatae* (Asteraceae–Asteroideae–Anthemideae–Artemisiinae) comprises 13 species, including 12 subspecies, of shrubs endemic to western North America, including the coastal areas of Baja California, the grasslands of the Great Plains, the basalt scablands of the Columbia Plateau, the western shrub lands of Canada, and the warm deserts of the Colorado Plateaus. The *Tridentatae* lineage underwent a period of rapid diversification and expansion, especially since the last glacial period. The greatest abundance of shrubs occurs within the arid Great Basin, a cold desert that was occupied by Pleistocene lakes. Taxa apparently representing ancestral lineages (*A. rigida* and *A. tripartita*) occur outside the margins of this inland desert. In spite of the extraordinary ecological specializations among the taxa, there is relatively little genetic differentiation, and morphological differences are often subtle. Differences in soil type, temperature, and moisture regimes distinguish the habitats of species as well as subspecies. Hybridization between species is rare, although hybridization among subspecies is common where populations are sympatric or habitats have been disturbed. Morphological differences among taxa primarily include discontinuities in growth form, the shape of the crown, the structure of the inflorescence, and habit (evergreen or deciduous, "root-sprouting" or not). Differences in leaf anatomy are significant and physiologically correlated, helping to define species boundaries but of no utility in field identification. Pollen varies notably in shape and size, and may prove to be useful in distinguishing species in stratigraphic profiles. Floral morphology varies little (florets and cypselae are nearly identical), but sexual arrangement within floral heads (capitula) defines sections: sect. *Tridentatae* is homogamous (all florets are perfect and fertile), and sect. *Nebulosae* is heterogamous (central florets are perfect or sterile, marginal florets are pistillate). An expanded circumscription and the geographic range of subg. *Tridentatae* is proposed. In order to accommodate morphological differences while keeping alliances indicated by molecular studies, subg. *Tridentatae* is divided into two new sections: sect. *Tridentatae* (10 species) and sect. *Nebulosae*; the latter includes *A. californica* and *A. nesiotica* (formerly placed in subg. *Artemisia*), and *A. filifolia* (formerly placed in subg. *Dracunculus*). Morphology and anatomy, ploidy levels, phytogeography, and phylogeny are discussed. Full synonymies and descriptions are provided for all taxa, as well as a key, specimen citations, illustrations, and maps.

INTRODUCTION

Artemisia L., with approximately 400 species, is the largest genus in tribe Anthemideae and one of the largest genera in the Asteraceae (Heywood & Humphries 1977; Bremer & Humphries 1993; Bremer 1994). Estimates of species numbers vary, primarily owing to differing opinions regarding the separation of lineages as segregate genera in the *Artemisia* alliance (Poljakov 1961; Ling 1994), or treatments of the genus in the broad sense (Bremer & Humphries 1993; Shultz 2006a). Treatments that place the woody taxa of subg. *Tridentatae* (Rydb.) McArthur as part of the genus *Seriphidium* (Besser ex Less.) Fourr. are based on the assumption that the North American species are derived from the woody species of the Asian highlands (Weber 1984; Ling1995b, 1995c). In my taxonomic treatment of *Artemisia* for the *Flora of North America* (Shultz 2006a), I maintained subg. *Tridentatae* as distinct from *Seriphidium* and included most of the species found in contemporary treatments (Beetle 1960; Winward & Tisdale 1977; McArthur et al. 1981; Shultz 1986a; Winward 2004). The current treatment varies in that I have expanded the circumscription of subg. *Tridentatae* to include three species that I previously included in subgenera *Artemisia* and *Dracunculus* (Shultz 2006a). Close relationships among species of *Artemisia* and the possibility of past hybridization events result in weakly resolved molecular phylogenies and problematical infrageneric circumscriptions (Watson 2005). The need for further work is a strong argument for a current broad circumscription of *Artemisia* (Shultz 2005, 2006a). It is apparent that we can no longer segregate subgeneric and generic groups on the basis of floral morphology, and the preponderance of evidence from molecular studies shows that the Asian and North American woody species have separate origins (McArthur et al. 1998a; Watson et al. 2000, 2002; Vallès et al. 2003; Riggins & Seigler 2006). The goal of this treatment is to clarify nomenclatural matters and propose sectional groups that serve as hypotheses for further study of relationships.

TAXONOMIC HISTORY

The first type specimen for a woody species of *Artemisia* in North America was collected by Meriwether Lewis on the banks of the Missouri River and was named *A. cana* by Frederick Pursh (1814). Thomas Nuttall (1841) subsequently named *A. tridentata*, the type of subg. *Tridentatae*, as well as most of the species of sagebrush that we recognize today. His descriptions were based on collections he made primarily during his third excursion into western North America in 1834 (see discussion in McKelvey, 1955) as well as the work of early collectors. Nuttall followed the route of the Oregon Trail, and from late June to late August he gathered plants mainly on the Snake River Plain, but unfortunately kept no journal or locality records (Reveal 1972). Three of the taxa he named in 1841 had already been collected and described: *A. foliosa* (= *A. californica*), *A. abrotanoides* (= *A. californica*), and *A. plattensis* (= *A. filifolia*), but most names persist: *A. arbuscula*, *A. rigida* (Nuttall's *A. trifida* var. *rigida*), *A. trifida* (= *A. tripartita*), and *A. tridentata*. Asa Gray (1884) named *A. bolanderi* (= *A. cana* subsp. *bolanderi*) and *A. rothrockii* in his synoptic treatment of North American genera of flowering plants, followed by his publication of *A. pygmaea* in 1886. Three of the thirteen currently recognized species—*A. nova*, *A. spiciformis*, and *A. nesiotica*—were described in the twentieth century.

The first comprehensive classification of *Artemisia* in North America was produced by Per Axel Rydberg in 1916. Rydberg recognized one hundred and nineteen species in the genus (with four subgenera, and twenty sections). He treated the woody taxa as subg. *Seriphidium*, with three unranked groups: *Tridentatae* (thirteen species), *Rigidae* (one species), and *Pygmaeae* (one species). Harvey M. Hall and Frederic Clements (1923) adopted a more conservative view in their phylogenetic study of *Artemisia*; they recognized only twenty-nine species in North America. In their sect. *Seriphidium*, which they used to accommodate all woody taxa in North America, they recognized five species. Early investigators worked with the disadvantages of scant collections and a limited knowledge of species in the field, a situation that was especially true for the relatively unexplored American West through the early twentieth century. The treatment for the *Flora of North America* provides descriptions for fifty species of *Artemisia* (Shultz 2006b).

A number of specialized studies of woody sagebrush species were initiated after 1950. George Ward collected widely through the western U.S.A. and documented patterns of polyploidy. He recognized seven species in sect. *Seriphidium* (Ward 1953). Ecological studies initiated by Alan Beetle established varying phenotypic patterns within species. Beetle recognized eleven species in sect. *Tridentatae* (1960) and argued for the importance of recognizing infraspecific taxa (1977). E. Durant McArthur and colleagues initiated expansive studies of chromosome number and structure in the 1970's (McArthur & Pope 1975; McArthur & Sanderson 1999), which led to collaborative studies regarding the role of hybridization in the species complex (McArthur 1984; McArthur et al. 1988, 1998a; Byrd et al. 1999) and the establishment of subg. *Tridentatae* (McArthur et al. 1981). Alma Winward described a number of new infraspecific taxa and variants, based on his study of ecological patterns and variation in vegetative structure (Winward 1970, 2004; Winward & Tisdale 1977).

Molecular analyses initiated in the 1990's have led to a better understanding of relationships within the genus *Artemisia* (Kornkven et al. 1998, 1999; McArthur et al. 1998a; Torrell et al. 1999; Watson et al. 2002; Vallès et al. 2003; Riggins & Seigler 2006). Phylogenetic incongruence complicates delimitation of subgeneric groups, but species circumscriptions have not changed as a result of these analyses.

MATERIALS AND METHODS

Inasmuch as possible I have used a biological species concept, but my circumscription of species is based on morphology. The species described here rarely interbreed, although hybridization among subspecies is common. The taxa show discontinuities in character states, but there can be a frustrating degree of overlap in some morphological characteristics. Subspecies are defined by subtle morphological differences, but their circumscription is extraordinarily important in ecosystem management. Knowledge of growth patterns and site condition is especially important for the identification of the widespread subspecies of *A. tridentata*, *A. cana*, and *A. arbuscula*. Since subspecies occupy unique ecological sites that can be defined by temperature and soil moisture, their identification is often used in the classification of ecological units. This is particularly true for the subspecies of *A. tridentata*, and further subdivision into varietal units may be warranted on ecological grounds. Even though I am cognizant of variation among subspecies in the field, I do not further subdivide the taxa into varieties or forms, because it is impossible to distinguish these patterns consistently. The same difficulty applies to zones of hybridization between subspecies, a situation which has resulted in the naming of several new taxa that I have designated here as nothotaxa. Hybrid zones are of particular interest in the study of adaptations and ecological segregation, but consistent identification on morphological grounds is not possible.

Descriptions and species circumscriptions are based on my observations in the field and collections of plants for more than three decades, measurements of herbarium specimens I have examined and annotated, and examination of type collections. Maps are based on the collections cited in the index, with points provided when a locality could be determined with accuracy within a 10 km diameter. The electronic database for all collections cited will be provided in response to requests. Herbarium citations are in accord with standard acronyms (Holmgren & Holmgren 1998). Noteworthy is that fact that some collections are cited even though they could not be mapped according to this standard. It is well known that widespread and common species are often underrepresented in herbaria, and it is certainly the case that populations occur in many areas not represented on the maps. This is especially true for the mapped representation of *A. tridentata* in the southern limits of Arizona and New Mexico.

The Intermountain Herbarium (UTC) of Utah State University served as my professional home for much of this work, and it is the primary repository for my voucher collections. Duplicates of collections made for this study are deposited primarily at Rancho Santa Ana Botanic Garden (RSA), New York Botanical Garden (NY), and the Gray

Herbarium (GH) of Harvard University. Records for *A. filifolia* were obtained from collection databases at the University of Kansas (KANU), Kansas State University (KSU), and the University of Tulsa (TUL), and some records for *A. californica* were obtained from various California herbaria through the CalFlora database. Herbaria that I visited or from which I obtained loans are listed in the Acknowledgments.

Anatomical material for descriptions of leaf, seed, pollen, wood, and floral structure are based on my collections fixed in the field in glutaraldehyde or FAA (formalin:acetic acid:alcohol) and (a) embedded in paraffin for thin sections of leaves, (b) freeze-dried for images of fruits and florets, or (c) air-dried for images of pollen. I took the scanning electron micrographs with an AMR-1000 microscope at the Utah State University Electron Microscopy Laboratory. A few images are based on air-dried material from herbarium specimens. Voucher specimens are cited with the figure captions and included in the index.

My reports of leaf anatomy are drawn from studies in which I compared plants grown in a common garden at the University of Wyoming (cited as Shultz and Beetle voucher collections) to those grown under normal conditions (Shultz 1983, 1986b). Descriptions of mesophyll structure are based on midleaf sections taken from mature leaves in the axillary bundle of the vegetative shoots and measurements of relative tissue volume in the leaf are calculated from a randomized sample of leaf sections (described in detail in Shultz, 1986b). Leaf clearings were made from tissue soaked in a concentrated solution of sodium hydroxide and stained with safranin. Thin sections (2–10 μm) are from paraffin-embedded tissue stained with safranin and fast green or toluidine blue-O (microtechnique following O'Brien and McCully, 1981).

For the determination of epidermal surfaces, I removed the dense trichome layer of the leaf surface with a single-edged razor blade. Scanning electron micrographs of leaf epidermal surfaces are from tissue fixed in glutaraldehyde, dehydrated with a critical-point freeze dryer, and coated with gold palladium. Scanning electron micrographs of pollen grains are from air-dried material coated with gold palladium.

Chromosome counts are based primarily on research by E. Durant McArthur and colleagues from the 1970's to the present (with more than 500 documented records), as well as early research by George Ward in the 1950's; the chromosome numbers reported here are referenced by publication. I examined the vouchers collected by Ward and McArthur, and annotated specimens according to my taxonomic circumscriptions.

MORPHOLOGY AND ANATOMY

HABIT. All species of *Artemisia* subg. *Tridentatae* are shrubs. They all have a well-defined trunk that branches from near the base of the plant. Most have a rounded crown overtopped by flowering branches. Exceptions are *A. nova* and *A. tridentata* subsp. *vaseyana*, which have a distinctively flat-topped crown (with flowering branches that appear to arise from the uppermost part of the crown). Flowering branches arise from the vegetative branches, and surpass the crown. Mature plants have bark that peels into elongated strips and is deeply furrowed. Intraxylary cork accounts for some of the unusual growth form, with stems that have the ability to split into dead and living portions. The average life span of plants of *A. tridentata* ranges from 50–100 years (Winward 1970), but there are reports of some populations of *A. tripartita* that mature and senesce in as little as three years (Rosentreter 2005). Some individuals of *A. tridentata* have been found that are more than 200 years old (Ferguson 1964).

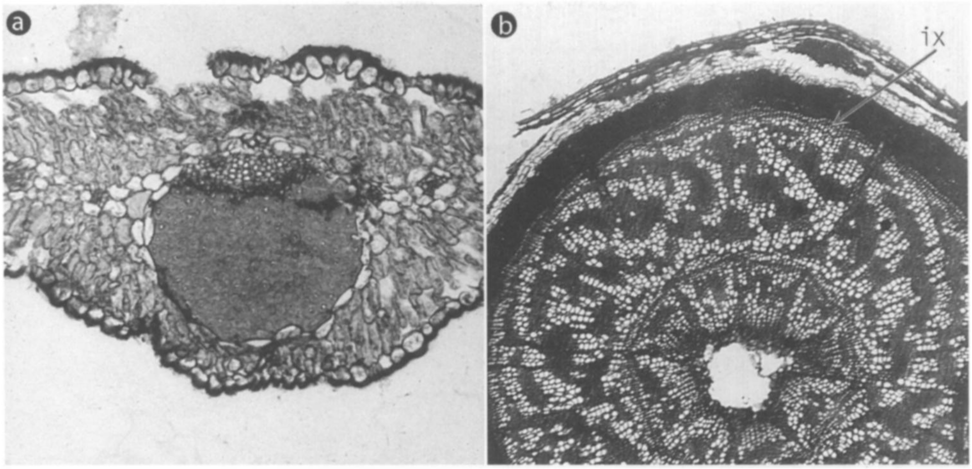

FIG. 1. Comparison of fiber bundles found in wood and leaves of *Artemisia;* micrographs show cross-sections. a. Leaf of *A. pygmaea* (*Shultz & Shultz 4560*) with large bundle of primary fibers in the center. b. Young stem of *A. rothrockii* (*Shultz & Shultz 5669*), showing intraxylary cork (ix) within the wood, near growth rings; note absence of ray cells.

ROOTS. Taxa of *Artemisia* subg. *Tridentatae* have two types of fibrous roots: coarse lateral roots that extend laterally near the soil surface and utilize moisture near the surface, and deep tap roots that have the ability to grow rapidly to great depths. The deep root systems have both fine and coarse branches. This bimodal pattern of root development allows plants to redistribute soil moisture from deep depths to surface levels (Ryel et al. 2002). Some species have the ability to "root sprout," a term that is not accurate as to origin, but is so universally applied that I am defining it here. "Root sprouters" are plants that can produce new shoots from adventitious buds arising from stem tissue, or crowns, below the ground. Plants that do not re-sprout after disturbance (e.g., fire, herbicide, or mechanical removal) lack this ability, which so dramatically affects successional stages in the ecosystem. The species that have the ability to re-sprout after disturbance are *A. arbuscula*, *A. cana*, *A. tripartita*, and *A. rigida*. These taxa have other characteristics considered to be basal within subg. *Tridentatae* (elongated pollen grains and large capitula), and for that reason I consider the ability to re-sprout an ancestral condition.

WOOD STRUCTURE. The wood of *Artemisia* is ring-porous, represented here by *A. rothrockii* (Fig. 1b). The cork layers between the growth rings and lack of ray cells in the first two years of growth are characteristic of all members of subg. *Tridentatae*. Cork layers are responsible for one of the sagebrush characteristics, stems with long thin strips of bark and irregular growth forms. The presence of intraxylary layers of cork was first reported by Moss (1940) in studies of *A. tridentata*. Intraxylary cork is also found in the closely related genus *Sphaeromeria* Nutt. (Holmgren et al. 1976). The presence of intraxylary cork, a characteristic that presumably confers an adaptive advantage in protecting the wood from desiccation and disease, as well as other specializations in *Artemisia* (Carlquist 1966a, 1966b, 1976, 1980), suggest a derivative form of wood morphology within the Anthemideae tribe. Ray cells are absent in the first two years of growth, first appearing in the third year of growth. This retention of juvenile characteristics, described as paedomorphic development (Carlquist 1962), supports the phylogeny showing *Artemisia* subg.

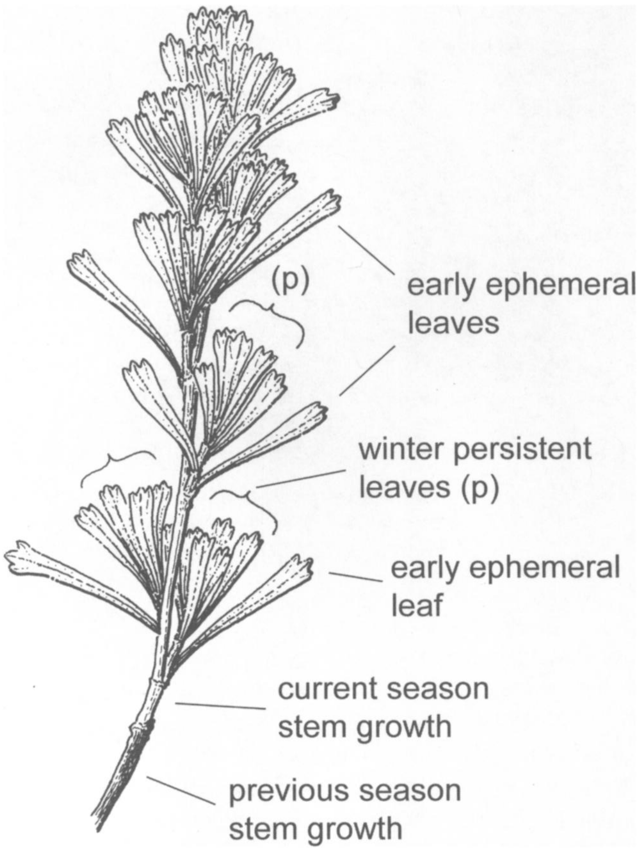

FIG. 2. Leaf morphology, comparing ephemeral and perennial leaves of *A. tridentata* subsp. *tridentata*. Ephemeral leaves are long-shoot leaves that occur below the fascicled (short-shoot) perennial leaves. (Based on *Goodrich 16468*; redrawn from Miller & Shultz 1987).

Tridentatae and *Sphaeromeria* as derived from a herbaceous lineage (Fig. 10). Woods of all examined species of *Artemisia* are ring-porous (Carlquist 1966a), as are those of the related genus *Sphaeromeria* (Holmgren et al. 1976). *Picrothamnus*, a genus sometimes included with the subg. *Tridentatae* (Sanz et al. 2008), differs in having diffuse-porous woods (Carlquist 1966a).

LEAVES. Leaves are simple, estipulate, and alternately arranged, with margins that are entire or lobed. Leaves are evergreen or deciduous, and usually occur in fascicles that are subtended by a single, deciduous leaf. This leaf is called ephemeral because it elongates in the spring, then senesces and drops about the time of flowering. The ephemeral leaves cause confusion in identification of species, because they resemble an abnormal, and variably sized, leaf of a sucker shoot (Fig. 2). Understanding the different positions of the two types of leaves will help to distinguish the fascicled leaves from the ephemeral leaves. Leaf descriptions in the taxonomic treatment refer to mature, fascicled leaves. The ephemeral and fascicled leaves vary in physiological and developmental aspects (Miller & Shultz 1987). Fascicled leaves on the vegetative branches are "short shoot" leaves that are

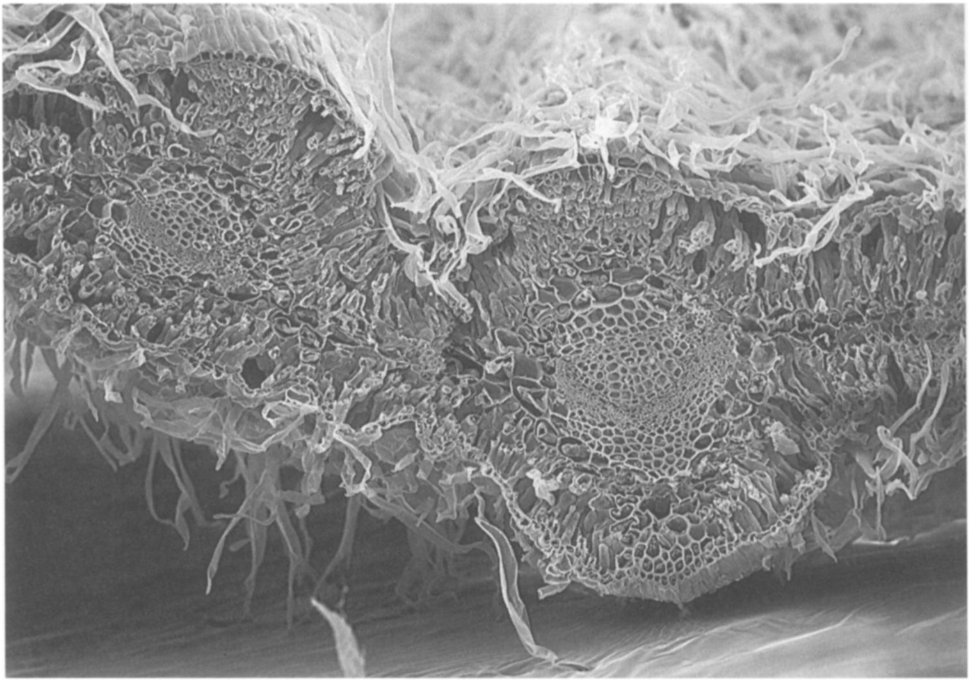

FIG. 3. Cross section of leaf, showing arrangement of mesophyll tissue typical of all members of *Artemisia* subg. *Tridentatae*. The mesophyll is isolateral, composed of palisade tissue present above and below the bundle sheath tissue; spongy mesophyll is absent. The bundle sheath parenchyma forms a large water-storage area, which surrounds the veins and extends between them. Although the structure has the appearance of C-4 morphology, the cells do not contain chloroplasts. Both dolabriform trichomes (on the surface of the epidermis) and glandular trichomes (in depressions of the epidermis) are visible. Based on scanning electron micrograph of *A. tridentata* subsp. *tridentata* (*Shultz & Shultz 4452*).

evergreen or deciduous. Ephemeral leaves are always deciduous and represent "long shoot" leaves. Flowering stems have leaves that are reduced in size and are either persistent or deciduous, a characteristic that is independent of the persistence of the leaves on the vegetative branches, and taxonomically variable. Unless otherwise specified, descriptions refer to the leaves of the vegetative stems.

Some attributes of leaf anatomy are common to all members of subg. *Tridentatae*, while other characteristics vary in significant ways. A typical leaf is shown in Fig. 3, represented by *A. tridentata.* Significant characters are discussed in the following paragraphs, ending with a discussion of functional significance.

Trichomes. Leaf trichomes are of two types: glandular or air-filled. The "living" trichomes are glandular and biseriate, and are the site of terpenoid synthesis. These occur on the leaves, flowers, and seeds of *Artemisia*. The T-shaped (or dolabriform) trichomes are air-filled and stalked. They create the "gray" look of sagebrush leaves and form dense layers in most species. Figure 4b shows the thin-walled dolabriform trichome, which is common to most species. Figure 4a shows the lignified trichome that is unique to *A. bigelovii.* Trichomes are extremely important functionally. Glandular trichomes are the site of synthesis of the monocyclic and acyclic monoterpenes (Stangl & Greger 1980) and sesquiterpene lactones (Kelsey & Shafizadeh 1980), which give the plants their bitter taste, and are

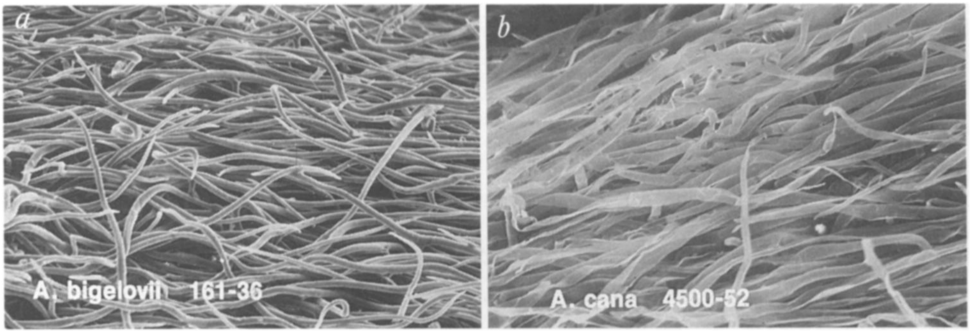

FIG. 4. Dolabriform (t-shaped) trichomes found on leaves and young stems of *Artemisia*; scanning electron micrographs of freeze-dried leaf tissue. a. Lignified trichomes of *A. bigelovii* (*Stockton 161*). b. Non-lignified trichomes of *A. cana* subsp. *viscidula* (*Shultz et al. 4500*), a defining characteristic of all other members of subg. *Tridentatae*.

known to exhibit a variety of biological activities (Rodriguez et al. 1972). The primary significance of the stalked trichomes appears to be the reflection of light and the consequent reduction of heat load (Ehleringer et al. 1976). The tough, lignified trichomes of *A. bigelovii* may provide herbivore deterrence.

Mesophyll Structure. The leaf mesophyll is isolateral (adaxial and abaxial sides similar), and the photosynthetic tissue is composed entirely of palisade cells (Figs. 3, 5), an arrangement that is common to arid-climate leaves that are arranged in an upright position on the stems. The palisade tissue is 2–3 cells deep on either side of the veins. Unlike the spongy mesophyll, with a large surface area, the cells are smooth and elongated, with an average length/width ratio ranging from 2:1 to 4:1. Palisade cells in the most xeromorphic species, *A. pygmaea* (shown in Fig. 1a), are at the lower range of this scale, with cells that are considerably shorter than those in the mesomorphic species *A. cana*. Air space within the mesophyll ranges in total volume from 5% in xeromorphic *A. tridentata* (Fig. 5a) to 25% in mesomorphic *A. cana* (Fig. 5b). Reduced air space and small surface-to-volume ratios for the palisade cells, presumably limiting water loss, appear to be significant adaptations to xeric habitats among species of subg. *Tridentatae*.

Venation. The typical pattern for leaves of subg. *Tridentatae* is three primary veins diverging from the base with lateral veins extending through most of the leaf blade, and a branching pattern that is actinodromous (Fig. 6). The primary veins are stout, the secondary and tertiary veins are fused just inside the margin, and the marginal vein is fimbrial. Secondary veins are moderately thick, diverging at moderate to wide angles (45–80°) from the primary veins. Tertiary veins are randomly reticulate. Vein areoles consist of incompletely closed meshes that are randomly arranged. The density of primary and secondary veins ranges from 4–15 veins per mm in the mid-portion of the leaf, and the average distance between tertiary veins is 60–70 μm (Shultz 1983, 1986b). This relatively high density of vascularization is typical of the sun leaves of deciduous dicots (Wylie 1951). The xylem consists entirely of open-ended vessel elements (Shultz 1983, 1986b). Vessels of the primary and secondary veins converge in the hydathodal region, and the pore that occurs at the leaf apex (Fig. 6b) apparently provides a mechanism for exuding excess water during periods of high positive root pressures. The region underlying the hydathodal openings at

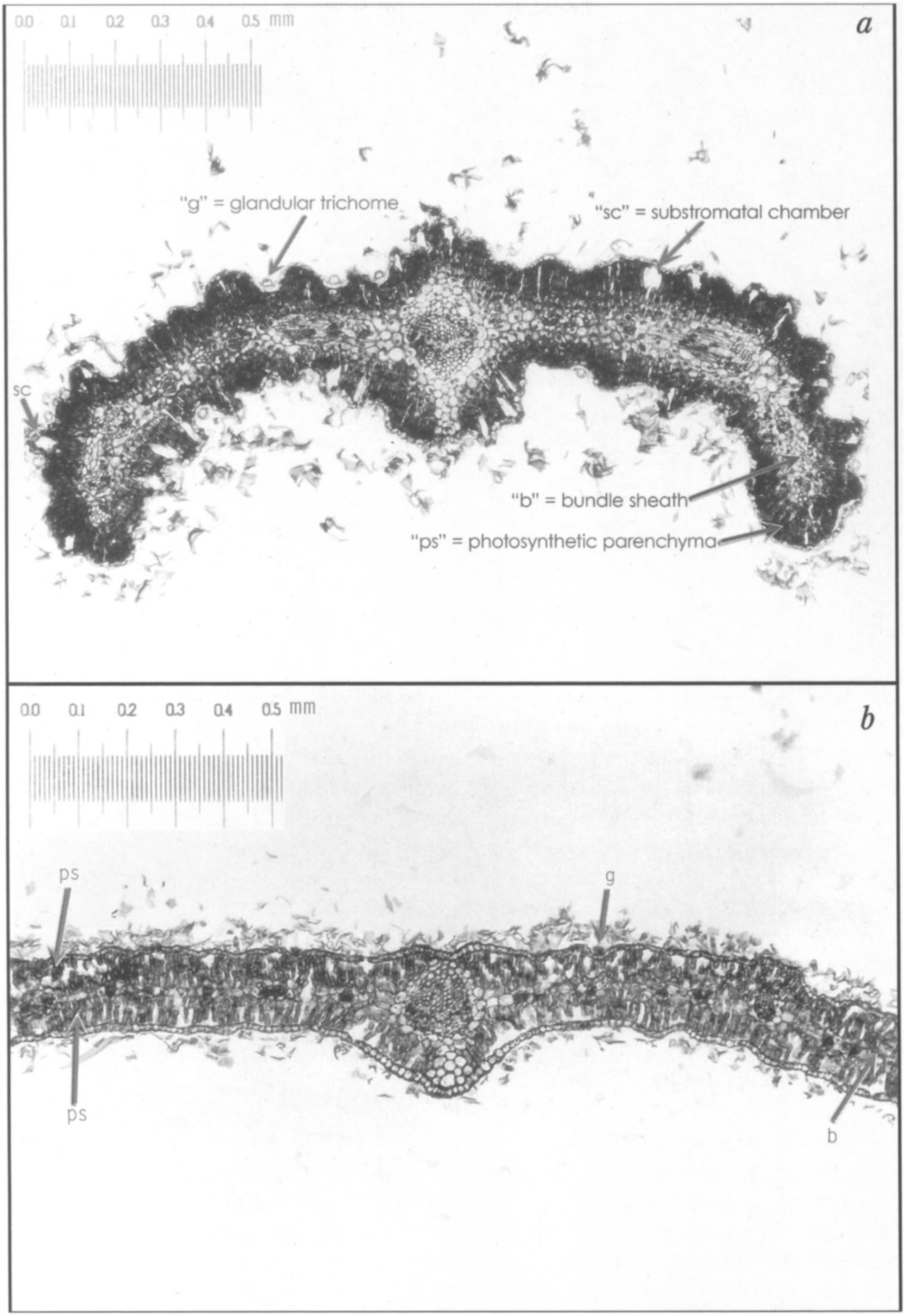

FIG. 5. Comparison of xeromorphic (a) and mesomorphic (b) leaf types of *Artemisia*. a. *A. tridentata* (*Shultz & Shultz 4600*): xeromorphic structure; note the compact mesophyll layer, large bundle sheath (water storage tissue), and small vessel diameters in the veins. b. *A. cana* (*Shultz et al. 4500*): mesomorphic structure; note the "open' mesophyll with high volume of air space, small area of bundle sheath cells, and large vessel diameters. [b = bundle sheath (non-photosynthetic parenchyma); g = glandular trichome; ps = photosynthetic parenchyma (palisade tissue)]

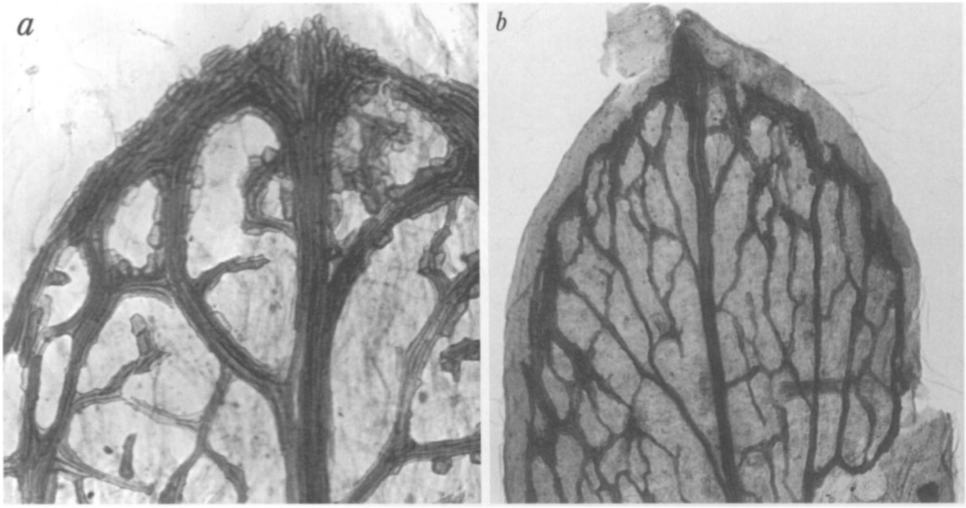

FIG. 6. Comparison of branching patterns of leaf veins in *Artemisia*. a. *A. tridentata* subsp. *parishii* (*Shultz & Shultz 4600*). b. *A. cana* subsp. *viscidula* (*Shultz et al. 4500*). Note secondary and tertiary veins, and hydathodal region near termination of veins.

the tips of the leaves consists of parenchyma cells, which may provide another important adaptation for arid land plants for water storage.

Sclerenchyma. Fibers are present in all the leaves of all species of subg. *Tridentatae*. The fibers are lignified with the exception of *A. rothrockii*, which has gelatinous fibers (Shultz 1986b). Fibers are unusually abundant in *A. pygmaea*, which has fibers aggregated in a dense central bundle, appearing "woody" in cross-section (Fig. 1a). The pattern of variation in fiber density follows an ecological gradient that may provide an adaptation to drought, as well as herbivore deterrence. Leaves with the highest fiber density occur in dry sites, while low-fiber-content leaves occur in mesic sites. Fiber densities range from an average of 15 fibers per leaf in high-elevation, relatively mesomorphic *A. tridentata* subsp. *vaseyana*, to 1,400 fibers per leaf in *A. pygmaea* (Shultz 1986b). Fibers displace the more delicate and easily dehydrated mesophyll cells; thus, leaves with numerous fibers (= high sclerenchyma volume) are able to maintain a sufficiently large surface area for high photosynthetic rates, while the fibers protect them from wilting. The large fiber bundle in *A. pygmaea* appears to be an effective adaptation to extremely xeric habitats, keeping the leaf from wilting in extreme heat.

Resin ducts. Resin ducts are found in all leaves of subg. *Tridentatae*. These ducts are schizogenous, positioned within the bundle sheath and adaxial to the xylem (Fig. 5a), and contain terpenes. Like the glandular trichomes, they are among the first structures differentiated in the leaf primordium and may also function in protecting the young leaf from herbivory. An abundance of resin ducts appears to correlate with phenology, ranging from rare (one per leaf) in deciduous species to moderate (2–3 per leaf) in evergreen species. The highest density (more than 5 ducts per leaf) is found in *A. rothrockii*, a species exuding a gummy residue when its leaves are crushed. The gelatinous leaf fibers of *A. rothrockii* stain green in the presence of safranin and fast green stain, while lignified fibers of all other species turn pink (Shultz 1983).

Epidermal surfaces and stomatal shape. Epidermal surfaces and cuticles are either striate or smooth, with round or elongate stomates (Fig. 7). Smooth epidermal surfaces and round stomata occur in diploid *A. tridentata* subsp. *tridentata* (Fig. 7a); blunt, square-shaped stomata are found in polyploid *A. tridentata* subsp. *wyomingensis* (Fig. 7b), *A. spiciformis* (Fig. 7c), and *A. rothrockii* (Fig. 7d). Elongate stomata occur in *A. rigida* (Fig. 7e). Striate cuticles and round stomata occur in *A. nova* (Fig. 7f), *A. bigelovii* (Fig. 7g), and *A. pygmaea* (Fig. 7h), a pattern also seen in *A. arbuscula*, *A. tripartita*, and *A. tridentata* subsp. *vaseyana*. While these differences are constant among species, they do not reflect phylogenetic patterns. Stomatal size varies greatly among the species of subg. *Tridentatae* and shows a relationship to ploidy level (Shultz 1991b). Large stomates (average length = 22 μm) occur in polyploid *A. tridentata* subsp. *wyomingensis* (Fig. 7b), *A. spiciformis* (Fig. 7c), and *A. rothrockii* (Fig. 7d), and smaller stomates (average length = 12 μm) occur in diploid populations of *A. tridentata* subsp. *tridentata* (Fig. 7f), *A. nova* (Fig. 7b), *A. pygmaea* (Fig. 7h), and *A. rigida* (Fig. 7e). Guard cells of tetraploid plants are nearly twice as large as in the stomates of diploid plants.

Water storage tissue. Large parenchyma cells with simple pits surround the veins (bundle sheaths) and extend between the veins as bundle sheath extensions (conspicuous in Fig. 3 and Fig. 5a). Originally reported as spongy mesophyll (Diettert 1938), these cells have no chloroplasts and give the leaves the superficial morphology of a plant with C-4 metabolism and large bundle sheaths; however, chemical tests reveal a C-3 metabolic pathway for *Artemisia* (Welkie & Caldwell 1970). I believe these cells represent an extraordinary adaptation in *Artemisia.* The internal "sheet" of parenchyma cells provides a hydrating layer within the leaf tissue and a means for water storage. Bundle sheath cells not only form a continuous layer between the veins, they also extend between the veins and the epidermis. While present in all species of subg. *Tridentatae*, the bundle sheath area is much larger in xeromorphic species, such as *A. tridentata* (Fig. 5a), than the more mesomorphic *A. cana* (Fig. 5b).

Functional significance of various aspects of leaf structure. Functionally advantageous features can be seen in a number of anatomical characteristics. The photosynthetic tissue in species of subg. *Tridentatae* is composed entirely of palisade cells. Palisade cells have less transpiration surface than spongy mesophyll, suggesting greater water-use efficiency. Palisade cells are shortest in *A. pygmaea*, the most xeromorphic taxon. A gradient from shortest to longest palisade cells in subg. *Tridentatae* correlates with the aridity of habitats, from driest to wettest (Shultz 1986b). The widest leaf vessels occur in *A. cana* and the narrowest in *A. pygmaea*. The variance from dry to wet habitats is remarkable, with species in the most xeric sites having the narrowest vessels, as well as the smallest proportional area of xylem (Shultz 1986b). Recent studies demonstrate gradients in resistance to water stress among subspecies of *A. tridentata* (Bonham et al. 1991; Black et al. 1994; Ryel et al. 2002) and suggest a strong functional relationship between the diameter of the xylem elements and potential water-use efficiency.

The amount of internal air space also follows an ecological gradient that varies by species. The total volume of internal air space ranges from as little as 5% in xeromorphic *A. pygmaea* (Fig. 1a) to as much as 25% in mesomorphic *A. cana* (Fig. 6b). Studies have shown that transpiration rates are positively correlated with the volume of intercellular air space (Turrell 1936, 1944), and intercellular air space decreases in response to drought stress (Nius 1931; Schröder 1937). The phenotypic plasticity in mesophyll configuration in

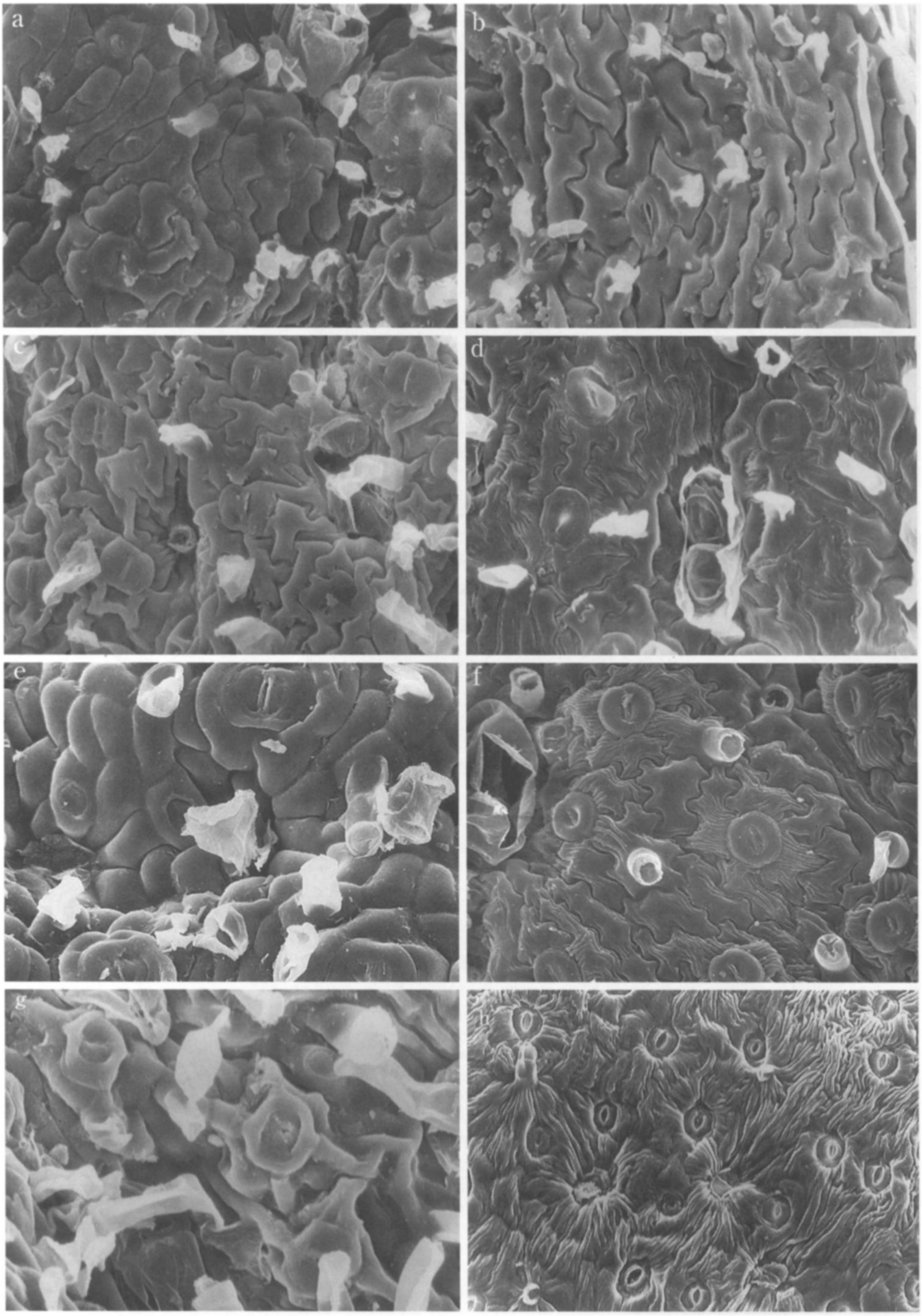

FIG. 7. Epidermal patterns and stomatal shapes in *Artemisia*; scanning electron micrographs of leaf surfaces from which dolabriform trichomes were removed. a. Smooth epidermal surfaces and round stomata of diploid *A. tridentata* subsp. *tridentata* (*Shultz & Thorne 4685*). b–d. Blunt, square-shaped stomata of polyploid taxa: b. *A. tridentata* subsp. *wyomingensis* (*Shultz & Shultz 5419*). c. *A. spiciformis* (*Shultz 5715*). d. *A. rothrockii* (*Shultz 5664*). e. Elongate stomata of *A. rigida* (*St. John 9107*). f–h. Striate cuticles and round stomata: f. *A. nova* (*Shultz & Shultz 4575*). g. *A. bigelovii* (*Stockton 161*). h. *A. pygmaea* (*Shultz & Shultz 4560*). A biseriate glandular trichome, surrounded by a thin cuticle, can be seen in "f"; "stubble" from the dolabriform trichomes is visible in all the figures except "h."

Artemisia appears to confer an adaptive advantage for a group of plants occupying extreme habitats. Higher rates of photosynthesis occur with the increased air space found in large leaves (Wiebe & Al-Saadi 1976), but water loss is reduced in small-leaved evergreens with lowered rates of photosynthesis (Mooney & Dunn 1970). Leaf morphology appears to conform to what is adaptive in a habitat where water is limited. In addition to mesophyll configuration, water conservation is provided by internal cuticularization (Scott 1948), a characteristic that can be seen by the thin refractive layer around the palisade tissue in species of sagebrush (visible in Fig. 5).

INFLORESCENCES. The flowering heads (capitula) of *Artemisia* are arranged in a panicle-like array that is technically called a capitulescence. In descriptions of the taxa, I use "inflorescence" to describe the capitulescence, because this is the more familiar (and easily understood) terminology. While inflorescences of the genus *Artemisia* are always panicle-like, the size and shape of the inflorescence are taxonomic characters that can be used to define taxa in subg. *Tridentatae*. Inflorescences can be broadly branched (here called paniculate), sparsely and narrowly branched with pedunculate heads (here called racemose), or narrow and little-branched with sessile heads (here called spicate). Even though the general shape and size of the inflorescence is highly variable, the inflorescence provides critical diagnostic features in distinguishing species and subspecies.

CAPITULA. Sexual arrangement of flowers within a capitulum has been the primary characteristic used to define subgeneric groups of *Artemisia* (Bremer & Humphries 1993; Shultz 2006a). Traditionally, subg. *Seriphidium* and subg. *Tridentatae* have been defined as having homogamous, perfect florets; subg. *Dracunculus* as having functionally staminate central florets (with an abortive ovary) and pistillate marginal florets; and subg. *Artemisia* as having perfect central florets and pistillate marginal florets. The redefinition of *Artemisia* subg. *Tridentatae* provided here challenges the importance of this character. *Artemisia* sect. *Tridentatae* has capitula that are homogamous and discoid, with tubular florets (except *A. bigelovii*, with 1–2 ray-like florets), whereas sect. *Nebulosae* has heterogamous capitula: *A. filifolia* with an arrangement characteristic of subg. *Dracunculus* (marginal florets pistillate, central florets functionally staminate), and *A. californica* and *A. nesiotica* with the capitular morphology of subg. *Artemisia* (marginal florets pistillate, central florets perfect).

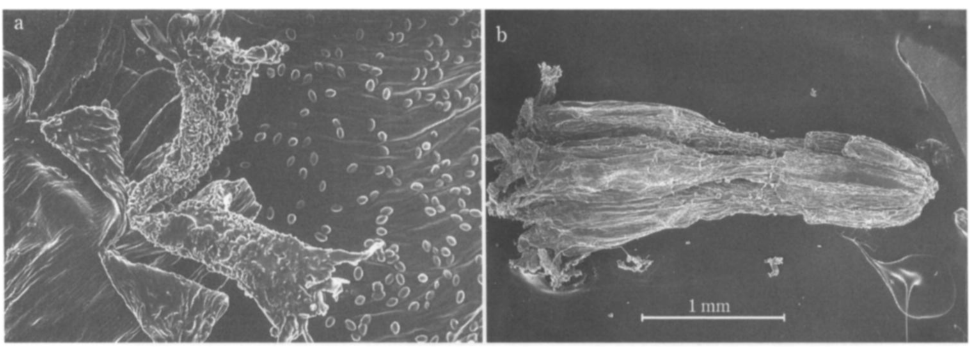

FIG. 8. Floral detail, florets and cypsela morphology typical of all members of *Artemisia* subg. *Tridentatae*. a. Style branches projecting from disc floret, with scattered pollen grains. b. Three disc florets with attached cypselae. Scanning electron micrographs of *A. cana* subsp. *viscidula* (*Shultz 4511*).

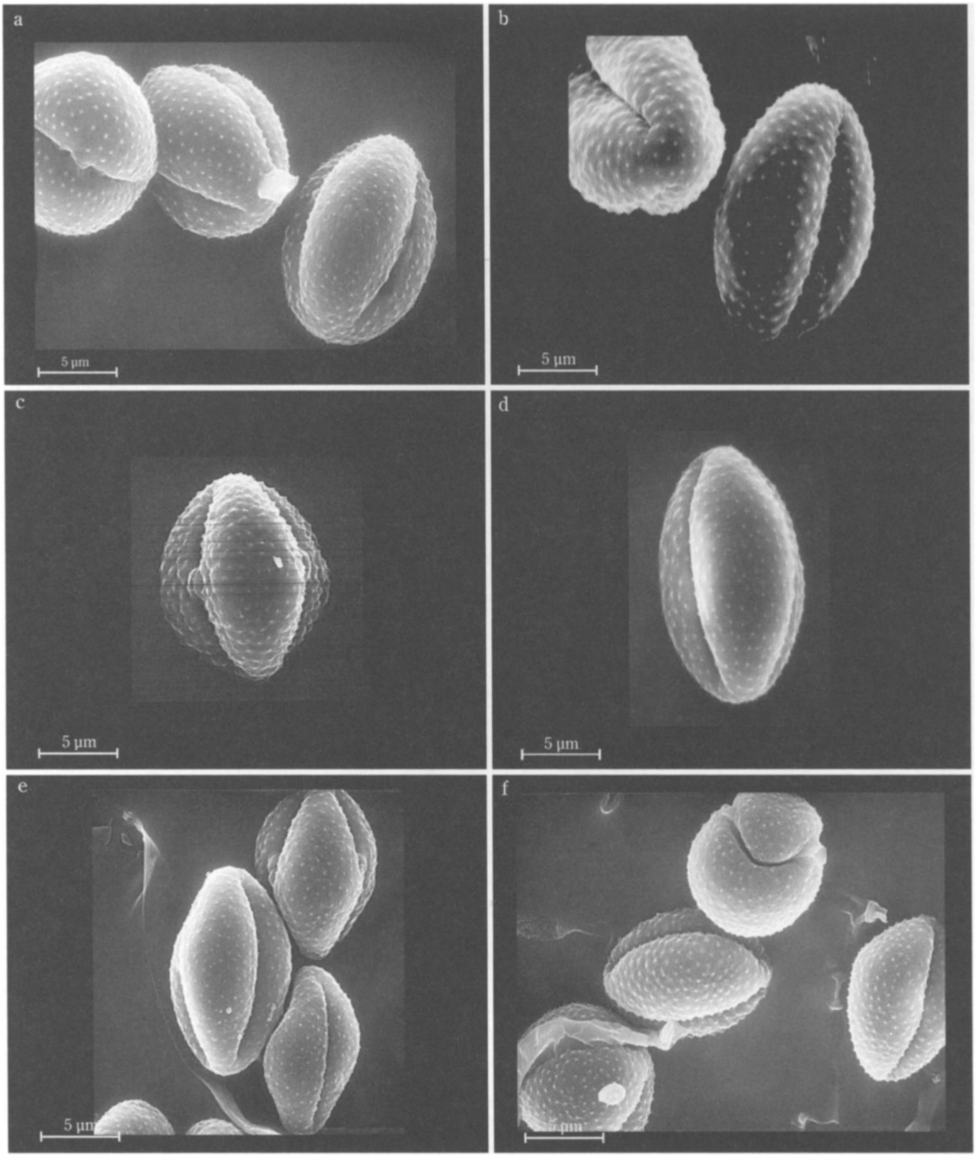

FIG. 9. Pollen morphology of *Artemisia* subg. *Tridentatae*; elongate-prolate pollen. a. *A. cana* subsp. *viscidula* (*Shultz 750*). b. *A. cana* subsp. *cana* (*Suksdorf 991*). c. *A. rigida* (*Shultz 7472*). d. *A. tripartita* subsp. *tripartita* (*Cronquist 1817*). e. *A. tripartita* subsp. *rupicola* (*Nelson 8941*). f. *A. spiciformis* (*Shultz 7438*).

FLOWERS. The flowers of *Artemisia* are minute and inconspicuous, and of little use in distinguishing species. Florets are typically tubular, perfect, and fertile. Exceptions are *A. bigelovii*, which rarely has one or two marginal florets that are pistillate (appearing as a rudimentary ligulate corolla); *A. californica* and *A. nesiotica,* with marginal florets that are pistillate; and *A. filifolia,* with central florets that are functionally staminate (ovary abortive). The remaining nine species have capitula that are homogamous, with tubular, perfect florets. Beyond the few exceptions in sexual arrangement within the capitulum,

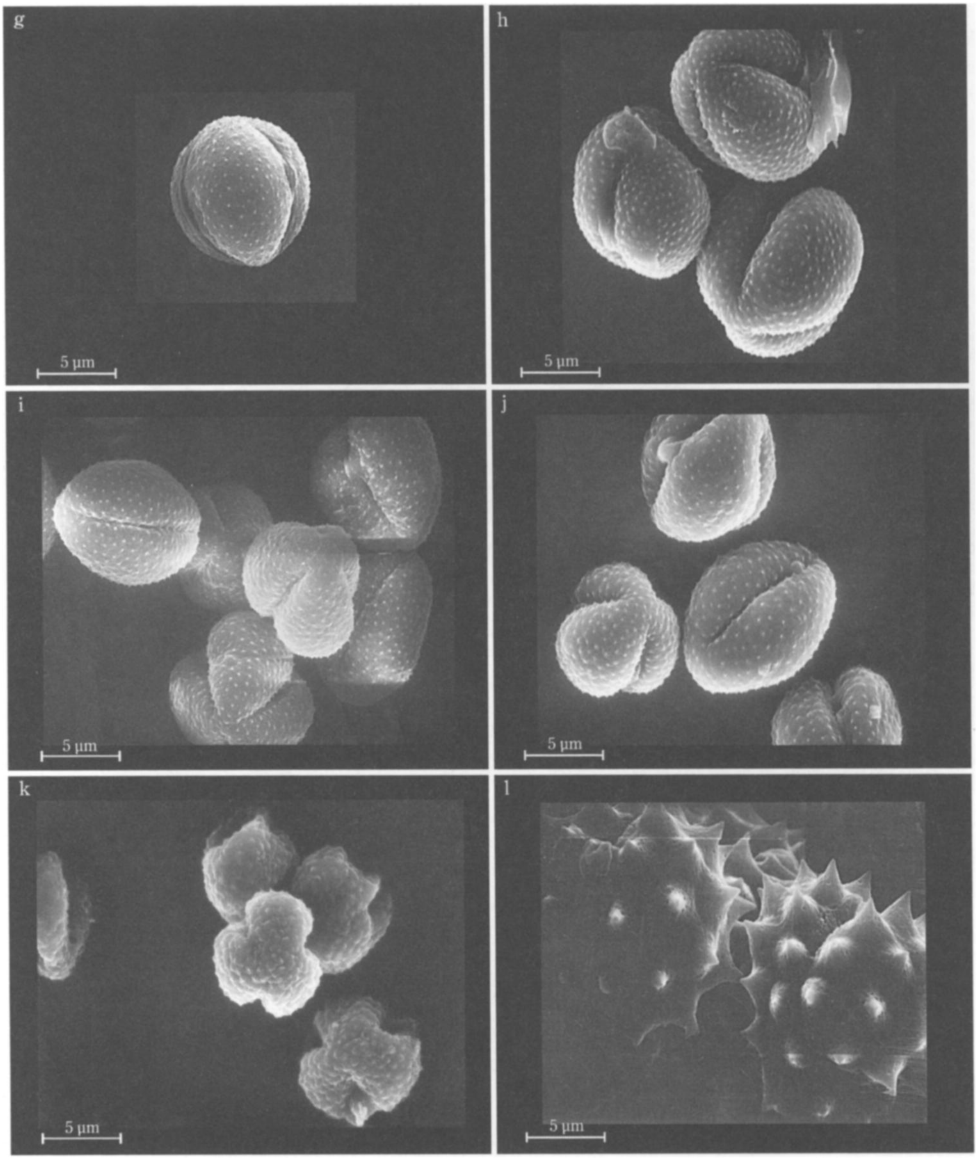

FIG. 9. (cont.) Pollen morphology of *Artemisia* subg. *Tridentatae* (spheroidal-oblate pollen) and *Achillea millefolium*. g. *A. tridentata* subsp. *tridentata* (*Shultz 10264*). h. *A. nova* (*Shultz 8150*). i. *A. cana* subsp. *bolanderi* (*Shultz 5692*). j. *A. rothrockii* (*Shultz 4713*). k. *A. arbuscula* subsp. *longiloba* (*Shultz 8109*). l. Spinulose pollen of *Achillea millefolium* (*Shultz 725*), a morphology characteristic of insect-pollinated taxa that are basal within the Anthemideae lineage.

there are no discernible differences in floral morphology. Florets of subg. *Tridentatae* range from 1.0–3.5 mm long, with sufficient variation occurring within a capitulum so that size is not useful diagnostically. Florets are glabrous or sparsely glandular, and pale yellow (except for sporadic populations of *A. tridentata*, with florets that become red with anthocyanin pigmentation in the fall). The receptacle is convex and smooth (epaleate). There is no true pappus, but a rudimentary fringe or microscopic and "pappoid" crown is apparent in three species (*A. rothrockii*, *A. californica*, and *A. nesiotica*). Style branches are linear or linear-spatulate, blunt, apically fringed, and flattened, with two stigmatic lines along the margins (Fig. 8a). The branches spread apart in fertile flowers, but wither or remain appressed in the one species with functionally staminate florets (*A. filifolia*). Anthers have a terminal deltate appendage, and the bases are obtuse with minute caudate appendages.

CYPSELAE. The fruits of *Artemisia* are cypselae (often described as "achenes" in the literature). They are minute (<2 mm), unwinged, and unornamented fruits, which are carried by the wind or blown along the top of crusted snow, rarely dispersed by birds when stuck to feathers or feet. Embryo sac development is monosporic, and the pericarp sometimes has myxogenic cells, lacking resin sacs. The cypselae of *Artemisia* are ellipsoid, slightly broadened at the apex (fusiform), light brown to dark brown, not compressed, smooth or sparsely glandular, obscurely ribbed, and generally indistinguishable at the species level. The cypselae of *Artemisia* subg. *Tridentatae* (Fig. 8b) are 1–2 mm in length, with an approximate length to width ratio of 3:1. The size of the mature fruit can vary by the season and its position within the head, and there appear to be no taxonomically useful characteristics as to ornamentation. The morphology of the fruit is more or less uniform for all species of subg. *Tridentatae*.

POLLEN. The pollen grains of *Artemisia* subg. *Tridentatae* are tricolporate with a smooth exine, and are spheroidal or prolate (Fig. 9). The grains are coarse-granular, having a two-layered exine: the inner thicker with coarse radial striae, and the outer thinner with very fine radial striae (Wodehouse 1935). The columellae have an "anthemoid" structural type, with cavities separating the columellae from the foot layer (Vezey et al. 1994). In contrast to most Anthemideae, the tectum is composed of three or more layers (Skvarla & Turner 1966). Questions about the significance of these structures to ontogeny and homology are addressed in comparative studies of *Artemisia* pollen (Skvarla & Larsen 1965; Vezey et al. 1994). Pollen of *Artemisia* (including *Crossostephium* Less.) falls into the general category of smooth, wind-pollinated grains, but shows no other distinguishing features (Skvarla & Turner 1966). Shapes of the spinules have a phylogenetic significance for some Asian species (Jiang et al. 2005), but spinules do not appear to vary among species in subg. *Tridentatae*. In a comparison of modern and fossil pollen of Eurasian species, primarily in subg. *Artemisia*, Martín et al. (2003) found no significant differences among the species.

Significant variation in pollen shape and size provides a remarkable and previously overlooked character that distinguishes species of subg. *Tridentatae* (Shultz 1988). Elongate, prolate grains with a length-to-width ratio >1.3 occur in *A. cana* subsp. *cana* and subsp. *viscidula*, *A. tripartita*, *A. spiciformis*, and *A. rigida* (Fig. 9a–f), whereas short, spheroidal pollen with a length-to-width ratio <1.2 is found in *A. tridentata*, *A. arbuscula*, *A. nova*, *A. rothrockii*, and *A. cana* subsp. *bolanderi* (Fig. 9g–k). Species with spheroidal grains usually occur in xeric habitats, and species with prolate pollen grains are generally found in more mesic habitats. *Artemisia rigida* is an exception and may provide evidence for an independent xeromorphic specialization within a mesomorphic lineage. Based on the differential patterns in pollen morphology for the mesomorphic and xeromorphic lineages of subg. *Tridentatae*, a renewed examination of stratigraphic profiles may help to determine the timing of desertification in western North America, the evolution of woodiness within *Artemisia*, and changing climatic patterns on a regional scale.

CHROMOSOME NUMBERS AND HYBRIDIZATION

There are three base numbers for *Artemisia*: x = 7 for dysploid *A. pattersonii* A. Gray (Wiens & Richter 1966), x = 8 for dysploid *A. vulgaris* L. (Vallès & McArthur 2001; Vallès et al. 2003), and x = 9 for all other species. Most species of subg. *Tridentatae* have diploid (2n = 18) and tetraploid (2n = 36) populations, with hexaploid and octoploid complements relatively infrequent. Chromosomes are rather small (2–8 µm), and the karyotypes tend to be symmetric (McArthur et al. 1981; Vallès & McArthur 2001). The unique condition of x = 8 for *A. vulgaris* represents a dysploid condition that is apparently derived through chromosomal fusion (Vallès & Siljak-Yakovlev 1997; Torrell et al. 2003).

McArthur established early in his research that polyploidy in subg. *Tridentatae* is derived through autopolyploidy (McArthur et al. 1981). The first report of chromosome morphology in subg. *Tridentatae* was published by Diettert (1938) for *A. tridentata*, followed by a comparative study and chromosome counts for all known taxa in subg. *Tridentatae* by Ward (1953). Breeding and cytological investigations conducted over the last three decades—primarily by E. D. McArthur, alone (1984, 2000) or in conjunction with colleagues (McArthur & Pope 1975; McArthur & Sanderson 1999; McArthur et al. 1979)—provide in-depth studies of chromosome morphology, reproductive systems, and ploidy levels among taxa of sect. *Tridentatae*. A summary table for more than 500 chromosome counts of species in sect. *Tridentatae* is provided by McArthur and Sanderson (1999) and Mahalovich and McArthur (2004).

Studies of chromosome morphology and cytogenetics for other subgenera of *Artemisia*, as well as allied genera in the Anthemideae, have been conducted by an alliance of European scientists during the last decade (for a review, see Torrell et al. 1999, 2003). The investigation of subg. *Seriphidium* (Torrell et al. 2003) supports the inclusion of this subgenus within *Artemisia* and its segregation from subg. *Tridentatae*.

Differences in chromosome numbers have helped characterize species and subspecies of *Artemisia* (Ward 1953; McArthur et al. 1981; McArthur & Sanderson 1999); however, because introgression among subspecies is relatively common (McArthur et al. 1979, 1988a, 1998b; McArthur 1984; McArthur & Sanderson 1999), a chromosome number alone is inadequate to identify the complexes. Infraspecific hybridization occurs on a relatively frequent basis, and the nature of hybrid complexes and the environmental conditions under which they occur have been studied extensively (Freeman et al. 1991, 1995; Byrd et al. 1999). The degree to which hybridization has contributed to speciation in *Artemisia* is a story that continues to unfold. Freeman et al. (1999) found that some hybrid populations are more developmentally stable than parental populations, and that the hybrid zones often create stable community types within undisturbed habitats.

These studies challenge standard assumptions concerning the presence of a dynamic equilibrium between selection and gene flow, and they demonstrate an ecological advantage of hybrid zones by showing stability in hybrid complexes as well as superior "fitness" of selected strains. It is clear from these studies that hybridization is an important driving force in maintaining genetic heterogeneity in populations, and it provides the material from which new lineages can be selected through either natural means or manipulation.

In spite of the morphological and ecotypic differentiation seen in the field and in common gardens among closely related taxa, genetic structuring among subspecies as well as species in subg. *Tridentatae* can be difficult to detect (Stanton et al. 2002; Miglia 2003). Certain molecular genetic patterns do characterize subspecies, species, and higher taxa (McArthur et al. 1998a, 1998b). Patterns are distinctive, even though unique markers are hard to find. K. J. Miglia (pers. comm.) found distinct markers for *A. tridentata* subsp. *tridentata* and subsp. *vaseyana* in the Salt Creek hybrid zone studied by McArthur and colleagues. Garrison (2006) found unique morphological patterns in her study of three subspecies of *A. tridentata* and was able to identify hybrid zones.

CLASSIFICATION

Tribal relationships. Artemisia belongs to tribe Anthemideae, subtribe Artemisiinae of subfamily Asteroideae of Asteraceae. The Asteroideae appear to be the most recently derived of all the major divisions in the Asteraceae (Panero & Funk 2002), and *Artemisia*, as one of the few wind-pollinated genera in the family, is among the most recently derived and highly specialized in reproductive morphology (Heywood & Humphries 1977; Kim & Jansen 1995). There are approximately 1,135 genera and 163,600 species in subfamily Asteroideae (Stevens 2006), and *Artemisia* is one of the largest of all the genera.

Generic relationships. Artemisia forms a clade consisting of species with flowering heads that are heterogamous-disciform or homogamous-discoid, pollen with short or without spines, and cypselae with smooth surfaces and thickened walls (Bremer & Humphries 1993). These characteristics apply to *Artemisia* as defined in most modern floras, but molecular analyses bring other genera into the *Artemisia* clade, including genera with radiate flower heads. The *Artemisia* group contains species that have been variously placed within the taxonomic boundaries of *Artemisia* sensu lato, as well as *Mausolea* Bunge ex Poljakov, *Neopallasia* Poljakov, and *Turaniphytum* Poljakov (Riggins & Seigler 2006; Sanz et al. 2008; Torrell et al. 1999, 2003; Vallès & McArthur 2001; Vallès et al. 2002; Watson et al. 2002), and *Sphaeromeria* Nutt. (Holmgren et al. 1976; Watson et al. 2002). Bremer and Humphries (1993) suggest that *Sphaeromeria* might be closely related to *Kaschgaria* Poljakov, but McArthur et al. (1998b), in a study of genetic similarities, found that the species are closely aligned with subg. *Tridentatae*, a conclusion that is tentatively supported by the work of Riggins and Seigler (2006).

These studies support investigations of anatomical structure and morphology that suggest that *Sphaeromeria* is more closely related to *Artemisia* than to New or Old World *Tanacetum* L. (Holmgren et al. 1976), but until a more inclusive study is done, the alignment of *Sphaeromeria* remains problematic (Lowrey & Shultz 2006). At least one species (*S. potentilloides*) is quite similar to *Picrothamnus desertorum* Nutt. (McArthur et al. 1998b). The monotypic genus *Picrothamnus* Nutt. (type species *P. desertorum*, formerly included in *Artemisia spinescens* D. C. Eaton) is segregated, in part, on the basis of its diffuse-porous wood anatomy and corymbiform inflorescences (Shultz 2006b). *Oligosporus* Cass. and *Crossostephium* Less. are treated as part of *Artemisia*.

Hypotheses of a congeneric relationship between the Old World genus *Seriphidium* and New World *Artemisia* subg. *Tridentatae* have been refuted by molecular studies (Kornkven et al. 1998, 1999; Torrell et al. 1999; Watson et al. 2002; Vallès et al. 2003; Riggins & Seigler 2006) as well as morphological and ecological analyses (Tkach et al. 2007), which indicate separate lineages for Old and New World species. I believe that the generic separation of *Artemisia* from *Seriphidium* (Ling 1995b, 1995c; Weber 1984), and the division of the genus into morphologically defined series (Poljakov 2000), confounds the emerging picture of relationships within *Artemisia*.

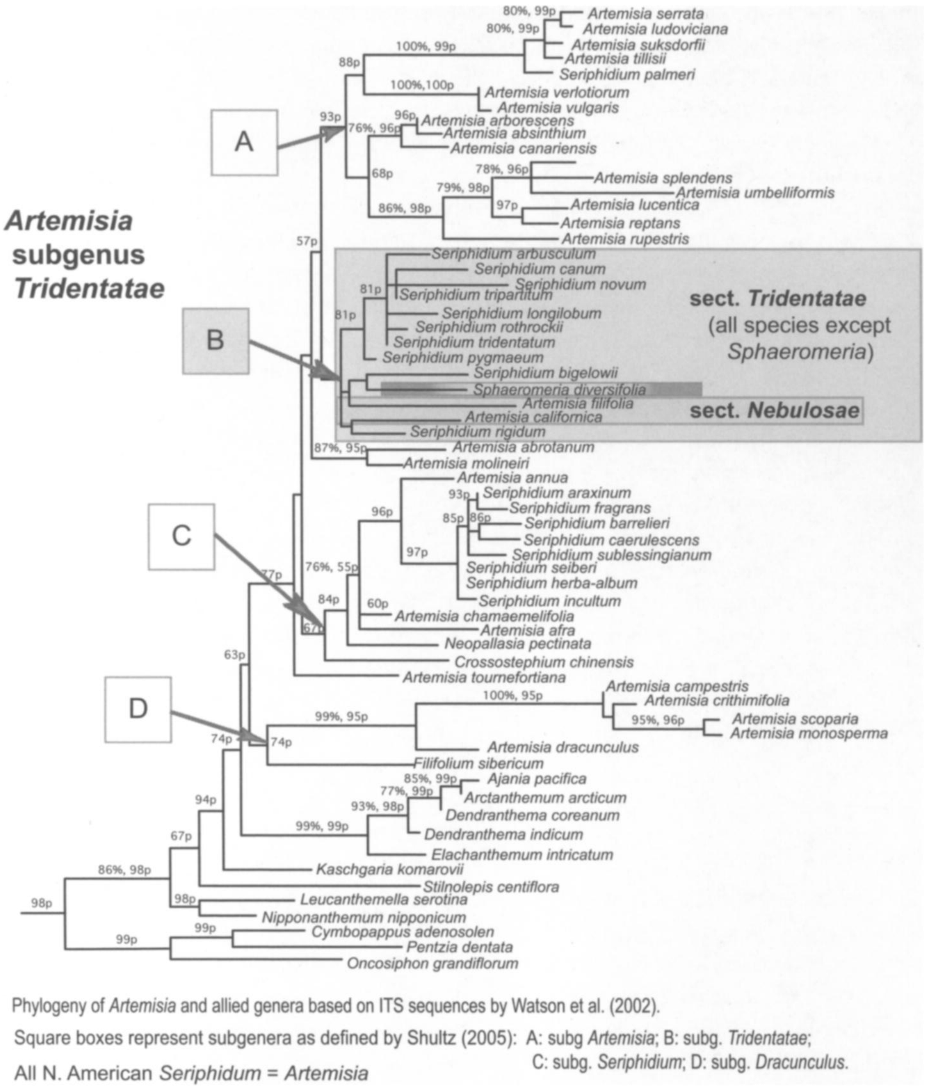

FIG. 10. Molecular phylogeny of Artemisia based on nuclear ITS sequences (modified from Watson et al. 2002; boxes show clades that correspond to subgenera here recognized). A. Subgenus *Artemisia*: comprises Old World and New World taxa, which are most closely related to subg. *Tridentatae* in North America (alignments of *A. abrotanum* and *A. molineiri* are noted in the text). B. Subgenus *Tridentatae*: includes most members of sections *Tridentatae* and *Nebulosae* (treated as *Artemisia*, not *Seriphidium*, and excluding *Sphaeromeria diversifolia*, as discussed in the text). C. Subgenus *Seriphidium* (sometimes recognized at generic level): includies *Artemisia annua*, *Neopallasia*, and Old World taxa of *Crossostephium*. D. Subgenus *Dracunculus* (sometimes recognized as genus *Oligosporus*; including *Filifolium sibericum*). Numbers above branches are bootstrap values.

Subgeneric classification. E. D. McArthur (in McArthur et al. 1981) established subg. *Tridentatae* to include species that had previously been treated within sections of *Artemisia* (Rydberg 1916; Hall & Clements 1923; Ward 1953; Beetle 1960; Winward & Tisdale 1977). I follow the subgeneric classification of McArthur, but instead treat the species he included in subg. *Tridentatae* as *Artemisia* subg. *Tridentatae* sect. *Tridentatae*.

This section is the only monophyletic taxon above species rank within *Artemisia* in the molecular phylogenies (Watson et al. 2002; Riggins & Seigler 2006), and its circumscription has remained unchanged since McArthur established the subgenus (McArthur et al. 1981). I believe the treatment of evolutionary lineages as subgenera of *Artemisia*, as opposed to generic segregates, is the best method and most practical way of reflecting species relationships; see Fig. 10.

Artemisia sect. *Nebulosae* is here established to accommodate three species (*A. filifolia*, *A. californica*, and *A. nesiotica*) within the *Tridentatae* clade. These three species share a number of morphological features, including marginal pistillate florets that have style branches with marginal stigmatic lines, and linear leaves that are non-fascicled. Independent molecular analyses place these species within the *Tridentatae* clade (Watson et al. 2002; Riggins & Seigler 2006), but because of the lack of strong support for this clade, the placement is tenuous. An ancient hybridization event may account for the affinity of *A. filifolia* with the *Tridentatae* clade (Watson 2005), and the same may be true for the *A. californica* lineage (including *A. nesiotica*). The name "*Nebulosae*" is intended to reflect a situation which is unknowable (i.e., nebulous) at this time.

The relationship of species of *Sphaeromeria* to subgenus *Tridentatae* also remains problematic (Holmgren et al. 1976), and may be part of the nebulous complex of species. With only *S. diversifolia* included in the molecular phylogeny shown in Fig. 10, I am unwilling to draw a conclusion regarding the relationships of the genus as a whole. Furthermore, a preliminary report by Riggins (2008) includes more species of *Sphaeromeria* that show relationships with other clades within *Artemisia*. Clearly, an understanding of evolutionary patterns within *Sphaeromeria* and its relationship to *Artemisia* has yet to be reached.

Species. My circumscriptions differ notably from modern treatments (Rosentreter & Kelsey 1991; Shultz 2006a; Welsh and Goodrich 1995; Winward & McArthur 1995; Winward et al. 1985): primarily in that I (1) treat *Artemisia longiloba* as a subspecies of *A. arbuscula*, (2) elevate *A. tridentata* subsp. *spiciformis* to species level, and (3) treat several recently described varieties as either hybrids (*A. arbuscula* subsp. ×*longicaulis*, *A. tridentata* subsp. ×*xericensis*, and *A.* ×*argilosa*) or relegate the name to synonymy (*A. tridentata* var. *pauciflora*) involving *A. tridentata*. *Artemisia* sect. *Nebulosae* includes *A. californica* and *A. nesiotica*, formerly placed in subg. *Artemisia* (Shultz 2006a), and *A. filifolia*, formerly treated in subg. *Dracunculus* (Shultz 2006a).

The species of subg. *Tridentatae* are reproductively isolated from one another, either by geographic isolation, phenology (separate flowering times), or reproductive incompatibility. Even though hybridization between subspecies frequently occurs in sympatric populations, hybridization between species is rare (McArthur et al. 1979). Past hybridizations have undoubtedly been an important factor in the evolution of species of *Artemisia*, thus confounding the molecular phylogeny. I believe three of the species in the complex—*A. arbuscula*, *A. spiciformis*, and *A. rothrockii*—are the result of past hybridizations between *A. cana* and *A. tridentata*, and between *A. tripartita* and *A. arbuscula* to form *A. arbuscula* subsp. *thermopola*. This is a relatively high degree of reticulate evolution that profoundly complicates the analysis of relationships, and makes a "true" phylogenetic tree difficult to reconstruct for subg. *Tridentatae*. The morphological characters I use to separate species vary in some notable hybrid swarms; in the discussions that follow the taxonomic descriptions I try to account for the variation I have encountered in the field.

Subspecies. Determination of infraspecific boundaries has been the most difficult aspect of this monographic study, and it is at this level of discrimination that users of the taxonomic key will have the greatest difficulty. A high degree of genetic mixing among subspecies (Byrd et al. 1999) is one of the most frustrating aspects of sagebrush classification. Genetic heterogeneity and phenotypic plasticity in *A. tridentata*, the most prolific and common species in the complex, undoubtedly contributes to its success in colonizing ecologically extreme environments. Subspecies of *A. arbuscula*, *A. cana*, *A. tridentata*, and *A. tripartita* occupy well-defined ecological gradients with extreme variation in thermal and moisture gradients as well as soil chemistry. In *A. tridentata* populations, for example, there may be as many as three subspecies growing sympatrically but separated in subtle ways. Microhabitats are defined by differences in soil texture and moisture, but introgression is common in the contact zones. Novel morphologies, as well as unique chemical constituents, arise in hybrid zones and provide a compelling argument for the importance of names assigned to nothotaxa in this treatment.

Inasmuch as it has been difficult to find distinct molecular markers to distinguish infraspecific taxa, I have maintained a broad circumscription of subspecies, which are not further subdivided into varieties. Some variants are widespread and appear to be ecologically distinctive. I note what I consider significant variants and refer to them as ecotypes in discussions that accompany the taxonomic descriptions. Usually, these variants represent populations of subspecies that have intermingled for many generations and are impossible to distinguish consistently. My guide has been the need to devise a practical, workable taxonomy that reflects evolutionary relationships as much as possible.

PHYTOGEOGRAPHY

Phytogeographic history suggests a relatively recent origin for woody *Artemisia* in western North America. The pollen record shows cold desert shrubs developing in the Great Basin during the Pliocene and early Pleistocene, with a predominance of *Artemisia* and *Pinus* L., beginning about 0.8 million years ago (Davis 1999). Modern desert assemblages were established as early as 12 million years ago on the lava flows extending from the Snake River Plain to the Columbia Plateau, appearing well before a desert assemblage appeared in the Great Basin (Davis 1998). Pleistocene lakes filled the intermountain valleys of western North America and created barriers to gene flow that might account, in part, for the pockets of endemism in subg. *Tridentatae* that occur around the fringes of the Great Basin. Subsequent diversification was stimulated as new habitats opened. As climates warmed and Pleistocene lakes dried to salt basins from 7000–4000 BP, sagebrush expanded into areas once occupied by conifer forests, and *A. tridentata* became the dominant shrub in the arid interior basin of western North America (Davis 2000). This warming period also provided for the northward expansion of *A. cana* and *A. tridentata* into the prairie provinces of Canada (Strong & Hills 2003). The change to a cooler, moister climate between 4000–2000 BP was followed by a return to aridity and high temperatures (Davis 2000). These rapid " pulses" of climate change followed by desertification created the kind of unstable conditions favoring a rapid expansion and diversification of species, with subsequent selection for the harsh conditions of the interior Great Basin. No other shrub complex rivals the success of woody *Artemisia*.

Herbaceous species of *Artemisia* first appeared in the pollen record during the Oligocene in north and central Asia (Ling 1992) and central Europe (Graham 1996).

Presumably, the early species were annuals and restricted to warm, moist climates (Ling 1992). Development and diversification of the genus in the Old World seems to have occurred in three major stages in the Late Cenozoic (during the Middle and Late Miocene), the Pliocene, and the Quaternary (W.-M. Wang 2004). The Pliocene was a major period for the development of *Artemisia* in western North America, and most authors assume that a primary factor was the appearance of woody species adapted to cold winters and long dry summers (Tidwell 1972). *Artemisia* is well represented in the pollen record in the Pliocene, but palynologists have not been able to distinguish between herbaceous and woody species. For that reason, there is no definitive time stamp on the first appearance of sagebrush.

The evolutionary history of New World species of *Artemisia* is complicated by the possibility of independent introductions (Tkach et al. 2007). In all likelihood, subtribe Artemisiinae and *Artemisia* sensu lato originated somewhere in Eurasia (Watson et al. 2000). North American lineages may have arisen with independent introductions from the Old World on both sides of the North American continent, as Beringian or amphi-atlantic migrations, and there appears to be at least one backmigration to the Old World (Shultz 2005; Watson 2005; Riggins & Seigler 2006). While the molecular phylogeny (Fig. 10) suggests paraphyly among Old World and New World lineages of *Artemisia*, sect. *Tridentatae* forms what may be the only monophyletic taxon above species rank within the genus. Most of the branches of the phylogenetic tree are not strongly supported, having less than 50% bootstrap support. Although no clear picture has emerged regarding relationships, I have attempted a phylogenetic circumscription of subgeneric groups within *Artemisia* based on the available evidence.

Within subtribe Artemisiinae, *Artemisia* shares a relatively ancient common ancestry with Asian members of subtribe Leucantheminae, as well as South African members of subtribe Matricariinae (Watson et al. 2000; Watson 2005). These related lineages all have radiate flower heads and are insect-pollinated. Reduced floral size, elongated inflorescences, and wind-pollinated flowers are shared derived characteristics that define the *Artemisia* clade (Bremer & Humphries 1993).

Most *Artemisia* specialists agree that the "ancestral" sagebrush would be a large-headed and deciduous-leaved herbaceous lineage occupying the cool, moist habitats that were prevalent during the early Pleistocene (Beetle 1960; McArthur 1979; McArthur et al. 1981; Shultz 1983, 2005; Bremer & Humphries 1993). Modern species, presumably derived from this early lineage (West 1983; McArthur 2000), are evergreen and small-leaved xerophytes, with small floral heads; they are specialists and occupy some of the harshest sites in North America. Palynological evidence suggests that the earliest woody lineage appeared in the region of the Columbia Basin in Oregon (Davis 1998). Leaf structure, both in terms of morphology and anatomy, corroborates the trend for xeromorphic specialization within the mesomorphic lineages (Shultz 1986b).

Sagebrush dominates much of the cool desert shrub lands of western North America (West et al. 1978, 1979). With the addition of the three species in sect. *Nebulosae*, the total range of subg. *Tridentatae* (Fig. 11) includes the Mediterranean coastal scrub of California and the Baja California Peninsula of Mexico, and the shrub-dominated portion of the Great Plains. These shrub lands are too dry to support forests, yet are either sufficiently cold or wet to result in exclusion of the other shrub and succulent species complexes that dominate the warm Sonoran, Mojave, and Chihuahuan deserts.

Studies by ecologists in the past three decades have done much to further our knowledge of sagebrush communities and of the dynamic interactions with wildlife, as well as

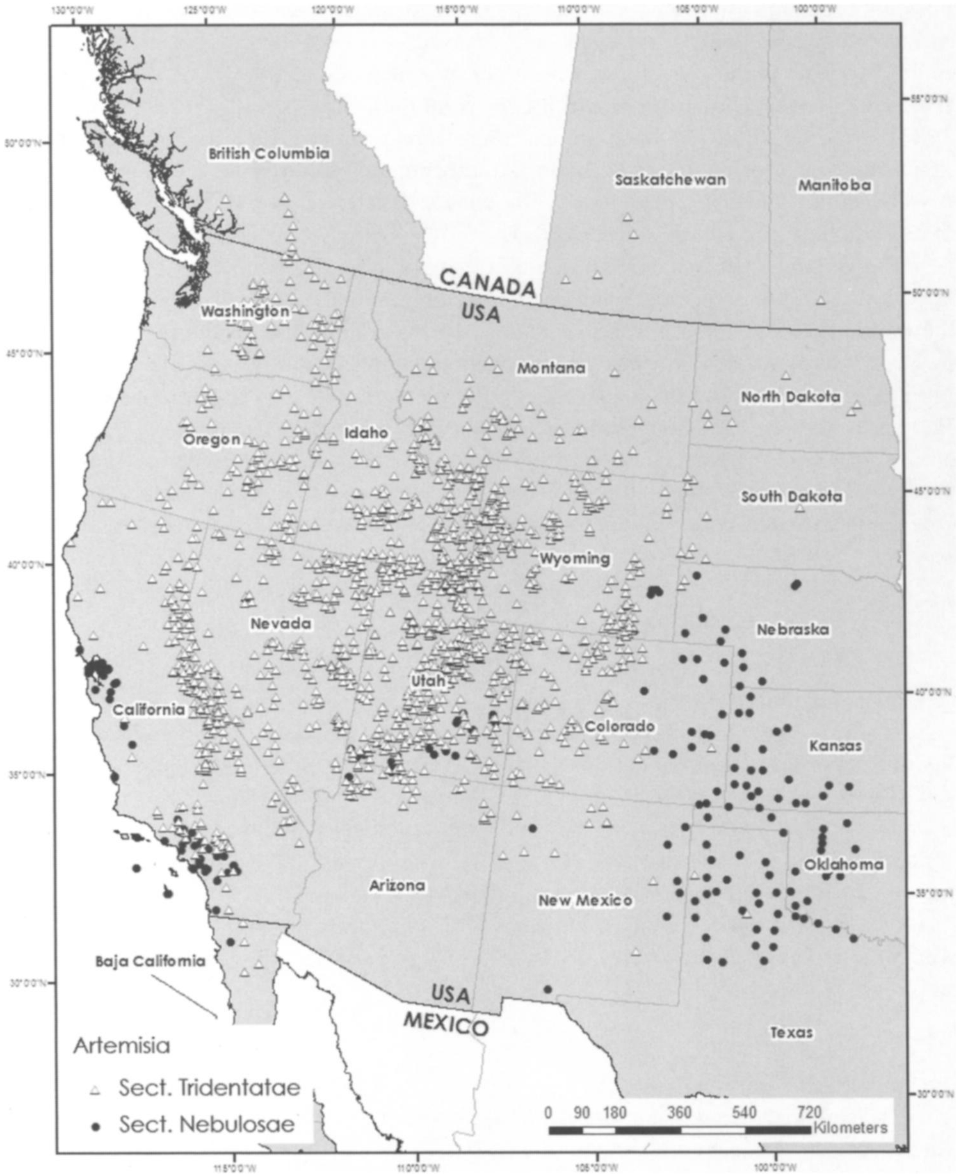

FIG. 11. Summary of the ranges of *Artemisia* sect. *Tridentatae* and sect. *Nebulosae*.

other plants, within the ecosystem. Ecological studies are too numerous for a thorough review here, but many include extensive bibliographies (e.g., Tisdale et al. 1965; M. West 1970; Winward 1970; M. West & Mooney 1972; Daubenmire 1975; McArthur & Plummer 1978; N. West et al. 1978, 1979; N. West 1979, 1988; McArthur & Welch 1982; Entwistle et al. 2000; Monsen et al. 2004; Goodrich 2005; Welch 2005).

Estimates of sagebrush dominance and diversity vary, but no one disputes that sagebrush has dominated the western landscape in modern times, with widespread dominance possibly occurring as recently as about 12,000 years ago (Martin 1970). In the Great Basin, *A. tridentata* commonly makes up more than 70% of the relative vegetation cover and more than 90% of the phytomass, regardless of succession status (N. West 1988). Thirty-five years ago, sagebrush cover was estimated at more than 62 million hectares (N. West 1983); however, there has been an alarming decrease in coverage through urbanization, agricultural development, and widespread die-off in the last three decades, either from unusually wet or unusually dry years, with some estimates of overall reduction as high as 50% since the early 1980's (Welch 2005).

The economic importance and complex evolutionary relationships of subg. *Tridentatae* will continue to present challenges to ecologists and systematists. Heterogeneity in the physical environment has led to genetic differentiation that results in ecotypes, varieties, or subspecies that are adapted for specific habitats, and rapid climate change probably has been one of the driving forces in the diversification of species and subspecies. Studies in sagebrush ecology demonstrate the close associations among soil type, precipitation cycles, temperature, and different *Artemisia* species and subspecies. The study of xeromorphic specializations in the context of emerging phylogenetic studies should provide some means of understanding vegetation response to changing climates.

PHENOLOGY

Flowering normally starts in late summer, and fruits mature in the fall. The only exception is *A. arbuscula* subsp. *longiloba*, which is spring-flowering. Species are either deciduous or evergreen. If evergreen, the leaves are of two types: ephemeral or perennial. The timing of leaf development depends on the type of leaf: the large "ephemeral" (long-shoot) leaves develop in early spring, and the fascicled (short-shoot) "perennial" leaves elongate throughout the growing season (see Fig. 2). Species with winter-deciduous leaves generally occur in moist habitats: *A. cana*, *A. spiciformis*, and *A. tripartita*. Evergreen-leaved species generally occur in xeric habitats: *A. arbuscula*, *A. bigelovii*, *A. pygmaea*, *A. nova*, *A. rothrockii*, and *A. tridentata*. Considerable phenological plasticity occurs within the species and subspecies, with the degree of variance corresponding to ecological amplitude (Shultz 1991a).

Ephemeral leaves last less than one growing season. They are long-shoot leaves that are attached singly, below the fascicled leaves. Ephemeral leaves elongate early in the growing season, are usually much larger than the fascicled leaves, and turn yellow and die as the season progresses. Their size is highly plastic and dependent on environmental conditions, much like leaves of sucker shoots of a tree. For that reason, measurements of ephemeral leaves are not used as a taxonomic character. Floral branches have leaves that are attached singly. These are smaller than the vegetative leaves, whether perennial or ephemeral, and are reduced upward on the flowering branch, eventually appearing as small bracts. The leaves of the flowering branches are persistent in the evergreen species, except for *A. arbuscula*. Measurements provided in the descriptions are for mature fascicled leaves on the vegetative (not floral) portion of the shrubs.

CHEMISTRY AND ETHNOBOTANY

Extensive studies of secondary compounds, especially sesquiterpene lactones occurring in subg. *Tridentatae*, were initiated circa the late 1960's (Geissman & Irwin 1969, 1970; Greger 1969; Irwin 1971; Hanks et al. 1973; Kelsey et al. 1976). Stangl and Greger (1980) showed that exudates of gland cells consist of monocyclic and acyclic monoterpenes, appearing as a transparent fluid that develops as the cell matures and the inner walls are broken down (Kelsey & Shafizadeh 1980). These authors described the molecular structure of unique compounds in most of subg. *Tridentatae* in detail, most of which are found only in one subspecies. Unfortunately, the biosynthetic pathways of these compounds are not understood, and therefore these studies are of minimal use in the construction of a phylogenetic tree.

Flavonoids are widely distributed in the Anthemideae, occurring predominantly as exudate flavones and flavonols (Greger 1977), and flavanones and dihydroflavonols (Valant-Vetschera & Wollenweber 2003). Terpenoid content varies among subspecies (Welch & McArthur 1981), and terpene levels differ among seasons, subspecies, individual plants, and different parts of the same plants (Byrd et al. 1999). Because hybrids produce novel terpenes for which biosynthetic pathways are not understood, the identification of terpenoids in hybrid populations does not elucidate genetic relationships among the species. McArthur et al. (1988) and Weber et al. (1994) describe distinct patterns of terpenes in synthetic and natural hybrids and parental stock. Convergence in secondary compounds is suggested in the study by Irwin (1971), who found similar lactone chemistry in sympatric populations of *A. nova* and *A. tripartita* subsp. *rupicola*. Exudate flavonoid production is linked to ecological factors, such as increased UV radiation in connection with alpine or xeric habitats (Valant-Vetschera & Wollenweber 2005).

The ultra-violet fluorescence of leaf chemicals has been widely used as a taxonomic tool, in a methodology first developed for alcohol extracts by Winward and Tisdale (1969). Stevens and McArthur (1974), McArthur et al. (1988), and McArthur and Sanderson (1999) expanded this tool by using water extracts. Because coumarins are abundant in some subspecies and not in others, the fact that coumarins fluoresce bright blue in the presence of an ultraviolet "black light" can be used to distinguish subspecies of *A. tridentata* (Winward 1970; Stevens & McArthur 1974; McArthur et al. 1988; Rosentreter 2005). Crushed leaves of subsp. *vaseyana* create a bright blue fluorescence under a black light, while leaves of subsp. *wyomingensis* do not fluoresce at all. Use of fluorescence for distinguishing these two taxa has been a useful tool in the field, even though it involves a rather cumbersome set-up involving a battery-powered black light and a "black box" for observation. Varying degrees of fluorescence have also been used to identify hybrid complexes (Garrison 2006). This test is helpful inasmuch as some subspecies provide superior forage for wildlife, and knowing that a particular subspecies is growing on a site can provide valuable information for managers.

Volatile compounds in sagebrush have a strong effect on patterns of herbivory. Sagebrush is known to release large amounts of methyl jasmonate, a volatile compound suspected of acting as a plant hormone (Karban et al. 2003). Presumably, the high terpenoid content in sagebrush is a deterrent to herbivores, thus conferring a selective advantage to high-terpenoid plants. Yet, production of these compounds has a metabolic cost, and the concentrations of secondary compounds vary from season to season. Terpenoid concentrations drop to their lowest levels after the plants have flowered. Ungulates that avoid grazing on young stems during the summer find sagebrush to be an important source of nutrients during the winter. After plants have flowered in the fall, terpenoid concentrations decline precipitously, after which the protein-rich inflorescences provide a superior winter food source for moose, antelope, and deer; sage grouse will eat leaves at any time of the year, as will ungulates, rodents, and other small mammals (see reviews of the literature in Shaw et al. 2001; Welch 2005).

Sesquiterpene lactones also affect browse patterns: they are bitter, and are known to exhibit a variety of biological activities (Rodriguez et al. 1972). The anti-herbivory significance of sesquiterpene lactones and bitter flavonoids is now generally accepted (Burnett & Jones 1978). In *Artemisia*, lactone levels drop during the winter months, when potential insect predation is low. This timing is advantageous, because *Artemisia* is browsed heavily during the winter, when it provides one of the better available protein sources for ungulates as well as domestic livestock (Rittenhouse & Vavra 1979), and the consumption of seed heads provides an effective means of seed dispersal. Sagebrush is moderately tolerant of grazing (Bilbrough & Richards 1993), and controlled studies suggest that insect predation does not significantly affect the reproductive potential of the plant (Messina et al. 2002). Messina et al. (1996) show differential patterns of herbivory by insects in sympatric populations of different subspecies of *A. tridentata*, with little effect on growth rate. They suggest that selection of advantageous hybrids may be occurring naturally and frequently. The work of Graham et al. (1999, 2001) shows that both habitat and host taxa play a role in the distribution of insects.

Although allelopathic effects are difficult to prove under field conditions, ecologists have long suspected that the volatile oils in sagebrush inhibit seed germination—an observation supported by the low species diversity and low biomass of other species in dense sagebrush communities. Recent studies show the effect of sagebrush on neighboring plants. Karban and colleagues (2003) showed that wild tobacco plants growing near sagebrush had elevated levels of proteinase inhibitors. Their work is remarkable in that it is the first study to demonstrate this effect on other plants under field-grown conditions.

Sagebrush has been valued for its antifungal, antimicrobial, analgesic, and anesthetic properties in traditional herbal medicine (Kane 2006), but it has not received much attention in modern medicine (Moerman 1998; Wright 2001). The growing importance of medicinal uses for other species of *Artemisia* (see discussion of *A. annua* below) is cause to re-examine the species of subg. *Tridentatae*. The use of sagebrush by aboriginals includes clean-burning fuel and the ceremonial "smoking" of fresh leaves as a "smudge" plant in cleansing rituals. This latter use continues to be popular in parts of the Southwest, and sagebrush bundles are often sold in tourist shops. The resinous vegetation burns for long periods and produces a pleasantly aromatic smoke, much like incense. Folk literature of the nineteenth century documents the use of sagebrush "incense" in fertility rites, a practice that may have been inspired by the plant's fecundity and ability to produce copious fruit.

There is a renewed interest in the medicinal value of *Artemisia* because of the increasing importance of artemisinin as an antimalarial drug. The drug is extracted from *A. annua*, and has been used in traditional Chinese medicine as a treatment for malaria for hundreds of years. It now appears to be the only effective drug in areas where the malaria-causing protozoon (genus *Plasmodium*) has developed resistance to chloroquine and mefloquine (Klayman 1985). The extraordinary importance of these findings has re-awakened interest in screening other species of *Artemisia* for their potential medical use (de Magalhaes et al. 1997; Mingsi et al. 2005). It also appears that artemisinin may be effective in restraining the proliferation of cancer cells (Xuliang & Huangronggang 2005) and enhancing immunosuppressive activity (Kanuja 2005). Owing to its medicinal importance and the recently suggested phylogenetic relationships (*A. annua* appears to be basal to subg. *Seriphidium* in Watson et al. 2002), the relationship of members of Old World subg. *Seriphidium* to New World subg. *Tridentatae* is of particular interest in pharmaceutical studies.

TAXONOMY

Artemisia L., Sp. pl. 2: 845. 1753.—LECTOTYPE, designated by Green, Prop. Brit. Bot.: 180. 1929: *Artemisia vulgaris* L.

Annual, biennial, or perennial herbs or shrubs, usually pungently aromatic. Leaves deciduous or evergreen, simple, alternate, without stipules, margins entire or lobed. Inflorescences of capitula arranged in panicles. Capitula discoid or disciform, campanulate, globose, ovoid, or turbinate. Phyllaries imbricate, in 2–4 unequal series, distinct, ovate to lanceolate, margins and apices usually green or white, rarely dark brown or black, scarious but often inconspicuously so, abaxial surfaces glabrous or hairy. Receptacles convex, glabrous or hairy, epaleate (except paleate in *A. palmeri*). Ray florets absent. Marginal florets pistillate or perfect. Central (disc) florets perfect and fertile or functionally staminate (with an abortive ovary). Heads heterogamous with pistillate (marginal) florets (the 1–3 pistillate florets in the heads of *A. bigelovii* sometimes 2-lobed, thus weakly raylike) or homogamous with florets all perfect and sexual. Corollas tubular, cylindrical, throats subglobose or funnelform; lobes 5, more or less deltate, glabrous, sparsely hirtellous, or glandular, usually pale yellow, sometimes red. Anthers 5, joined, longer than the filaments, obtuse basally, not tailed, with an ovate appendage apically. Style 2-cleft; branches more or less recurved, linear, erose or fimbriate along the margin of the truncate apex, without appendages, abaxially glabrous or papillate, stigmatic lines adaxial in two series, extending from the base to the apex. Cypselae ellipsoid-fusiform, minute (less than 2.5 mm long), ribs 0–5, surfaces glabrous or pubescent, often gland-dotted. Pappus absent (or rarely present as a rudimentary membranous crown). Chromosome number: n = 9 (n = 7 in *A. pattersonii*, Wiens & Richter 1966; and n = 8 in the *A. vulgaris* group; Vallès & McArthur 2001; Vallès et al. 2003).

Species ca. 400; mostly Northern Hemisphere (North America, Eurasia), several species in South America and Africa.

The following definitions of subgeneric groups are proposed to reflect better phylogenetic relationships within the genus. This account diverges from my treatment for the *Flora of North America* (Shultz 2006a), in that I treat sections *Artemisia* and *Absinthium* of *Artemisia* subg. *Artemisia* as separate subgenera. Based on my interpretation of the molecular phylogeny shown in Fig. 10, I recognize four subgenera of *Artemisia* (Shultz 2005), including two newly erected sections within subg. *Tridentatae*.

KEY TO THE SUBGENERA AND SECTIONS OF ARTEMISIA

1. Herbs; capitula heterogamous: central florets perfect, marginal florets pistillate. — 1. *Artemisia* subg. *Artemisia*
    2. Receptacle glabrous. — 1a. *Artemisia* sect. *Artemisia*
    2. Receptacle hairy. — 1b. *Artemisia* sect. *Absinthium*
1. Shrubs or suffrutescent herbs; capitula homogamous (florets all perfect) or heterogamous (central florets sterile or perfect, marginal florets pistillate).
    3. Capitula heterogamous: central florets with an aborted ovary and stigmas; marginal florets perfect; style branches with marginal stigmatic lines, erect, not recurved.
        4. Plants herbaceous, sometimes low-growing suffrutescent herbs (Old World and New World). — 4. *Artemisia* subg. *Dracunculus*
        4. Plants shrubby with a distinct trunk (New World: western North America grasslands and warm deserts—*A. filifolia, A. californica, A. nesiotica*). — 3b. *Artemisia* subg. *Tridentatae* sect. *Nebulosae*
    3. Capitula homogamous (all perfect) or heterogamous with marginal florets pistillate; style branches apically fringed, recurved.

5. Florets without a pappus.
   6. Middle or basal leaves 2–4-pinnatifid; plants suffrutescent or shrubby; Eurasia. 2. *Artemisia* subg. *Seriphidium.*
   6. Leaves entire (usually apically 3-lobed) or once-pinnatifid; shrubs; North America. 3a. *Artemisia* subg. *Tridentatae* sect. *Tridentatae*
5. Florets with a crown-like pappus. 3b. *Artemisia* subg. *Tridentatae* sect. *Nebulosae*

Synoptic Descriptions of Subgenera and Sections

1. **Artemisia** subg. **Artemisia.**

This subgenus includes most of the herbaceous species of the Old and New World. It is the most problematic of the four subgenera in that relatively few of the species have been sampled (see clade A shown in Fig. 10). In its traditional circumscription, subg. *Artemisia* includes the paraphyletic *A. tournefortiana, A. annua, A. chamaemelifolia, A. afra, Neopallasia pectinata,* and *Crossostephium chinensis* in clade C, and *A. abrotanum* and *A. molineiri* in the branch that includes clades A and B. According to the molecular phylogeny of Watson et al. (2002; Watson 2005), the only way to make subg. *Artemisia* monophyletic is to include all the species of *Artemisia* with the exception of those belonging to subg. *Dracunculus,* a solution which I consider untenable.

1a. **Artemisia** sect. **Artemisia.**

This section, which includes most of the herbaceous Old and New World species, is clearly problematic in that it does not form a monophyletic clade within *Artemisia.* Future phylogenetic studies will undoubtedly help to determine relationships among the species, but no clear pattern has emerged from the relatively few species that have been analyzed so far. In agreement with the suggested relationships from ITS sequence data (Watson et al. 2002), I am transferring *A. californica*, a species formerly included in this section, to subg. *Tridentatae*. The inclusion of *A. nesiotica* is in agreement with Riggins and Seigler (2006), who found 100% similarity between *A. california* and *A. nesiotica* based on the ITS sequence. Old World *A. vulgaris* is the type species for *Artemisia*, and thus is the type of the section. *Artemisia* sect. *Artemisia* comprises ca. 220 species.

1b. Artemisia sect. **Absinthium** (Miller) DC. in DC. & Lamarck, Fl. Franç., ed. 3, 4(1): 189. 1805. *Absinthium* Miller, Gard. dict. abr., ed. 4, 1: [unpaginated]. 1754. *Artemisia* subg. *Absinthium* (Miller) Lessing, Linnaea 6: 217. 1831. *Artemisia* subsect. *Absinthium* (Miller) Darijima, Bot. Zhurn. (Moscow & Leningrad) 73: 1469. 1988.—Type: not designated.

Species of sect. *Absinthium* are characterized by having hairy receptacles, and form a monophyletic group that is nested within subg. *Artemisia* (clade A-1 in Fig. 10). The section includes Old and New World species, and is the topic of the recent dissertation by Riggins (2008), a work that details information about the included species. My alignment subsumes the genus *Absinthium* as a section of subg. *Artemisia* and includes all of the species I that I included in subg. *Absinthium* for the *Flora of North America* treatment (Shultz 2006). *Artemisia* sect. *Absinthium* comprises ca. 40 species.

2. Artemisia subg. **Seriphidium** Besser ex Lessing, Syn. gen. Compos. 264. 1832, as "*Seriphida*." *Seriphidium* (Besser ex Lessing) Fourreau, Ann. Soc. Linn. Lyon, ser. 2, 17: 89. 1869.—TYPE: *Artemisia maritima* L.

This subgenus is here defined primarily as an Old World alliance of shrubby species of *Artemisia* even though some herbaceous species are included (see clade C, Fig. 10). In the molecular phylogeny of Watson et al. (2002), subg. *Seriphidium* appears to include *Neopallasia* and *Crossostephium chinensis*, as well as some species formerly included within subg. *Artemisia*. The herbaceous *Artemisia annua* L. (in subg. *Artemisia*) may or may not be included in the *Seriphidium* clade. [The frequently noted citations "*Artemisia* sect. *Seriphidium* Besser" (Bull. Soc. Imp. Naturalistes Moscou 18: 222. 1829) and "*Artemisia* sect. *Seriphidium* Besser in Hooker" (Fl. bor.-amer. 1: 325, 1833) refer to a name that was not validly published, because no description was provided.] *Artemisia* subg. *Seriphidium* comprises ca. 100 species.

3. Artemisia subg. **Tridentatae** (Rydberg) McArthur — see p. 30.

This subgenus is a New World alliance of shrubby species endemic to western North America and includes 13 species.

3a. Artemisia sect. **Tridentatae** L. M. Shultz — see p. 33.

Species of this section have homogamous capitula, with florets that are perfect and fertile (except *A. bigelovii*, which occasionally has 1–2 marginal florets that are pistillate and raylike). *Artemisia* sect. *Tridentatae* comprises 10 species.

3b. Artemisia sect. **Nebulosae** L. M. Shultz — see p. 97.

This section is erected to accommodate three woody species with heterogamous capitula that are aligned with species in subg. *Tridentatae* in molecular analyses (Watson et al. 2002; Riggins & Seigler 2006). It includes two species formerly placed in subg. *Artemisia* (*A. californica* and *A. nesiotica*), and one species formerly placed in subg. *Dracunculus* (*A. filifolia*). Although molecular evidence suggests that *Sphaeromeria* is weakly aligned within this clade (Watson et al. 2002; Riggins & Seigler 2006), I am not proposing a transfer until more species are sampled and the relationships to other species of *Artemisia* are clearly resolved. Rydberg (1916) placed *A. pedatifida* in his [unranked] *Filifoliae*, but I retain that species within subg. *Dracunculus*.

4. Artemisia subg. **Dracunculus** (Besser) Rydberg, N. Amer. Fl. 34: 251. 1916. *Artemisia* sect. *Dracunculus* Besser, Bull. Soc. Imp. Naturalistes Mouscou 8: 3, 8. 1835.—TYPE: *Artemisia dracunculus* L.

Oligosporus Cassini, Bull. Sci. Soc. Philom. Paris 1817: 33. 1817.—TYPE: *Oligosporus campestris* Cassini [=*Artemisia dracunculus* L.]

This subgenus is defined as having heterogamous capitula with central florets that are functionally staminate owing to an aborted ovary. The style branches in the central florets are visible, but they do not elongate and do not open. This group of Old and New World species appears to have diverged early in the evolution of *Artemisia*. It was treated as the segregate genus *Oligosporus* by Cassini (1817), an alignment followed in some modern floras (notably Weber 1984). It is basal within the *Artemisia* clade (Watson et al. 2002; Riggins & Seigler 2006; Sanz et al. 2008), and appears to be monophyletic if *A. filifolia* is excluded, a species I include in subg. *Tridentatae* sect. *Nebulosae*. The recent analysis by Sanz et al. (2008) suggests that four Asian genera, *Filifolium* Kitamura, *Mausolea* Poljakov, *Neopallasia* Poljakov, and *Turaniphytum* Poljakov, should be included in this subgenus. *Artemisia* subg. *Dracunculus* comprises ca. 80 species.

Taxonomy of Artemisa Subgenus Tridentatae

Artemisia subg. **Tridentatae** (Rydberg) McArthur, Amer. J. Bot. 68: 590. 1981. *Artemisia* [unranked] *Tridentatae* Rydberg, N. Amer. Fl. 34: 282. 1916. *Artemisia* ser. *Tridentatae* (Rydberg) Poljakov, Fl. URSS 26: 626. 1991.—Type: *Artemisia tridentata* Nuttall.

Shrubs, pubescent or glabrous, mildly to pungently aromatic; caudices woody, often profusely branched; roots fibrous, with both a lateral and a vertical deep root system; rhizomes absent, some species producing stems that sprout from the underground caudex, thus giving the appearance of sprouting from the roots (as in *A. arbuscula*, *A. cana*, *A. rigida*, and *A. tripartita*). Bark gray to gray-brown, usually shredding in long strips with age; juvenile stems usually pubescent. Leaves deciduous or evergreen, erect, sessile, usually narrowly or broadly cuneate and apically 3-lobed with rounded lobes (except acute in *A. bigelovii* and some leaves of *A. spiciformis*), rarely pinnatifid (*A. pygmaea*), sometimes entire and lanceolate, usually in fascicles on the vegetative stems and subtended by an elongated "long-shoot" or ephemeral leaf attached singly in the inflorescence; texture pliable (except rigid and brittle in *A. pygmaea* and *A. rigida*). Capitula of sect. *Tridentatae* discoid and homogamous, all florets tubular, perfect, and fertile (except *A. bigelovii*, with occasional, 1–2, pistillate and ray-like marginal florets); capitula of sect. *Nebulosae* heterogamous (*A. californica* and *A. nesiotica* with marginal florets pistillate, central florets perfect; *A. filifolia* with central florets functionally staminate, marginal florets perfect). Receptacle naked, glabrous. Florets 2–40, tubular, slightly funnelform (rarely ray-like in *A. bigelovii*), pale yellow or (rarely) becoming red-tinged in the fall, glabrous or occasionally dotted with glands, 1–3.5 mm long. Style branches slender, linear, included (occasionally exserted in *A. nova*), spreading and apically fringed in species of sect. *Tridentatae*; sect. *Nebulosae* all with pistillate marginal flowers with style branches not fringed, with marginal stigmatic lines: erect style branches in central florets of *A. filifolia,* apically fringed style branches in central perfect florets of *A. californica*, and *A. nesiotica*). Cypselae fusiform, minute, ca. 3 times as long as wide, sparsely glandular or glabrous, not differing significantly among species. Pappus absent or rudimentary (coroniform in *A. californica* and *A. nesiotica*, and sometimes on the outer florets of *A. rothrockii*).

The 13 species of subg. *Tridentatae* occur in western North America (Fig. 11).

Character States of Artemisia Subgenus Tridentatae

Because the flowers and fruits of species of subg. *Tridentatae* are uniform in shape and size, and the details microscopic, the following key to the subgenus relies heavily on vegetative characteristics. Until the user of the key becomes familiar with the variation found in different parts of the plant, characteristics of leaf morphology may be difficult to interpret. The following notes will help guide the use of the key. *Unless otherwise noted, leaf characteristics in the key apply to leaves of the vegetative branches. If a characteristic applies to the leaves of the flowering stems, it is so noted.* Descriptions of leaf size and lobing refer to the leaves of the lateral vegetative shoots or "fascicles" (see earlier discussion of leaves). Measurement of the elongated "ephemeral" leaf is not reliable as a taxonomic character, since the leaf size is highly variable, and the leaves usually fall off early in the growing season (a notable exception is *A. spiciformis*, which retains its ephemeral leaves through most of the growing season). Fascicled (or "perennial") leaves can be evergreen or deciduous, making the term "perennial" a common misnomer. I have chosen the term "persistent" to distinguish fascicled leaves from the ephemeral leaves. Leaves are anatomically isolateral (more or less equivalent on both sides), with the abaxial and adaxial surfaces similar in color and pubescence. Height refers to mature shrubs.

The order of species is systematic. I have placed the large-headed taxa of sect. *Tridentatae* at the beginning of the treatment, followed by smaller-headed (and presumably derived) taxa. The three species in sect. *Nebulosae* are placed after sect. *Tridentatae*. The taxon arrangement is meant to be phylogenetic, with related species (which are usually morphologically similar) placed near to one another as much as possible. Patterns of reticulate evolution are problematic in this linear order, but when a taxon appears to be of hybrid origin, supporting evidence is provided in the discussion.

The morphological characteristics that are most useful in distinguishing species show a great deal of phenotypic plasticity. These characteristics include size and growth form of the shrubs (height and branching patterns), degree of lobing and size of the vegetative leaves, size and shape of the flowering capitula, and size and shape of the inflorescence (capitulescence). Thirteen species are recognized in this treatment, with eight additional taxa at the rank of subspecies.

The following synoptic list is provided in order to highlight characteristics that are useful in distinguishing species and subspecies of sagebrush. Numbers correspond to the taxa enumerated in the paragraph that follows this list. *Numbers in parentheses indicate that the character state is uncommon.*

Low-growing shrubs: 2b, 3b, 4, 5a, 5b, 5c, 6, (7), (9d), 10, 13
Tall shrubs: 9a, 9b, (9c), (9d), 11, 12
Leaves evergreen: 1, (3a), 5, 6, 7, 8, 9, 10, 11, (12)
Leaves primarily deciduous: 2, 3, 4, 8, 11, 12, 13
Leaves entire: (1), 2, (4), (7), 8, 11, (12)
Leaves 3-lobed: 1, (2c), 3, 4, 5, 6, 7, 8, 9, (11), 12, 13
Leaves pinnately lobed: 10, (13)
Leaves irregularly lobed: (2c), 8
Phyllaries glabrous: 6, 10, 12

In approximate phylogenetic order, species are numbered from what may be morphologically the most basal member of subg. *Tridentatae* to the most derived, as follows: (1) *A. bigelovii*; (2) *A. cana*; (3) *A. tripartita*; (4) *A. rigida*; (5) *A. arbuscula*; (6) *A. nova*; (7) *A. rothrockii*; (8) *A. spiciformis*; (9) *A. tridentata*; (10) *A. pygmaea*; (11) *A. californica*; (12) *A. filifolia*; and (13) *A. nesiotica*. Notes regarding derivative polyploid taxa (such as octoploid *A. cana* subsp. *cana* and tetraploid populations of *A. tridentata* subsp. *wyomingensis*) are provided.

KEY TO THE SPECIES OF ARTEMISIA SUBG. TRIDENTATAE

1. Leaves entire or lobed with filiform segments (divided more than 1/3 total length with segments less than 2 mm wide), attached singly or in fascicles; vegetative leaves mostly deciduous (dropping during winter or with extreme drought), leaves of the flowering branches deciduous (in *A. arbuscula,* a characteristic that can be seen early in the season, or from flowering branches of the previous year) or evergreen.
   2. Leaves mostly entire, usually more than 2 mm wide, narrowly elliptic to lanceolate, some irregularly lobed. 2. *A. cana*
   2. Leaves deeply lobed, lobes less than 2 mm wide, linear and filiform.
      3. Stems wandlike, forming delicate rounded shrubs; growing on loose sandy soils in the Mojave Desert, Colorado Plateau, and central N. American grasslands. 12. *A. filifolia*
      3. Stems not wandlike, coarse and broadly branched; habitat various, from the Great Basin to California chaparral to the Columbia Plateau.
         4. Leaves rigid and brittle; inland areas, not occurring in California.
            5. Leaves bright green, pinnatifid; growing on barren white knolls; Colorado, Nevada, New Mexico, and Utah. 10. *A. pygmaea*
            5. Leaves silvery gray, deeply lobed with filiform segments; basalt scablands of the Columbia Plateau portion of Oregon, Washington, and extreme western Idaho. 4. *A. rigida*
         4. Leaves pliable, not rigid or brittle; California, Great Basin, and Columbia Plateau.
            6. Leaves attached singly, not in fascicles; florets with a rudimentary coroniform scale; chapparal plants of coastal California and Baja California, incl. Channel Islands.
               7. Prostrate shrubs mostly less than 0.5 m tall, coarsely branched; phyllaries densely canescent; leaf margins not revolute; endemic to the Channel Islands of California. 13. *A. nesiotica*
               7. Erect shrubs more than 0.5 m tall, coarsely branched or with wandlike stems; phyllaries sparsely canescent; leaf margins revolute; coastal chaparral of California and Baja California. 11. *A. californica*
            6. Leaves attached in fascicles; florets without a scalelike attachment; widespread, inland mountains and valleys, not coastal.
               8. Inflorescence leaves of flowering stems mostly entire; medium-sized to tall shrubs, usually more than 2 dm tall (subsp. *rupicola* sometimes shorter); usually growing on deep loamy soils. 3. *A. tripartita*
               8. Inflorescence leaves of flowering stems deeply lobed; low-growing shrubs less than 3 dm tall; usually growing on rocky soils. 5. *A. arbuscula*, in part
1. Leaves shallowly and broadly 3-lobed (less than 1/3 blade length), rarely with some that are both entire and irregularly lobed (*A. spiciformis*), lobes usually rounded (except some acute in *A. bigelovii* and *A. spiciformis*), more than 2.0 mm wide, attached in fascicles to vegetative stems (single only on flowering stems), mostly evergreen (except partially deciduous in *A. spiciformis* and *A. arbuscula*).
   9. Inflorescences broadly paniculate, or if narrow, then leaves at least partially deciduous; shrubs 50–200 (–250) cm tall.
      10. Leaves mostly deciduous, variable in size and shape (irregularly 3–6-lobed or entire), lobes rounded or acute; ephemeral leaves 3–5+ cm long, usually turning yellow early in the growing season. 8. *A. spiciformis*
      10. Leaves persistent, cuneate and generally uniform in shape, lobes to 1/3 blade length; ephemeral leaves less than 3 cm long, remaining green throughout the growing season.
         11. Capitula broad, ovoid, 3–5 mm high and 4–6 mm wide; florets 10–20; leaves dark gray-green and sticky-resinous (or gray-pubescent in the White Mountain form); stems felty-pubescent; endemic to California. 7. *A. rothrockii,* in part
         11. Capitula narrowly turbinate or cylindric, 1–4 mm long and 1–3 mm wide; florets 3–11; leaves gray-green, not sticky-resinous; stems sparsely pubescent or glabrous; widespread throughout western North America 9. *A. tridentata*, in part
   9. Inflorescences narrowly paniculate, or if broad, then leaves evergreen; shrubs 5–50 cm tall.
      12. Capitula nodding, globose; marginal florets sometimes pistillate and ligulate; leaf lobes acute. 1. *A. bigelovii*
      12. Capitula erect, campanulate, ovoid or turbinate; marginal florets always perfect and not ligulate; leaf lobes rounded.

13. Capitula sessile or nearly so, phyllaries pubescent; leaves on flowering stems early-deciduous, three-lobed; widespread, " low sagebrush" of mountains and valleys. 5. *A. arbuscula,* in part
13. Capitula pedunculate, phyllaries glabrous or pubescent; leaves on flowering stems persistent, usually entire.
    14. Crowns flat-topped; inner phyllaries glabrous (rarely pubescent), shiny, and straw-colored; capitula narrowly turbinate (sides nearly parallel). 6. *A. nova*
    14. Crowns rounded, irregular; phyllaries densely pubescent and gray-green; capitula ovoid (sides rounded).
        15. Capitula 1–2 mm wide; stems sparsely or densely pubescent, but not felty-tomentose; leaves not sticky-resinous; widespread and common. 9. *A. tridentata,* in part
        15. Capitula 3–6 mm wide; stems felty-tomentose; leaves sticky-resinous; endemic to central and southern Sierra Nevada and White Mountains of California. 7. *A. rothrockii,* in part

Artemisia sect. **Tridentatae** L. M. Shultz, sect. nov.—TYPE: *Artemisia tridentata* Nuttall.

Artemisia [unranked] *Pygmaeae* Rydberg, N. Amer. Fl. 34: 284. 1916.—TYPE: *Artemisia pygmaea* A. Gray.

Artemisia [unranked] *Rigidae* Rydberg, N. Amer. Fl. 34: 284. 1916.—TYPE: *Artemisia rigida* (Nuttall) A. Gray.

Artemisia ser. *Bigelovianae* Y. R. Ling in Hind, Jeffrey & Pope, Advances in Compositae Systematics 271. 1995.—TYPE: *Artemisia bigelovii* A. Gray.

Frutices, capitulis homogamis, foliis fasciculatis.

Shrubs evergreen or deciduous, strongly aromatic. Leaves fasciculate on vegetative branches, mostly shallowly 3-lobed (tridentate), sometimes entire, irregularly lobed apically, or pinnatifid; on flowering branches attached singly, and reduced in size and often entire. Capitula homogamous (except *A. bigelovii*), arranged in narrow or broad panicles. Florets 1–3.5 mm long, pale yellow (rarely tinged with red), all tubular, perfect, and fertile (except *A. bigelovii* with occasional, 1–2 pistillate and ray-like marginal florets); style branches spreading and apically fringed, stigmatic lines on margins (except in pistillate flowers of *A. bigelovii*). Cypselae 0.5–2.3 mm long, fusiform; pappus absent (rarely coroniform in marginal florets of *A. rothrockii*).

1. Artemisia bigelovii A. Gray in Torrey, Pacif. Railr. Rep. 4(5): 110. 1857. *Seriphidium bigelovii* (A. Gray) K. Bremer & Humphries, Bull. Nat. Hist. Mus. London, Bot. 23: 118. 1993.—TYPE: U.S.A. Texas: rocks and canyons on the Upper Canadian River and Llano Estacado, 25th Parallel, 18 Sep 1853, *J. M. Bigelow 768* (holotype: GH!; isotypes: K! NY).

Artemisia petrophila Wooton & Standley, Contr. U.S. Natl. Herb. 16: 193. 1913.—TYPE: U.S.A. Arizona: north end of Carrizo Mountains, 28 Jul 1911, *P. C. Standley 7355* (holotype: US!; isotype: NY!).

Short to medium-sized evergreen shrubs, 2–4 (–6) dm tall, mildly aromatic; crowns rounded; not sprouting from underground caudices. Stems silvery-canescent, delicate and arched or stout, branched from the base; bark gray-brown, pubescent. Leaves gray-green, deciduous, pliable; blades 0.5–1.8 (–3) cm long, 0.2–0.5 cm wide, narrowly cuneate, entire or 3 (–5)-lobed, lobes acute and narrow (1.5–2 mm wide), less than 1/3 blade length, surfaces silvery-canescent; ephemeral leaves similar in shape, lobing, and pubescence, but at the upper limit (3 cm) of length. Capitula 1.5–3 mm high, 1.5–2 mm wide, globose, nodding. Phyllaries ovate, canescent or tomentose. Inflorescences narrowly paniculate, 6–15 (–25) cm long, (0.5) 1–2 (–4) cm wide; branches erect or curved outward. Florets 1–1.5 mm long; marginal florets 0–2 (if present, then raylike and up to 1 mm wide), pistillate; central florets 1–3, perfect. Style branches apically fringed, recurved. Cypselae 0.5–1 mm long, 5-ribbed, glabrous. Pappus absent. Chromosome number: 2n = 18 (McArthur & Sanderson 1999; McArthur et al. 1981; Ward 1953); 2n = 36 (McArthur & Sanderson 1999; McArthur et al. 1981); 2n = 72 (McArthur & Sanderson 1999). Figs. 4a, 7g, 12.

Common names. Bigelow sagebrush, Plateau sagebrush.

Phenology. Flowering early summer to late fall.

Distribution (Fig. 13). U.S.A.: Arizona, California, Colorado, Nevada, New Mexico, Texas, Utah; in sandy or fine-grained (clayey) alkaline soils or rock outcrops, in warm or cold deserts (Mohave Desert, Colorado Plateau, and Great Basin); 1000–2500 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** ARIZONA: Apache Co.: Spider Rock Overlook, *Beetle 12824* (UTC), *Beetle 12991* (UTC); Canyon del Muerto, *Halse 743* (UTC). Coconino Co.: 5 mi W of Fredonia, *Beetle 12973* (UTC). La Paz Co.: W of Holbrook, 30 Apr 1948, *Cook s.n.* (UTC); Billings, *Jones 4571* (UTC). Mohave Co.: Kaibab Indian Reservation, *Shultz & Shultz 9833* (UTC). Navajo Co.: Monument Valley, *Beetle 12839* (UTC); Kayenta, *Eastwood & Howell 6557* (UTC).—CALIFORNIA: San Bernardino Co.: E Mohave Desert, *Prigge 2207* (UTC); E Mohave Desert, *Thorne et al. 47974* (UTC), *Thorne et al. 50703* (UTC); Middle Gilroy Canyon, *Thorne et al. 51739* (UTC).—COLORADO: Mesa Co.: Coke Oven Overlook, *Shaw 4223* (UTC). Montezuma Co.: McElmo Canyon, *Weber & Whittmann 17264* (UTC). Pueblo Co.: St. Charles River bluffs, *Weber & Arp 14068* (UTC); Pueblo, *Woodward s.n.* (UTC).—NEVADA: Clark Co.: W end of Fossil Ridge, *Ackerman 30930* (UTC); SE Frenchman drainage basin, 21 Aug 1968, *Beatley s.n.* (UTC); N end of Ranger Mtns, 15 Oct 1968, *Beatley s.n.* (UTC); Red Rock Canyon Recreation Lands, *Landau 3615* (UTC). Lincoln Co.: N end of Desert Range, *Ackerman 83-734* (UTC); W slope of E Mormon Mtns, *Shultz & Shultz 7588* (UTC); Meadow Valley Wash, *Tiehm 8371* (UTC). Nye Co.: N-facing slope of Red Mtn, *Reveal 1772* (UTC).—NEW MEXICO: Bernalillo Co.: near Albuquerque, *Jones s.n.* (POM). Catron Co.: without locality, *Lyngholm & Smith 26* (UTC). Chavez Co.: Comancheau Bluffs, W of Roswell, *Waterfall 5718* (GH). Quay Co.: 1952, *Hornsby s.n.* (DS). San Juan Co.: S of Burnham Trading Post, 7 Jun 1980, *Shultz s.n.* (UTC). Valencia Co.: Grant, *Jones 4353* (UTC).—TEXAS: Llano Co.: Llano Estacado, *Bigelow & Bigelow 768* (NY, K). Oldham Co.: 7 mi W of Adrian, *Cory 50397* (GH, UC, WS).—UTAH: Beaver Co.: 38 mi W of Milford, *Hatch 39* (UTC). Duchesne Co.: San Rafael Desert, *Bryan & Redd 8-8* (UTC); Tavaputs Plateau, Nutters Canyon, *Goodrich 5041* (UTC); Horse Canyon, *Kass & Collins 1272* (UTC); San Rafael Swell, Mussentuchit Creek drainage, Blue Flats, *Shultz & McReynolds 20286* (UTC); 10 mi S of Duchesne, Emery Co.: San Rafael Desert, *Shultz & Shultz 7309* (UTC); San Rafael Desert, *Shultz & Shultz 7310* (UTC); near Little Flat Top on road (dirt) to Hans Flat, *Shultz & Shultz 7313* (UTC); 20 mi N of Hanksville, 12 Jun 1947, *Stoddart & Cook s.n.* (UTC); 2 mi W of Duchesne, 13 Aug 1936, *Stoddart & Passey s.n.* (UTC). Garfield Co.: Hall's Creek drainage, *Camp 1979* (UTC); E bank of Calf Creek, *Fertig 21405* (UTC); The Fins, *Loope 196* (UTC). Grand Co.: 15 mi E of Green River, *Albee 4424* (UTC); 1 mi E of Moab bridge, S Rock Cove, *Bryan and Moab School 1-7* (UTC); isolated ridge above Little Grand Wash, *Stockton 160* (UTC); one-half mi up Millcreek Canyon, *Stockton 172* (UTC); 14 mi SE of Moab, *Van Cott V-176* (UTC). Kane Co.: abandoned Pareah townsite, near Paria River, *Shultz & Shultz 9933* (UTC). San Juan Co.: Butler Wash Rd, *Davis & Blair 541* (UTC); Kane Creek Rd, *Shultz & McReynolds 20178* (UTC); Calf Canyon, vicinity of Bluff, *Holmgren 3806* (UTC); 14 mi NW on Beef Basin Rd, *Holmgren & Lewis 16299* (UTC); Lavender Mesa, *Holmgren & Lewis 16376* (UTC); seep areas N of Bluff, *Shultz & Shultz 7791* (UTC); Forgotten Canyon, *Shultz & Shultz 8975* (UTC); between Bluff and Mexican Hat, 12 Apr 1938, *Smith et al. s.n.* (UTC); Fry Point, *Wilson 102* (UTC); middle of Blue Notch Canyon, *Wilson 300* (UTC); middle of Blue Notch Canyon, 18 Jun 1966, *Wilson s.n.* (UTC). Uintah Co.: Seep Ridge Rd, 1 mi N of Buck Canyon, *Neese 6524* (UTC); Buck Canyon, *Shultz & Shultz 3853* (UTC); Buck Canyon, between Willow Creek and Bitter Creek, *Shultz & Shultz 5192* (UTC). Wayne Co.: Elaterite Basin, *Loope 144* (UTC); NE rim of Main Fork of Happy Canyon, *Neely & Sigler 684* (UTC); Benchtop ridge overlooking the Maze, *Neely & Sigler 695* (UTC); S Fork of Happy Canyon, *Neely & Sigler 696* (UTC); near Flat Top, *Shultz & Shultz 6966* (UTC); N Caineville Mesa, *Shultz & Shultz 6990* (UTC); Orange Cliffs, *Shultz & Shultz 7326* (UTC); Horse Canyon benches, *Shultz & Shultz 7364* (UTC); Horse Canyon benches, *Shultz & Shultz 7364-a* (UTC); N end of Boulder Mountain, *Shultz & Shultz 7871* (UTC); Sunglow campground, *Shultz & Shultz 8068* (UTC); E of Government Creek and W of Teasdale, *Shultz et al. 7985* (UTC).

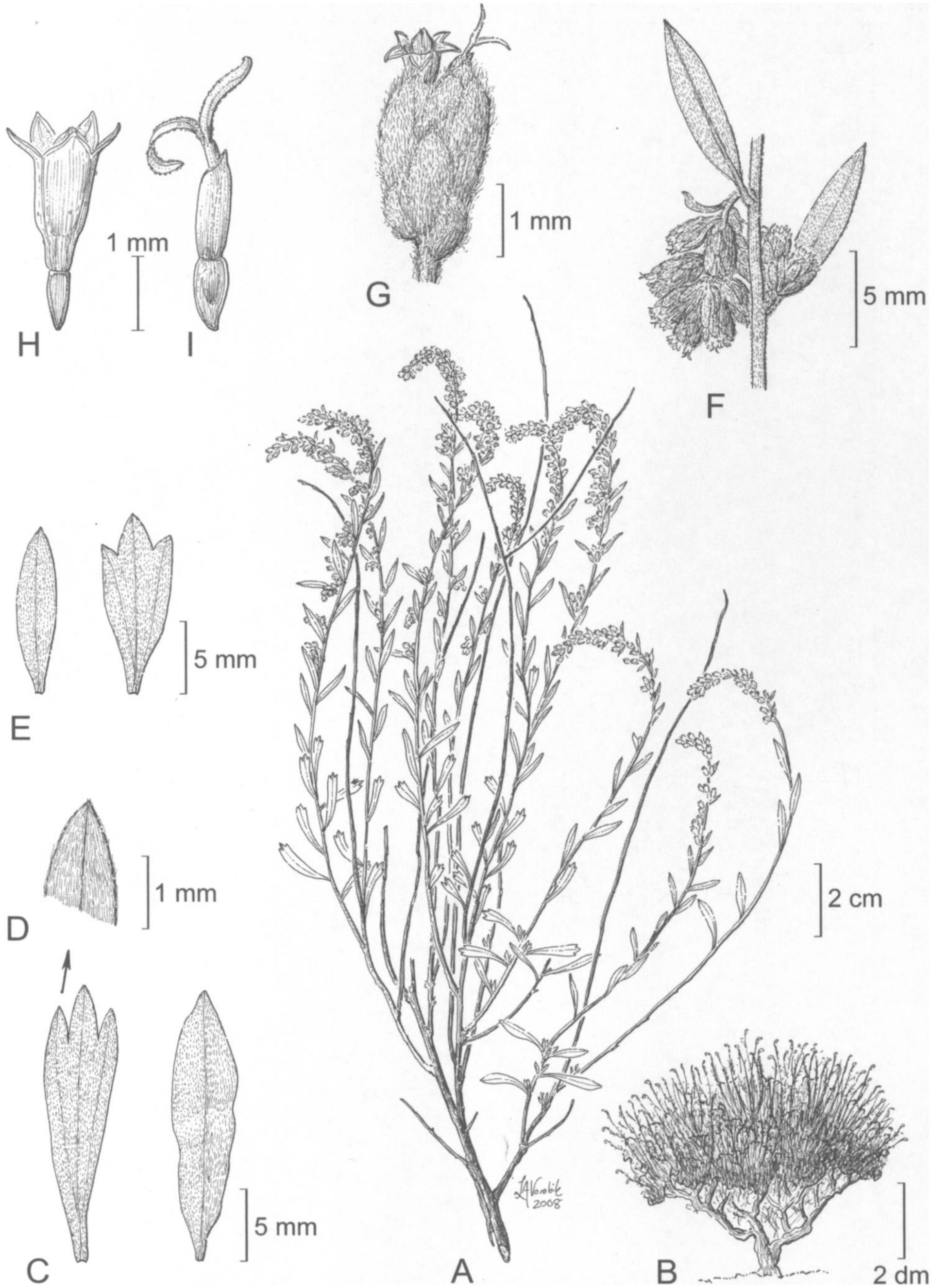

FIG. 12. *Artemisia bigelovii*. A. Flowering branches. B. Habit. C. Leaves. D. Leaf tip. E. Inflorescence leaves. F. Inflorescence branch. G. Capitulum. H. Disk floret and cypsela. I. Ray flower and cypsela. (Based on *Tiehm 8371*.)

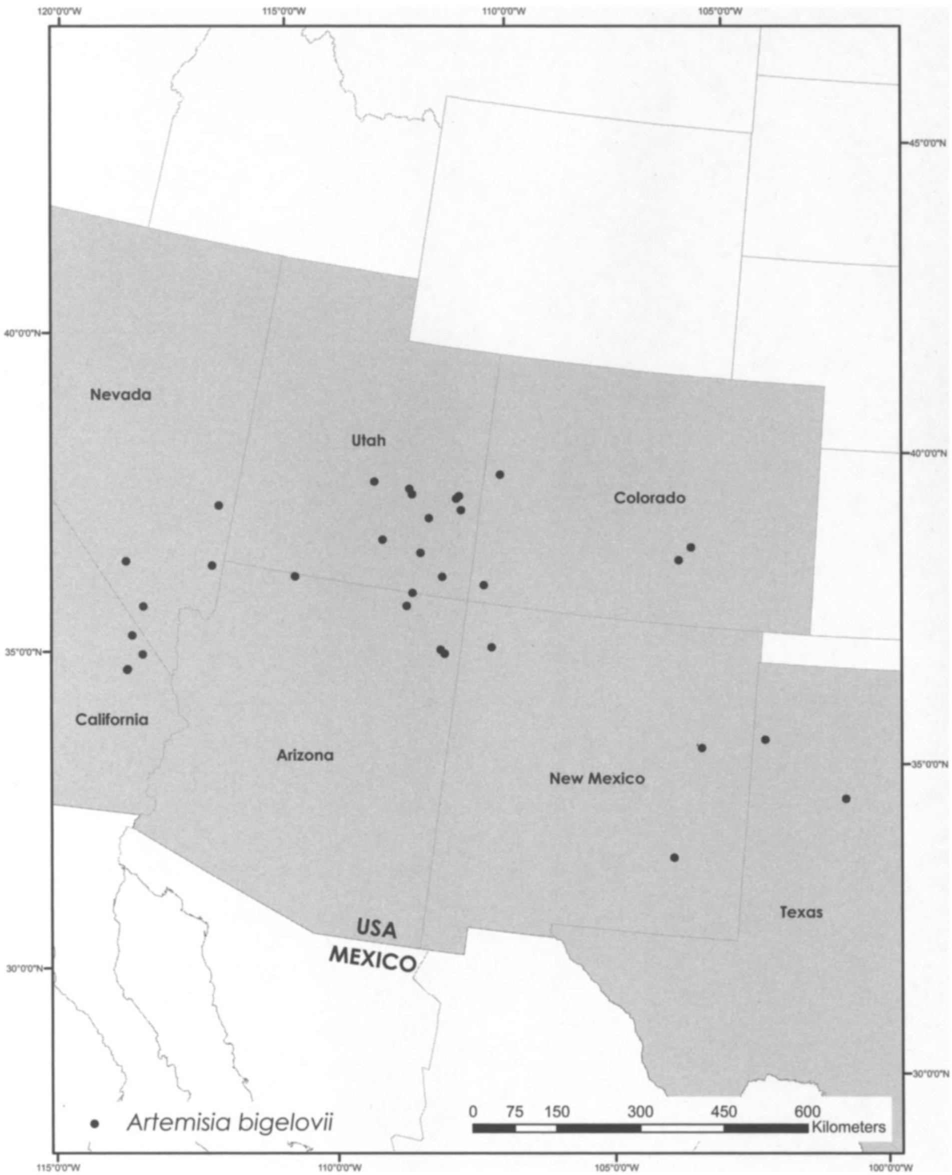

FIG. 13. Distribution of *Artemisia bigelovii*.

Artemisia bigelovii is sometimes mistaken for *A. tridentata*, but it is well distinguished ecologically and morphologically. Its range overlaps with that of *A. tridentata* in the Colorado Plateau, but it also occurs in warm Mohave desert habitats where *A. tridentata* is absent.

The species is unusual in several respects. It is the only member of subg. *Tridentatae* with raylike marginal florets (though these occur rarely), and the only member with vestigial spines on the pollen grains (first reported by Wodehouse, 1935). These characteristics are shared with basal species in the Artemisiinae lineage. It is also the only species with "lignified" trichomes (Fig. 4a; also see Shultz. 1986b). Small nodding flowering heads, arched slender branches, and leaves with acute apical lobes will distinguish *A. bigelovii* from dwarf forms of *A. tridentata*, with which it is sometimes confused.

Molecular analysis places the species with other members of subg. *Tridentatae* (Watson et al. 2002), but morphological characteristics suggest a relationship with the subg. *Artemisia* clade.

The specific epithet honors John Milton Bigelow (1804–1878), botanist for the Whipple Expedition, who collected the species in 1853.

2. Artemisia cana Pursh, Fl. Amer. sept. 521. 1814. *Seriphidium canum* (Pursh) W. A. Weber, Phytologia 55: 7. 1984.—TYPE: U.S.A. "On the bluffs of the Missouri River," *M. Lewis 60* (lectotype, here designated: PH-LC 18!).

Small to medium-sized deciduous shrubs, 1–15 dm tall, pleasantly aromatic; crowns rounded or flat-topped; sprouting from underground caudices. Stems light brown to gray-green, woody, somewhat pliable, leafy, persistently canescent or glabrescent, branched from just above the well-defined trunk; bark gray. Leaves whitish gray to dark gray-green, pliable, deciduous, attached singly (not fascicled); blades 1.5–8 cm long, 0.2–1 cm wide, narrowly elliptic to lanceolate, usually entire, sometimes irregularly lobed, surfaces sparsely to densely hairy. Capitula 3–4 mm high, 2–5 mm wide, narrowly to broadly campanulate, sessile or short-pedunculate, subtended by conspicuous green leafy bracts. Phyllaries ovate or lanceolate, margins scarious, nearly invisible, densely canescent. Inflorescences congested and leafy (leaves not bractlike), 10–20 cm long, 0.2–7 cm wide. Florets 4–20, all perfect and tubular; corollas 1.8–2.5 mm long, resinous; style branches to 2.3 mm long, ellipsoid, exserted, gland-dotted, apically fringed, recurved. Cypselae 1–2 mm long, light brown, resinous. Pappus absent. Chromosome number: $2n = 18, 36, 72$.

The type specimen of *A. cana* was collected along the Missouri River by Meriwether Lewis and labeled simply as "on the bluffs." According to an annotation by L. H. Shinners in 1946, the location would have been "Lookout Bend of the Missouri, now called Little Bend, near the mouth of the Big Cheyenne River."

KEY TO THE SUBSPECIES OF ARTEMISIA CANA

1. Shrubs mostly 10–15 dm tall; leaves 2–8 cm long, entire; east of the Continental Divide. — 2a. *A. cana* subsp. *cana*
1. Shrubs mostly 1–9 dm tall; leaves 1.5–4 cm long, somewhat irregularly lobed; west of the Continental Divide.
   2. Stems felty-tomentose; leaves dull gray or whitish gray (rarely bright green); capitula usually 4–5 mm wide; endemic to the western side of the Great Basin, in mesic and dry sites in California, extreme western Nevada, and southern Oregon. — 2b. *A. cana* subsp. *bolanderi*
   2. Stems pubescent or glabrous (not felty-tomentose); leaves gray-green, often yellow or dark green; capitula usually 2–3 (–4) mm wide; widespread in montane, mesic habitats. — 2c. *A. cana* subsp. *viscidula*

2a. Artemisia cana subsp. **cana.**

Artemisia columbiensis Nuttall, Gen. N. Amer. pl. 2: 142. 1818.—TYPE: U.S.A.: "on arid & saline hills that border the Missouri & lesser streams, commencing ca. 30 miles below the White River (plant called 'wild sage' by Lewis & Clark)," [1811], *T. Nuttall s.n.* (holotype: PH!).

Medium-sized shrubs, 10–15 dm tall; crowns rounded. Stems white to light gray or brown, stout and usually strictly erect. Leaves whitish gray; blades 2–8 cm long, 0.3–1 cm wide, narrowly elliptic to lanceolate, usually entire, sometimes irregularly lobed, surfaces densely silvery-canescent. Capitula 3–4 mm high, 3–5 mm wide, broadly campanulate. Phyllaries broadly ovate, mostly obtuse, densely hairy. Inflorescences leafy, 10–20 cm long, 5–7 cm wide. Florets 10–20. Cypselae 1–1.2 mm long. Chromosome number: 2n = 72 (McArthur & Sanderson 1999) [reports in the literature of 2n =18 and 36 are based on G. H. Ward (1953) collections that I have annotated as *A. cana* subsp. *bolanderi*]. Figs. 9b, 14A–F.

Common names. Silver sagebrush, Plains silver sagebrush.

Phenology. Flowering mid- to late summer.

Distribution (Fig. 15). Canada: Alberta, Manitoba, Saskatchewan; U.S.A.: Colorado, Montana, Nebraska, North Dakota, South Dakota, Wyoming; in sandy loam soils, often along streams; 1000–1500 m.

ADDITIONAL SPECIMENS EXAMINED. **Canada.** ALBERTA: W of Hazlett, *Barkworth 1135* (UTC); between Coutts and Milk River, *Beetle 13964* (RM); Cypress Hills, *Breitung 5601* (DAO); near Del Bonita, *Moss 432* (GH); E of Woolford, *Shinners 585* (WIS).—MANITOBA: Melita (SW corner), *Scoggan 9906* (GH).—SASKATCHEWAN: Outlook, *Argus 4723* (GH, RM); Souris River Valley, *Boivin 7972* (DAO); 2 mi W of Elbow, *Boivin 14127* (DAO, GH, RM); Cypress Hills, *Breitung 5387* (DAO, MO); Whiteshore Lake, 2 Aug 1906, *Herrott s.n.* (GH). **U.S.A.** COLORADO: Larimer Co.: Near Tinmath, *Crandall 2653* (COLO).—MONTANA: Beaverhead Co.: Red Rock Pass, *Ewan 18410* (DS). Big Horn Co.: Lodge Grass, *Beetle 12223* (UTC). Custer Co.: near Miles City, *Jack 1632* (RM). Gallatin Co.: N of Bozeman, *Chase 14215* (UC); near Bozeman, 23 Sep 1898, *Blankinship 251* (MO, WS); Gallatin Valley, *Nelson & Nelson 377* (RM); 6 mi E of Livingston, *Shultz & Hysell 11960* (UTC); 6 mi E of Livingston, *Shultz & Hysell 11961* (UTC). Jefferson Co.: Helena, 7 Jul 1891, *Kelsey s.n.* (UC). Prairie Co.: near Terry, *Rose 448* (WS). Rosebud Co.: Tongue River Valley, 3 Aug 1957, *Bennett s.n.* (DS, UC). Stillwater Co.: Absaroka, 10 Jul 1926, *Hawkins s.n.* (WIS); 0.7 mi E of Sweet Grass County line, *Shultz & Hysell 11972* (UTC). Sweet Grass Co.: Crazy Mtns, *Shultz & Hysell 11969* (UTC); valley E of Crazy Mtns, *Shultz & Hysell 11970* (UTC). Yellowstone Co.: Billings, *Bartholomew 5164* (RM); 9.3 mi E Pompey's Pillar, *Beetle 12231* (UTC); 20 mi S of Billings, *Beetle 12234* (COLO, RM); 10 mi S of Ringling, *Beetle 12247* (WS); W of Billings, 21 Jul 1934, *Osterhout s.n.* (MO); 12 mi E of Livingston, *Shultz & Hysell 11965* (UTC); Suksdorf's Gulch, *Suksdorf 232* (MO, WS), *Suksdorf 971* (DS, MO); NW of Wilsall, *Suksdorf 991* (COLO, DS, UTC).—NEBRASKA: Dawes Co.: Crawford, 1 Aug 1889, *Webber s.n.* (MO). Sioux Co.: Glen, 16 Jun 1897, *Bates s.n.* (RM); common in clay soils, *Kramer 200* (MO).—NORTH DAKOTA: Fort Pappy, *Hayden 260* (MO); abundant on Yellowstone and Missouri Rivers, Aug 1853, *Hayden s.n.* (MO). Barnes Co.: Valley City, *Stevens 2929* (ND, RM, UC). Billings Co.: southern edge of Kinley Plateau, 21 Aug 1992, *DiGiacomo & Leuszler s.n.* (UTC); Medora, 2 Sep 1884, *Seymour s.n.* (WIS). Golden Valley Co.: Sentinel Butte, *Bergman 1174* (ND, RM). Stark Co.: Dickinson, 7 Sep 1908, *Holgate s.n.* (MO).—SOUTH DAKOTA: Butte Co.: Belle Fourche, *Beetle 12164* (RM); NW Mud Buttes, Jun 1958, *Rauzi s.n.* (UTC). Corson Co.: Bear Creek, *Over 2341* (COLO). Fall River Co.: Evans Siding, Hot Springs, *McIntosh 164* (RM); Edgemont, *Over 16279* (RM); 20 mi SW of Hot Springs, *Ward 2549* (RM). Harding Co.: Edgemont, *Hayward 529* (RM); Badland, 5 Sep 1896, *Perrine s.n.* (RM); Box Elder Creek, *Visher 389* (RM); Billings, 2 Sep 1894, *Williams s.n.* (RM). Interior Co.: without locality, *Over 6200* (COLO). Lyman Co.: near Chamberlain, *Palmer 36096* (MO). Pennington Co.: near Wall, *Palmer 37306* (MO).—WYOMING: Albany Co.: 9 mi N of Laramie, *Beetle 13184* (MO, WS); Centennial, *Gooding 2118* (MO, COLO); W of Laramie, 10 Sep 1919, *Hall s.n.* (DS); Sheep Mtn, *Nelson & Nelson 1144* (RM); Pole Mtn, 13 Nov 1956, *Palmer s.n.* (MO); N Fork of Sybille Creek, *Porter 4102* (RM, UC); Medicine Bow Mtns, *Porter & Porter 10071* (UC); Sheep Range, *Reed & Reed 1730* (ID). Campbell Co.: without locality, *Stromberg 10* (WIS). Converse Co.:

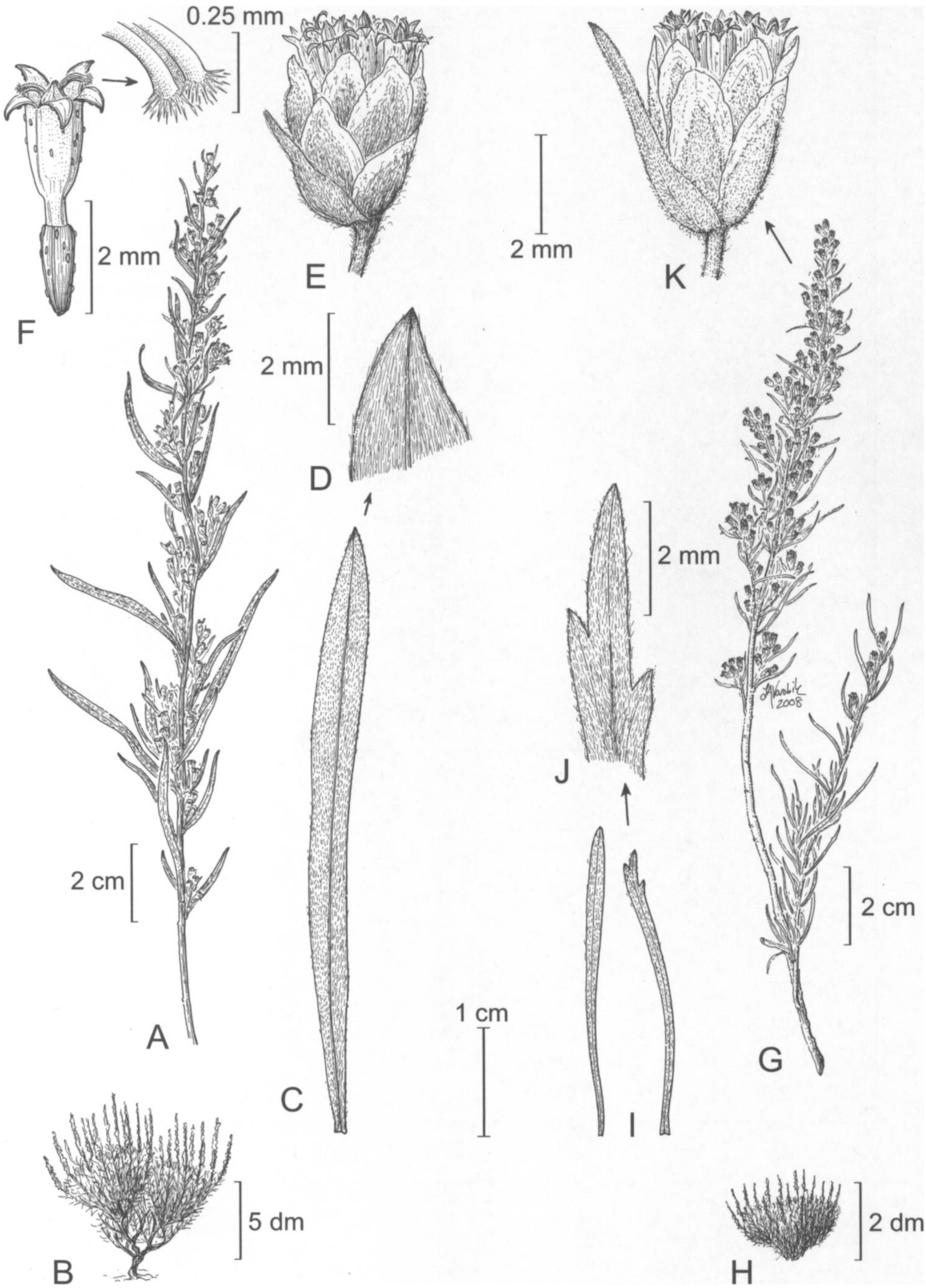

FIG. 14. *Artemisia cana*. A–F: *A. cana* subsp. *cana*. A. Flowering branch. B. Habit. C. Leaf. D. Detail of leaf tip. E. Capitulum. F. Disk floret and cypsela with detail of style branches. G–K: *A. cana* subsp. *bolanderi*. G. Flowering branch. H. Habit. I. Leaves. J. Detail of leaf tip. K. Capitulum. (Based on: A–F, *Suksdorf 945*; G–K, *Shultz & Shultz 5708*.)

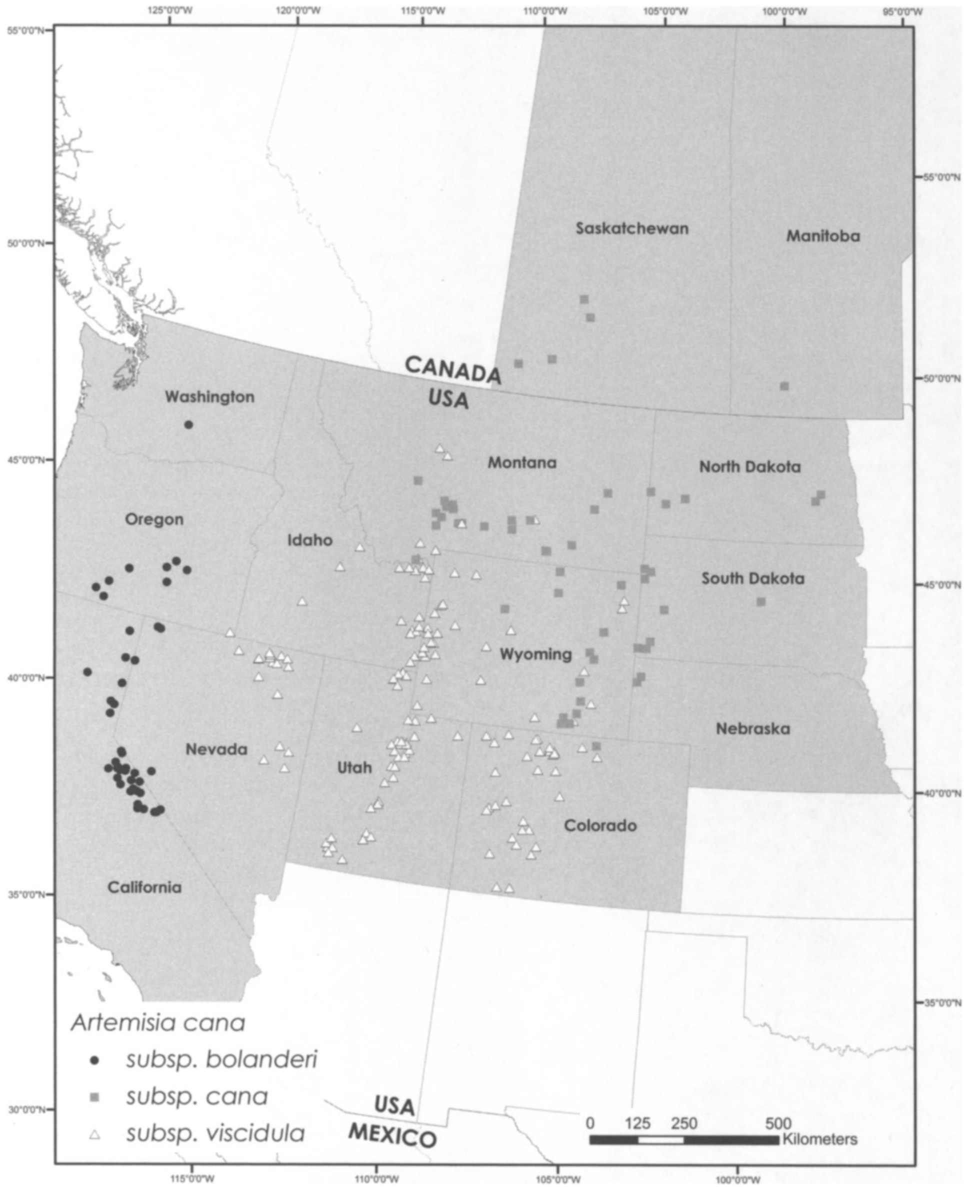

FIG. 15. Distribution of *Artemisia cana* subsp. *cana*, subsp. *bolanderi*, and subsp. *viscidula.*

Douglas, *Pfadt 192* (RM). Crook Co.: base of Devil's Tower, *Beetle 12143* (MO, RM). Goshen Co.: NW of Torrington, *Nelson 2451* (RM). Hot Springs Co.: S of Thermopolis, *Beetle 13199* (MO). Johnson Co.: near Buffalo, *Tweedy 3060* (WS). Natrona Co.: 5 mi S of Casper, *Shultz 11514* (UTC); Independence Rock, *Shultz 11522* (UTC). Niobrara Co.: S of Mule Creek junction, *Beetle 12156* (MO, UC). Sheridan Co.: Sheridan, Jun 1897, *Pammel s.n.* (MO).

Artemisia cana subsp. *cana* occurs in grasslands and along stream banks in the northern Rocky Mountains of the United States and the prairie provinces of Canada. One population has been determined by E. D. McArthur from west of the continental divide (Colorado, Moffatt Co.: Maybell), but I have not confirmed the identification. Wide-leaved populations of *A. cana* subsp. *viscidula* have most of the characteristics of subsp. *cana*. Not only is it possible to confuse the two subspecies, it is likely that restoration projects have resulted in the establishment of a subspecies beyond its normal range.

This is one of the few taxa for which there is no evidence of hybridization with other subspecies or species. *Artemisia cana* subsp. *cana* appears to be a polyploid derivative within the *A. cana* complex (McArthur & Sanderson 1999). With its large, entire leaves, it is sometimes confused in herbarium collections with fragmentary samples of herbaceous *A. longifolia* Nutt. or *A. ludoviciana* Nutt. subsp. *ludoviciana.*

2b. Artemisia cana subsp. **bolanderi** (A. Gray) G. H. Ward, Contr. Dudley Herb. 4: 192. 1953. *Artemisia bolanderi* A. Gray, Proc. Amer. Acad. Arts 19: 50. 1883. *Artemisia tridentata* subsp. *bolanderi* (A. Gray) H. M. Hall & Clements, Publ. Carnegie Inst. Wash. 326: 139. 1923. *Artemisia cana* var. *bolanderi* (A. Gray) McMinn, Man. Calif. shrubs 609. 1939. *Seriphidium canum* subsp. *bolanderi* (A. Gray) W. A. Weber, Phytologia 55: 7. 1984. *Seriphidium bolanderi* (A. Gray) Y. R. Ling in Hind, Jeffrey & Pope, Advances in Compositae Systematics 288. 1995.—TYPE: U.S.A. California: Mono Co., Mono Pass, 1866, *Bolander 6149* (holotype: GH!; isotypes: BM! K! MO! NY! UC!).

Low-growing to medium-sized shrubs, (1–) 2–6 (–8) dm tall; crowns rounded or slightly flat-topped. Stems white, felty-tomentose when young. Leaves dull gray or whitish gray (rarely bright green), early-deciduous (in fall); blades (1.5–) 3–4 cm long, 0.2–0.6 cm wide, linear to narrowly lanceolate, usually entire, sometimes irregularly lobed. Capitula 2–3 per branch, broadly campanulate, 3–4 mm high, 4–5 mm wide. Phyllaries narrowly ovate-lanceolate, acute (outer) or obtuse, densely hairy. Inflorescences sparsely leafy, 12–18 cm long, 1–2 cm wide. Florets 8–16. Cypselae 1–1.5 mm long. Chromosome number: 2n = 18, 36 (Ward 1953). Figs. 9i, 14G–K.

Common names. Sierran sagebrush, California silver sagebrush, Bolander wormwood.

Phenology. Flowering mid- to late summer.

Distribution (Fig. 15). U.S.A.: California, Nevada, Oregon, Washington; in gravelly soils, in mountain meadows, stream banks, or fine-grained basins; 1600–3300 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** CALIFORNIA: Alpine Co.: 5 mi W of Heenan Lake, *Embree 209* (RSA, UC); 2 km E of Monitor Pass, *Cronquist 12179* (NY, UTC); Dardanelles, Poison Valley, *Gifford 747* (UC); just W of Monitor Pass, 24 Oct 1964, *Howell s.n.* (UTC); 0.5 mi W of Sonora Pass Summit, *Wiggins 9297* (DS, RM, UT); 0.5 mi W of Sonora Pass summit, 27 Aug 1939, *Wiggins s.n.* (UTC). Inyo Co.: Heart Lake, *Ferris 11078* (DS); Rock Creek basin, 25 Aug 1945, *Ferris & Lorraine s.n.* (UTC); Rock Creek, *Peirson 9107* (UC); Rock Creek Lake, *Shultz & Shultz 5680* (UTC), *Shultz & Shultz 5691* (UTC), *Shultz & Shultz 5692* (UTC); John Muir Wilderness Area, *Shultz & Shultz 5700* (UTC); trail to Mono Pass, *Shultz & Shultz 5702* (UTC), *Shultz & Shultz 5703* (UTC); Rock Creek drainage, *Shultz & Shultz 5704* (UTC), *Shultz & Shultz 5705* (UTC); White Mtns, *Shultz et al. 19809* (UTC), *Shultz et al. 19810* (UTC), *Shultz et al. 19812* (UTC); Rock Creek Basin, above Tom's place, *Wright 227* (UTC). Lassen Co.: between Ravendale and Termo, *Beetle 12892* (MO, RM, UTC); Litchfield, *Beetle 12910* (MO, UC); between Ravendale and Termo, 13 Aug 1957, *Beetle s.n.* (UTC). Modoc Co.: 15 mi S of Alturas, *Beetle 12764* (MO); Devil's Garden, *Wheeler 3931* (MO). Mono Co.:3.3 mi E of Sonora Pass, *Anderson 2932* (RM, UTC); S end of Bridgeport Valley, *Applegate 6860* (DS); S of Mono Lake, *Applegate 6897* (DS); E base of Sonora Pass, *Beetle 12576* (MO); base of Sonora Pass, *Beetle 12578* (MO, RM); northern border of Mono County at Sonora Pass, *Beetle 12583* (MO, UTC, WS); Dry Creek, *Beetle 12992* (ID), *Beetle 12955.1*

(MO, RM); on Dry Creek, S of Mono Lake, 13 Aug 1957, *Beetle s.n.* (UTC); Mono Pass, *Bolander 6149* (MO); Campito Meadow, near the Patriarch Grove, in White Mtns, *Cronquist 12086* (UTC); Sonora Pass in the Sierra Nevada, *Cronquist 12088* (UTC); Mono Lake, 16 Aug 1898, *Congdon s.n.* (DS); Walker Lake, 16 Aug 1898, *Congdon s.n.* (WS); 1.5 mi S of Bridgeport, *Graham 269* (UC); 3.5 mi S of Chinese Camp, *Graham 276* (RSA, UC); 14 mi N of Bridgeport, *Hall 11690* (UC); Sand Flat, S of Mono Lake, *Hall 11877* (MO, RM); Mammoth, *Hall 11901* (CAS); 4 mi N of Bridgeport, *Howell 21523* (CAS, RSA); near summit of Sonora Pass, *Keck 5030* (UC); on W slopes of Leavitt Lake, Sierra Nevada Mtns, 6 Jul 1979, *Mozingo & Ryser s.n.* (UTC); Owen's Valley, *Peirson 1447* (RSA); without locality, *Reveal 1169* (UTC); Crooked Meadow, 8 Sep 1962, *Reveal s.n.* (UTC); 4 mi E of Mono Hill, 27 Aug 1964, *Reveal s.n.* (UTC); Waford Springs on Pole Line Rd, 29 Aug 1964, *Reveal s.n.* (UTC); White Mtns, *Roos & Roos 5875* (RSA); Crooked Creek, 23 Aug 1959, *Ross s.n.* (UTC); Rock Creek Canyon, *Shultz & Shultz 5708* (UTC); 14 mi N of Bridgeport, *Shultz et al. 19777* (UTC), *Shultz et al. 19778* (UTC); Sand Flat, *Ward & Birmingham 964* (WS); Sand Flat, S of Mono Lake, *Ward & Birmingham 962* (DS); Sonora Pass, *Ward & Birmingham 974* (DS, WS); along Virginia Creek, *Wolf 2529* (POM, RSA); Mono Mills, *Wolf 2556* (CAS, POM); Sand Flat, *Wolf 2557* (RSA). Placer Co.: Silver Peak, *Pyle 1978* (CAS). Plumas Co.: 2.5 mi S of Bagley Pass, *Albertus 271* (RSA, UC); Grizzly Creek, *Balls 15664* (RSA); 6 mi S of Beckworth, *French 556* (UC); near Beckworth, *Howell 34971* (CAS, UTC); Feather River, *Howell 36922* (CAS, UTC). Sierra Co.: Sierra Valley, *Lemmon 17* (MO); near Little Truckee River, *Sonne 431* (MO); Loyalton, 3 Sep 1920, *Strong s.n.* (CAS). Tuolumne Co.: W of Sonora Pass, *Reveal 189* (CAS, UC); 2.5 mi W of Sonora Pass summit, *Wolf 5471* (DS, RSA).—NEVADA: Lyon Co.: Sweetwater Mtns, *Tiehm et al. 9331* (UTC). Mineral Co.: 8 mi SE of Simpson, *Graham 98* (UC). Washoe Co.: 7 mi SW of Huffaleer, *Lee 202* (UC); Hunter Lake, 27 Jul 1968, *McCintock s.n.* (CAS); S of Verdi, *Tiehm 12762* (UTC); Madelin Mesa, *Tiehm 13770* (UTC); Madelin Mesa, *Tiehm 13770* (UTC); Big Meadows, *Williams 256* (CAS).—OREGON: Crook Co.: near Prineville, *Leiberg s.n.* (UTC). Harney Co.: Town of Burns, *Bailey 7693* (OSC); Squaw Butte Experiment Station, Sep 1956, *Barkley et al. s.n.* (OSC, WS); Squaw Butte Experiment Station, W of Burns, *Beetle 12911* (UTC); Burns, *Butte 12797* (WS); Steens Mtns, *Hansen 547* (OSC); Anderson Valley, *Henderson 8493* (CAS); Harney Valley, *Parsell 576* (OSC); Squaw Butte Experiment Station, *Pursell 24* (OSC); 15 mi N of Wagontire, *Ward 954* (DS, WS). Klamath Co.: Brookside Ranch, *Applegate 282* (DS); Klamath Falls, *Beetle 12950* (UTC); Klamath Falls, 13 Aug 1957, *Beetle s.n.* (UTC); between Dairy and Olene, *Beetle 12955* (MO, RM); near Klamath Falls, *Peck 2882* (OSC). Lake Co.: town of Silver Lake, *Beetle 12586* (MO, RM); E side of Drew's Gap, *Beetle 12857* (MO); Thompson's Valley, *Cusick 2737* (OSC); near Bullon, *Leiberg 792* (WS); upper end of Warner Canyon, *Reeder & Merkle 103* (OSC); Old Jacob's place, 15 Jul 1931, *Scheiffer s.n.* (OSC). Malheur Co.: Lookout Lake, *Packard 76163* (UTC); damp bank of Owyhee River, *Peck 21819* (OSC).—WASHINGTON: Yakima Co.: without locality, 13 Jun 1972, *Daubenmire s.n.* (WS).

Artemisia cana subsp. *bolanderi* is restricted to the western range of the species, and occurs only in California, Oregon, Washington, and western Nevada. The leaf morphology and growth form of the subspecies are extremely variable, but the tomentose stems and light gray pubescence distinguish it from subsp. *viscidula*. The narrow-leaved form of subsp. *bolanderii* typically occurs in fine-grained soils of valley basins. A broader-leaved form occurs at high elevations, typically in rocky soils of mountain habitats. To what degree these populations vary genetically has not been determined.

The specific epithet honors Henry Nicholas Bolander (1831–1897), a German-born botanist, who collected extensively in California from 1860 to 1886.

2c. Artemisia cana subsp. **viscidula** (Osterhout) Beetle, Rhodora 61: 84. 1959. *Artemisia cana* var. *viscidula* Osterhout, Bull. Torrey Bot. Club 27: 507. 1900. *Artemisia viscidula* (Osterhout) Rydberg, Bull. Torrey Bot. Club 33: 157. 1906. *Seriphidium canum* subsp. *viscidulum* (Osterhout) W. A. Weber, Phytologia 55: 8. 1984. *Seriphidium canum* var. *viscidulum* (Osterhout) Y. R. Ling in Hind, Jeffrey & Pope, Advances in Compositae Systematics 286. 1995.—TYPE: U.S.A. Colorado: Routt Co., Steamboat Springs, 1 Sep 1899, *Osterhout 2012* (holotype: RM!; isotype: NY!).

Medium-sized shrubs, (2–) 4–7 (–9) dm tall; crowns more or less flat-topped. Stems white (sparsely tomentose) or brown (glabrous), stout. Leaves dark green (viscid) to gray-green (pubescent), deciduous in late fall or winter; blades (1.5–) 2–3 (–4) cm long, 0.2–0.4 cm wide, linear to narrowly lanceolate, often irregularly lobed, surfaces sparsely hairy or glabrescent, usually viscid with glandular hairs; ephemeral leaves mostly entire, up to 1.3 times as long as the persistent (fascicled) leaves. Capitula 2–3 per branch, 3–5 mm high, 2–3 (–4) mm wide, narrowly campanulate, erect, sessile. Phyllaries narrowly lanceolate, acute (outer) or obtuse, sparsely hairy. Inflorescences sparsely leafy, 12–20 cm long, 1–2 cm wide. Florets 4–8. Cypselae 1–2 mm long. Chromosome number: 2n = 18 (McArthur & Sanderson 1999); 2n = 36 (McArthur et al. 1981; McArthur & Sanderson 1999). Figs. 4b, 5b, 6b, 8, 9a, 16.

Common names. Mountain silver sagebrush, Sticky sagebrush.

Phenology. Flowering mid- to late summer.

Distribution (Fig. 15). U.S.A.: Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Wyoming; in seasonally moist mountain meadows, stream banks, or rocky areas with late-lying snows; 2000–3300 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** COLORADO: Archuleta Co.: 7 mi above Arbolis, *Flowers 135* (UC, UT). Grand Co.: 6 mi N of Grand Lake, *Douglass & Douglass 60406* (CS); near Grand Lake, 23 Aug 1965, *Mickelson s.n.* (WIS); near Middle Park, *Parry 1862* (MO); near Mt Bryant, *Sawyer & Rutter 110* (UC). Gunnison Co.: Marshall Pass, *Baker 880* (MO, RM); head of Beaver Creek, *Barrell 675* (RM); S of Taylor Reservoir, *Iltis & Iltis 19011* (WIS); Castle Park, *Langenheim 4471* (WS); 10 mi S of Sapinero, *Rollins 1999* (MO, RM); 1 mi from Crested Butte, *Ward 1727* (RM); Ohio Creek valley, *Weber 14521* (COLO, CS, UTC). Jackson Co.: 2 mi W of Coalmont, Nov 1956, *Beetle s.n.* (UTC); near town of Coalmont, *Shultz & Shultz 5421* (UTC); near Coalmont, *Shultz & Shultz 5430* (RSA, UTC); North Park, *Weber 12430* (WIS); Coalmont, *Wilken 13583* (UTC); W of Hebron, *Wiley-Eberle 454* (UTC); Coalmont townsite, *Wiley-Eberle 824* (CS). Larimer Co.: North Park, *Osterhout 1829* (RM), *Osterhout 2269* (RM). Mesa Co.: Buzzard Creek, 1 Sep 1969, *Kufeld s.n.* (CS); Uncompahgre Plateau, *Rollins 1582* (MO); along Rim Drive Rd, 29 Aug 1981, *Wilken s.n.* (UTC). Moffat Co.: Big Hole Gulch, *Deming 25-6* (UTC); W of Maybell, *Beetle 13017* (MO, RM); 8 mi NW of Craig, *Nielson 88742* (WIS); between Greystone and Sunbeam, *Weber 12702* (COLO); Cold Spring Mtn, *Weber 14293* (COLO, UT). Montrose Co.: 26 mi N of Montrose, *Rollins 1603* (WIS). Routt Co.: 12 mi S of Oak Creek, *Beetle 2340* (RM); 2 mi S of Oak Creek, *Beetle 11947* (MO); Steamboat Springs, *Beetle 12206* (MO), *Osterhout 2256* (RM, UTC); Hayden Flats, *Osterhout 2258* (RM, WIS), *Osterhout 2259* (WIS); Steamboat Lake Campground, *Wilken 12812* (CS, UTC). Saguache Co.: along Archuleta Creek, 11 Jun 1960, *Johnson s.n.* (CS). San Miguel Co.: Dallas divide, *Arp 171313* (COLO). Summit Co.: Breckenridge, 27 Aug 1896, *Cowen s.n.* (MO); near Breckenridge, *Mackenzie 262* (COLO, MO).—IDAHO: Bear Lake Co.: Snowslide Canyon, *Shultz & Shultz 8185* (UTC). Bingham Co.: N end Blackfoot Mtn, *Beetle 13305* (UTC); N end of the Blackfoot Mtns, 21 Aug 1958, *Beetle s.n.* (UTC); Henry's Lake, *Nelson & Nelson 6795* (WS). Bonneville Co.: Caribou Natl Forest, *Beetle 13407* (UTC). Canyon Co.: playas just E of turnoff to Steens Mtns, *Packard 78260* (UTC). Caribou Co.: Blackfoot River, *Davis 385* (WS); Grays Lake Natl Wildlife Refuge, Outlet Valley, *Neely 1575* (UTC); E of Soda Springs, *Shultz 20191* (UTC). Clark Co.: above Spencer, *Cronquist 866* (UTC);11 mi E of Kilgore, *Maguire 17103* (UTC). Custer Co.: 10 mi N of Stanley, *Cronquist 2782* (MO). Elmore Co.: near Camas Prairie, mile 130, Hwy 20, *Shultz 20399* (UTC). Fremont Co.:S side of Targhee Pass, *Beetle 12227* (MO); Camas Creek, *Rust 776* (ID); SE of Henry's Lake, *Ward & Ward 910* (DS, WS). Gooding Co.: City of Rocks, *Shultz & Shultz 8444* (UTC). Lemhi Co.: Antelope Pasture, *Olsen 9115* (RM). Lincoln Co.: Tom Gooding Lake, *Beveridge 7* (ID). Oneida Co.: Pocatello Valley, *Smith 3* (UC, UTC); Pocatello Valley, 31 Sep 1939, *Smith & Corey s.n.* (UTC). Owyhee Co.: near Big Springs, *Falker 45* (ID). Twin Falls Co.: Shoshone Ranger Station, *Gierisch 819* (UTC).—MONTANA: Beaverhead Co.: above Elk Lake, 0.5 mi NE of lodge, *Lesica 8997* (UTC). Cascade Co.: 10 mi SE of Great Falls, *Beetle 14107* (UTC). Gallatin Co.: Hwy 191 to Bozeman, *Shultz & Hysell 11956* (UTC); Fawn Pass, *Shultz & Hysell 11957* (UTC); Wallrock Basin, about 12 mi NW of Wilsall, *Suksdorf 945* (UTC). Madison Co.: Beaverhead Forest, *Ellison 440* (ID). Teton Co.: near Pendroy, 7 Aug 1956, *Beetle s.n.* (UTC). Yellowstone Co.: 9.3 mi E of Pompey's Pillar, *Beetle 12231* (UTC); 12 mi E of Livingston, *Shultz & Hysell 11965.1* (UTC).—NEVADA: Elko Co.: Sun Creek, *Gullion 574* (RM, UC); Wild Horse Reservoir, *Holbo 3* (UTC); 30 mi N of Midas, *Holmgren 716* (UTC, WS); Bull Run Basin, *Holmgren 732* (UTC, WS); North Fork, *Holmgren 1878* (UC, UTC); Maggie Creek, *Kennedy 642* (RM); 5 mi S of Charlston, 10 Aug 1943, *Maguire &*

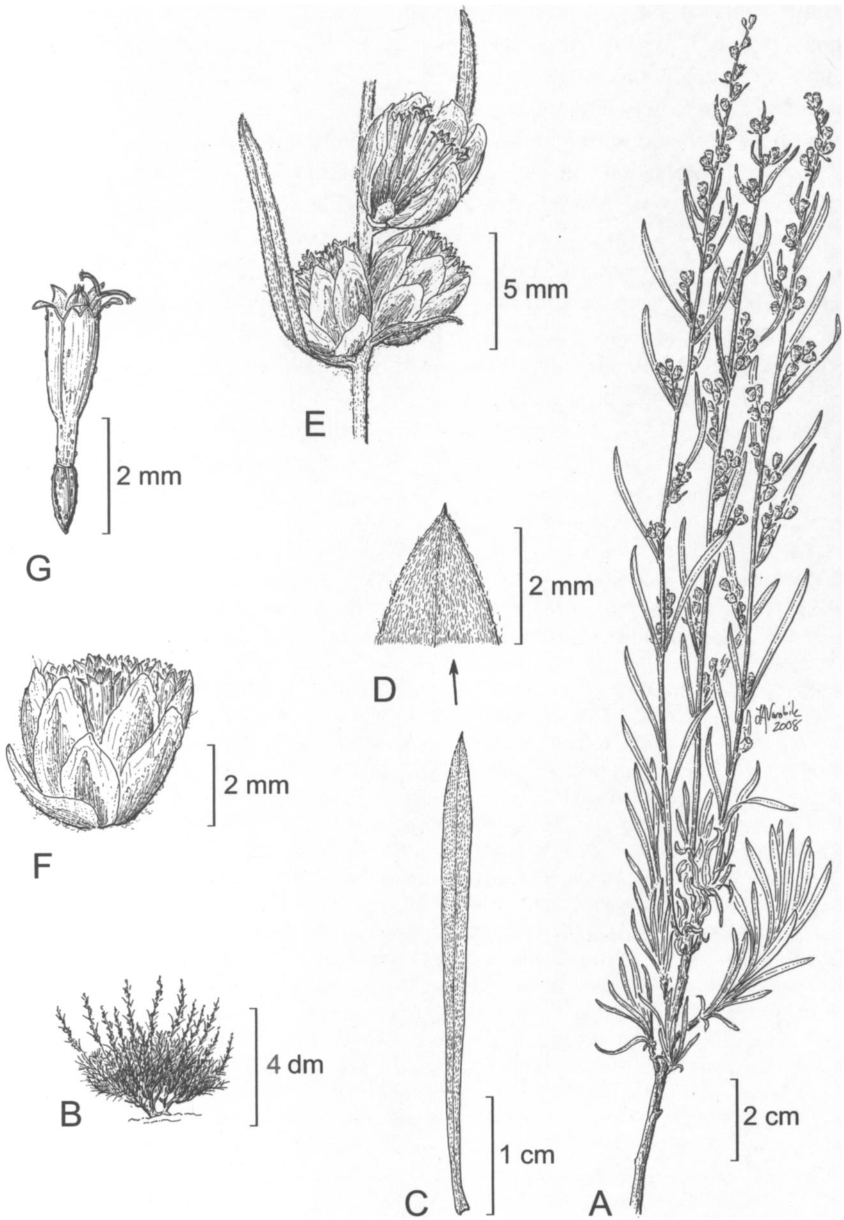

FIG. 16. *Artemisia cana* subsp. *viscidula*. A. Flowering branch. B. Habit. C. Leaf. D. Detail of leaf tip. E. Portion of inflorescence branch; part of involucre removed in distal capitulum to show receptacle. F. Capitulum. G. Disk floret and cypsela. (Based on: A–D, *Shultz & Shultz 4500*; E–G, *Maguire & Maguire 15584*.)

Holmgren s.n. (UC, UTC); Humboldt Natl Forest, *Leonard 79976* (UTC); Sunflower Flat, *Lewis 3670* (UTC); Belcher's Meadow, *Williams & Tiehm 79-139-2* (UTC); Bull Run Reservoir, *Williams & Tiehm 84-116-1* (UTC); 2.1 mi E of Beaver Creek Ranch house, *Williams & Tiehm 84-120-5* (UTC). Humboldt Co.: Humboldt Natl Forest, *Lewis 3679* (UTC). White Pine Co.: Hamilton, *Gullion 506* (UTC); near Telegraph Peak, *Pinzl & Work 12598* (UTC); Schell Creek Range, *Tart & Howell 2714* (UTC); between Steptoe and Duck Creek, *Train 1029* (DS, MO).—UTAH: Cache Co.: 3 mi N of Hardware Ranch, *Cottam et al. 15947* (DS, UT); 11 mi up Blacksmith Fork, *Maguire 17774* (UTC, WS); Beaver Basin, *Maguire 20148* (UC, UTC); 11 mi up Blacksmith Fork Canyon, 22 Jun 1939, *Maguire s.n.* (UTC); islands on Beaver Basin area, 10 Sep 1940, *Maguire s.n.* (UTC); Logan Canyon, *Piep 04.078* (UTC); Amazon Hollow, E of Beaver Creek, *Shultz 4511* (UTC); Amazon Hollow, *Shultz 4513* (UTC); S face of Logan Peak, *Shultz 7439* (UTC); Logan Canyon, *Shultz & Shultz 8207* (UTC); between Girl's Camp and Blacksmith Fork Canyon, *Shultz et al. 7443* (UTC); Logan Canyon, *Shultz et al. 19820* (UTC); Mud Springs, 7 Sep 1937, *Smith s.n.* (UTC); near head of Logan Canyon, *Ward & Ward 925* (DS, RM). Carbon Co.: E Soldier Summit, *Flowers 1089* (UT). Duchesne Co.: Summit of Daniel's Canyon, *Garrett 8045* (COLO, UT); Blind Stream, Duchesne Ranger District, *Goodrich 1571* (UTC); Blind Stream, Uinta Mtns, *Huber 3138* (UTC). Emery Co.: Lower Sheep Flat, *Lewis 7591* (UTC). Garfield Co.: Aquarius Plateau, Jul 1968, *Hall s.n.* (UT), *Maguire et al. 15582* (UTC), *Reese 1019* (UTC), *Ward 593* (MO). Iron Co.: Hwy 14, *Annable & Hurst 2603* (UTC); Cedar Breaks, *Bruhn 1200* (UT); Dixie Natl Forest, summer 1936, *Gierisch s.n.* (UTC); vicinity of Cedar Breaks, 29 Aug 1934, *Maguire & Maguire s.n.* (UTC); 8 mi SE of Cedar Breaks, *Maguire & Richards, Jr. 15583* (UTC). Juab Co.: Chicken Creek Canyon, *Welsh 2571* (WIS). Kane Co.: 3 mi W of Navajo Lake, *Maguire 19659* (RM, UTC); Markagunt Plateau, *Niles 1136* (UTC). Rich Co.: 1 mi E of summit, Logan Canyon, Bear River Range, *Maguire 20126* (UTC); Deseret Land and Livestock Ranch, *Shultz et al. 20303* (UTC), *Shultz et al. 20304* (UTC). Sanpete Co.: Hop Creek, *Cottam 16069* (UT); near Ephraim, 5 Aug 1972, *Epstein s.n.* (UTC); San Pitch Mtns, *Harris 28183* (MO); Upper Gooseberry, *Lewis 7173* (UTC); Beaver Dam Reservoir, *Thorne & Hugie 731* (BRY, UTC). Sevier Co.: near Fish Lake, *Garrett 6830* (MO); near Yogo Creek, *Harrison 21* (UTC); Marvine Peak, *Maguire 19907* (RM, UTC); Lost Lake, 20 mi SE of Salina, *Maguire 19976* (UC, UTC, WS); near Fish Lake, 1 Aug 1934, *Maguire & Richards, Jr. s.n.* (UTC). Summit Co.: near Bear River, *Goodman 308* (RM); E fork of Bear River, *Goodman 2018* (ISU, MO); 11.5 mi NW of Kings Peak, *Goodrich 16346* (BRY, UT); Uinta Mtns, *Neely et al. 2497* (UTC); without locality, *Van Warmer 44* (UTC). Tooele Co.: Stansbury Mtns, *Taye 333* (UTC). Uintah Co.: along Vernal–Manila Rd, *Graham 10191* (MO). Utah Co.: summit of Strawberry Reservoir, *Beetle 13102* (UC); meadow of Soldier Summit, *Garrett 4557* (UT); Colton, 1 Apr 1908, *Jones s.n.* (UTC). Wasatch Co.: W end of Strawberry Valley, *Anderson 1010* (KSC, UTC); Strawberry Valley 35 km SW of Heber City, *Cronquist et al. 12038* (UTC); near summit, N Fork Duchesne drainage of the Uinta Mtns, *Harrison & Garrett 8863* (BRY, UC, UTC); 1.2 mi N of Strawberry Peak, *Huber 3246* (UTC); 5 mi E of Strawberry Valley, *Maguire 16751* (UC); 5 mi E of Strawberry Reservoir, 20 Aug 1939, *Maguire s.n.* (UTC); 2 mi NE of Strawberry Reservoir, *Shultz & Shultz 7290* (UTC), *Shultz & Shultz 7291* (UTC), *Shultz & Shultz 7292* (UTC); 0.5 mi S of Daniels Pass, *Stockton 173* (UTC); slopes ca. 3/4 mi S of Currant Creek Dam, *Tuhy 2306* (UTC). Wayne Co.: Boulder Mtn, *Shultz 9026* (UTC); Aquarius Plateau, Boulder Mtn, *Shultz & Shultz 8026* (UTC).—WYOMING: Albany Co.: 22 mi W of Rawlins, *Hall 10991* (UC); 5 mi E of Sybille Experiment Station, 18 Sep 1917, *Landon & Varcalli s.n.* (UTC); North Park Rd, *Osterhout 1369* (RM); junction of Buffalo River and Dubois, 2 Nov 1956, *Smith s.n.* (WS). Carbon Co.: Platte Valley, *Gooding 1931* (MO); French Creek Campground, 19 Sep 1973, *Nelson & Nelson s.n.* (RM); N Boat Creek Rd, *Ward 78* (RM). Converse Co.: Medicine Bow Mtns, *Beetle 10346* (RM). Crook Co.: ca. 17–18 km W of Sundance, *Cronquist 12173* (UTC). Fremont Co.: ca. 22.5 mi NE of Riverton, *Haines 4988* (UTC); Wind River Range, *Fisser 744* (RM), *Porter & Porter 8827* (RM, UC). Lincoln Co.: Smoot, *Beetle 12314* (MO); near Evanston, *Hall 10992* (UC); Star Valley, *Holte 22* (WS); Fossil Station, *Letterman 93* (MO, UC); E of Fossil Butte Natl Monument, *Neely & Carpenter 1361* (UTC); near Kemmerer, *Nelson 8103* (MO); Kemmerer, 27 Aug 1900, *Nelson s.n.* (UTC); S end of Star Valley, *Porter 3807* (RM); Salt River Range, *Shultz 750* (UTC, RM); Salt River Range, near the Salt River drainage, *Shultz 10837* (UTC); Allred Flat Campground, *Shultz 11552* (UTC); W slope of Grayback Ridge, *Shultz & Shultz 3565* (COLO, RM, UTC); Star Valley, *Ward & Ward 920* (WS). Park Co.: Grand Canyon of the Yellowstone at Canyon Junction, 30 Aug 1955, *Beetle s.n.* (UTC); Gros Ventre Mtns, 2 Nov 1956, *Smith s.n.* (MO). Sublette Co.: Wyoming Range, *Shultz 680 p.p.* (UTC); Snider Basin, 34 mi W of Big Piney, *Shultz & Shultz 2821* (UTC); 21 mi N of Cora, near Gypsum Springs, Pinedale District, *Shultz 19844* (UTC); Snider Basin, *Shultz & Shultz 2822* (RM, UTC); headwaters of Corral Creek, above Grey's River drainage, *Shultz et al. 4500* (UTC). Sweetwater Co.: without locality, *Ownbey 1113* (COLO, MO, UTC). Teton Co.: Little Granite Creek Watershed, *Beetle 11899* (MO); Granite Creek, *Beetle 11901* (MO, UTC); Moran, *Beetle 12180* (MO); Bridger-Teton Natl Forest, *Beetle 12218* (UTC); Yellowstone Lake, *Hall 11486* (UC); Yellowstone Natl Park, 17 Aug 1919, *Hawkins s.n.* (WIS); Yellowstone Natl Park, *Nelson & Nelson 6679* (MO); Yellowstone Lake, *Rydberg 5200* (WS); near Snow King ski lift in Jackson Hole, *Shultz 11555* (UTC); Blacktail Butte, *Shultz et al. 10520* (UTC). Weston Co.: 2 mi N of Upton, *Beetle 12152* (UTC); Bacon Creek, *Nelson 1042* (WS).

Artemisia cana subsp. *viscidula* is the common silver sagebrush of the Intermountain region. It differs from subsp. *bolanderi* and subsp. *cana* in its darker green foliage and sparsely (rather than densely) tomentose or glabrous stems, as well as by geography and growth habit. *Artemisia cana* subsp. *viscidula* stands out from sympatric populations of *A. tridentata* subsp. *vaseyana*, especially in the late summer when its semi-deciduous leaves begin to yellow and drop. Identification is problematic where ranges overlap in Oregon; some anomalous gray-leaved forms occur in the central Wasatch Mountains of Utah.

Artemisia cana subsp. *viscidula* is common in high elevation grasslands and shrub-steppe; silver-sagebrush communities support large herds of buffalo and elk in Yellowstone and Teton National Parks, and domestic livestock elsewhere. It resprouts after fire, but even after disturbance it rarely dominates the shrub community. It is usually found in association with a luxuriant growth of native herbs and grasses, often in wetlands or along streamsides and ditches in otherwise dry habitats.

3. Artemisia tripartita Rydberg, Mem. New York Bot. Gard. 1: 432. 1900. *Artemisia trifida* Nuttall, Trans. Amer. Philos. Soc., n.s., 7: 398. 1841, non *Artemisia trifida* Turczaninow, 1832. *Artemisia tridentata* subsp. *trifida* (Nuttall) H. M. Hall & Clements, Publ. Carnegie Inst. Wash. 326: 137. 1923. *Artemisia tridentata* var. *trifida* (Nuttall) McMinn, Man. Calif. Shrubs 608. 1939. *Seriphidium tripartitum* (Rydberg) W. A. Weber, Phytologia 55: 8. 1984.—TYPE: "Plains of the Rocky Mts.," [probably Idaho, 1834], *T. Nuttall s.n* (holotype: BM!; isotypes: GH! PH!).

Small or medium-sized, semi-deciduous shrubs, 0.5–25 (–40) dm tall, aromatic; crowns rounded; sprouting from underground adventitious buds or not. Stems pale gray, stout, glabrescent; bark gray. Leaves gray-green, pliable, deciduous or evergreen, finely divided; blades 1.5–4 cm long, 0.5–2 cm wide, broadly cuneate, deeply 3-lobed, lobes acute, 1–1.4 mm wide; ephemeral leaves early-deciduous, similarly lobed, up to 1.5 times as long as the persistent (fascicled) leaves. Capitula 2–4 mm high, 1.5–3 mm wide, globose or turbinate. Phyllaries broadly lanceolate, margins scarious, obscured by the densely canescent indument. Inflorescences narrowly paniculate or spiciform, (5–) 8–15 (–35) cm long, (0.5–) 1–5 cm wide; inflorescence leaves both entire and 3-lobed. Florets 3–11, 2–2.5 mm long, all perfect and tubular, sparsely glandular; style branches apically fringed, recurved. Cypselae 1.8–2.3 mm long, unequally ribbed, glabrous or resinous. Pappus absent. Chromosome number: 2n = 18, 36.

KEY TO THE SUBSPECIES OF ARTEMISIA TRIPARTITA

1. Medium-sized shrubs, 2–25 (–40) dm tall; leaf lobes linear and narrow (less than 0.5 mm wide); on stony or loamy soils of igneous origin and occurring west of the Continental Divide, widespread from the central to northern Rocky Mountains. 3a. *A. tripartita* subsp. *tripartita*
1. Small shrubs, 0.5–2 dm tall; leaf lobes lanceolate (1–1.5 mm wide); soils various, occurring in grasslands east of the Continental Divide, endemic to southwestern Wyoming. 3b. *A. tripartita* subsp. *rupicola*

3a. Artemisia tripartita subsp. **tripartita.**

Artemisia tripartita var. *hawkinsii* E. H. Kelso, Rhodora 39: 151. 1937.—TYPE: U.S.A. Wyoming: Teton Co., Yellowstone National Park, Old Faithful, 2–7 Jul 1922, *P. Hawkins 513* (holotype: US).

Small to medium-sized shrubs, 2–25 (–40) dm tall; sprouting from underground adventitious buds (in some populations) or not. Leaves evergreen or deciduous, 1.5–4 cm long, 0.5–1.5 cm wide, lobes linear, to 0.5 mm wide; persistent (fascicled) and ephemeral leaves similar in shape and size. Capitula 2–3 mm high, 2 mm wide, mostly sessile. Inflorescences leafy, spicate, 6–15 (–35) cm long, (1–) 4–5 cm wide. Florets 4–8. Cypselae 0.8–1.2 mm long. Chromosome number: 2n = 18, 36 (Ward 1953; McArthur et al. 1981; McArthur & Sanderson 1999). Figs. 9d, 17A–F.

Common name. Three-tipped sagebrush.

Phenology. Flowering mid-summer to late fall.

Distribution (Fig. 18). Canada (British Columbia) and U.S.A. (Idaho, Montana, Nevada, Oregon, Utah, Washington, Wyoming); in deep loam or stony soils, the soils usually volcanic or granitic; 1500–1900 m.

Additional Specimens Examined. **Canada.** British Columbia: 5 mi E of Osoyoos, *Beetle 13464* (MO); 20 mi N of Penticton, *Beetle 13988* (MO); N of Penticton, *Beetle 13997* (UTC); Dog Lake, 20 Apr 1906, *Henderson s.n.* (WS). **U.S.A.** Idaho: Bannock Co.: City Creek, *Cronquist 379-36* (UTC); Mink Creek Canyon, *Lingenfelter 754* (COLO, ID, RS); 2 mi N of McCannon turnoff from I-16, *Shultz 10263* (NY, RSA, UTC); benches W of Pocatello, *Shultz & McReynolds 19856* (UTC), *Shultz & McReynolds 19858* (UTC); Bannock Range, *Shultz & Shultz 8114* (UTC). Bear Lake Co.: Mill Creek Rd, *Anderson & Anderson 5* (UTC); E of Nounan Valley, *Cottam 15544* (UT); on S slope of the Gannett Hills, *Shultz 10840* (UTC). Bingham Co.: N end of Blackfoot Mtns, *Beetle 13304* (UTC); 2 mi E of Grace, *Cottam et al. 16286* (DS, UT); Fort Hall Indian Reservation, 30 Aug 1939, *Smith s.n.* (UTC). Blaine Co.: 26 mi E of Carey, *Hugie & Passey 148* (UTC). Bonneville Co.: W of Idaho Falls, *Beetle 14126* (UTC); Long Gulch, *Dieffenbach 505* (UTC) *Dieffenbach et al. TNF-505* (UTC); Palisades Creek drainage, *Shultz 7920* (UTC); Palisades Creek, *Shultz & Shultz 7919* (UTC). Butte Co.: 5 mi E of Arco, *Beetle 14127* (UTC); Lemhi Range, *Henderson 4231* (ID). Caribou Co.: Blackfoot Reservoir, *Albee 663* (UT); Chesterfield, *Cronquist 1817* (UTC); Blackfoot River, 16 Aug 1937, *Davis s.n.* (WTU); Hwy 34, *Shaw 3300* (UTC). Clark Co.: near Spencer, *Beetle 12270* (WS); N of Dubois, *Beetle 13940* (MO). Custer Co.: N end of Little Lost River Valley, *Andersen 115* (ID); N of Arco, 19 Aug 1982, *Epstein s.n.* (UT); N of Ketchum, 14 Jul 1983, *Epstein s.n.* (UT, UTC). Fremont Co.: ca. 3 mi N of Ashton, *Shultz & Shultz 7932* (UTC, WS); E of Marysville, *Ward & Ward 900* (DS, UC, WS); SE of Henry's Lake, *Ward & Ward 907* (WS). Jefferson Co.: 5 mi NW of Roberts, 7 Jul 1965, *Schloemer s.n.* (UTC); NE of East Butte, *Shultz et al. 10258* (UTC); Snake River Plain, *Shultz et al. 10260* (COLO, NY, UTC); between Idaho Falls and Dubois, summer 1934, *Hall s.n.* (UC, UTC); Hwy 91, between Idaho Falls and Dubois, summer 1934, *Hall s.n.* (UC, UTC). Lemhi Co.: near Leadore, *Ballard 6* (RSA, UTC); Gilmore divide, *Beetle 13933* (UTC, WS); vicinity of Gilmore Summit, *Beetle 13944* (MO); E of Tendoy, *Rosentreter 2688* (ID). Lincoln Co.: N of Shoshone, *Albee 18* (UT); on a mud flat of Tom Gooding Lake, *Beveridge 75-6* (UTC); Shoshone, *Nelson & MacBride 1183* (DS, MS); 12 mi NE of Richfield, *Ward & Ward 894* (DS, WS, WTU). Madison Co.: Mill Hollow, *Thomas 75* (UT). Owyhee Co.: Big Springs, *Falker 43* (ID). Power Co.: Bannock Range, *Shultz & Shultz 8113* (UTC). Teton Co.: between Felt and Lamont, *Beetle 11903* (UTC).—Montana: Beaverhead Co.: 14 mi W of Dillon, *Beetle 12241* (UTC); Montana/Idaho state line, *Beetle 12243* (UTC); 10 mi SE of Jackson, *Beetle 12264* (UTC, MO, UC, WS); Monida Pass, *Beetle 12268* (UTC); Centennial Valley, 1 Sep 1958, *Morris s.n.* (UTC); General over the hills around Monida, *Ward 1714* (UTC). Madison Co.: Madison River, *Beetle 12123* (COLO, MO, RM); near Flathead Lake, *Jones 8768* (POM); Alaska Basin, *Nelson 6809* (GH, MO). Missoula Co.: Bonner, 30 Aug 1892, *Sandberg s.n.* (POM).—Oregon: Baker Co.: 8 mi SE of Baker, *Beetle 12849* (MO, WS); 12 mi SE of Baker, *Ward 885* (UC); 12 mi SE of Baker, *Ward & Ward 886* (DS, WS, UC). Malheur Co.: Blue Mtn Pass, *Beetle 14154* (MO); road to Morton Springs, *Packard 167* (UTC).—Utah: Rich Co.: Deseret Land and Livestock Ranch, *Shultz et al. 20298* (UTC), *Shultz et al. 20302* (UTC).—Washington: Adams Co.: Ritzville, *Suksdorf 1613* (WS). Benton Co.: without locality, *O'Farr & O'Farr 275* (WS). Chelan Co.: S side of Mt Cooper, *Beetle 12866* (GH, MO, UC). Douglas Co.: between Bridgeport and Leahy, *Beetle 12819* (MO); between Chelan and Wenatchee, *Beetle 12833* (MO); Chelan, 5 Jul 1911, *Jones s.n.* (POM); near Egbert Spring, *Sandberg 366* (UTC); between Waterville and Douglas, on Hwy 2, *Shultz 20248* (UTC); N side of Lake Chelan, *Ward & Ward 851* (DS, WS); E edge of Chelan, *Ward & Ward 854* (WS). Ferry Co.: Curlew, *Spiegelberg 494* (WS). Kittikas Co.: Wenatchee Mtns, *Cotton 1793* (WS); without locality, 22 Jun 1955, *Moomaw s.n.* (WS). Lincoln Co.: near Sprague, 12 Jun 1918, *Moomaw s.n.* (WS). Okanogan Co.: W of Omak, *Fiker 501* (WS); Oroville, 5 Aug 1911, *Jones s.n.* (DS, POM, UC); Twisp, *Murie 205* (GH); E edge of Chelan, *Ward & Ward 855* (UTC). Stevens Co.: Kettle Falls, *Spiegelberg 492* (WS). Whitman Co.: near Cottonwood Creek, *Cotton 966* (WS). Yakima Co.: Yakima region, *Cotton 482* (GH, WS, WTU).—Wyoming: Hot Springs Co.: near summit of Owl Creek Mtns, *Beetle 11786* (COLO, RM); 11 mi S of Thermopolis, 25 Jul 1961, *Passey & Hugie s.n.* (UTC). Park Co.: Yellowstone Natl Park, 8 Mar 1905, *Moore s.n.* (MO). Teton Co.: near JTS Ranch,

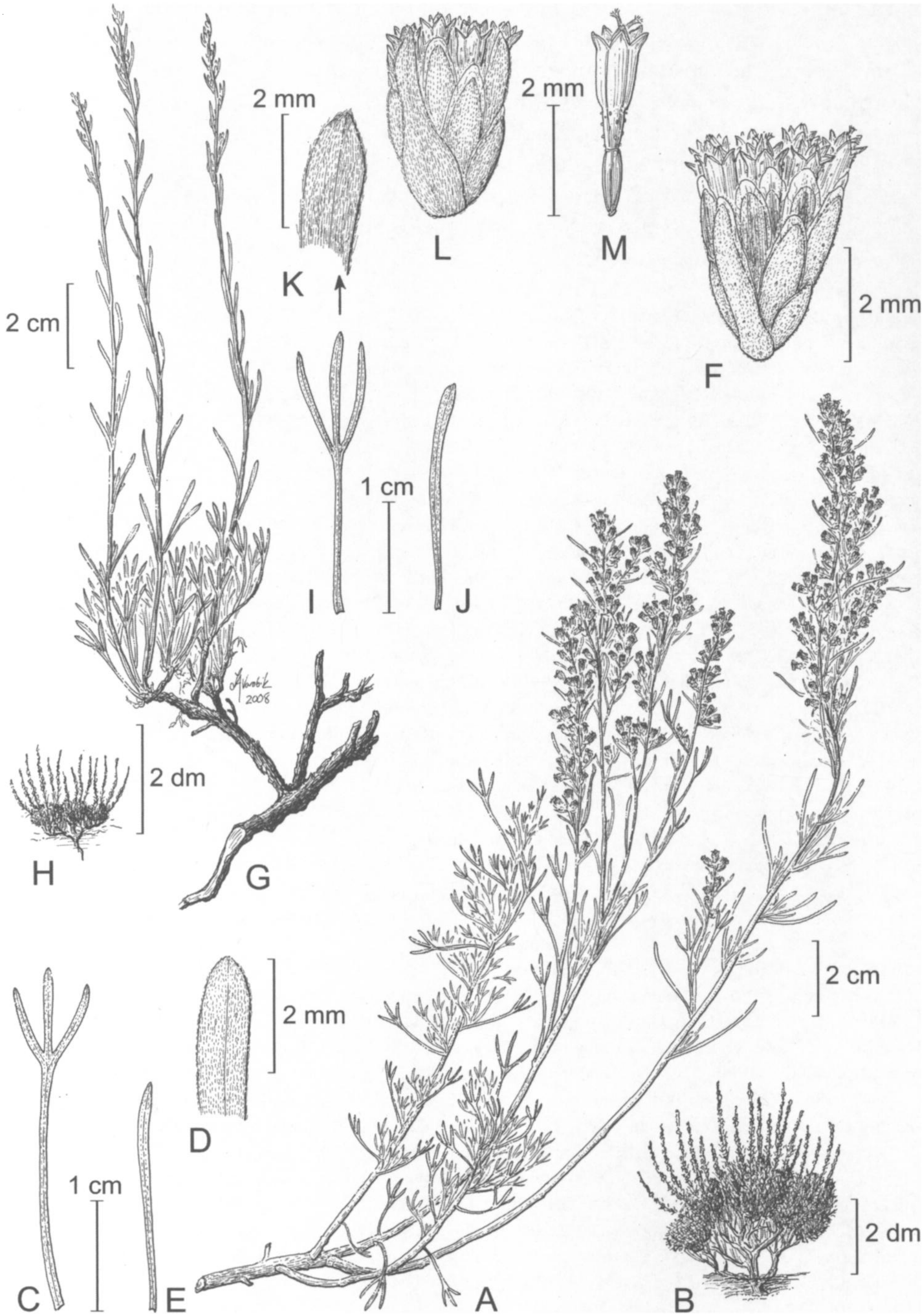

FIG. 17. *Artemisia tripartita*. A–F: *A. tripartita* subsp. *tripartita* A. Flowering branches. B. Habit. C. Leaf. D. Inflorescence leaf. E. Detail of leaf tip. F. Capitulum. G–M: *A. tripartita* subsp. *rupicola*. G. Branch with flowering shoots. H. Habit. I. Leaf. J. Inflorescence leaf. K. Detail of leaf tip. L. Capitulum. M. Floret and cypsela. (Based on: A–F, *Shultz 10263*; G–M, *Shultz 5439*.)

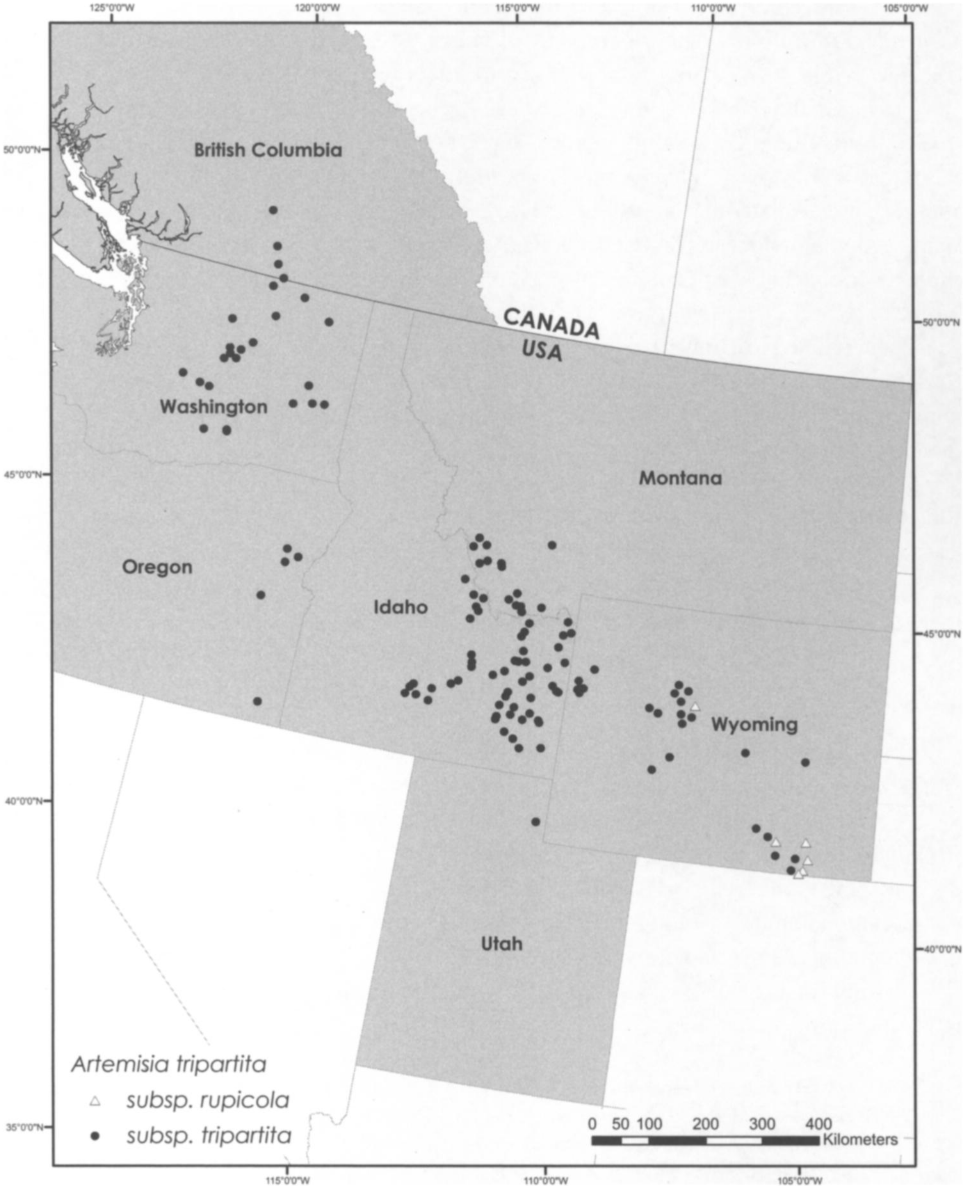

FIG. 18. Distribution of *Artemisia tripartita* subsp. *tripartita* and subsp. *rupicola*.

Bailey 72 (UC); Sheep Creek, *Beetle 11592* (UTC); Jackson Hole, *Beetle 11596* (MO, UTC, WS); 3 mi S of Jackson, *Beetle 11594* (UTC); 2 mi N of Jackson Hole, *Beetle 11605* (MO, UTC); Elk Refuge, *Beetle 11808* (UTC); Sheep Creek, *Beetle 17756* (UTC); Hoback Canyon, 6 Jul 1949, *Beetle s.n.* (UTC); between Felt and Lamont, 23 Aug 1956, *Beetle s.n.* (UTC); around Jackson Hole, *Hall 11471* (UC); N of Leigh Lake Cabin, 29 Jul 1975, *Shaw s.n.* (UTC); ca. 2 mi N of Jackson, *Shultz 10833* (UTC); near Snow King ski lift in Jackson Hole, *Shultz 11554* (UTC); near Moran Junction, *Shultz 11556* (UTC); between Wilson and Jackson Hole, *Shultz 20196.1* (UTC); 3 mi SW of Jackson Hole, *Ward & Ward 914* (DS, WS).

Artemisia tripartita subsp. *tripartita* occurs primarily in the Snake and Columbia river basins, and north into southern British Columbia. These areas are dominated by soils of volcanic origin with relatively high moisture (average annual precipitation of 375–800 mm). Because the habitat for the subspecies is generally defined by deep loamy soils suitable for agriculture (especially potatoes, sugar beets, and alfalfa hay fields), much of the habitat for three-tip sage has been lost to farming. Existing populations of subsp. *tripartita* often occur as isolated islands along drainages, rocky outcrops, and valleys, and on north-facing mountain slopes. The deeply-lobed leaves are distinctive, and similar to the morphology found in *A. arbuscula* subsp. *thermopola*; I suggest that hybridization of *A. tripartita* with *A. arbuscula* gave rise to this taxon.

The phenology of subsp. *tripartita* is unusual in that plants can be evergreen or deciduous, and may or may not sprout from an underground caudex. West et al. (1979) note that some populations mature and senesce within an exceptionally short time (as little as three years), an unusual condition within subg. *Tridentatae*.

3b. Artemisia tripartita subsp. **rupicola** Beetle, Rhodora 61: 82. 1959. *Artemisia tripartita* var. *rupicola* (Beetle) Dorn, Vasc. Pl. Wyoming 295. 1988. *Seriphidium tripartitum* var. *rupicola* ['*rupicolum*'] (Beetle) Y. R. Ling in Hind, Jeffrey & Pope, Advances in Compositae Systematics 286. 1995.—TYPE: U.S.A. Wyoming: Albany Co., Pole Mt., Medicine Bow National Forest, 7 Sep 1958, *A. Beetle 13185* (holotype: RM!).

Small shrubs, 0.5–2 dm tall; sprouting from underground adventitious buds. Leaves evergreen, broadly cuneate, 1.5–3.5 cm long, 1–2 cm wide, deeply lobed, lobes 1–1.5 mm wide. Capitula 2–4 mm high, 1.5–3 mm wide, sessile. Inflorescences densely leafy, spicate or paniculate, 2–20 cm long, 1.8–2 cm wide. Florets 3–11. Cypselae 1.2–2.3 mm long. Chromosome number: 2n = 18 (Garcia et al. 2007). Figs. 5a, 6a, 9e, 17G–M.

Common name. Wyoming three-tip sagebrush.

Phenology. Flowering early to late summer.

Distribution (Fig. 18). U.S.A.: central Wyoming; in shallow rocky soils, in grasslands; 2400–2900 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** WYOMING: Albany Co.: Roger's Canyon, *Asplund 26* (RM); Pole Mtn, *Beetle 12146* (UTC); Forest, Pole Mtn, *Beetle 13185* (UC, WS); Laramie Range, *Finzel 415* (RM); Laramie Hills, 5 Sep 1901, *Gooding s.n.* (RM); S of Laramie, 9 Sep 1919, *Hall s.n.* (DS); Tie Siding, *Heller 14321* (DS); Sherman, 12 Sep 1873, *Jones s.n.* (POM); 25 mi W of Cheyenne, *Maguire & Piranian 15591* (UTC); 5.5 mi N of Colorado-Wyoming state line, *Neely 2655* (UTC); Centennial Valley, *Nelson 5271* (POM); Cooper Hill, *Nelson 8941a* (UTC); S end of Laramie Plains, *Osterhout 1827* (RM); Laramie Plains, *Osterhout 7082* (POM, RM); near Tie Siding, *Osterhout 2272* (COLO, POM, RM, UTC); Pole Mtn region, *Porter 6849* (RM); near Tie Siding, *Shultz et al. 5434* (RSA, UTC); near Tie Siding, *Shultz et al. 5439* (UTC); 20 mi S of Laramie, near Hwy 231, *Shultz et al. 6150* (UTC). Carbon Co.: Northern part, *Beetle 12917* (RM); Elk Mtn, *Gartner 78* (RM); Sheephead Mtn, *Hammel & Hartman 607* (RM), *Hartman & Hammel 5004* (RM). Fremont Co.: near Atlantic City, *Beetle 10558* (WS); South Pass, *Beetle 13196* (WS); Wind River Range, *Fisser 65* (RM); SE of Thermopolis, *Fisser 154* (RM); SW of Thermopolis, *Fisser 291* (RM); Wind River, *Fisser 768* (RM). Hot Springs Co.: SE of Thermopolis, *Fisser 302a* (RM); SW of Thermopolis, *Fisser 307* (RM); SE of Thermopolis, *Fisser 737* (RM); Granite Canyon, *Nelson & Nelson 344* (RM); intersection N of Wyoming Hwy 461, 25 Jul 1961, *Passey & Hugie s.n.* (UTC); S of Thermopolis, 25 Jul 1961, *Passey & Hugie s.n.* (RM, UTC). Natrona Co.: Casper Mtn, *Jozwik 324* (RM).

Artemisia tripartita subsp. *rupicola* is restricted to the high, windy plains of south-central Wyoming. Because of its limited distribution and scant representation in herbarium collections, this distinctive taxon was overlooked until it was described by Beetle. Its ecology and dwarf habit sharply distinguish it from subsp. *tripartita*. Until the genetic relationship of these subspecies is resolved, the phylogenetic placement of subsp. *rupicola* remains problematic.

4. Artemisia rigida (Nuttall) A. Gray, Proc. Amer. Acad. Arts 19: 49. 1883. *Artemisia trifida* var. *rigida* Nuttall, Trans. Amer. Philos. Soc., n.s., 7: 398. 1841. *Seriphidium rigidum* (Nuttall) W. A. Weber, Phytologia 55: 8. 1984.—TYPE: U.S.A. [presumably Washington]: "plains of the Lewis [Snake] River" [presumably 1834], *T. Nuttall s.n.* (holotype: BM!; isotype: PH!).

Low-growing deciduous shrubs, 1.5–4 dm tall, mildly aromatic; crowns rounded; not sprouting from underground caudices. Stems gray, coarse, brittle, pubescent, widely branching; bark gray, exfoliating. Leaves silver-gray, deciduous, 1.5–4 cm long, 0.5–0.7 cm wide, deeply 3–5-lobed (rarely entire), rigid and brittle; blades linear (if entire) or broadly spatulate (if lobed), abruptly narrowed at the base, lobes divided more than 1/2 blade length, divisions narrow (ca. 1 mm wide), surfaces densely pubescent. Capitula borne singly or in glomerules, 4–5 mm high, 2.5–3.5 mm wide, narrowly campanulate. Phyllaries densely leafy, spicate or paniculate, elliptic (acute to obtuse), densely canescent. Inflorescences 2–20 cm long, 2 cm wide; inflorescence leaves deeply lobed and surrounding the capitula. Florets 4–8, all perfect and tubular; corollas 2–2.8 mm long, yellowish red to red; style branches oblong, truncate, exserted, apically fringed, recurved. Cypselae 1–1.5 mm long, 4–5 ribbed, glabrous. Pappus absent. Chromosome number: $2n = 18, 36$ (Ward 1953; McArthur & Sanderson 1999; McArthur et al. 1981). Figs. 7e, 9c, 19.

Common names. Scabland sagebrush, Columbia Plateau sagebrush, Stiff sagebrush, Rigid wormwood.

Phenology. Flowering mid-summer to early fall.

Distribution (Fig. 20). U.S.A.: Oregon, Idaho, Washington; in dry rocky scablands, primarily on volcanic plains of the Columbia Plateau; 500–1800 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** IDAHO: Ada Co.: 15 mi SE of Boise, *Beetle 12776* (RM). Adams Co.: 1 mi S of Council, *Christ & Ward 8782* (ID); along the hwy past the turnoff to Jefferson Creek, *Packard 275* (UTC). Idaho Co.: Whitebird Grade, 12 May 1972, *Tisdale s.n.* (ID). Nez Perce Co.: 3 mi N of Zaza, *Baker 14358* (ID); near Zaza, *St. John 9107* (WS). Payette Co.: without locality, *Henry 510* (SRP). Washington Co.: Seven Devil Mtns, *Jones 6414* (MO).—OREGON: Crook Co.: near Sicsequa Creek, *Coville & Applegate 728* (GH); Ochoco Mtns, *Cronquist 7754* (WS); Ochoco Forest, *Ingram 758* (OSC). Douglas Co.: near Alkaline Lake, *Leiberg 417* (MO). Gilliam Co.: Lost Valley, *Leiberg 888* (GH, MO). Harney Co.: Squaw Butte Experiment Station, 6 Sep 1956, *Barkley et al. s.n.* (OSC); NE of Burns, *Beetle 12868* (WTU); between Buchanan and Burns, *Beetle 13914* (UTC); Stinking Water Mtn, *Parsell 14* (OSC), *Parsell 19* (OSC); near Burns, *Parsell 40* (OSC); Drewsey, Jun 1937, *Parsell s.n.* (OSC); near Burns, *Peck 2826* (GH). Malheur Co.: lower slopes of Cottonwood Mtn, *Packard 76* (OSC, UTC); road to Morton Springs, *Packard 77163* (OSC); Wallowa Mtns, *Sheldon 8848* (MO); 5.5 mi N of Westfall, on Clover Creek Rd, *Shultz et al. 7471* (UTC); 12 mi W of Westfall, on Clover Creek Rd, *Shultz et al. 7472* (UTC). Umatilla Co.: Blue Mtns, *Beetle 12850* (GH, MO, RM, UC), *Cooke 12090* (OSC); S of Pilot Rock, *Standley 4640* (OSC). Union Co.: E flank of Show Mtn, *Beetle 12851* (UTC); without locality, *Cusick 533* (GH); 1 mi SE of Union, *Ward & Ward 882* (DS, RM, UC). Wasco Co.: near Deschutes River, *Peck 2670* (OSC); 6 mi E of Maupin, *Steward & Steward 7020* (GH, OSC, UTC); 20 mi S of Maupin, *Ward & Ward 833* (WS).—WASHINGTON: Adams Co.: 2 mi E of Paxton, *Eastwood & St. John 13274* (WS). Asotin Co.: S rim of.—WASHINGTON: Blue Mtns, *Cronquist & Preece 6813* (OSC, WS, WTU). Douglas Co.: near Alkali Lake, *Sandberg & Leiberg 417* (GH). Garfield Co.: 7 mi S of Pomeroy, 27 Oct 1937, *Allen s.n.* (UTC). Grant Co.: 2 mi

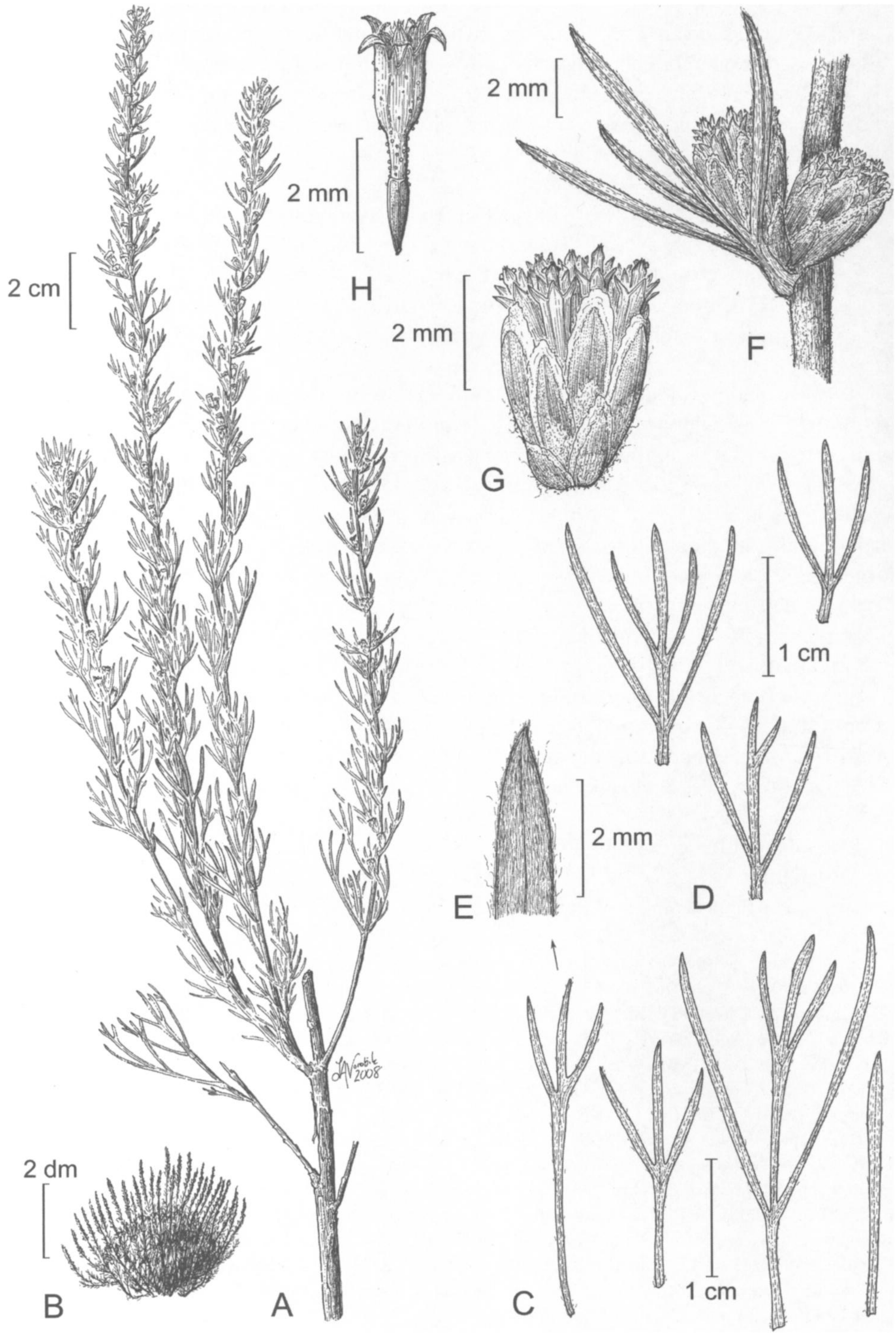

FIG. 19. *Artemisia rigida*. A. Branch with flowering shoots. B. Habit. C. Leaves. D. Inflorescence leaves. E. Detail of leaf tip. F. Portion of inflorescence branch. G. Capitulum. H. Floret and cypsela. (Based on: *Packard 77-275*.)

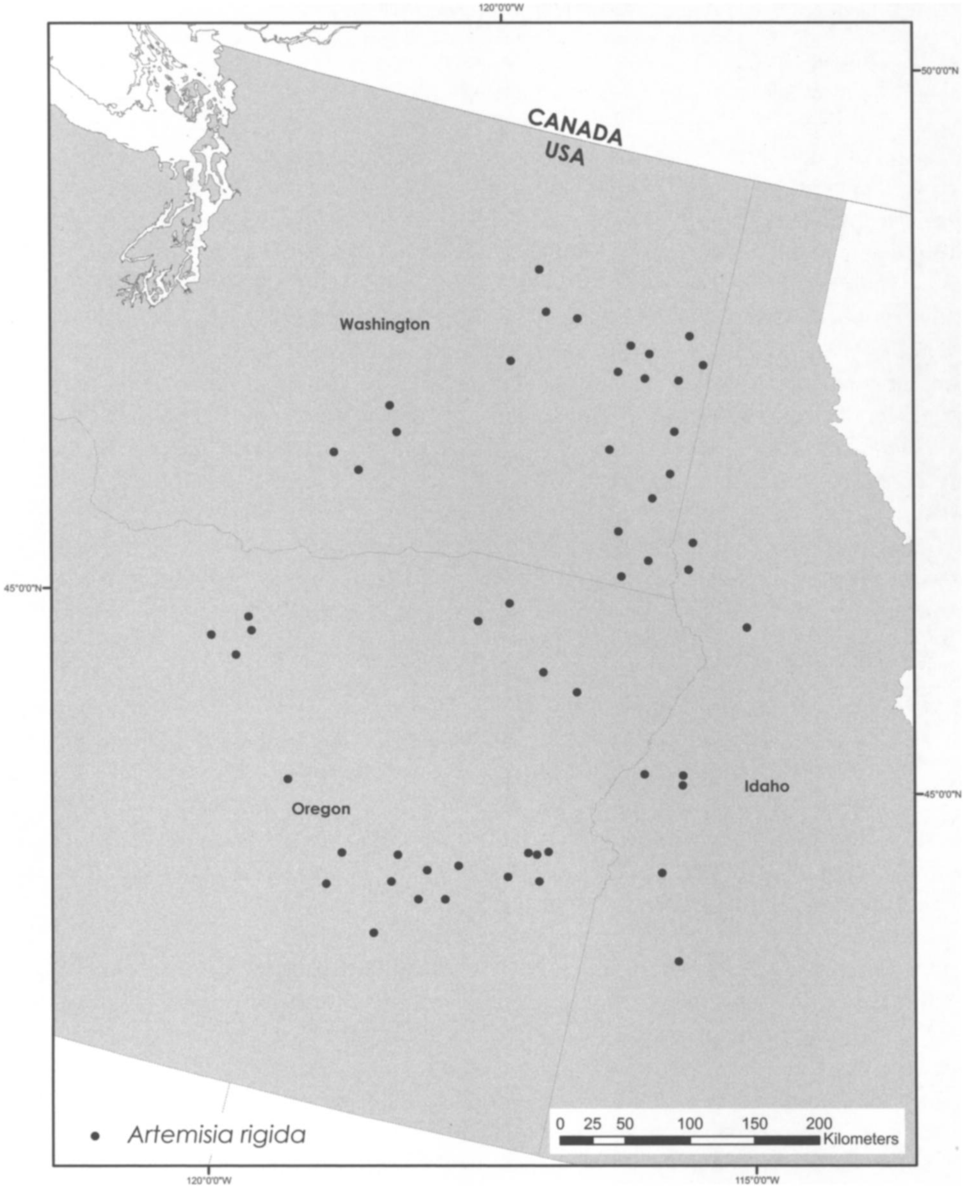

FIG. 20. Distribution of *Artemisia rigida*.

S of Marlin, *Bacon 206* (WS, WTU); near Trinidad, 24 Sep 1933, *Jones s.n.* (WTU); above Grand Coulee, *Mastrogiuseppe 1988* (WS); S bank of Columbia River, *Musselman 3716* (WIS). Kittitas Co.: Saddle Mtns, *Mastrogiuseppe 2188* (WS); W rim of Columbia Gorge, *Smith 2000* (WTU); 11 mi W of Vantage, *Ward & Ward 839* (WS). Lincoln Co.: 25 mi W of Spokane, *Beetle 12822* (UTC); near Wilbur, *Beetle 12844* (GH, MO); SW of Sprague, *Beetle 12846* (UTC); near Creston, 12 Aug 1980, *Tanner s.n.* (WS). Spokane Co.: 3 mi N of Spokane, *Beetle 13995* (MO); near Spangle, *Christ 1629* (ID); Columbia Plateau, 23 Sep 1917, *Hawkins s.n.* (WIS); without locality, *Lawrence 3782* (OSC); above Bonnie Lake, *St. John et al. 3196* (WS); W side Medical Lake, *St. John et al. 6768* (WS); sterile rocky places, *Suksdorf 933* (GH, MO, WTU); near Spangle, *Suksdorf 12981* (WS); Rock Creek, *Suksdorf 12982* (WS). Whitman Co.: 4 mi N of Rosalia, *Beetle 14106* (RM); Steptoe Canyon Rd, *Lyon*

271 (ID); bluffs above Wawawai, *Piper 3814* (GH, WS); above Wawawai, *St. John 6730* (WS); 6 mi S of Revere, *St. John et al. 7154* (WS); Wawawai Canyon, *Ward & Ward 859* (WTU). Yakima Co.: Yakima region, ca. 1885, *Brandegee s.n.* (GH); near Fort Simcoe, *Cotton 1564* (WS); above Priest Rapids Dam, *Mastrogiuseppe et al. 2156* (WS); 15 mi S of Toppenish, *Ward & Ward 837* (WS).

In both morphology and ecology, *A. rigida* differs markedly from other species in subg. *Tridentatae*. It is endemic to scabland soils of the Columbia Plateau, where it often forms a climax community; the soils on which it grows are typically shallow to moderately deep loams or montmorillonic clays over fractured basalt bedrock (Hironaka et al. 1983).

Artemisia rigida is similar to *A. cana*, *A. tripartita*, and *A. arbuscula* in having large flowering heads that are sessile on the flowering stem, but it is easily distinguished in the field by its brittle-textured leaves and occurrence on basalt scablands. Because it shares similar stomatal and pollen shapes (see discussion in the section on anatomy), it may well represent an ecological specialization, or an entity that is basal to the large-headed *A. cana*, *A. tripartita*, and *A. arbuscula*. If a large-headed clade with elongated pollen grains proves to represent a separate lineage within subg. *Tridentatae*, with so-called "primitive" traits, then *A. rigida* would represent a xeromorphic specialization within that group.

Palynological evidence suggests that the earliest development of a modern desert flora was in the area of basalt flows present in Oregon (Davis 1998). Because *A. rigida* and *A. tripartita* form widespread community types in this area, the populations may well be decendants of the ancestral type of woody sagebrush.

5. Artemisia arbuscula Nuttall, Trans. Amer. Philos. Soc., n.s., 7: 398. 1841. *Artemisia tridentata* subsp. *arbuscula* (Nuttall) H. M. Hall & Clements, Publ. Carnegie Inst. Wash. 326: 138. 1923. *Artemisia tridentata* var. *arbuscula* (Nuttall) McMinn, Man. Calif. shrubs 608. 1939. *Seriphidium arbusculum* (Nuttall) W. A. Weber, Phytologia 55: 7. 1984.—TYPE: U.S.A. [presumably Washington]: "arid plains of the Lewis [Snake] River" [presumably 1834], *T. Nuttall s.n.* (holotype: BM!; isotypes: GH! K! PH!).

Low-growing evergreen shrubs, 1–3 (–5) dm tall, aromatic; crowns rounded; capable of (though rarely) sprouting from underground caudices. Stems gray-green to brown, brittle, coarsely branched, glabrate, diffusely branched from the bases, appearing to arise from the soil surface and lacking a well-defined trunk; bark gray. Leaves gray-green, mostly evergreen (except inflorescence leaves), pliable, 3–10 mm long, 2–4 mm wide; blades broadly to narrowly cuneate; persistent (fascicled) leaves obtuse (or acute in subsp. *thermopola*), shallowly or deeply 3-lobed; ephemeral leaves gray-green, obtuse or acute, shallowly or deeply 3-lobed (or, rarely, with laterals bi- to trifid), lobes oblong-linear, mostly 1–3 mm wide, surfaces densely hairy. Capitula usually borne singly (rarely 2–4 in a cluster), (1.5–) 2–4 (–7) mm high, (1.5–) 3–5 (–6) mm wide, campanulate or globose-ovoid, erect, sessile (rarely short-pedunculate). Phyllaries ovate to oblong, pubescent or densely tomentose, margins green. Inflorescences leafy, narrowly spiciform, 2–10 cm long, 0.5–2 cm wide; branches slender; inflorescence leaves mostly early-deciduous and deeply 3-lobed. Florets 4–6 (–10), all perfect and tubular, 1.5–2 mm long, glabrous; style branches apically fringed, recurved. Cypselae 0.7–0.8 mm long, light brown, resinous. Pappus absent. Chromosome number: $2n = 18, 36$.

Artemisia arbuscula is one of the most perplexing species complexes in subg. *Tridentatae*, second only to *A. tridentata*. Its large capitula, early-deciduous leaves on the flowering stem, root-sprouting habit, striate epidermis, and elongated stomates suggest a relationship with the *A. cana* lineage (Shultz 1986b). Variation in anatomical and morphological characteristics among the subspecies suggests multiple hybrid origins, with different parental species (i.e., *A. tripartita* and *A. tridentata*) involved in the ancestry of the various subspecies.

The subspecies described as *A. arbuscula* subsp. ×*longicaulis* Winward & McArthur (with 2n = 54) is particularly problematic. The authors suggested that it is a polyploid complex involving hybridization between *A. arbuscula* subsp. *arbuscula* and *A. tridentata* subsp. *wyomingensis*. I am listing this taxon as a nothotaxon (see p. 109), but most herbarium collections will be identified as one of the parents.

Even though I suspect separate hybrid origins for each of the subspecies (see discussions after descriptions of subspecies), populations of *A. arbuscula* are reproductively robust, and communities of "low sagebrush" occupy distinct ecological niches. In fact, identification of subspecies by morphological characteristics alone can be unsatisfactory, but a characterization of ecological site conditions can be used to distinguish the three subspecies.

KEY TO THE SUBSPECIES OF ARTEMISIA ARBUSCULA

1. Leaves deeply lobed (ca. 1/2 leaf length), lobes ca. 1 mm wide, filiform and acute; blades narrowly cuneate; growing on soils of volcanic origin, usually glacial moraines; Idaho, Wyoming, and Utah. 5c. *A. arbuscula* subsp. *thermopola*
1. Leaves shallowly lobed (less than 1/3 leaf length), lobes more than 2 mm wide and obtuse; blades broadly cuneate; usually growing on rocky or calcareous clay soils of sedimentary origin; widespread.
    2. Leaves with a middle lobe not overlapping the lateral lobes; montane habitats, usually on rocky soils; flowering mid- to late summer. 5a. *A. arbuscula* subsp. *arbuscula*
    2. Leaves with a middle lobe that overlaps the lateral lobes, lobes of the ephemeral leaves divided (almost 1/3 leaf length); growing in valleys or mountains on fine-textured clay soils; flowering late spring to early summer. 5b. *A. arbuscula* subsp. *longiloba*

5a. Artemisia arbuscula subsp. arbuscula.

Leaves broadly cuneate, 3-lobed, lobes rounded, ca. 2 mm wide, divisions less than 1/3 blade length; persistent (fascicled) leaves 3–11 mm long, 2–4 mm wide; ephemeral leaves considerably elongated, 10–20 mm long, 2–4 mm wide. Capitula 2–4 (–5) mm high, 2–4.5 mm wide. Chromosome number: 2n = 18 (Ward 1953; McArthur et al. 1981; McArthur & Sanderson 1999); 2n = 36 (McArthur et al. 1981; McArthur & Sanderson 1999). Fig. 21.

Common names. Low sagebrush, Dwarf sagebrush, Little sagebrush.

Phenology. Flowering mid- to late summer.

Distribution (Fig. 22). U.S.A.: California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, Washington, Wyoming; in rocky soils of sedimentary origin, in high valleys, mountain slopes, basins, or windswept ridges; 1500–3800 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** CALIFORNIA: Alpine Co.: Highland Lake, *Gierisch & Esplin 3626* (RM); Silver Peak, *Hardham 21885* (CAS). Amador Co.: Silver Lake, Oct 1893, *Hansen s.n.* (DS); E of Silver Lake Dam, *McNeal 2790* (UTC). El Dorado Co.: 2 mi from Shingle, 23 Sep 1920, *Kennedy s.n.* (UC). Glenn Co.: Mendocino Pass, *Knight & Knight 2531* (CAS); Telephone Camp, *Ward & Ward 1076* (CAS, DS); Lassen Co.: Diamond Mtn, *Hardham 1837* (CAS); Hay Valley, *Robbins 2156* (GH, UC); Truckee, *Sonne 372* (COLO). Mendocino Co.: summit of Coast Ranges, *Hall 12931* (DS). Modoc Co.: Warner Mtns, *Howell 12098a* (CAS, US); E of Goose Lake, *Ward 957* (DS); Green Spring, *Wheeler 3962* (GH, US). Mono Co.: E base of Sonora Pass,

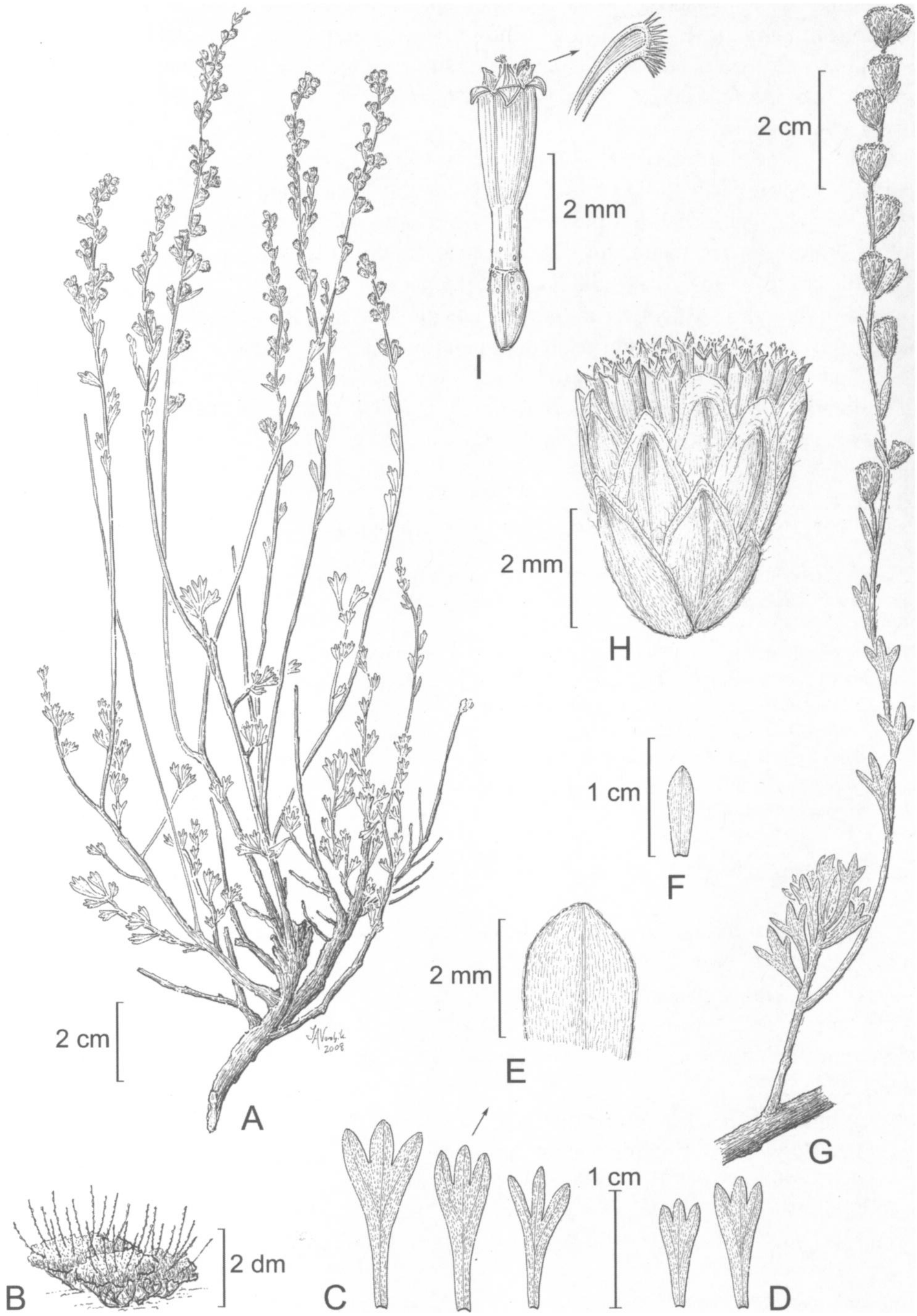

FIG. 21. *Artemisia arbuscula* subsp. *arbuscula*. A. Branches with flowering shoots. B. Habit. C. Ephemeral leaves. D. Persistent leaves. E. Detail of leaf tip. F. Inflorescence leaf. G. Flowering shoot. H. Capitulum. I. Floret and cypsela; detail of apex of one style branch. (Based on: A, B, C, E, *Pinzl 9231*; D, *Williams 80-209-16*; F, G, *Cronquist 7673*.)

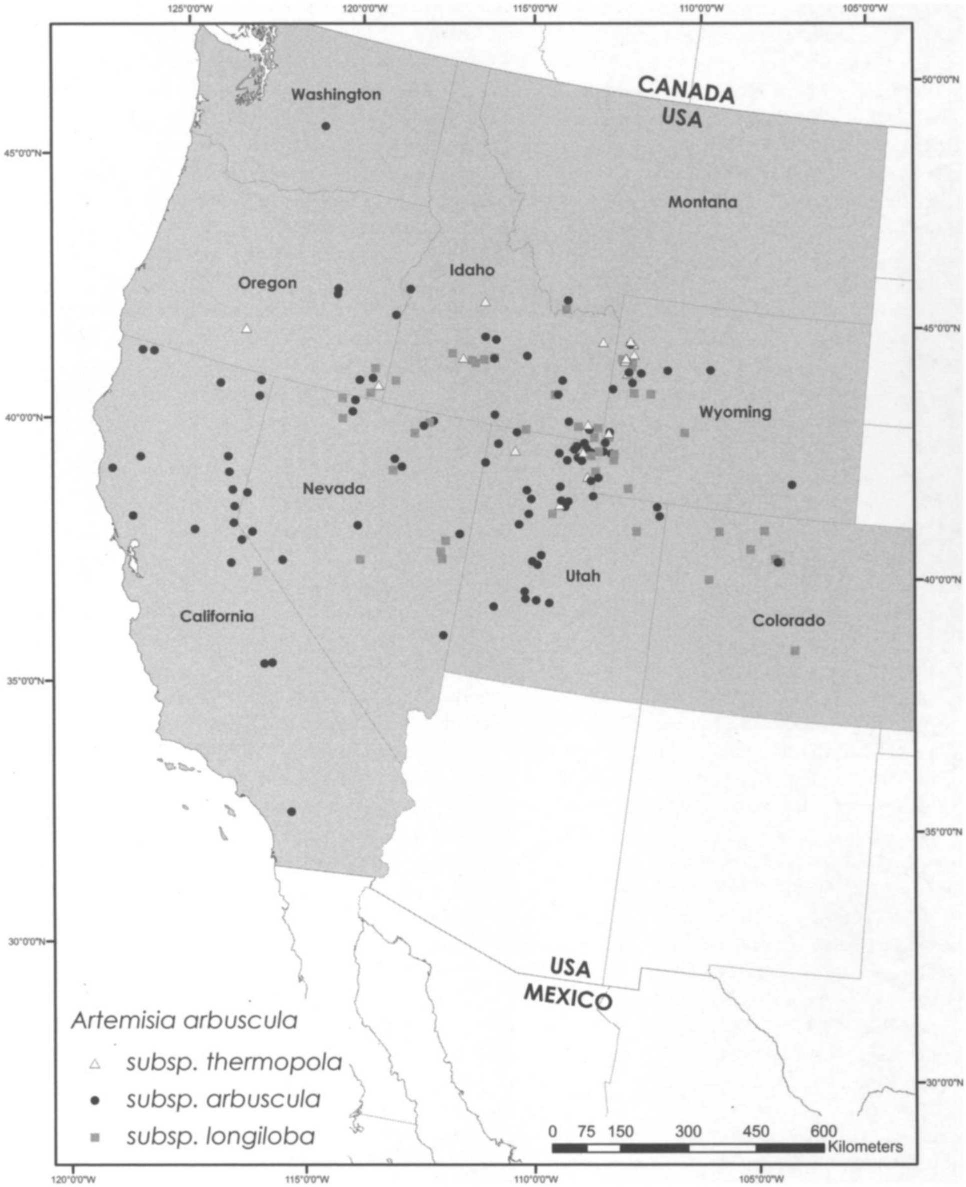

FIG. 22. Distribution of *Artemisia arbuscula* subsp. *arbuscula*, subsp. *longiloba*, and subsp. *thermopola*.

Beetle 12577 (RM); S side of Glass Mtns, *Beetle 12897* (RM); Bodie to Bridgeport Rd, 19 Aug 1898, *Condon s.n.* (DS); Upper Horse Meadow, *Reveal 1173* (GH, UTC). Napa Co.: hills W of Calistoga, *Shultz & Shultz 10231* (UTC). Nevada Co.: S of Donner Pass, *Heller 7184* (DS); W side of Donner Pass, *Howell 18413* (CAS); White Rock Lake, *Trowbridge 8033* (CAS); Castle Pass, *True & Howell 2817* (CAS). Placer Co.: Donner Pass, *Heller 12914* (COLO, DS); 8 mi N of Tahoe, *Ward & Ward 948* (UC). Plumas Co.: Davis Lake area, *Albertus 272* (RM); S of Bagley Pass, *Albertus 273* (UC); SE of Thompson Peak, *Hardman 21784* (CAS). Riverside Co.: Garner Valley, 15 Aug 1964, *Ziegler s.n.* (CAS, RSA). Sierra Co.: Sierra Valley, *Howell 37825* (CAS). Siskiyou Co.: Black Mtn, *Howell 15054* (CAS); Marble Mtns, *Muth 504* (CAS); Siskiyou Mtns, *Wheeler 3226* (DS). Tulare Co.: Olancha Peak, *Purpus 1868* (UC); Monache Meadow, *Twisselmann 18662* (CAS); Kern Plateau, *Twisselmann et* *al. 17294* (CAS). Tuolumne Co.: Granite Lake area, *Bolt 432* (RM).—COLORADO: Grand Co.: above the Colorado River at the junction with Willow Creek, *Shultz & Shultz 10488* (UTC). Routt Co.: Hayden Flats, *Osterhout 2260* (COLO).—IDAHO: Bannock Co.: 20 mi W of Pocatello, *Stoddart 21* (UTC). Bear Lake Co.: Preuss Range, *Shultz & Shultz 8186* (UTC). Blaine Co.: Sun Valley, *Beetle 13412* (RM); hillside above Ketchum, *Nelson & MacBride 1190* (COLO, RM); Trail Creek summit, *Shultz 7474* (UTC); S of Bellevue, *Shultz & McReynolds 19853* (UTC). Butte Co.: 40 mi SW of US Sheep Experiment Station, *Pechanec 883* (UTC); Craters of the Moon, *Ward & Ward 896* (DS, UC), *Ward & Ward 897* (DS, UC). Cassia Co.: 9.5 mi SW of Oakley, *Goodrich et al. 17892* (UTC). Clark Co.: 20 mi W of Mack's, *Beetle 12271* (RM). Washington Co.: Seven Devils Mtn, *Jones 6415* (DS); Weisir, 9 Jun 1929, *Phelps s.n.* (CAS),—MONTANA: Beaverhead Co.: Monida, *Beetle 12267* (RM).—NEVADA: Douglas Co.: near Topaz Lake, *Sanderson & McArthur 1594* (SSLP); near Double Spring, *Beetle 12889* (RM). Elko Co.: North Fork, *Holmgren 1977* (NY, UTC); Mahue Canyon, *Holmgren 2030* (NY, UC); Mountain City, *Lewis 3650* (UTC); 4.2 mi S of Point of Rocks, *Williams & Tiehm 80-209-16* (UTC). Esmeralda Co.: 1.5 mi E of Tonopah on US Hwy 6, *Barkworth 5033* (UTC). Eureka Co.: 8 mi W of Carlin, 22 Sep 1960, *Passey & Hugie s.n.* (NY, RM); Jarbidge Mtns, *Train 641* (UTC). Humboldt Co.: Santa Rosa Mtns, *Lewis 3504* (RM, UTC); Jarbidge Mtns, *Lewis 3748* (UTC); Santa Rosa Mtns, *Munz 16157* (DS); 0.5 mi E of Santa Rosa, *Robertson 353* (RM). Lander Co.: Toiyabe Range Ophir Wash, *Goodrich 10104* (UTC); summit Reserve, *Kennedy 4592* (UC); just E of Austin, *Ward & Ward 947* (DS, RM). Lincoln Co.: 5 mi E of Panaca, *Ward 1804* (DS, RM). Lyon Co.: Pine Nut Mtns, *Sanderson & McArthur 1595* (SSLP). Mineral Co.: SW slopes of Mt Grant, *Anderson & Ruffin 3405* (KSC, UTC). Nye Co.: Toiyabe Range, *Goodrich 12201* (UTC); Bunker Hill Range, *Tidestrom 10921* (BH). Pershing Co.: Mt Rose, *Heller 9883* (DS); 4 mi N of Toulon, *McArthur & McArthur 1683* (SSLP); mtns W of I-80 Toulon exit, *Sanderson & McArthur 1593* (BRY, RENO, UTC); NW of Reno, just E of Nevada County line, *Shultz & Garrison 20324* (UTC). Washoe Co.: Little Valley, *Mozingo & Williams 4* (CAS); Last Chance Ranch, *Tiehm & Rogers 4710* (UTC); Hell Creek, *Tiehm & Rogers 4732* (UTC); High Rock Canyon, *Tiehm & Schoolcraft 10205* (NY, UTC). White Pine Co.: Lehman Cave Campground, *Lewis 2041* (UTC).—OREGON: Clark Co.: Buck Creek, *Parsell 36* (SRP). Deschutes Co.: Bear Creek Buttes, *Steward 6958* (SRP); Harney Co.: 3 mi S of Silvies, *Cronquist 7673* (UTC). Lake Co.: Button Spring, *Leiberg 788* (GH, UC); N of Dairy Creek, *Steward & Steward 7476* (WTU). Malheur Co.: Blue Mtn Pass, *Beetle 14155* (RM); Owyhee, *Leiberg 2173* (DS); Leslie Gulch, *Shultz & Shultz 8505* (UTC). Morrow Co.: near Hay Creek, *Leiberg 858* (GH). Owyhee Co.: Succor Creek, *Shultz & Shultz 8506* (UTC).—UTAH: Beaver Co.: San Francisco Mtns, *Baird 323* (BRY). Box Elder Co.: Raft River Mtns, *Atwood 8243* (UTC); Grouse Creek Mtns, *Shultz & Shultz 8148* (UTC); Bald Eagle Mtn, *Shultz & Shultz 10206* (UTC). Cache Co.: Dry Lake, *Garrett 6475* (UTC), *Harrison & Garrett 10507* (BRY, UC); near summit, Logan Canyon, *Maguire 20133* (UTC); Logan Canyon N side of Hwy near summit, *Maguire 20135* (UTC); near summit, Logan Canyon, *Maguire 20137* (GH, UTC); Beaver Basin, *Maguire 20146* (UTC); Logan Canyon, *Piep 04.079* (UTC); Logan Canyon, *Shultz 4512* (UTC); near summit of Bear River Range, *Shultz 4788* (RSA, UTC); Logan Canyon, *Shultz & Kama 6504* (UTC), *Shultz et al. 19823* (UTC); Logan, *Smith 2006* (UTC); Upper Blacksmith Fork, *Tuhy 2284* (UTC); Mollens Hollow, ca. 22 mi SE of Logan, *Tuhy 2295* (UTC); near head of Logan Canyon, *Ward & Ward 927* (DS). Daggett Co.: Goslin Mtn, *Goodrich 22228* (UTC). Davis Co.: E of Bountiful, *Arnow 2920* (COLO, UT); E of Bountiful, 22 Sep 1909, *Clements s.n.* (RM, UC, UT); Lake Blanche, 26 Aug 1895, *Jones s.n.* (DS). Duchesne Co.: 5 mi E of Duchesne, *Forsling 622* (RM). Juab Co.: Canyon Mtns, *Goodrich 16466* (BRY); 9 mi N of Nebo Ranger Station, *Maguire 20090* (UTC). Millard Co.: Pavant Range, *Cronquist et al. 12043* (UTC); Canyon Mtns, *Goodrich 15130* (BRY, UT); head of Pole Canyon, *Goodrich 15254* (UTC); Pavant Mtns, *Goodrich 17920* (BRY), *Shultz et al. 10162* (UTC). Rich Co.: 3 mi W of Garden City, *Maguire 3874* (RM, UC); 2 mi W of Garden City, *Maguire & Stoddart 21662* (UTC); S of Hwy 89, *Shultz et al. 20293* (UTC); Deseret Land and Livestock Ranch, *Shultz et al. 20296* (UTC); 4 mi W of Garden City, *Ward & Ward 922* (DS, RM). Salt Lake Co.: Red Butte Canyon, *Arnow 2517* (COLO, UT); Emigration Canyon, *Beetle 11954* (RM, UTC); just S of Neff's Canyon, *Cronquist & Neese 12051* (BRY, NY, UTC); City Creek Canyon, *Garrett 2060* (RM, UTC); Oquirrh Mtns, 3 Aug 1966, *Simonson s.n.* (BRY); Emigration Canyon, *Smith 1864* (RM, UTC). Sevier Co.: 21 mi S of Fillmore, *Goodrich 17933* (BRY, UTC); head of Second Creek in the Pavant Mtns, *Shultz et al. 10165* (COLO, RS, UTC). Summit Co.: China Meadow, *Garrett 2941* (UTC); Echo Creek, *Goodrich 16482* (BRY). Tooele Co.: Snow Hollow, *Frisenknecht 195* (BRY); Hickman Pass in E Hickman Canyon, *Taye 1281* (BRY, UTC). Uintah Co.: 0.25 mi S of Crouse Reservoir, *Goodrich 22412* (UTC).—WASHINGTON: Chelan Co.: near border with Kittitas County, *Ward 843* (DS, GH).—WYOMING: Albany Co.: NE of Rock River, *Porter 6864* (UC). Lincoln Co.: Lincoln County border, *Beetle 12305* (RM); N of Evanston, *Kamb 660* (UC); 14 mi N of Cokeville, 23 Jul 1957, *Palmer & Palmer s.n.* (UTC); near entrance to Fossil Butte Natl Monument, *Shultz 19835* (UTC); 2 mi N of Thayne, *Ward & Ward 917* (DS). Sublette Co.: 2 mi S of Daniel, *Maguire et al. 12603* (UTC). Teton Co.: NE side of Lower Slide Lake, *Beetle 11804* (RM); Hoback Canyon, *Beetle 11904* (RM); S entrance to

Yellowstone Natl Park, *Beetle 12810* (UTC); E side of Snake River, *Ward & Ward 192* (DS), *Ward & Ward 912* (UC).

Diversification in the *Artemisia arbuscula* complex appears to be the result of hybridization involving different taxa in different parts of the geographic range of the species. Morphological characteristics suggest that this short-statured subspecies may be the result of past hybridization between *A. cana* (with large heads) and *A. tridentata* (with three-lobed leaves). Unfortunately, molecular analyses are not sufficiently well resolved to support this hypothesis. The large heads of subsp. *arbuscula* suggest a relationship with *A. cana*. I believe the morphological variation within this subspecies, from the eastern to western parts of its range, may be explained by ancestral hybridizations with different elements within the *A. cana* complex—elements that have been differentiated as separate subspecies. The element described as *A. arbuscula* subsp. ×*longicaulis* appears to be the result of introgression between *A. arbuscula* subsp. *longiloba* and *A. tridentata* subsp. *wyomingensis* in western Nevada.

5b. Artemisia arbuscula subsp. **longiloba** (Osterhout) L. M. Shultz, Sida 21: 1637. 2005. *Artemisia spiciformis* var. *longiloba* Osterhout, Muhlenbergia 4: 69. 1908. *Artemisia longiloba* (Osterhout) Beetle, Rhodora 61: 84. 1959. *Seriphidium arbusculum* subsp. *longilobum* (Osterhout) W. A. Weber, Phytologia 55: 7. 1984. *Artemisia arbuscula* var. *longiloba* (Osterhout) Dorn, Vascular Plants of Wyoming 295. 1988. *Seriphidium longilobum* (Osterhout) K. Bremer & Humphries, Bull. Nat. Hist. Mus. London, Bot. 23: 119. 1993.—TYPE: U.S.A. Colorado: Grand Co., Sulphur Springs, 8 Aug 1907, *Osterhout 3592* (holotype: RM!; isotype: GH!).

Leaves broadly cuneate, often irregularly lobed, lobes rounded, middle lobes overlapping the lateral lobes; persistent (fascicled) leaves 4–11 mm long, 2–5 mm wide; ephemeral leaves 10–17 mm long, 4–7 mm wide, divisions ca. 1/3 leaf length. Capitula 4–7 mm high, 2–3 mm wide. Chromosome number: 2n = 18, 36 (McArthur et al. 1981; McArthur & Sanderson 1999). Figs. 9k, 23A–G.

Common names. Alkali sagebrush, Long-lobed low sagebrush.

Phenology. Flowering early to late spring.

Distribution (Fig. 22). U.S.A.: California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, Wyoming; in clay soils of alkaline basins and valleys, occasionally on outwash plains of mountains; 1500–2800 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** CALIFORNIA: Mono Co.: 8 mi S of Bridgeport, W side of Hwy 395, *Shultz et al. 19779* (UTC).—COLORADO: Fremont Co.: Cañon City, *Shultz 5464* (RSA, UTC). Grand Co.: near Arapaho Forest, *Gierisch & Schwan 1671* (RM); Sulphur Springs, *Osterhout 3592* (COLO); 2 mi NW of Granby, *Shultz 10490* (UTC). Jackson Co.: North Park, *Shultz & Shultz 5429* (RSA, UTC). Moffat Co.: county road, *Parks 550* (CS). Routt Co.: 2 mi S of Oak Creek, *Beetle 11946* (COLO).—IDAHO: Bannock Co.: Bannock Range, *Shultz & Shultz 8109* (UTC). Bear Lake Co.: Sheep Creek Hills, *Ertter 76291* (UTC). Blaine Co.: 5 mi S of Bellevue, *Shultz & McReynolds 19642* (UTC). Camas Co.: Bennett Hills, 0.5 mi SE of Divide Reservoir, *Ertter 2398* (NY, UTC). Cassia Co.: Black Pine Mtns, *Shultz & Shultz 4159* (UTC). Elmore Co.: W of Hill City, *Romero 4* (MO). Gooding Co.: near City of Rocks, 15 Aug 1978, *Phillips s.n.* (UTC). Owyhee Co.: SE Jordan Valley, *Bates 272* (UTC).—MONTANA: Beaverhead Co.: Beaverhead Mtns, *Lesica 5863* (UTC), *Lesica 5866* (UTC).—NEVADA: Elko Co.: Tennessee Mtn, *Lewis 3676* (UTC); head of Taylor Canyon, 6 Jul 1961, *Passey & Hugie s.n.* (UTC); S of Point of Rocks, *Williams & Tiehm 80-209* (BRY). Eureka Co.: 8 mi W of Carlin, *Passey & Hugie s.n.* (UTC). Humboldt Co.: Humboldt Natl Forest, *Lewis 3720* (OGD, UTC); Windy Gap Rd, *Lewis*

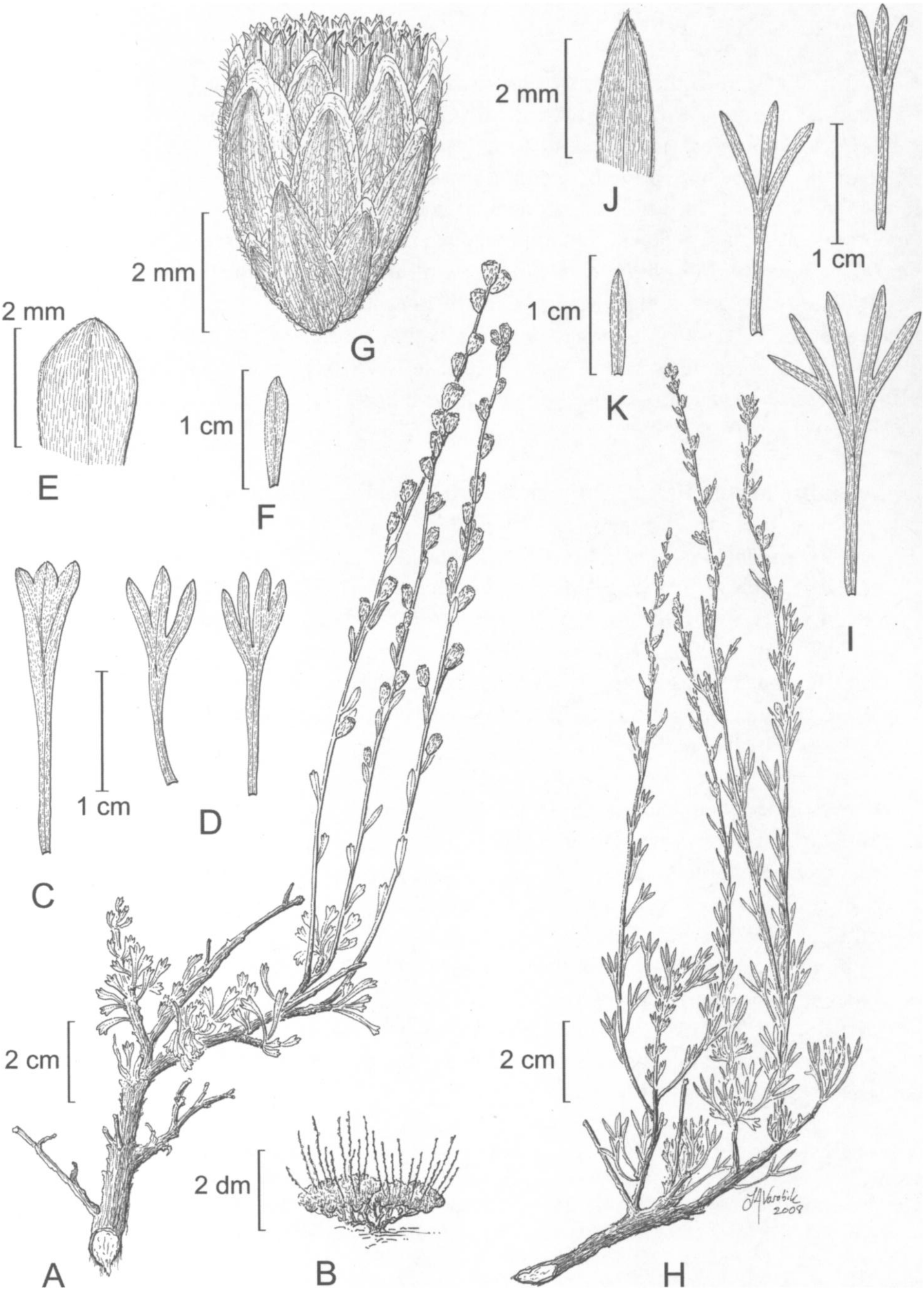

FIG. 23. *Artemisia arbuscula*. A–G: *A. arbuscula* subsp. *longiloba*. A. Branch with leafy and flowering shoots. B. Habit (also for subsp. *thermopola*). C. Leaf. D. Leaves. E. Detail of leaf tip. F. Unlobed inflorescence leaf (lobed leaves not shown: early-deciduous). G. Capitulum. H–K: *A. arbuscula* subsp. *thermopola.* H. Branch with leafy and flowering shoots. I. Leaves. J. Detail of leaf tip. K. Inflorescence leaf. (Based on: A–C, E–G, *Neese et al. 14554*; D, *Goodrich & Atwood 17213*; H–K, *Shultz 2826*.)

3721 (OGD, UTC); Humboldt Mtns, *Torrey 247* (GH, MO). White Pine Co.: Schell Creek Range, *Tart & Howell 2715* (UTC), *Tart & Howell 2716* (UTC); Kalamazoo Summit, *Tart & Howell 2723* (UTC).—OREGON: Malheur Co.: Blue Mtns, *Cusick 2055* (GH); near Anderson Crossing, *Mansfield 4040* (CIC); Hunter Ranch, *Packard 169* (CS, UTC); Succor Creek, *Shultz et al. 7455* (COLO, RSA, UTC).—UTAH: Rich Co.: 16 mi NW of Evanston, *Neese et al. 14554* (BRY, UTC); near Sage Junction, 24 Jul 1957, *Palmer & Palmer s.n.* (UTC); E of Laketown, *Shultz 20295* (UTC); N of Deseret Range, *Shultz & Peterson 20361* (UTC); Negro Dan Hollow, *Thorne et al. 3282* (BRY, UTC). Salt Lake Co.: Wood Hollow Canyon, *Shultz & Tart 19760* (UTC), *Shultz & Tart 19762* (UTC). Uintah Co.: 2 mi from La Point, *Goodrich 15265* (UTC).—WYOMING: Carbon Co.: W of Little Robber Dike, 1 Jun 1957, *Lang s.n.* (UTC). Fremont Co.: near South Pass City, *Beetle 13555* (UTC). Lincoln Co.: Green River Basin, *Carpenter 88* (UTC); between N Fork of Twin Creek and Hay Hollow, *Neely & Carpenter 1230* (UTC); 10 mi S of Cokeville, 14 Jul 1957, *Palmer & Palmer s.n.* (UTC); Tunp Range, *Shultz & Shultz 2606* (UTC, COLO). Sublette Co.: N of Pinedale, *Shultz 4460* (RSA, UTC); S of Hoback River Rd, *Young s.n.* (UTC). Sweetwater Co.: Leucite Hills, *Harrison 13105* (BRY). Teton Co.: Jackson Hole, *Beetle 11627* (UTC); Lower Slide Lake, *Beetle 12814* (UTC); Gros Ventre drainage, *Goodrich 24948* (UTC); Gros Ventre Canyon, *Shultz 11953* (UTC); Horsetail Creek drainage, *Shultz & Shultz 10096* (UTC). Uinta Co.: 8 mi N of Lonetree, *Goodrich & Atwood 17213* (BRY, UTC).

Artemisia arbuscula subsp. *longiloba* is reproductively isolated from the other late-blooming subspecies of the *A. arbuscula* complex by blooming in early spring. In fact, it is the only member of subg. *Tridentatae* that will flower as soon as the ground begins to thaw at the end of winter. This subspecies is ecologically distinguished from the other subspecies of *A. arbuscula* by its occurrence at low elevations on fine-grained clay soils. Beetle (1960) treated it as a species because of ecological differences, but in morphology and growth form, it is very difficult to distinguish from other subspecies of *A. arbuscula*.

5c. Artemisia arbuscula subsp. **thermopola** Beetle, Rhodora 61: 83. 1959. *Seriphidium arbusculum* var. *thermopolum* (Beetle) Y. R. Ling in Hind, Jeffrey & Pope, Advances in Compositae Systematics 288. 1995.—TYPE: U.S.A. Wyoming: Teton Co., along the banks of the Snake River, near the entrance to Yellowstone National Park, 10 Aug 1957, *Beetle 12631* (holotype: RM!; isotype: MO!).

Leaves narrowly cuneate, 5–10 mm long, 3–6 mm wide, deeply lobed, lobes at least 1/2 blade length, acute, divisions fine, less than 1 mm wide. Capitula (1.5–) 2–2.5 mm high, 1.5–2 mm wide. Chromosome number: 2n = 18 (Mahalovich & McArthur 2004). Fig. 23H–K.

Common names. Hot springs sagebrush, Three-tipped low sagebrush.

Phenology. Flowering mid- to late summer.

Distribution (Fig. 22). U.S.A.: Idaho, Oregon, Utah, Wyoming; in rocky soils of igneous origin; 2200–2800 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** IDAHO: Bear Lake Co.: off Mill Creek Rd, *Andersen & Andersen 5* (UTC). Custer Co.: 20 mi NW of Stanley, *Beetle 17140* (RM, UTC). Elmore Co.: near Camas Prairie, mile 130, Hwy 20, *Shultz 20393* (UTC). Fremont Co.: St. Anthony Dunes, *Rosentreter 16052* (SRP).—OREGON: Klamath Co.: Sycan Marsh, *Christy 2718* (SRP). Malheur Co.: Jack Creek, *Mansfield 581* (CIC).—UTAH: Box Elder Co.: W slope of Wellsville Mtns, *Shultz & Dennis 2458* (UTC); N slope of Raft River Mtns, *Shultz et al. 20365* (UTC). Cache Co.: Logan Canyon, *Shultz 8088* (UTC); mouth of Green Canyon, *Shultz 10141* (UTC); Franklin Basin, *Shultz 11559* (UTC); Hardware Canyon, *Shultz et al. 20261* (UTC), *Shultz et al. 20262* (UTC). Garfield Co.: near Antimony, *Owens s.n.* (UTC). Rich Co.: Deseret Land and Livestock Ranch, *Shultz et al. 20300* (UTC). Salt Lake Co.: Cottonwood, *Ward 1724* (RM). Tooele Co.: Stansbury Mtns, *Taye 658* (UTC).—WYOMING: Lincoln Co.: 14 mi N of Cokeville, up Smith's Fork, 23 Jul 1957, *Palmer & Palmer s.n.* (UTC). Teton Co.: Flagg Ranch, banks of Snake River, *Beetle 11618* (RM, UTC); on Pilgrim Creek N of Moran, *Beetle 12315* (UTC); banks of Snake River, *Beetle 12631* (RM); entrance to Paintbrush Canyon, *Beetle 11913* (UTC); Yellowstone Natl Park, Jul 1925, *Kraus s.n.* (WIS); Grand Teton Natl Park, *Shaw 4609* (UTC); Grand Teton Natl Park, 1956, *Shaw s.n.* (UTC); N of Leigh Lake cabin, 29 Jul 1975, *Shaw s.n.* (UTC); Baseline Flat, *Shultz 10099* (UTC); Taggart Lake turnoff, *Shultz 11951* (UTC); Yellowstone Natl Park, *Shultz & Shultz 7952* (UTC); cultivated, seed from Grand Teton Natl Park, *Shultz & Beetle 5457* (RSA, UTC).

Because of its deeply lobed leaves, *A. arbuscula* subsp. *thermopola* has been confused with *A. tripartita*. The deeply lobed leaves of the flowering stem, short stature, and geographic distribution of subsp. *thermopola* suggest *A. tripartita* and *A. arbuscula* as possible parents of this taxon. In the valley east of the Teton Mountains, this taxon forms a dominant community type on shallow, igneous-derived, morainal soils. I have observed seedlings in these populations every year since 1988, and I have seen no evidence of introgression with *A. arbuscula* subsp. *arbuscula* or *A. tripartita* subsp. *tripartita*. Whatever its origin, subsp. *thermopola* is apparently reproductively isolated from sympatric populations of its putative parents, and it occupies a distinct ecological niche.

6. Artemisia nova A. Nelson, Bull. Torrey Bot. Club 27: 274. 1900. *Artemisia tridentata* subsp. *nova* (A. Nelson) H. M. Hall & Clements, Publ. Carnegie Inst. Wash. 326: 137. 1923. *Artemisia tridentata* var. *nova* (A. Nelson) McMinn, Man. Calif. Shrubs 608. 1939. *Artemisia arbuscula* subsp. *nova* (A. Nelson) G. H. Ward, Contr. Dudley Herb. 4: 183. 1953. *Artemisia arbuscula* var. *nova* (A. Nelson) Cronquist, Vascular Plants of the Pacific Northwest 5: 58. 1955. *Seriphidium novum* (A. Nelson) W. A. Weber, Phytologia 55: 8. 1984.—TYPE: U.S.A. Wyoming: Medicine Bow Mts., Aug 1898, *A. Nelson 4095* (lectotype, designated by Hall & Clements, 1923: RM!).

Artemisia nova var. *duchesnicola* S. L. Welsh & Goodrich, Great Basin Naturalist 55: 361. 1995.—TYPE: U.S.A. Utah: Uintah Co., 16 km W of Vernal (T5S, R20E), *S. Goodrich 23215* (holotype: BRY!; isotypes: NY! UTC!).

Low-growing evergreen shrubs, 1–3 (–5) dm tall, aromatic; crowns flat-topped; not root-sprouting. Stems brown, glabrescent, widely and loosely branched, trunks well defined, short; vegetative stems of approximately equal height, giving plants a "hedged" appearance; bark dark gray, exfoliating with age. Leaves characteristically dark green (sometimes gray-green), evergreen, pliable; blades of vegetative branches cuneate, shallowly 3-lobed (rarely 4- or 5-lobed), lobes rounded, sinus less than 1/5 blade length, usually less than 1.5 mm deep, surfaces sparsely hairy, glandular hairs exposed, giving the leaves their characteristic gland-dotted and dark green appearance; persistent (fascicled) leaves 4–7 mm long, 2–4 mm wide; ephemeral leaves longer and more deeply lobed (up to 1/3 blade length), 9–15 mm long, 2–5 mm wide; leaves of the inflorescence branches entire and evergreen. Capitula 2–4 mm high, 1–2 mm wide, narrowly turbinate, erect on slender peduncles. Phyllaries ovate to elliptic, straw-colored or light green, margins hyaline, shiny-resinous, sparsely hairy or glabrous, of two types, the outermost miniscule and hairy, the inner elliptic, usually resinous and glabrous. Inflorescences slender, paniculate, 4–10 cm long, 0.5–3 cm wide; branches more or less erect. Florets 2–6, all perfect and tubular; corollas 1.8–2 (–3) mm long, glabrous or dotted with small glands, style branches apically fringed, recurved, usually included but sometimes exserted. Cypselae 0.8–1.5 mm long, ribbed, glabrous or resinous. Pappus absent. Chromosome number: $2n = 18, 36$ (Ward 1953; McArthur et al. 1981; McArthur & Sanderson 1999); $2n = 54$ (Mahalovich & McArthur 2004, for var. *duchesnicola*). Figs. 7f, 9h, 24.

Common names. Black sagebrush, Black sage.

Phenology. Flowering mid-summer to late fall.

Distribution (Fig. 25). U.S.A.: Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Wyoming; in shallow soils, in desert valleys, and on exposed mountain slopes; 1500–2300 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** ARIZONA: Coconino Co.: S rim of Grand Canyon, *Beetle 12834* (RM); N rim of Grand Canyon, *Eastwood & Howell 7042* (CAS); House Rock Valley, 23 Aug 1956, *Ferguson s.n.* (ARIZ, UTC); Oak Creek Canyon, *Gooding 433* (UT); Cape Royal, 9 Aug 1950, *Ward s.n.* (UTC), *Ward 1803* (UTC). Mohave Co.: Grand View, *Hall 11188* (UC); near Poverty Mtn, *Shultz 19602* (UTC); San Francisco Mtns, 10 Sep 1894, *Toumey s.n.* (UC); Grand Canyon, *Weber 14000* (COLO).—CALIFORNIA: Inyo Co.: 8 mi E of Laws, *Applegate 6939* (DS); summit of Westguard Pass, *Beetle 12896* (RM); Death Valley Natl Monument, 23 Jun 1958, *Ferguson s.n.* (ARIZ, RM); Panamint Mtns, *Hoffmann 290* (DS); Cerro Gordo Rd, 12 Oct 1937, *Kerr s.n.* (CAS); White Mtn Rd, *Mooney 668* (DS); Wild Rose Canyon, *Roos 2810* (DS); White Mtns, 6 mi ENE of Big Pine, *Shultz & Shultz 5024* (UTC); White Mtns, *Shultz et al. 19801* (UTC). Lassen Co.: 8 mi SE of Ravendale, *Balls 20971* (RSA, UTC); Susanville, *Hoover 4634* (UC); 25 mi N of Susanville on Hwy 395, *Lyman 4241* (UTC), *Lyman 4242* (UTC); 41 mi N of Susanville on Hwy 395, *Shultz & Shultz 8602* (UTC); between Litchfield and Alturas, *Tiehm & Schoolcraft 14368* (UTC). Mono Co.: W side of Crowley Lake, *Beetle 12940* (UTC); 2.8 mi E of Country Farm, *Hendrix 638* (UC); Campground Creek, *Reveal 219* (UTC); about 5 mi N of Danberg Beach, *Reveal 220* (UTC); N of Convict Canyon, *Shultz et al. 19794* (UTC). San Bernardino Co.: Upper Holcomb Valley area, 10 Sep 1957, *Ferguson s.n.* (UTC); New York Mtns, *Hendrickson 10892* (DS); canyon below Keystone Spring, *Munz 13870* (UTC); summit of Johnson's Grade, *Peirson 5157* (DS, UC); Bear Valley, *Roos 2768* (DS); New York Mtns, *Thorne et al. 47998* (UTC); Mohave Desert, *Wolf 7585* (DS).—COLORADO: Gunnison Co.: Sapinero, *Hall 507* (UT); Gunnison Airport, 21 Aug 1961, *Iltis s.n.* (WIS); outskirts of Gunnison, *Weber 9327* (DS). La Plata Co.: without locality, 1 Sep 1934, *Loughridge s.n.* (CS). Mesa Co.: between Mesa and Skyway, *Beetle 13559* (UTC); Colorado Natl Monument, *Porter & Porter 10585* (RM); Liberty Cap Trail, on W side of Monument Mesa, *Siplivinsky 5053* (UTC). Moffat Co.: near John Weller ranch, *Deming et al. 20-1* (UTC); Mesa, *Deming et al. 23-8* (UTC); Douglas Mtn, *Harris 8732* (CS); Irish Lakes, *Weber 14240* (COLO); between Greystone and Gates of Lodon, 26 Jun 1965, *Weber s.n.* (COLO). Montezuma Co.: Mesa Verde Natl Park, *Beetle 12813* (RM); W rim of Mesa Verde, *Neely 4481* (UTC). Montrose Co.: Cedar Creek, *Neely 2900* (UTC); ca. 0.5 mi WNW of junction of Dry Cedar Creek and South Canal, *Neely 2951* (UTC); ca. 2.4 mi due E of Uncompahgre Memorial Gardens, along Hwy 50, *Neely 2955* (CS, UTC); Atkinson Creek Canyon, *Ratzloff 1653* (COLO); 9 mi NE of Nucla, *Weber 3579* (DS, UTC). Park Co.: South Park, *Walter 921* (CS). Rio Blanco Co.: Spring Creek, *Waters 82-56* (CS). San Miguel Co.: 13.5 mi N of Dove Creek, *Harrington 8480* (CS).—IDAHO: Bannock Co.: Pocatello, *Beetle 11989* (RM), *Jack 1637* (GH); benches W of Pocatello, *Shultz & McReynolds 19857* (UTC); Bannock Range, *Shultz & Shultz 8102* (BRY, UTC), *Shultz & Shultz 8107* (UTC). Bear Lake Co.: Fish Haven, *Davis 1601* (UTC). Butte Co.: Lost River Range, *Beetle 13168* (RM); along road to Arco, *Pechanec 882* (UTC); road to Arco, *Pechanec 882-37* (UTC). Cassia Co.: Albion Mtns, *John 1037* (UTC). Custer Co.: Bear Canyon, *Nelson & MacBride 1428* (RM). Jefferson Co.: Middle Butte, *Shultz 10261* (UTC). Twin Falls Co.: 5 mi N of Nevada state line, *Beetle 14116* (RM).—MONTANA: Jefferson Co.: at Lewis and Clark Cavern, *Beetle 12255* (RM). Livingston Co.: along Yellowstone River, 1 Jul 1947, *Wright s.n.* (GH, MONT, RM).—NEVADA: Clark Co.: Mt Irish, *Purpus 6333* (UC); Deadman Canyon, *Train 1774* (UC). Douglas Co.: 1.5 mi N of Como Peak, *Graham 576* (UC); Markleville, *Lee 93* (UC); Pine Nut Mtns, *Tiehm 14364* (UTC), *Tiehm 14365* (UTC), *Tiehm & Nachlinger 14369* (UTC), *Tiehm & Nachlinger 14370* (UTC), *Tiehm & Nachlinger 14372* (UTC). Elko Co.: 3.5 mi W of Wendover, *Beetle 13152* (UTC); ca. 30 km S of Wendover, *Cronquist 12049* (NY, UTC); Jarbidge Mtns, *Curto & Allen 1583* (UTC); 30 mi NW of Wendover, on road to Wells, *Shultz & Garrison 20316.2* (UTC); W side of Pequop Mtns, *Shultz & Garrison 20329* (UTC); 17 mi S of Wendover, *Shultz & Shultz 4550* (RSA, UTC), *Shultz & Shultz 4551* (UTC); Pilot Mtns, *Shultz & Shultz 8150* (UTC); Pilot Mtns, below Copper Mtns, *Shultz & Shultz 10191* (UTC); base of Copper Mtn, *Shultz & Shultz 10192* (UTC); SW side of White Horse Pass, *Ward & Ward 9381* (DS); Winecup Rd, *Williams & Tiehm 84-113* (UTC); N on Hwy 93, *Williams & Tiehm 84-113-2* (UTC). Esmeralda Co.: Trail Canyon, 23 Jun 1958, *Ferguson s.n.* (ARIZ, GH, RM); Goldfield Hills, *Pinzl 9875* (UTC); Soda Springs, *Shockley 678* (UC); Lida Summit, *Shultz & Shultz 5033* (UTC). Eureka Co.: Monitor Range, *Goodrich 13102* (UTC); E slope of Emigrant Pass, Jul 1961, *Hugie & Passey s.n.* (UTC); 8 mi W of Carlin, *Passey & Hugie 21* (NY, RM, RSA, UTC); E of Battle Mountain, between Dunphy and Elko, near I-80 milepost 272, *Shultz & Garrison 20326* (UTC); 6 mi W of Eureka, *Ward & Ward 944* (DS, UT, UTC). Humboldt Co.: near trough, Windy Gap Rd, Santa Rosa Mtn, *Lewis 3715* (UTC); between Big Springs Table and Railroad Point, *Nachlinger & Combs 2155* (UTC). Lander Co.: Toiyabe Range, *Goodrich 9961* (UTC), *Goodrich 9962* (BRY,

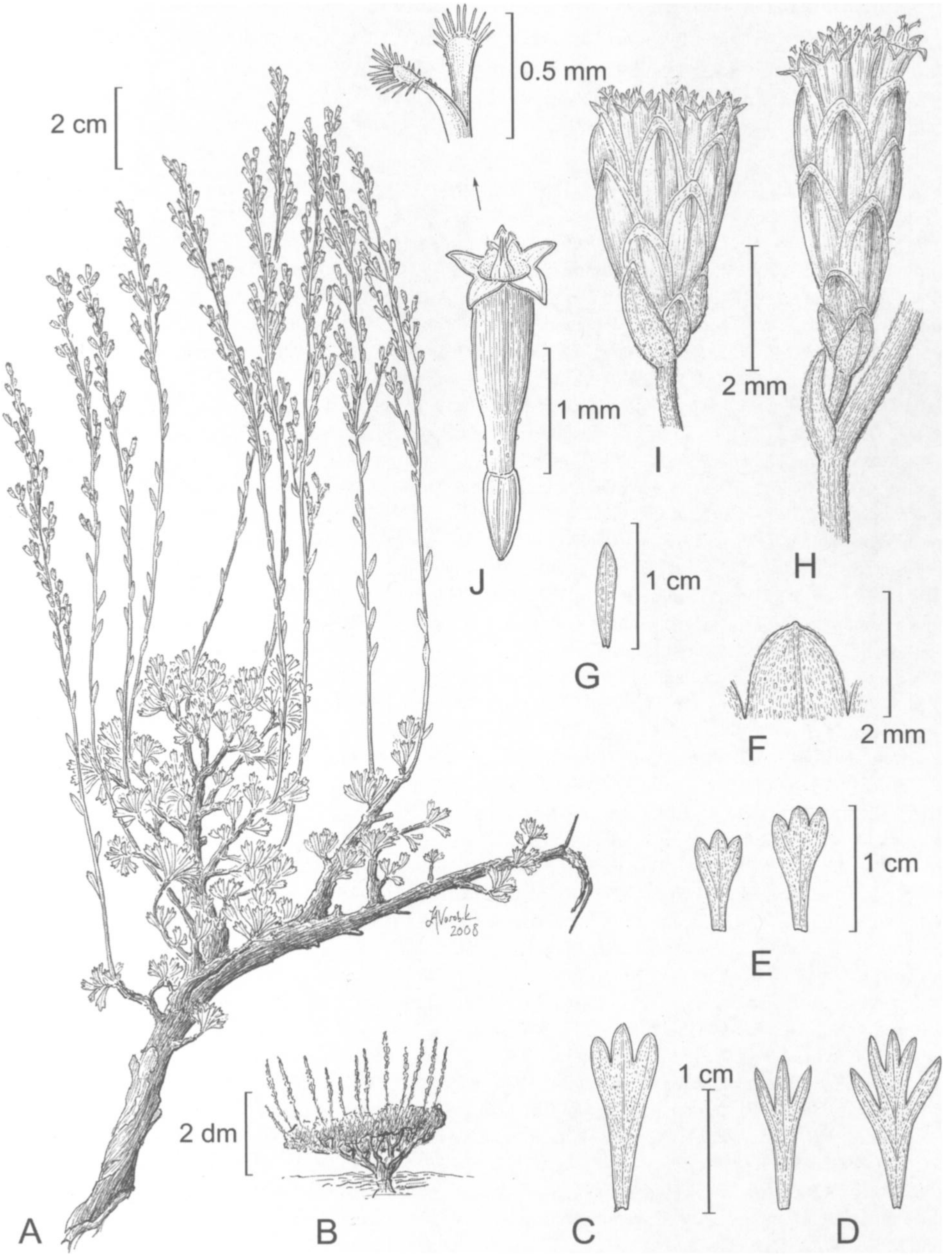

FIG. 24. *Artemisia nova*. A. Branch with leafy and flowering shoots. B. Habit. C. Ephemeral leaf. D. Ephemeral leaves. E. Persistent leaves. F. Detail of leaf tip. G. Inflorescence leaf. H. Capitulum. I. Capitulum. J. Floret and cypsela; detail showing style branches. (Based on: A, E–H, *Fertig 20904*; C, I, J, *Shultz & Shultz 3820*; D, *Tiehm 14372*.)

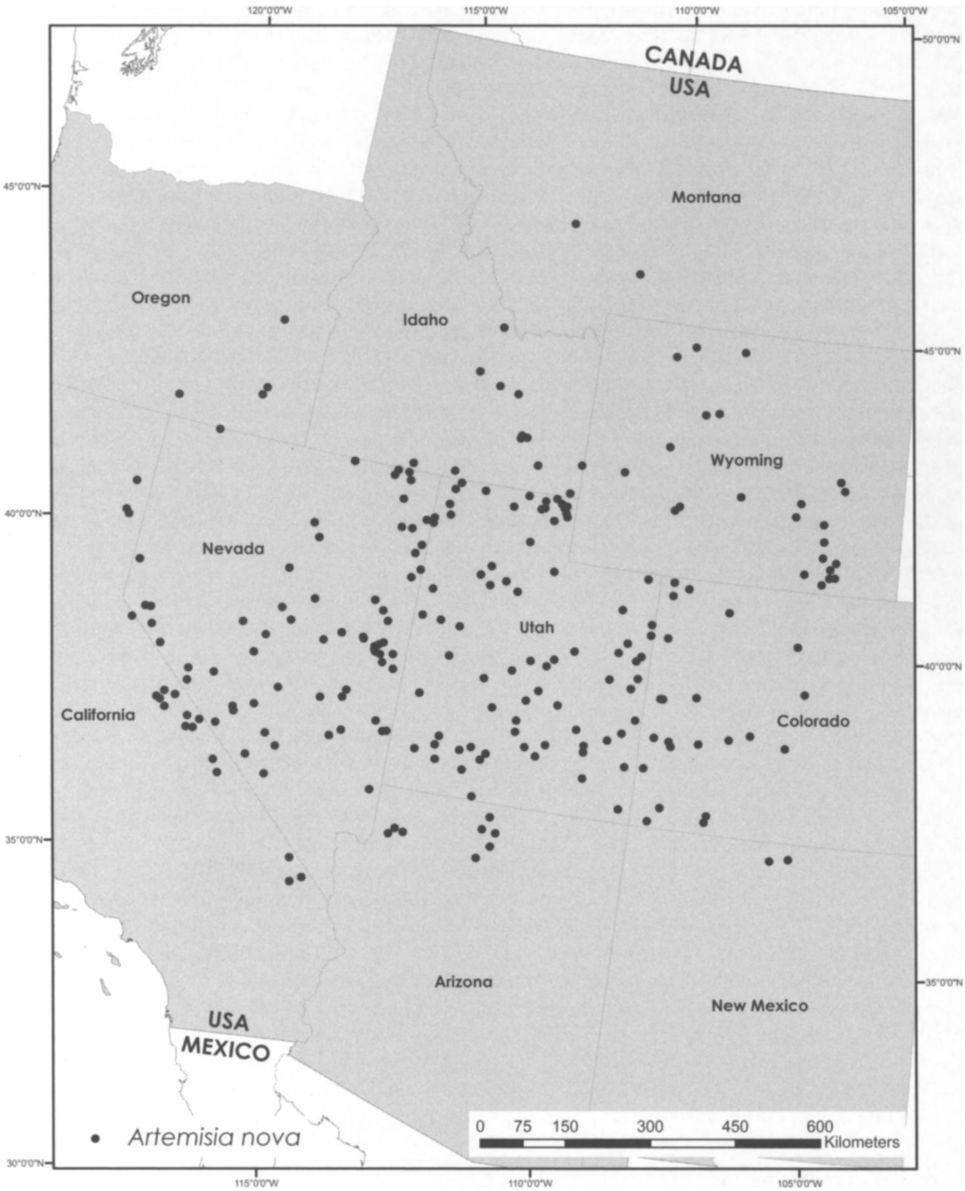

FIG. 25. Distribution of *Artemisia nova*.

UTC); Hickison summit, *Shultz & Shultz 8642* (UTC). Lincoln Co.: N slope of ridge, 0.2 mi NE of hill, *Ackerman 30959* (UTC); Deer Lodge, *Hall 8407* (BRY, UTC); Mahogany Mtns, near Big Summit, *Shultz & Shultz 6244* (UTC); W slope of E Mormon Mtns, *Shultz & Shultz 7595* (UTC); 3 mi NW of Panaca, *Train 2481* (UC). Lyon Co.: 9.5 mi SE of Rockland, *Hendrix 657* (UC); 5 mi SE of Wellington, *Holmgren 153* (UTC); Sweetwater Rd, *Williams & Tiehm 84-131* (UTC); 3.2 mi W of Nevada Hwy 22, *Williams et al. 84-131-3* (UTC). Mineral Co.: White Mtns, *Archer 7173* (DS, UTC); 2 mi W of Esmeralda County line on Hwy 6, *Shultz & Shultz 4595* (UTC, RSA). Nye Co.: NW Yucca Basin, *Beatley 3911* (DS); N Cactus Range, *Beatley 9603* (UTC); E of Forty-Mile drainage, 15 Oct 1968, *Beatley s.n.* (UTC); E slopes of Monitor Range, *Goodrich 10756* (UTC); between Hot Creek and Kawich Ranges, *Pinzl 9756* (UTC); Central Pahute Mesa, *Reveal 1991* (UTC); Pahute Mesa, *Reveal*

2026 (UTC); 1.5 air mi NW of Tippipah, *Reveal 2093* (DS, UTC); Thirsty Canyon, *Reveal 6986* (DS, UT); canyon in Central Belted Range, *Rasp 5390* (DS); white knolls near McGill Reservoir, *Shultz & Shultz 4575* (RM, RSA, UTC); slopes S of Cherry Creek Summit, *Williams & Tiehm 81-141-2* (UTC); Quinn Canyon Range, *Williams & Tiehm 84-141-2* (UTC); 30 mi S of Eureka, 30 Sep 1967, *Zamora s.n.* (UTC). Washoe Co.: Peavine Mtn, *Howell & Williams 49044* (CAS); Range Spring, *Train 2899* (UTC). White Pine Co.: Lehman Caves Natl Monument, *Beetle 13040* (RM); Egan Range, *Shultz & Nachlinger 12769* (UTC); 7 mi WSW of Ely, *Shultz & Shultz 4557* (UTC, RSA); Schell Creek Range, *Tart & Howell 2702* (UTC), *Tart & Howell 2704* (UTC), *Tart & Howell 2706* (UTC), *Tart & Howell 2710* (UTC), *Tart & Howell 2717* (UTC), *Tart & Howell 2720* (UTC), *Tart & Howell 2722* (UTC); Mokomoke Mtns, *Tiehm 10189* (UTC); Robinson Summit, *Train 11989* (UC); 5 mi N of McGill, *Ward & Ward 939* (DS); summit of Conner's Pass, *Ward & Ward 941* (DS).—NEW MEXICO: Rio Arriba Co.: NW of Tres Piedras, *Springfield 375* (RM). Taos Co.: 3 mi N of Tres Piedras, *Beetle 12999* (UC).—OREGON: Lake Co.: Hart Mtn, *Steward 7258* (OSU, UTC). Malheur Co.: 50 mi W of Vale, *Loftfield 2092* (DS); without locality, 1 Sep 1959, *Yoakum s.n.* (RM).—UTAH: Beaver Co.: Wah Wah Mtns, *Holmgren 428* (BRY), *Neely & Chambers 2067* (UTC); San Francisco Mtns, *Shultz & Shultz 5267* (UTC). Box Elder Co.: Raft River Mtns, *Cottam 3071* (UT); slopes below Bovine Mtns, *Curto et al. 1290* (UTC); Promontory Point, *Flowers 1035* (UT); Hansen Valley, *Gierisch 828* (UTC); W slope of Wellsville Mtns, *Shultz 5466* (UTC); 19 mi E of Nevada border, *Shultz & Shultz 4315* (RM, RSA); Dove Creek Pass, *Shultz & Shultz 8142* (UTC); E of Copper Mtn, *Shultz & Shultz 10202* (UTC); Bald Mtn, *Shultz & Shultz 10205* (UTC); road to exclosure S of Raft River Mtns, *Shultz et al. 20268* (UTC); 5 mi W of Lucin, *Sommerville 47* (UTC). Cache Co.: base of Logan Canyon, *Beetle 11964* (RM); foothills of Bear River Range, *Maguire 260* (UTC); E edge of Logan Country Club, *Shultz & Shultz 7229* (UTC); mouth of Green Canyon, *Shultz 10031* (UTC), *Shultz 10047* (UTC), *Shultz 10148* (UTC); Upper Blacksmith Fork, *Tuhy 2281* (UTC), *Tuhy 2283* (UTC). Carbon Co.: near Price, 18 Sep 1929, *Flowers s.n.* (UT); between Price and Helper, *Goodrich 25391* (UTC); 5 mi E of Wellington, *Neese 8555* (BRY, UTC). Daggett Co.: Goslin Mtn, *Goodrich 22227* (UTC). Duchesne Co.: NE of Bridgerland, *Goodrich 15168* (BRY). Emery Co.: N Dragon Creek, *Lewis 4524* (UTC); near Taylor Flat, *Shultz et al. 3126* (UTC); E of Emery, *White 98* (BRY). Garfield Co.: E end of Panguitch Lake, *Barkworth & Hallsten 4441* (UTC); Doves Hollow, 13 Sep 1961, *Folks s.n.* (UTC); Plot 80, 17 Aug 1986, *Gottschalk s.n.* (UTC); Widstoe, *Hinckley 2230* (UT); Panguitch Lake, *Jones 5997* (UC, UTC); head of Red Canyon, *Maguire 19051* (UTC); King Ranch, *Markham B-23* (UTC); S fork of Happy Canyon, *Shultz & Shultz 6951* (UTC); Orange Cliffs, *Shultz & Shultz 7352* (UTC); Aquarius Plateau, *Shultz & Shultz 8014* (UTC); Bryce Canyon, *Thackery 551* (UC). Grand Co.: Sevasey Peak, *Albee 800* (UT); N slope of LaSal Mtns, *Howell & True 44870* (CAS); W ridge of Gold Hill, *Maguire et al. 15588* (UTC, RM, US); Book Cliffs, *Neely 231* (UTC), *Neely 239* (UTC); ridge above East Canyon, *Neely 331* (UTC). Iron Co.: near junction of Dry Wash and Little Pinto Creek, *Shultz & Shultz 7716* (UTC); 30 mi SE of Milford, *Shultz et al. 10174* (UTC); 13 mi W of Parowan, *Turner & Turner 198* (ARIZ, GH, UTC). Juab Co.: Trout Creek, *Becraft & Starr 391 d-6* (UTC); 20 mi E of Trout Creek, *Maguire 2850* (UTC); along Sand Pass Rd, *Maguire & Becraft 2850* (UTC); Deep Creek Mtns, *Shultz & Aitken 17383* (UTC); N end of Drum Mtn, *Stewart 10* (UTC). Kane Co.: 10 mi W of Mt Carmel, *Beetle 12920* (GH); Vermilion Cliffs, *Fertig 20904* (UTC); Dixie Natl Forest, *Gierisch 254* (UTC). Millard Co.: Desert Range Experiment Station, *Alder 85* (UT); Church Mtns, *Goodrich 15223* (BRY); Antelope Spring, *Kass 1070* (BRY); E of Sevier Lake, *Shultz & Shultz 7420* (UTC). Rich Co.: vicinity of Sunrise Campground, *Leidolf 2230* (UTC); 1 mi E of Laketown, *Maguire & Stoddart 21610* (UTC); 2 mi W of Garden City, *Maguire & Stoddart 21661* (NY, US); 0.5 mi E of Laketown, *Maguire & Stoddart 21719* (UTC); 1 mi E of Laketown, *Shultz 4524* (RM, RSA, UTC); E shore of Bear Lake, ca. 1 mi N of Hwy 30 junction, *Shultz 19832* (UTC); S of Hwy 89, *Shultz et al. 20294* (UTC); 1 mi E of Laketown, *Stoddart & Maguire 21658* (UC, UTC); 2 mi W of Garden City, *Welsh 18248* (BRY, UTC). San Juan Co.: Montezuma Canyon, *Rydberg & Garrett 9685* (UT); Montezuma Creek Canyon, 20 Aug 1988, *Shultz & Furlong s.n.* (UTC); Kane Creek road, *Shultz & McReynolds 20177* (UTC); top of Fry Mesa, *Wilson 285* (UTC). Sanpete Co.: Maple Canyon, *Collins 161* (BRY); S of Manti City garbage dump, *Lewis 6990* (UTC); 1 mi W of Gunnison, *Shultz & Shultz 7407* (UTC); Antelope Valley, 15 Sep 1965, *Williams et al. s.n.* (UT). Sevier Co.: Clear Creek, *Lewis 7688* (UTC; Marysvale Canyon, *Munz 29* (UT). Summit Co.: 5 mi S of Kamas, *Despain 115* (BRY). Tooele Co.: Skull Valley, *Flowers 45* (UT, UTC); Lakeside Mtns, *Ludwig 4761* (UT); 2 mi N of Goldhill, *Shultz & Shultz 8162* (UTC); 0.5 mi SE of Big Spring, *Taye 1015* (BRY, UTC); 10 mi S of Stockton, *Wipff et al. 346* (UTC). Uintah Co.: 2 mi N and E 62 deg. of Lapoint, *Goodrich 18000* (UTC); Uintah Basin, 2 mi NE of Lapoint, *Goodrich 18105* (UTC); 2 mi NE of Lapoint, *Goodrich 22225* (UTC); 10 mi W of Vernal, *Goodrich 23215* (BRY); Seep Ridge Rd, 20 mi S of White River, *Neese 6522* (BRY, RM, UTC); 17.3 mi S of Hill Creek Bridge, *Shultz & Shultz 3802* (UTC); 9.8 mi N of Grand County line, on Seep Ridge road, *Shultz & Shultz 3820* (UTC); Uinta Basin, 26 mi NE of Walsh Knolls, *Shultz & Shultz 5405* (RM, RSA); Walsh Knolls Area, *Shultz & Shultz 5409* (UTC); E Tavaputs Plateau, *Vickery & Wiens 1734* (UT). Utah Co.: Cedar Valley, *Nebeker 335* (BRY); Transverse Mtns, *Shultz et al. 19660*

(UTC). Washington Co.: Beaverdam Mtns, *Higgins 711* (BRY). Wayne Co.: Henry Mtns, *Everitt 220* (COLO, POM); Parker Mtn, 25 Sep 1969, *Jensen & Smith s.n.* (UTC). Weber Co.: Malan Basin, *Clark 1617* (UTC); Bryce Canyon Natl Park, 12 Aug 1986, *Gottschalk s.n.* (UTC).—WYOMING: Albany Co.: Sherman Hill Recreation Area, *Asplund 29* (RM); along Horse Creek Rd, *Barr 1030* (RM); Centennial, Ramber Rd, *Gooding 2073* (RM, UTC); Buford, *Hartman 5105* (RM); Centennial Valley, *Nelson 5272* (RM, UTC); open plains, *Nelson 8185* (UTC); S Laramie Plains, *Osterhout 1824* (RM); W of Tie Siding, *Osterhout 6622* (RM); 0.5 mi W of University of Wyoming rock quarry, 1 Aug 1957, *Palmer & Palmer s.n.* (UTC); Laramie Plains, *Porter 6866* (RM); W side of Laramie hills, *Shultz & Hartman 5445* (RSA, UTC). Big Horn Co.: near Lyman Creek, *Despain 408* (RM); Shell Canyon, *Johnson 1824* (COLO). Carbon Co.: Shirley Basin, E of Casper, 17 Jul 1978, *Current s.n.* (RM); Willow Creek, *Haines 4542* (UTC); near Difficulty, *Porter 6785* (RM). Converse Co.: junction of LaBonte River and Platte River, *Beetle 12174* (UTC); Douglas, *Nelson 5043* (RM). Fremont Co.: Wind River Range, *Fisser 740* (RM). Hot Springs Co.: Owl Creek Range, *Fisser 730* (RM); 2.5 mi NW of Thermopolis, *Kemmerer & Martin 1236* (RM). Park Co.: Absaroka Mtns, *Evert 3933* (RM, UTC); N of Cody, *Pearson 324* (RM). Sublette Co.: W of Big Piney, *Beetle 11623* (COLO, GH). Sweetwater Co.: Lucerne Valley, *Flowers 134* (UT); without locality, *Ownbey 1119* (UC, UTC, WS).

Artemisia nova is the common, low-growing, dark green ("black") sagebrush of desert valleys or south-southwest-facing slopes. It is prized by sheep ranchers as forage in areas where little else is available for grazing. It is conspicuous by its low growth habit, dark green foliage, and, in late season, by its pale orange to light brown flowering branches that rise above the vegetative growth. Often misidentified in herbarium collections as *A. arbuscula*, in most instances *A. nova* can be easily distinguished from *A. arbuscula* by the entire leaves of the flowering stems, pedunculate and narrowly turbinate capitula, and phyllaries that are straw-colored and glabrous. Glandular trichomes are usually visible on the leaves, giving black sage (*A. nova*) its characteristically dark color and punctate surface.

Artemisia nova var. *duchesnicola* is a large-headed variant with pubescent phyllaries. It may warrant formal recognition at the level of subspecies. Described from an isolated population in the Uinta Basin of Utah, it has hairy involucral bracts and is hexaploid (2n = 54). This is a sporadic but unusual variant that occurs in other populations in Utah, Nevada, and California. This hairy form of *A. nova* may be a polyploid derivative that occurs in xeric habitats, but until we know more about its genetics and distribution patterns, I am reluctant to give it formal status.

7. Artemisia rothrockii A. Gray in Brewer, Watson & Gray, Bot. California 1: 618. 1876. *Artemisia tridentata* subsp. *rothrockii* (A. Gray) H. M. Hall & Clements, Publ. Carnegie Inst. Wash. 326: 137. 1923. *Artemisia tridentata* var. *rothrockii* (A. Gray) McMinn, Man. Calif. shrubs 608. 1939. *Seriphidium rothrockii* (A. Gray) W. A. Weber, Phytologia 55: 8. 1984.—TYPE: U.S.A. California: Tulare Co., Monache Meadows, 1875, *J. T. Rothrock 298* (holotype: GH!; isotype: UC!)

Small to medium-sized evergreen shrubs, (1–) 2–10 dm tall, sticky-resinous and dark green throughout, aromatic; crowns rounded; not root-sprouting. Stems white, becoming dark gray with age, canescent, trunks relatively narrow; bark gray, exfoliating. Leaves dark gray-green (or light gray in White Mountain populations), evergreen, pliable; blades long-cuneate or lanceolate, shallowly 3-lobed or entire, lobes rounded, to 1/3 blade length, surfaces densely to sparsely canescent, gland-dotted, sticky-resinous; persistent (fascicled) leaves 8–15 mm long, 2–3 mm wide; ephemeral leaves 9–25 mm long, 2–5 mm wide. Capitula 3–5 mm high, 3–6 mm wide, broadly ovoid or campanulate, erect, sessile or pedunculate. Phyllaries ovate, light brown or green, glutinous or sparsely canescent. Inflorescences narrowly paniculate, 5–15 cm long, 1–2 (–3) cm wide; inflorescence leaves evergreen, bractlike, entire. Florets 10–20, all perfect and tubular; corollas 2.5–3.5 mm long; style branches apically fringed, recurved. Cypselae 0.8–2 mm long, smooth, resinous. Pappus absent. Chromosome number: 2n = 36 (Ward 1953; McArthur & Sanderson 1999); 2n = 54, 72 (McArthur & Sanderson 1999). Figs. 1b, 7d, 9j, 26.

Common names. Rothrock sagebrush, Sticky sagebrush, White Mountains low sagebrush.

Phenology. Flowering mid-summer to fall.

Distribution (Fig. 27). U.S.A.: California; in clay soils of montane meadows; 2350–3100 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** CALIFORNIA: Alpine Co.: Ebbet's Pass, *Brewer 1996* (UC); Crater Lake, *Holbo 35* (RM). Inyo Co.: Cottonwood Lakes, *Alexander & Kellogg 3342* (DS, MO, POM, UTC); Monache Meadows NE of airstrip, *Graham 1036* (UTC); Coyote Ridge, *Raven 202* (CAS); White Mtns, *Shultz et al. 19802* (UTC); *Shultz et al. 19803* (UTC); *Shultz et al. 19804* (UTC); Cottonwood Lakes, *Ward 1812* (RM). Lassen Co.: between Susanville and Alturas, *Balls 20971* (RSA, WS). Madera Co.: 2 mi SE of Mt Florence, *Akey 340* (UC); Devil's Postpile Natl Monument, *Beetle 12860* (RM). Mariposa Co.: 0.5 mi W of Ireland Lake, *Thomas 470* (UC). Mono Co.: near Sonora Pass, *Anderson 2933* (KSC, RM); Mammoth Lakes, *Beetle 12862* (RM); Walker Lakes, *Congdon 9990* (GH); Campito Meadow, near the Patriarch Grove in White Mtns, *Cronquist 12085* (UTC); N slopes of Sheep Mtn, *Maguire & Holmgren 26121* (UTC); entrance to Patriarch Area, *Mooney 667* (DS); Sara Creek, *Purpus 5165* (UC); Crooked Meadow, *Reveal 198* (CAS, RM, RSA, UTC); White Mtns, *Shultz et al. 19817* (UTC); Carnegie Timberline Station, *Ward 959* (DS); Warren Creek, *Ward 961* (DS). Placer Co.: 0.5 mi W of Lake Van Norden, *French 462* (UC). San Bernardino Co.: Holcomb Valley, *Ewan 4873* (RM); Holcomb Valley, 10 Sep 1957, *Ferguson s.n.* (ARIZ, RM, RSA); E end of Bear Valley, *Roos 2777* (DS); Holcomb Valley, *Shultz & Thorne 4706* (RM, UTC), *Shultz & Thorne 4707* (UTC); near Holcomb Creek, *Shultz & Thorne 4708* (UTC); Holcomb Valley, *Shultz & Thorne 4711* (UTC), *Shultz & Thorne 4712* (UTC), *Shultz & Thorne 4713* (UTC), *Shultz & Thorne 4714* (UTC), *Shultz & Thorne 4715* (UTC); Erastre Flats, *Shultz & Thorne 4695* (UTC); Big Bear Lake, *Ward 979* (DS, WS); E end of Bear Lake, *Ward 980* (DS, WS); Mojave River at Oro Grande, *Wheeler 2261* (DS); Big Bear Valley, *Wolf 2487* (DS, RSA). Tulare Co.: Big Meadow, 16 Sep 1912, *Childs s.n.* (CAS); ca. 55 km NNE of Kernville, *Cronquist & Frame 12182* (UTC); 15 km NE of Kernville, *Cronquist & Renner 12163* (UTC); 40 km NE of Kernville, *Cronquist & Renner 12166* (UTC); Volcano Meadows, *Hall 5490* (CAS, UC); Chagoopa Plateau, *Howell 17572* (CAS); Rock Creek, *Howell 26102* (CAS, WS); Horse Meadow, *Howell 41714* (CAS); Siberian Outpost, *Jensen 434* (UC); S Fork Kern River, *Leskinen 973* (CAS); Troy Meadow, *Meng 493* (CS); Cottownwood Lakes, *Morton 11776* (CAS, US); Chagoopa Plateau, *Sharsmith 3829* (WS); Monache Meadows, *Shultz & Shultz 5600* (RM, UTC); Southern Sierra Nevada Mtns, *Shultz & Shultz 5652* (UTC), *Shultz & Shultz 5653* (UTC), *Shultz & Shultz 5654* (UTC); SW edge of Monache Meadows, *Shultz & Shultz 5660* (UTC), *Shultz & Shultz 5661* (UTC), *Shultz & Shultz 5662* (NY, UTC), *Shultz & Shultz 5664* (UTC), *Shultz & Shultz 5669* (RSA, UTC); Little Troy Meadows, *Shultz & Shultz 5670* (NY, RSA, UTC), *Shultz & Shultz 5671* (UTC), *Shultz & Shultz 5672* (NY, RSA, UTC), *Shultz & Shultz 5673* (UTC); Monache Meadow, 8 Aug 1911, *Taylor s.n.* (UC); Paloma Meadow, *Twisselmann 13843* (CAS); Monache Meadow, *Twisselmann 14817* (CAS); Siberian Pass Creek, *Twisselmann 17415* (CAS); Casa Vieja Meadow, *Twisselmann 18143* (CAS); Osa Meadow, *Twisselmann 18420* (CAS); W slope Argue Peak, *Twisselmann 19060* (CAS). Tuolumne Co.: Yosemite Natl Park, *Beetle 12858* (RM); Mt Dana, *Bolander 6018* (UC); Tioga Pass, *Hall 10847* (UC); Tenaya Lake, *Hall 12105* (UC); Matterhorn Canyon, *Hawbecker 18546* (UC); Mt Gibbs, *Smiley 762* (GH); Mt Dana, *State Survey 6078* (UC).

Artemisia rothrockii occurs sporadically in the mountains of California, at high elevations, but is most abundant in the central and southern Sierra Nevada and the White Mountains. Persistent reports of *A. rothrockii* from the Rocky Mountains are based on misidentifications of *A. spiciformis*. Distinctive chemistry and anatomical features, such as gelatinous fibers (Shultz 1986b), support the segregation of *A. rothrockii* from *A. spiciformis* and *A. tridentata*, but it is often confused with these taxa. The high concentration of resins in the leaves of *A. rothrockii* is apparent by the sticky texture of the leaves and flowering heads. Several morphological features suggest that the species could be a result of

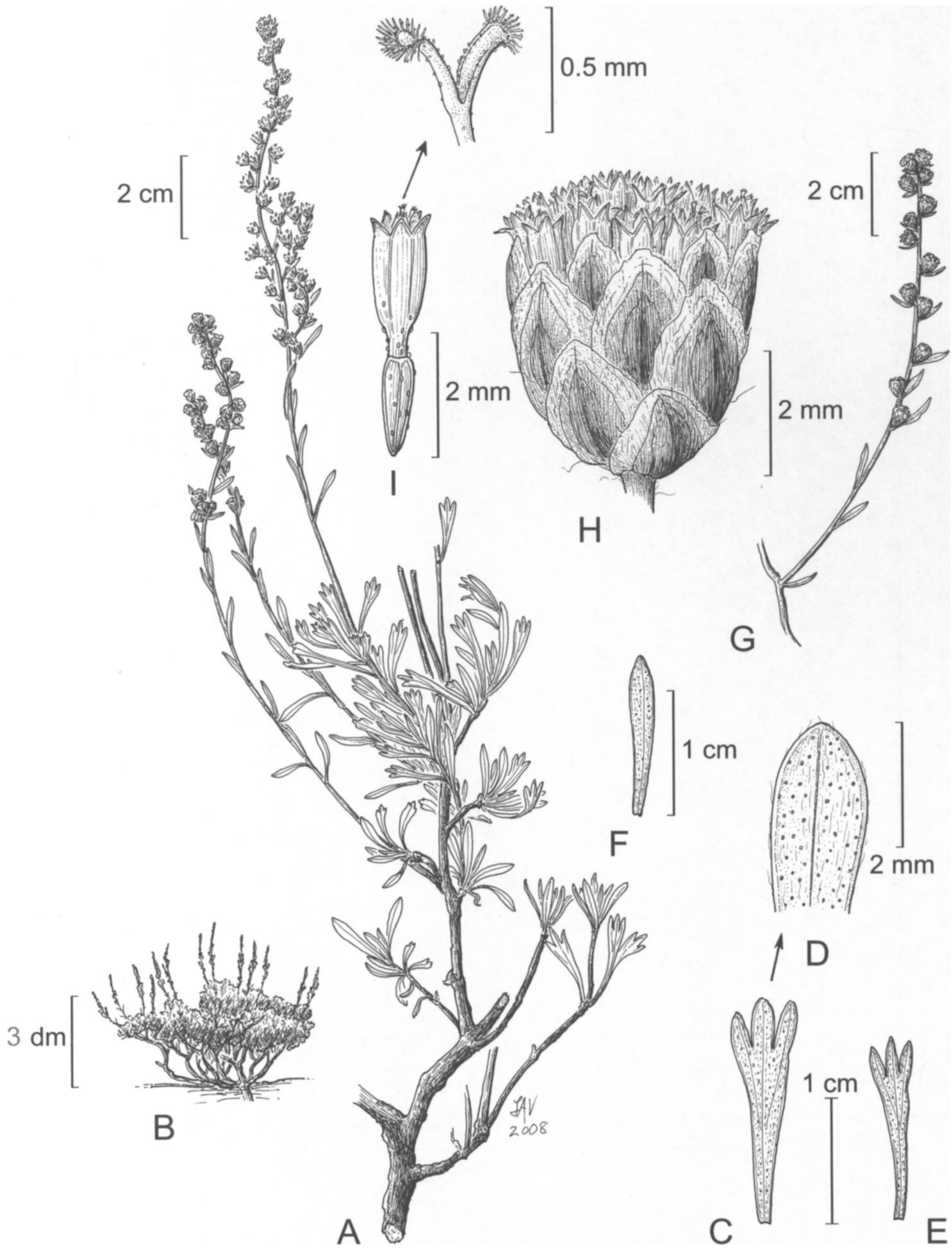

FIG. 26. *Artemisia rothrockii*. A. Branch with leafy and flowering shoots; the distalmost inflorescence shoot branches at the base and bears open (older) capitula. B. Habit. C. Ephemeral leaf. D. Detail of leaf tip. E. Persistent leaf. F. Inflorescence leaf. G. Inflorescence branch. H. Capitulum. I. Floret and cypsela, with detail of style branches. (Based on: *A–F, Shultz 5660*; G–I, *Alexander & Kellogg 3342*.)

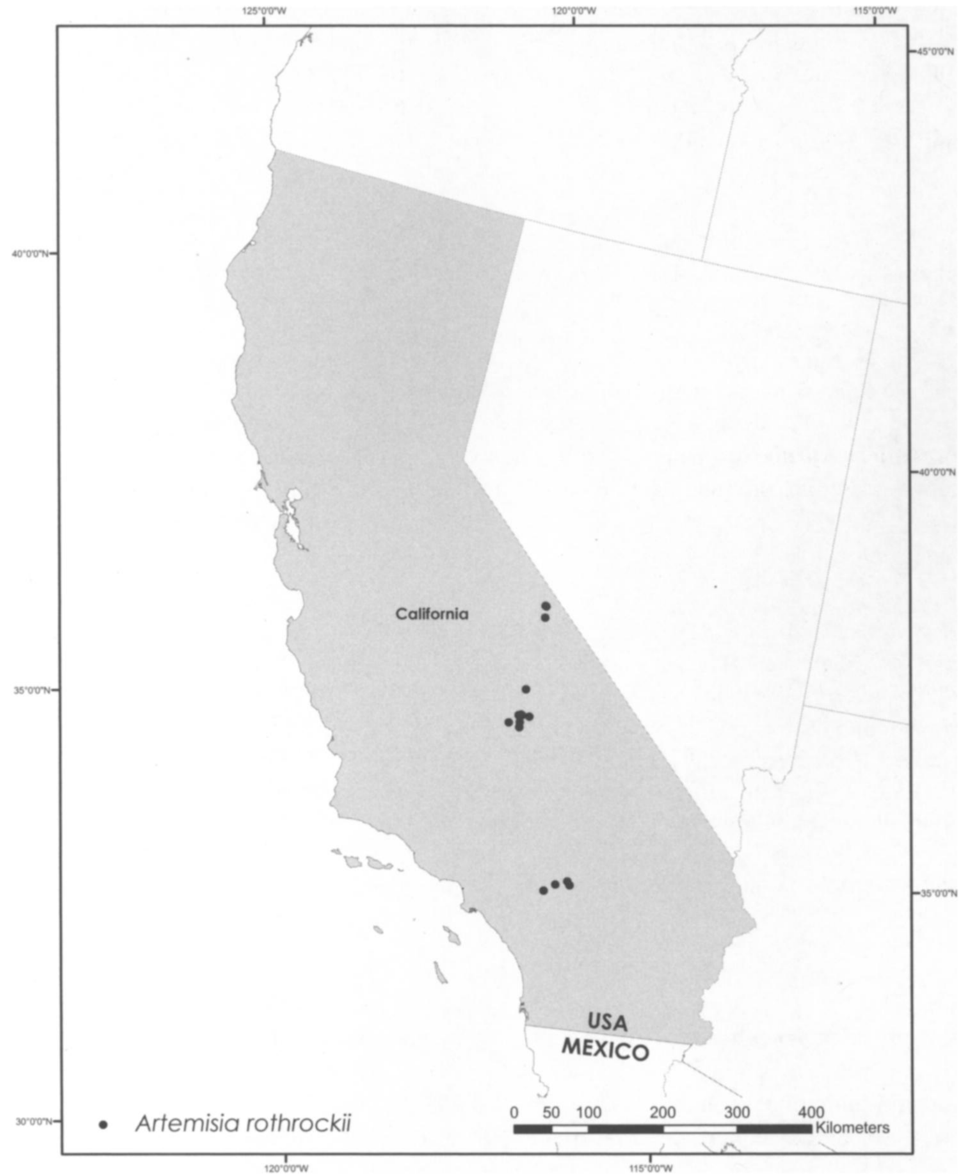

FIG. 27. Distribution of *Artemisia rothrockii*.

reticulate evolution involving *A. cana*, *A. tridentata*, and possibly *A. arbuscula*. The large heads of *A. rothrockii* are similar to those of *A. cana*, the shape of the inflorescence is similar to that of *A. tridentata*, and its short stature suggests the influence of *A. arbuscula*. The species is polyploid with several ploidy levels (McArthur et al. 1981), a finding that supports the possibility of a hybrid origin for the species.

The distinctively white-pubescent form of *A. rothrockii* found in the White Mountains may represent a subspecific taxon. This White Mountain form (informally annotated as "*A. hallii*" by Arthur Cronquist in a collection in the Intermountain Herbarium) has a shorter stature, denser pubescence, and more variation in leaf size and lobing. Yet, because the White Mountain populations may represent an introgressed swarm involving local populations of *A. tridentata* and *A. cana*, I am reluctant to recognize them as a distinct subspecies or variety without further study.

The specific epithet honors Joseph Trimble Rothrock (1839–1922), collector for the Wheeler Expedition of 1875.

8. Artemisia spiciformis Osterhout, Bull. Torrey Bot. Club 27: 507. 1900. *Artemisia tridentata* f. *spiciformis* (Osterhout) Beetle, Rhodora 61: 83. 1959. *Artemisia tridentata* subsp. *spiciformis* (Osterhout) Kartesz & Gandhi, Phytologia 71: 59. 1991. *Seriphidium spiciforme* (Osterhout) Y. R. Ling in Hind, Jeffrey, and Pope, Advances in Compositae Systematics 288. 1995. *Artemisia tridentata* var. *spiciformis* (Osterhout) Dorn, Vasc. Pl. Wyoming, ed. 3: 375. 2001.—TYPE: U.S.A. Colorado: Larimer Co., North Park, 3 Sep 1899, *Osterhout 2011* (holotype: RM!; isotype: NY!).

Medium-sized, semi-deciduous shrubs, 5–8 dm tall, aromatic; crowns rounded; sprouting from underground caudices, the stems "layering" and rooting. Stems numerous, brown or grayish green, erect, gray-tomentose, widely branched; bark gray. Leaves more or less deciduous, most turning yellow by late summer, but some persisting into the winter months, pliable; blades lanceolate or oblanceolate, highly variable in size and lobing; persistent (fascicled) leaves considerably shorter than the ephemeral leaves, 2.5–5.5 cm long, 0.8–1.2 cm wide, entire or irregularly 3–6-lobed, lobes rounded or acute, ca. 1.5 mm wide, to 1/3 blade length, surfaces more or less sericeous or tomentose; ephemeral leaves deciduous, irregularly lobed, ca. 1.5 times as long (up to 7 cm long) as the fascicled leaves. Capitula (2.5–) 4 mm high, 6 (–7) mm wide, ovoid, erect, sessile (lowermost sometimes pedicellate). Phyllaries lanceolate, sparsely to densely hairy. Inflorescences leafy, paniculate, 8–15 (–25) cm long, 0.5–3 (–4) cm wide; leaves of the flowering stems persistent or deciduous, reduced, entire. Florets 8–18 (–27), all perfect and tubular; corollas 2.5–3.5 long, glabrous; style branches apically fringed, recurved. Cypselae 1–1.5 mm long, glabrous or resinous. Pappus absent. Chromosome number: 2n = 18, 36 (McArthur & Sanderson 1999); 2n = 54 (McArthur et al. 1981). Figs. 7c, 9f, 28.

Common names. Snowfield sagebrush, Subalpine sagebrush.

Phenology. Flowering mid-summer to fall.

Distribution (Fig. 29). USA.: California, Colorado, Idaho, Montana, Nevada, Oregon, Utah, Washington, Wyoming; in moist open slopes, rocky meadows, streamsides, woodlands, and late-lying snowfields; 2100–3700 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** CALIFORNIA: Inyo Co.: Thorndike Camp, 13 Jun 1958, *Ferguson s.n.* (UTC). Mono Co.: High Altitude Research Station, *Bacigalupi et al. 8062* (UTC); W of Lee Vining, *Cronquist 12087* (UTC); slopes along the NE shore of Ellery Lake, *Cronquist & Renner 12169* (UTC); overlooking N side of Ellery Lake, *Cronquist & Renner 12170* (UTC); Tioga Pass, *Reveal 216* (UTC); Tioga Pass, *Reveal 221* (UTC); Mono Pass, at the head of Bloody Canyon, *Reveal 1055* (UTC); Ellery Lake, *Shultz & Shultz 5713* (UTC), *Shultz & Shultz 5715* (UTC); Virginia Lakes Rd, *Shultz et al. 19782* (UTC); just W of Tioga Pass, *Shultz et al. 19787* (UTC), *Shultz et al. 19788* (UTC); Lake Mary, *Shultz et al. 19793* (UTC); White Mtns, just N of Inyo/Mono County line, *Tucker 2224* (UTC). Tulare Co.: ca. 40 km NE of Kernville, *Cronquist & Renner 12167* (UTC).—COLORADO: Gunnison Co.: Watershed, *Baker 810* (POM). Jackson Co.: S of Coalmont, *Beetle 11912* (UTC); North Park, *Osterhout 2255* (UTC). Lake Co.: Empire Hill, *Neely 3250* (UTC). Rio Blanco Co.: 15 mi S of Meeker, *Maguire & Piranian 12513* (UTC, GH).—IDAHO: Bear Lake Co.: 0.5 road mi below Minitonka Cave, *Piep et al. 00.155.1* (UTC); 2 mi E of Minetonka Cave, *Shultz 4514* (UTC). Blaine Co.: 2 mi N of Hailey, *Anderes*

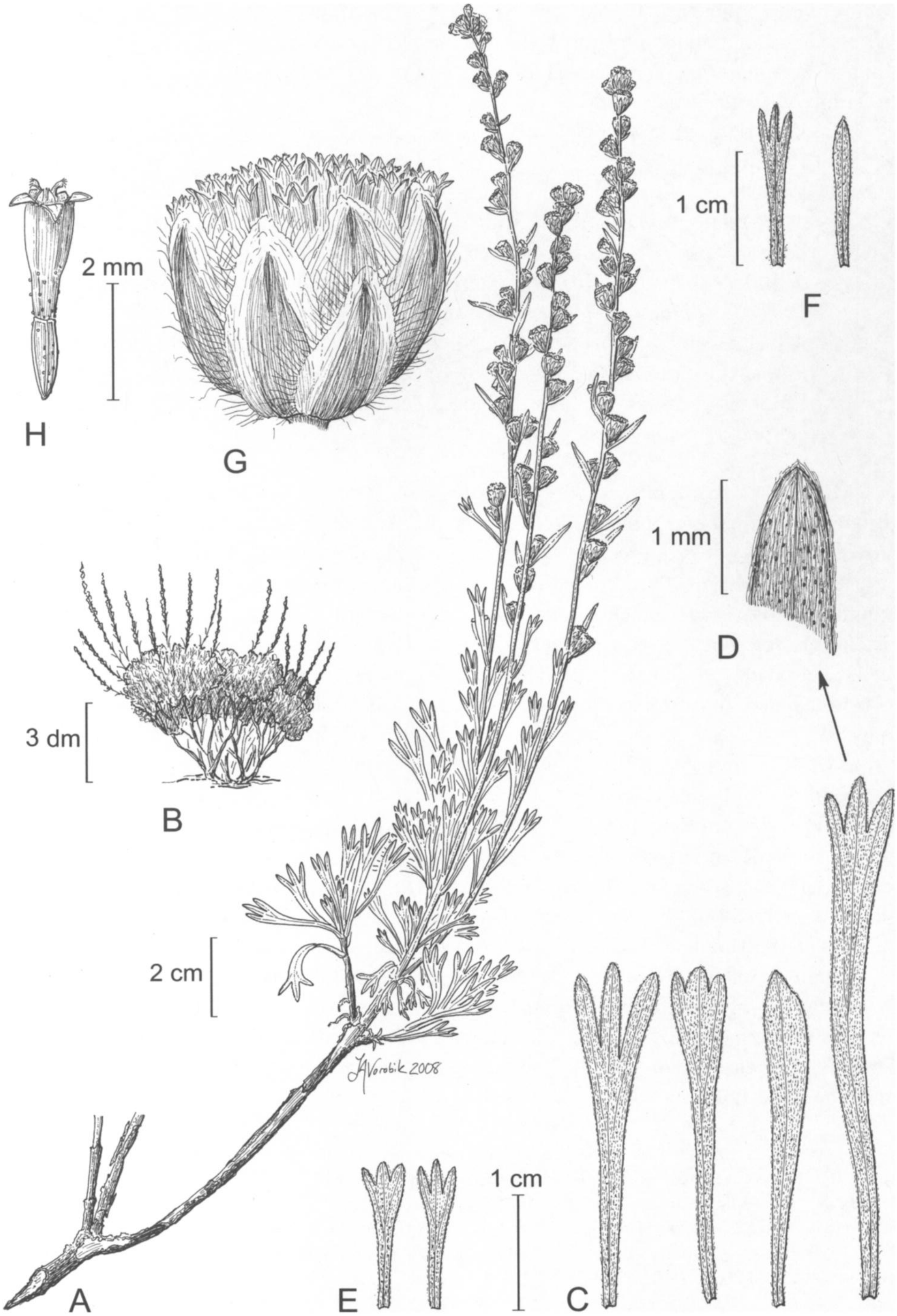

FIG. 28. *Artemisia spiciformis*. A. Branch with leafy and flowering shoots. B. Habit. C. Ephemeral leaves. D. Detail of leaf tip. E. Persistent leaves. F. Inflorescence leaves. G. Capitulum. H. Floret and cypsela. (Based on: A–B, G–H, *Cronquist 12169*; C, *Messina s.n.*, Aug 1990; E, F, *Shultz & Shultz 7444*.)

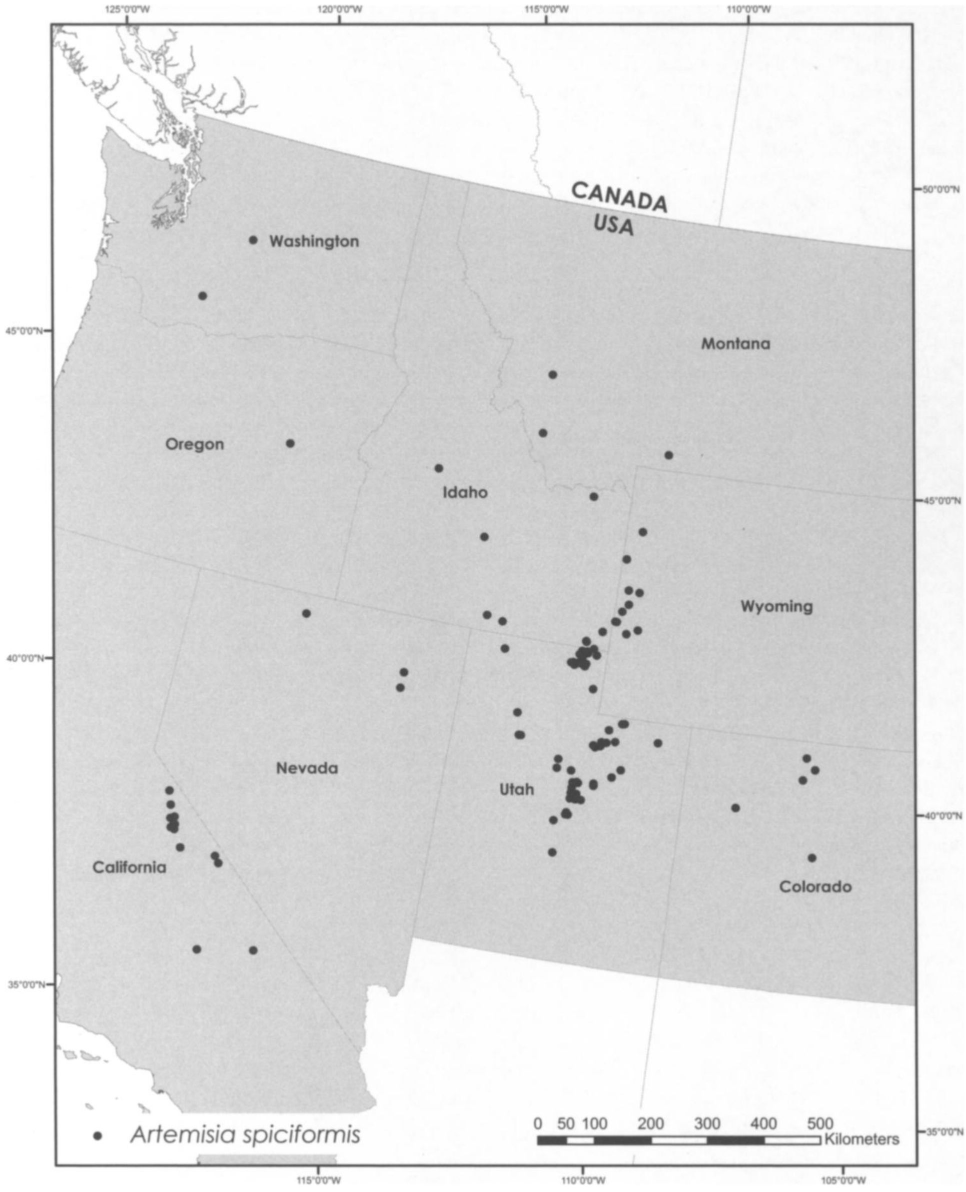

FIG. 29. Distribution of *Artemisia spiciformis*.

15-11 (UTC). Caribou Co.: Franklin Basin, *Shultz et al. 20212* (UTC), *Shultz et al. 20213* (UTC), *Shultz et al. 20214* (UTC), *Shultz et al. 20216* (UTC); Franklin Basin, N of Ranch site, *Shultz et al. 20217* (UTC). Cassia Co.: Thompson Flat, *Shultz & Shultz 8116* (UTC). Clark Co.: along Ching Creek, *Cronquist 2005* (MO, RM, UTC). Valley Co.: head of Bear Valley, *Beetle 14138* (MO).—MONTANA: Beaverhead Co.: 10 mi SE of Jackson, *Beetle 12262* (UTC). Flathead Co.: Georgetown Lake, 19 Aug 1958, *Beetle s.n.* (UTC).—NEVADA: Elko Co.: Angel Lake, *Raven 20625* (DS). Humboldt Co.: Lye Creek Campground, *Wilken et al. 12506* (UTC).—OREGON: Grant Co.: ca. 15 mi SE of John Day, *Acker 109* (UTC).—UTAH: Cache Co.: Top of Logan Canyon, *Beetle 11965* (UTC), *Beetle 11966* (UTC); Cache Creek, *Beetle 11968* (UTC), *Beetle 11969* (UTC); Sheep Creek Springs, 6 Aug 1939, *Corey s.n.* (UTC); Temple Fork Rd, *Horner-Till 929* (UTC); ca. 8 mi E of Logan, *Johnson 350402*

(UTC); Logan Peak, *Maguire 250* (UTC); Tony Grove, *Maguire 3875* (UTC); Beaver Basin area, *Maguire 20145* (UTC); Franklin Basin, *Maguire 20149* (UTC); Logan Canyon, *Maguire & Stoddart 21666* (UTC), *Maguire & Stoddart 21728* (UTC); near Beaver Peak, Logan Canyon, 23 Aug 1990, *Messina* (UTC); Bear River Range, *Neely 661* (UTC), *Neely 670* (UTC), *Neely 677* (UTC); Logan Canyon, *Piep 04.080* (UTC); Beaver Mtn, *Reese 1187* (UTC); 15 mi up Logan Canyon, 13 Sep 1934, *Richards Jr. s.n.* (UTC); Bear River Range, Temple Fork Road, Mill Trace, *Shultz 19829* (UTC); S face of Logan Peak, *Shultz 7431* (UTC), *Shultz 7436* (UTC), *Shultz 7438* (UTC); Bear River Range, *Shultz & McReynolds 20182* (UTC); Tony Grove area, *Shultz & Shultz 6388* (UTC); Logan Canyon, *Shultz & Shultz 8204* (UTC); S face of Logan Peak, *Shultz et al. 7440* (UTC), *Shultz et al. 7442* (UTC); between Girl's Camp and Blacksmith Fork Canyon, *Shultz et al. 7444* (UTC); Logan Canyon, *Shultz et al. 19821* (UTC); Hardware Canyon, *Shultz et al. 20260* (UTC); N of Tony Grove Lake 2 Sep 1937, *Snell s.n.* (UTC); Logan Canyon, *Thorne 2781* (UTC), *Thorne 2974* (UTC), *Thorne 3007* (UTC). Duchesne Co.: head of Rhoades Canyon, *Goodrich 651* (UTC); Reservation Ridge, *Goodrich 1581* (UTC), *Goodrich 1583* (UTC), *Goodrich 1584* (UTC), *Goodrich 1585* (UTC); Tavaputs Plateau, *Goodrich 1586* (UTC); E rim of N Fork Duchesne Canyon, *Goodrich 1589* (UTC); 10.5 mi and 337 deg. from Tabonia, *Goodrich 15118* (UTC); Uinta Mtns, *Goodrich 25395* (UTC); head of Swift Creek, *Huber & Goodrich 2384* (UTC). Emery Co.: Castle Valley Ridge, *Lewis 7641* (UTC). Rich Co.: vicinity of gravel pit on NE side of US Hwy 89, *Barkworth et al. 166.0* (UTC); 1 mi E of summit of Logan Canyon, *Maguire 20120* (UTC, UC, MO); near summit, Bear River Range, *Maguire 20128* (UTC); E of Randolph, Old Canyon, Bear River Range, *Shultz & Peterson 20421* (UTC). Sanpete Co.: Wasatch Plateau, 31 Aug 1969, *Detling s.n.* (UTC, UT); above Ephraim, 30 Sep 1978, *Epstein s.n.* (UT, UTC); 13 mi E of Ephraim, 30 Sep 1978, *Epstein s.n.* (UTC); Ephraim Canyon, *Lewis 4432* (UTC); head of Clear Creek, *Lewis 4514* (UTC); S of junction of Skyline Drive and Hwy 31, *Lewis 7611* (UTC); Skyline Drive, *Lewis 7613* (UTC), *Lewis 7614* (UTC); Skyline Drive junction with Hwy 31, *Lewis 7615* (UTC); head of Bolger Canyon, *Lewis 7648* (UTC), *Lewis 7649* (UTC); near Skyline Drive, *Lewis 7650* (UTC); near Lake Guard Station, *Lewis 7651* (UTC); E of gravel pile, *Lewis 7655* (UTC), *Lewis 7656* (UTC); head of Johnson Ridge, *Lewis 7660* (UTC); N of junction of Skyline Drive and US Hwy 31, *Lewis 7664* (UTC); Lower Claybank Ridge, *Lewis 7670* (UTC); Ridley Ridge, *Lewis 7671* (UTC). Sevier Co.: Fishlake, *Jones 5824* (MO); about Fish Lake, *Maguire & Richards, Jr. 15587* (UTC). Summit Co.: E Fork of Bear River, *Goodman 2021* (MO); Uinta Mtns, *Goodrich 16200* (UTC), *Goodrich 16237* (UTC). Tooele Co.: Stansbury Mtns, *Taye 1241* (UTC, BRY), *Taye 1259* (UTC, BRY). Uintah Co.: Unitah Mtns, *Maguire & Richards, Jr. 15590* (UTC). Utah Co.: head of Lake Fork, *Lewis 7652* (UTC); Clear Creek, *Lewis 7654* (UTC); Bear area, *Lewis 7662* (UTC), *Lewis 7663* (UTC); head of Left Fork of Clear Creek, *Lewis 4444* (UTC); 10 mi S of Payson railroad station, *Maguire 20095* (UTC); Upper Payson Creek drainage, 1 Oct 1963, *Parker s.n.* (UTC). Wasatch Co.: Wolf Creek Summit, *Blake 10257* (MO); Wolf Creek Pass, *Graham 10257* (GH); N Fork Duchesne Canyon, *Goodrich 14886* (UTC); Uinta Mtns, *Goodrich 15123* (BRY, MO, UTC); Wolf Creek, *Goodrich 15124* (UTC); head of Trail Hollow, *Huber & Goodrich 3243* (UTC).—WASHINGTON: Kittitas Co.: Swauk River Valley, *Sharples 260* (GH). Yakima Co.: Mt Paddo, *Suksdorf 72* (GH).—WYOMING: Lincoln Co.: 29 mi W of Big Piney, *Maguire et al. 12607* (UTC); Greys River, *Shultz 735* (UTC); Allred Flat Campground, *Shultz 11553* (UTC); Green Knoll, *Shultz & Shultz 2858* (COLO, RM, UTC); Salt River Range, *Shultz & Shultz 7965* (UTC); W slope of the Salt River Range, *Shultz & Shultz 8692* (MO, UTC). Sublette Co.: Deadline Ridge, *Shultz 359* (UTC); Wyoming Range, *Shultz 680 p.p.* (UTC). Teton Co.: top of Teton Pass, *Beetle 11603* (UTC, MO); Wind River Range, *Porter 10305* (GH); SE shore of String Lake, *Shultz 10098* (NY, UTC).

Artemisia spiciformis has not been recognized at the species level in Floras until recently (Shultz 1993, 2006). Although it has been treated as a subspecies of *A. tridentata*, it forms a widespread and stable community type at high elevations and is worthy of specific status. Because of its large heads and leaves, it has been confused with *A. rothrockii*. This confusion is the basis for the reports of *A. rothrockii* in Wyoming by Beetle (1960), whose treatment was followed in a number of subsequent Floras. The species differ in morphology as well as anatomy, e.g., *A. spiciformis* lacks the sticky-resinous leaves and the internal resin ducts of *A. rothrockii* (Shultz 1983, 1993). Introgression sometimes occurs at sites where *A. spiciformis* grows adjacent to *A. tridentata* subsp. *vaseyana* and/or *A. cana* subsp. *viscidula*, making it difficult to determine species boundaries. These hybrid populations tend to show more plasticity in leaf size and lobing than is typical for *A. spiciformis*.

9. Artemisia tridentata Nuttall, Trans. Amer. Philos. Soc., n.s., 7: 398. 1841. *Seriphidium tridentatum* (Nuttall) W. A. Weber, Phytologia 55: 8. 1984.—TYPE: U.S.A. "plains of the Columbia River," [probably in Oregon or Washington, 1834 or 1835], *T. Nuttall s.n.* (lectotype, designated by Cronquist, 1994: PH!).

Low, medium, or tall evergreen shrubs, 3–20 (–30) dm tall, with gray herbage, aromatic; crowns rounded or somewhat flat-topped; not root-sprouting. Stems gray-brown, glabrate, trunks relatively thick; bark gray, exfoliating in strips. Leaves gray-green, evergreen, pliable, usually 3 times longer than wide; blades usually narrowly cuneate and shallowly 3-lobed, lobes rounded, 1.5+ mm wide, to 1/3 blade length, surfaces densely hairy. Inflorescences not conspicuously leafy, broadly to narrowly paniculate, leaves persistent on the flowering branches, reduced and bractlike. Capitula 1–4 mm high, 1–3 mm wide, ovoid or campanulate, mostly erect, on slender peduncles. Phyllaries oblanceolate, densely tomentose. Florets 3–11, all perfect and tubular; corollas 1.5–2.5 mm long, glabrous; style branches apically fringed, recurved. Cypselae 1–2 mm long, hairy or glabrous, glandular. Pappus absent. Chromosome number: $2n = 18, 36$.

Artemisia tridentata comprises four subspecies; however, the species has undergone considerable taxonomic revision in the past century, and the circumscription of subspecies remains controversial. There is considerable morphological variation across the range of the species. The identification of subspecies is often used as a guide in the development of land classification systems because of the fidelity of subspecies to a particular suite of ecological conditions. The infraspecific taxa vary in discrete morphological and chemical characteristics, but the boundaries become blurred in areas where the subspecies hybridize. Zones of hybridization usually occur in the ecotone between the different habitats of two subspecies. Although the subspecies are genetically similar, genetic differences appear to increase with geographic distance (Downs 2000).

I list a number of recently described infraspecific taxa in synonymy and maintain a conservative circumscription, inasmuch as genetic differences have not been quantified. Chemical differences between subspecies can be distinguished by aroma, and these differences are sometimes used to determine subspecies in the field.

KEY TO THE SUBSPECIES OF ARTEMISIA TRIDENTATA

1. Leaves more than 3 times longer than wide, elongate; inflorescences broadly paniculate, > 8 cm long; lower inflorescence branches elongate and widely spreading; medium to tall shrubs (sometimes dwarfed in subsp. *tridentata*), 10–30 dm tall.
   2. Capitula 1.5–2.5 mm high, 1–2 mm wide, erect; leaves ca. 4 times as long as wide; cypselae glabrous; on deep, well-drained (usually sandy) soils in valley bottoms and lower montane slopes, often along drainages; widespread primarily in cold desert habitats, with dwarfed forms (less than 10 dm) in some areas. 9a. *A. tridentata* subsp. *tridentata*
   2. Capitula 2–4 mm high, 1–2 mm wide, nodding; leaves greater than 5 times as long as wide; cypselae pubescent; usually on loose, sandy soils; restricted to warm deserts. 9b. *A. tridentata* subsp. *parishii*
1. Leaves less than 3 times longer than wide; inflorescences narrowly paniculate; lower inflorescence branches short; low-growing to medium-sized shrubs, 2–15 dm tall (see also stunted forms of subsp. *tridentata*).
   3. Crowns flat-topped; inflorescences 10–15 cm long; capitula 2–3 mm high, 1.5–3 mm wide; shrubs 4–8 (–15) dm tall (crowns not covered with old inflorescence branches); leaf lobes usually not overlapping; usually in comparatively moist montane meadows or on north-facing slopes. 9c. *A. tridentata* subsp. *vaseyana*

3. Crowns rounded; inflorescences 2–8 (–10) cm long; capitula (1–) 1.5–2 mm high, 1.5–2 mm wide; shrubs 2–5 (–15) dm tall (old inflorescence branches retained from previous year's growth, giving rounded crowns a "twiggy" appearance); outer margins of leaf lobes "bell"-shaped; usually in cold desert basins and high plateaus, sometimes in foothills (usually on drier sites than subsp. *vaseyana*). 9d. *A. tridentata* subsp. *wyomingensis*

9a. Artemisia tridentata subsp. tridentata.

Artemisia tridentata var. *angustifolia* A. Gray, Proc. Amer. Acad. Arts 19: 49. 1883. *Artemisia angusta* Rydberg, N. Amer. Fl. 34: 283. 1914.—Type: U.S.A. Nevada, 1877, *J. D. Hooker & A. Gray s.n.* (lectotype, here designated: GH!).

Medium-sized to tall shrubs, 10–25 (–30) dm tall; crowns rounded; vegetative branches nearly equaling the inflorescence branches. Leaves 0.5–1.2 (–2.5) cm long, 0.2–0.3 (–0.6) cm wide, cuneate or lanceolate, elongate, more than 3 times as long as wide, 3-lobed, lobes rounded, to 1/3 blade length. Capitula 1.5–2.5 mm high, 1.5–2 mm wide, ovoid, erect. Inflorescences broadly paniculate, nearly pyramidal in outline, (6–) 8–15 (–30) cm long, (1.5–) 5–6 cm wide; inflorescence leaves persistent, entire, reduced, inconspicuous. Florets 4–6. Cypselae glabrous. Chromosome number: 2n = 18, 36 (McArthur et al. 1981; McArthur & Sanderson 1999; Ward 1953). Figs. 2, 3, 7a, 9g, 30.

Common names. Great Basin sagebrush, Big sage, Basin big sage.

Phenology. Flowering mid-summer to late fall.

Distribution (Fig. 31). Canada: British Columbia; U.S.A.: Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, Wyoming; Mexico: Baja California; usually in deep, well-drained soils, in valley bottoms or lower montane slopes, often along drainages; 1300–2200 m.

Additional Specimens Examined. **Canada.** British Columbia: Osoyoos, *Beetle 12939* (RM); near Penticton, *Beetle 13466* (RM); 18 mi N of Penticton, *Beetle 13938* (UTC); N end of Lake Skaha, *Beetle 13996* (RM); 3 mi W of junction of Hwys 3 and 9, *Löve 7370* (COLO, MONT); Kamloops, 19 Sep 1928, *MacFadden s.n.* (RM); Kamloops, *McCabe 1947* (UC); cobble desert, *Thompson 4442* (UC). **U.S.A.** Arizona: Apache Co.: S rim near the turnoff for Sliding Rock Overlook, *Halse 754* (UTC). Coconino Co.: E entrance of Grand Canyon Natl Park, *Beetle 12987* (RM); W entrance of Grand Canyon Natl Park, *Beetle 13927* (RM); 14.4 mi N of Jacob Lake, 23 Aug 1956, *Ferguson s.n.* (UTC); near Houser, *Gardenhire 23* (RM); Grand Canyon, Rowe Well, *Nelson 10212* (RM). Mohave Co.: Grand Canyon Natl Park, *Eastwood 3602* (CAS); Point Lookout Rd, 26 Aug 1956, *Ferguson s.n.* (UTC); 23 mi S of Wolf Hole, 26 Aug 1956, *Ferguson s.n.* (ARIZ, RM); Marshall Ranch Rd, 25 Aug 1956, *Ferguson s.n.* (UTC); Coyote Valley, *Shultz & Shultz 9982* (UTC).—California: Inyo Co.: W of Lone Pine, *Beetle 12938* (RM); 9 mi S of Independence, 15 Jun 1958, *Ferguson s.n.* (UTC); Owens Valley, *Shultz & Shultz 6015* (UTC); White Mtns, *Wolf 2592* (DS). Kern Co.: Cummings Creek, *St. John 18797* (RM). Lassen Co.: 3 mi S of Heerlong, *Nord N-103* (RM); Harvey Valley, *Robbins 2157* (UTC); Burgess Spring, *Short 505* (UC); Long Valley Creek drainage, *Shultz & Shultz 8611* (UTC). Los Angeles Co.: Newhall, *Beetle 13081* (RM); Del Valle, *Evan 5296* (RM); Pallett, *Jensen 75999* (RM); Rock Creek, *Jensen 76116* (RM); 0.75 mi NE of Newhall, *Johannsen 76113* (RM); Oak Spring, 1 Feb 1934, *Lewis s.n.* (RM); S of Lancaster, *Ward 977* (DS); pass 3 mi W of Benton, *Wolf 2567* (UTC, RSA). Modoc Co.: 15 mi S of Alturas, *Beetle 12914* (RM); Jess Valley, Clarke Ranch, *Smith 976* (RM). Mono Co.: N of Benton Station Rd, *Beetle 12902* (RM); S side of Mono Lake, *Beetle 12929* (RM); Lee Vining Canyon, *Keck 5017* (DS); Mill Creek crossing, *Reveal & Reveal 462* (UTC, RM); Johnny Meadow, *Reveal 199* (UTC); N side of Mono Lake, *Reveal 209* (UTC); 8 mi S of Bridgeport, *Shultz et al. 19780* (UTC); Mono Basin, *Shultz et al. 19783* (UTC); Adobe Valley, *Shultz et al. 19785* (UTC); Sherwin Grade, *Shultz et al. 19795* (UTC); below Warren Creek, *Ward 960* (DS). Nevada Co.: Boca Dam, *Shultz & Shultz 10222* (UTC). Orange Co.: Santa Ana River bottom, *Howell 3165* (CAS); near camp, *Wiggins 1010* (DS). Plumas Co.: between Quicy and Reno, ca. 2 mi W of Vinton, *Shultz & Garrison 20320* (UTC). Riverside Co.: San Jacinto Mtns, 25 May 1982, *Wisura s.n.* (UTC). San Benito Co.: New Idira, *Hardman 14253* (CAS). San Bernardino Co.: Bear Lake, *Beetle 13003* (UTC); 5 mi NE of Cajon Pass, *Reveal 227* (UTC); 10 mi S of Adelanto, along Hwy 395, *Reveal 239* (UTC); N side of the Kingston Range, 6 Aug 1950, *Roos s.n.* (UTC); Burnt Flats, *Shultz 4704*

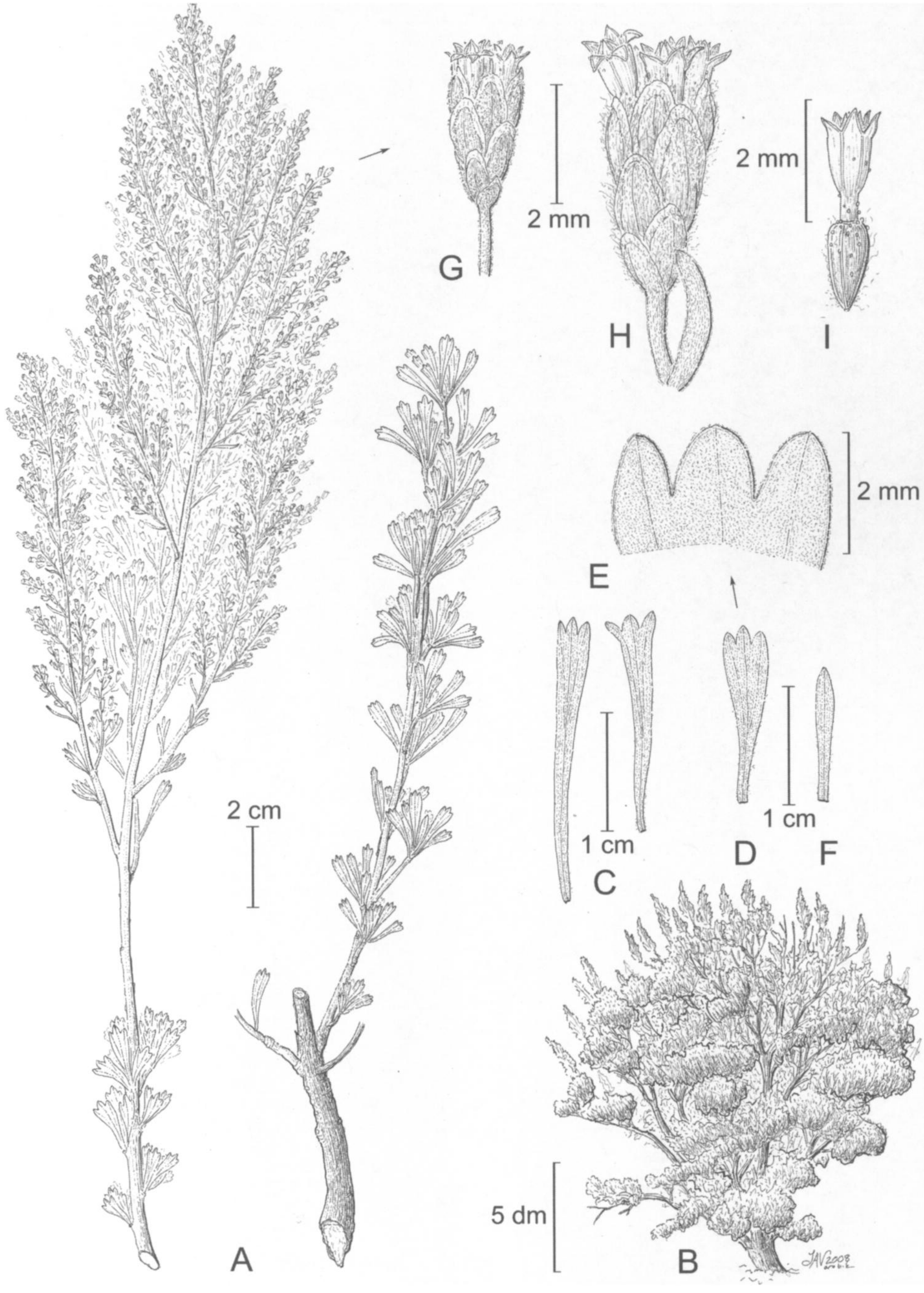

FIG. 30. *Artemisia tridentata* subsp. *tridentata*. A. Flowering branch. B. Habit. C. Ephemeral leaves. D. Persistent leaf. E. Detail of leaf tip. F. Inflorescence leaf. G. Capitulum. H. Capitulum. I. Floret and cypsela. (Based on: *A, G, Pinzl 12679*; C, *Maguire 15589*; B, D–F, H–I, *Goodrich 16468*.)

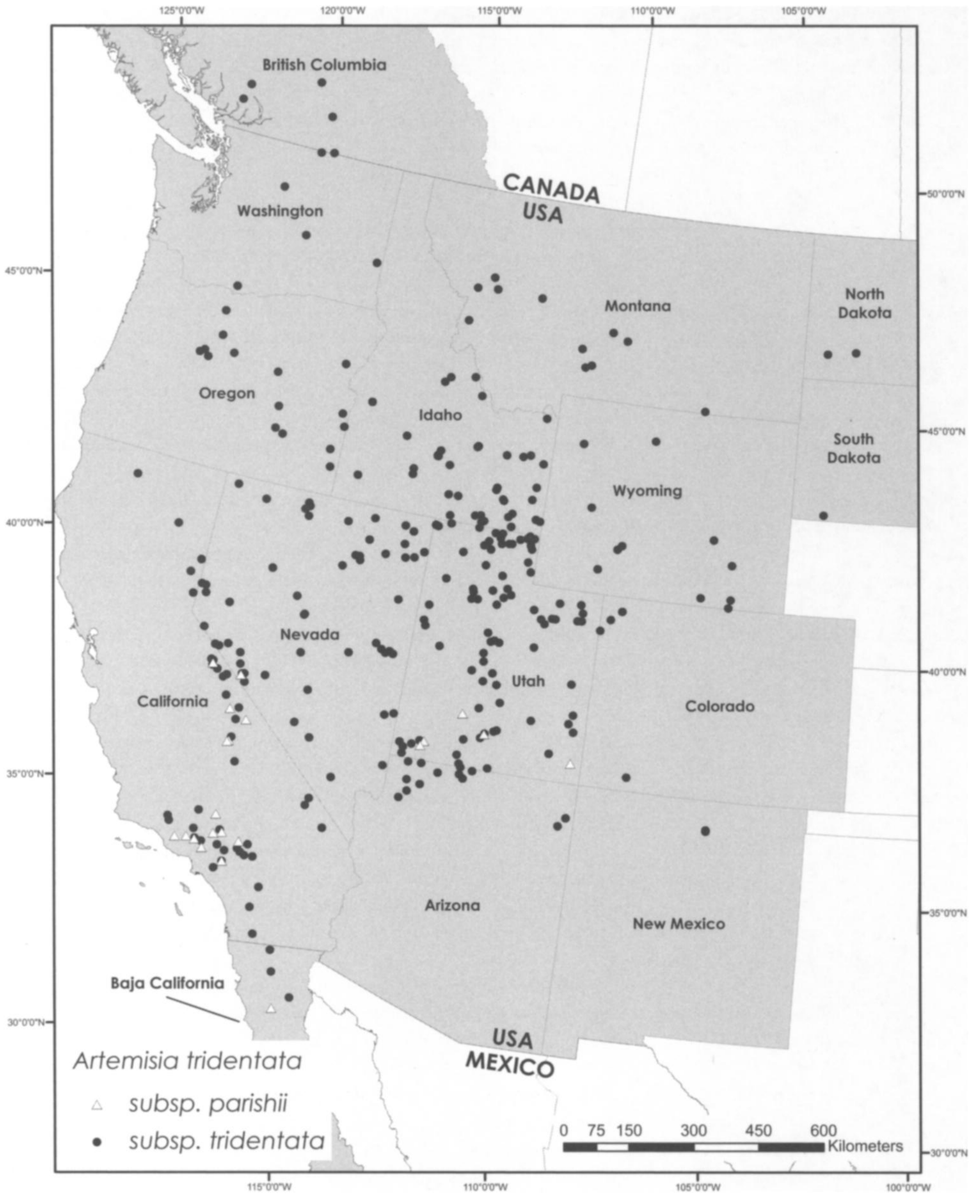

FIG. 31. Distribution of *Artemisia tridentata* subsp. *parishii* and subsp. *tridentata*.

(RSA, UTC); Kingston Mtns, *Shultz & Thorne 4685* (UTC); Holcomb Valley, *Shultz & Thorne 4719* (UTC); Cottonwood Canyon, *Stein 154* (UTC); Cottonwood Canyon, in New York Mtns, *Thorne et al. 48614* (UTC); head of Porcupine Canyon, *Thorne et al. 54785* (UTC). San Diego Co.: Oak Valley, *French 763* (RM); Canada Aguanga, *Raymond 76327* (RM). Siskiyou Co.: Butte Valley, *Butler 1883* (RM); Shasta Valley, *Jensen 81881* (RM); 15 mi NE of Weed, *Ward & Ward 828* (RM). Ventura Co.: Apache Canyon, *Sowder 83228* (RM); Sespe Creek, *Thompson 1104* (UC).—COLORADO: Gunnison Co.: Gunnison Airport, *Iltis 18940* (WIS), *Iltis 18942* (WIS); 9 mi W of Monarch, *Ugent 63* (WIS). Jackson Co.: between Cowdrey and Walden, *Beetle 12325* (RM). La Plata Co.: Durango, *Baker et al. 990* (COLO, MO). Mesa Co.: 1 mi up Prairie Canyon Rd from Baxter Pass, *Walter & Walter 9683* (MO). Moffat Co.: 2 mi E of Utah border, *Shultz 4383* (UTC). Montezuma Co.: Mesa Verde Natl Park, *Haas*

33 (RM). Montrose Co.: Cimmaron, 21 Aug 1896, *Crandall s.n.* (MO); Paradox, *Walker 197* (RM). Rio Blanco Co.: S Fork White River, *Pint 30* (RM).—IDAHO: Ada Co.: Boise, hillsides everywhere, *Clark 336* (MO, RM). Bannock Co.: 2 mi N of Oxford, *Maguire 3877* (UTC); 2 mi N of McCannon turnoff from I-16, *Shultz 10264* (UTC); benches W of Pocatello, 7 Nov 2004, *Shultz & McReynolds s.n.* (UTC); Bannock Range, *Shultz & Shultz 8100* (UTC). Bear Lake Co.: Montpelier Canyon, *Shultz & Shultz 3035* (UTC). Blaine Co.: ca. 50 mi N of Twin Falls, *Shultz 20314* (UTC); sagebrush meadow near Picabo, *Shultz & McReynolds 19851* (UTC), *Shultz & McReynolds 19852* (UTC); S of Bellevue, *Shultz & McReynolds 19854* (UTC). Bonneville Co.: 5 mi E of Ririe, *Beetle 11984* (UTC); W of Idaho Falls, *Beetle 14125* (UTC); without locality, *Brown 73-459* (UTC), *Brown 459* (UTC). Butte Co.: 5 mi E of Arco, *Beetle 14128* (UTC); 3 mi W of Craters of the Moon, *Ward & Ward 898* (DS, RM, UC). Caribou Co.: Caribou Natl Forest, *Brown 73-58* (UTC); near Wood Canyon, *Brown 73-580* (UTC); Rasmussen Valley, *Peterson P-40* (RM). Cassia Co.: Burley, *Beetle 12783* (UTC); Albion Mtns, *John 1032* (UTC). Franklin Co.: 1 mi W of Preston, *Maguire 3876* (UTC); 6 mi W of Soda Springs, *Solheim 669* (RM). Fremont Co.: near Bishop's Ranch, *Aldous 240* (RM); 1.5 mi S of Island Park, *Shultz & Shultz 7951* (UTC); 1 mi NE of Warm River, *Ward & Ward 901* (DS, RM, UC). Gem Co.: ca. 15 mi N of Emmett, *Henry 501* (UTC). Gooding Co.: Hagerman, *Davis 1771* (UTC); along Hwy 46 near City of Rocks, 15 Aug 1978, *Phillips s.n.* (UTC). Lemhi Co.: near North Fork, *Ballard 2* (UTC); near Leadore, *Ballard 2a* (UTC); near Leadore, *Ballard 4* (UTC); Meyers Cove, *Davis 1409* (UTC). Lincoln Co.: 12 mi NE of Richfield, *Ward & Ward 895* (DS). Oneida Co.: Switzer Rd turnoff, *Shultz 19651.1* (UTC); Curlew Valley Natl Grassland, *Shultz et al. 20151* (UTC), *Shultz et al. 20152* (UTC), *Shultz et al. 20154* (UTC); Glen Canyon area, *Welsh & Welsh 17085* (RM). Owyhee Co.: SW of Bruneau, *Johnson 211* (DS, OSU). Payette Co.: Payette, *Harper s.n.* (WIS). Washington Co.: Nutmeg Mtns, E of Weiser, *Ertter 585/3* (UTC).—MONTANA: Beaverhead Co.: without locality, 8 Mar 1905, *Moore s.n.* (MO). Big Horn Co.: West Decker, *Mayer 974* (RM). Clark Co.: 23 mi N of Helena, at Lewis and Clark Landing, *Beetle 11992* (UTC). Golden Valley Co.: 5 mi W of Ryegate, *Beetle 12278* (UTC). Missoula Co.: Sunset Prarie Ranger Lookout, *Barkley 1755* (UTC); Grant Creek, *Rose 527* (UC, UTC). Park Co.: Livingston, 25 Jul 1901, *Scheuber s.n.* (UC); 12 mi E of Livingston, *Shultz & Hysell 11968* (UTC); NW of Wilsall, *Suksdorf 993* (UTC). Ravalli Co.: 10 mi N of Hamilton, *Beetle 13936* (MO). Wheatland Co.: 0.5 mi E of Harlowton, 21 Aug 1956, *Rauzi s.n.* (UTC).—NEVADA: Churchill Co.: Carson Sink region, *Kennedy 1672* (MO); E shore of Lake Lahontan, *Shultz & Shultz 8635* (UTC); W side of the Toiyabe Mtns, *Shultz & Shultz 8638* (UTC). Clark Co.: Kyle Canyon, *Clokey 7386* (UTC). Elko Co.: 8.5 mi E of Carlin, *Beetle 13384* (RM); Grande Ranch, *Holmgren 1988* (UTC); on the Boyes Ranch, N of Wells, *Johansen 18* (UTC); Cobre, 1 Sep 1906, *Jones s.n.* (UTC); Big Bend Creek, *Leonard 191* (UTC); S of Brush Creek Ranch, 21 Sep 1938, *Passey s.n.* (UTC); Adobe Range, *Pinzl 9250* (UTC), *Pinzl 12679* (UTC); W side of Pequop Mtns, *Shultz & Garrison 20330* (UTC); E side of pass through Independence Mtns, *Shultz & Shultz 2382* (UTC); 51 mi S of Wendover, on alt. Hwy 93 to Ely, *Shultz & Shultz 4552* (UTC); Pilot Mtns, below Copper Mtn, *Shultz & Shultz 8149* (UTC); base of Copper Mtns, *Shultz & Shultz 10189* (UTC); Star Valley, *Shultz & Shultz 10251* (UTC); valley 5 mi W of Elko, *Shultz et al. 7446* (UTC). Esmeralda Co.: Fishlake Valley, 23 Jun 1958, *Ferguson s.n.* (UTC). Eureka Co.: E of Battle Mountain, between Dunphy and Elko, near I-80 milepost 272, *Shultz & Garrison 20328* (UTC). Humboldt Co.: 5 mi N of Paradise Valley, *Beetle 14142* (RM); Pine Forest Range, *Holmgren & Reveal 1702* (UC, UTC); Indian Creek, *Lewis 3710* (UTC); Dutch John Creek crossing, Santa Rosa Mtns, *Lewis 3713* (UTC); Dutch John Creek crossing, *Lewis 3714* (UTC); W side of the Santa Rosa Range, *Pinzl 12676* (UTC); 33 mi S of McDermitt, *Porter & Porter 7705* (RM); Humboldt, *Redfield 180* (MO). Lander Co.: Austin Summit, *Beetle 13397* (UTC); along Bodi Creek, near Hwy 50, *Genz 8966* (UTC); between Neve Pass summit and Mt Air summit, *Shultz & Shultz 8640* (UTC). Lincoln Co.: Panaca, 6 Sep 1912, *Jones s.n.* (UTC); Mahogany Mtns, near Big Summit, *Shultz & Shultz 6243* (UTC); Toquop Wash, *Shultz & Shultz 7609* (UTC). Lyon Co.: Sweetwater Ranch, *Reveal 238* (UTC). Mineral Co.: without locality, *Graham 289* (RM); Carson Sink region, *Kennedy 1692* (DS);Wassuk Range, *Pinzl 11726* (UTC); 15 mi S of Hawthorne, at Whiskey Flat, *Reveal 214* (CAS, NY, UT, UTC); 2 mi W of Esmeralda County line, on Hwy 6, *Shultz & Shultz 4601* (RM, UTC). Nye Co.: vicinity of Currant, *Bentley 1915* (MO, RM); Toquima Range, *Genz 9049* (UTC); Shoshone Mtn, *Reveal 1969* (UTC); Deadhorse Flat, *Reveal 2032* (UTC). Pershing Co.: Humboldt Range, *Pinzl 12663* (UTC); Hills NW of Reno, just E of Nevada County line, *Shultz 20325* (UTC). Storey Co.: S of Carson Valley, *Shultz et al. 19775* (UTC). Washoe Co.: 6 mi N of Reno, *Shultz 10247* (UTC); S of Reno, *Shultz 19772* (UTC); 6 mi N of Reno, *Shultz & Shultz 10246* (UTC); Bald Mtn, *Tiehm & Rogers 4775* (UT, UTC). White Pine Co.: Berry Creek Ranger Station, *Moore M-535* (RM); 7 mi WSW of Ely, *Shultz & Shultz 4558* (RM, UTC); Schell Creek Range, *Tart & Howell 2705* (UTC); Schell Creek Range, *Tart & Howell 2719* (UTC).—NEW MEXICO: Rio Arriba Co.: Tierra Amarilla, *Benner 6068* (RM); Carson Natl Forest, *Copple 329* (RM); Tierra Amarilla divide, *Talbot 15* (RM). Taos Co.: 5 mi SW of Ute Mtn, *Hendricks et al. 1034* (RM); Sunshine Mesa, Ranchos de Taos, *Shultz 19675* (UTC), *Shultz 19676* (UTC); Sunshine Mesa, *Shultz & McReynolds 20170* (UTC).—NORTH DAKOTA: Slope Co.: Black Butte, *Moir 2299* (ND, UC).—OREGON: Baker Co.: 12 mi SE of

Baker, *Ward & Ward 888* (DS). Deschutes Co.: 3 mi N of Sisters, *Cronquist 6849* (UTC); 3 mi N of Sisters, *Steward 6849* (UTC); 5 mi N of Bend, *Ward & Ward 831* (DS, RM, UC). Grant Co.: Dayville, *Beetle 12864* (RM). Harney Co.: 32.4 mi S of Burns, *Acker 52* (UTC); ca. 6.9 mi NW of Diamond, *Acker 73* (UTC); ca. 7.6 mi NW of Diamond, *Acker 90* (UTC); Burns, *Beetle 12793* (UTC). Jefferson Co.: without locality, *Ward & Ward 832* (UC). Lake Co.: 0.5 mi E of Dismal Creek, *King 29* (RM). Malheur Co.: Snively Gulch Ford on Owyhee Dam Rd, *Ertter 273a/4* (UTC); Succor Creek drainage, *Shultz et al. 7453* (UTC), *Shultz et al. 7456* (UTC), *Shultz et al. 7470* (UTC); 8 mi N of Vale, *Ward & Ward 891* (RM). Umatilla Co.: McKay Creek, *Ingram B-291* (RM). Wasco Co.: near Maupin, *Abrams 9549* (DS); sandy soil along railroad tracks, *Ward & Ward 829* (DS, UC).—SOUTH DAKOTA: Fall River Co.: 2 mi E of Oelrichs, *Barr 1024* (RM).—UTAH: Beaver Co.: Needle Range, *Holmgren 413* (RM); Wah Wah Mtns, *Holmgren 427* (RM). Box Elder Co.: Dry Canyon Mtn, *Dixon 1098* (UTC); Hogup Mtns, 23 May 1986, *Gilbert s.n.* (UTC); Promontory Point, *Holmgren 1562* (UTC), *Holmgren 15661* (UTC); 3 mi W of Snowville, *Maguire & Knowlton 2246* (MO, UC, UTC); base of Raft River Mtns, *Shultz & Shultz 10184* (UTC); base of W slope of the Wellsville Mtns, *Shultz 5472* (RM, UTC); S of Howell, *Shultz 20149* (UTC); Promontory Mtns, near Big Fill, *Shultz & Shultz 4134* (UTC); Promontory Mtns, *Shultz & Shultz 4135* (UTC); 10 mi N of Grouse Creek, *Sommerville 3* (UTC); W Grouse Creek Mtns, *Sommerville 5* (UTC); E side of section, *Sommerville 7* (UTC); Giant W on Meadow Creek Butte, *Sommerville 8* (UTC); 0.5 mi E of Meadow Creek Butte, *Sommerville 9* (UTC); 1 mi NW of intersection going to Goose Creek, *Sommerville 10* (UTC); Meadow Creek Butte area, *Sommerville 12* (UTC). Cache Co.: foothills of Bear River Range, *Maguire 261* (UTC); mouth of Green Canyon, *Shultz 10143* (UTC); E of Hatchery, *Shultz & Kobler 4447* (UTC). Carbon Co.: canal bank W of Price, 3 Aug 1947, *Flowers s.n.* (UT). Duchesne Co.: 17 km NW of Tabonia, *Cronquist et al. 12035* (UTC); 2.5 mi SE of Tabonia, on hwy, *Goodrich 20234* (UTC); town of Mt Emmons, *Harrison & Larsen 7744* (BRY, UTC); 5 mi W of Mt Emmons, 8 Sep 1936, *Stoddart & Passey s.n.* (UTC). Garfield Co.: Pet Hollow, *Fertig 21417* (UTC); Dixie Natl Forest, 8 Sep 1961, *Folks s.n.* (UTC); Short Canyon, *Hallsten 2555* (UTC); 5 mi W of Escalante, *Maguire 15589* (UTC), *Maguire & Richards, Jr. 15589* (UTC); 12 mi NE of Escalante, *Welsh 19282* (RM). Grand Co.: Sego Canyon, *Stockton 162* (UTC). Juab Co.: 5.75 mi E of Nephi, *Goodrich 16468* (UTC); Nephi, *Hatch 130* (UTC); Trout Creek, *Have 130* (UTC); 3.5 mi W of Nephi, *Jones 219* (RM); E of Deep Creek Mtns, *Shultz & Shultz 8164* (UTC); above Yuba Dam Reservoir, *Shultz et al. 10154* (UTC). Kane Co.:Vermilion Cliffs, *Fertig 20903* (UTC); 15 miles E of Kanab, *Fertig 20909* (UTC); at the head of Kaibab Gulch, *Shultz 9971* (UTC); Johnson Canyon, *Shultz & Shultz 9908* (UTC). Millard Co.: Pavant Range, *Shultz & Shultz 7408* (UTC); Swasey Spring, *Stewart 6* (UTC); Swasey Spring, *Stewart 7* (RM). Piute Co.: Grass Valley, *Shultz 6779* (UTC). Rich Co.: 0.5 mi S of Ideal Beach, *Maguire & Stoddart 21656* (UTC), *Maguire & Stoddart 21721* (UTC), *Maguire & Stoddart 21722* (UTC), *Maguire & Stoddart 21723* (UTC); E Shore of Bear Lake, *Piep 04.082* (UTC); E of Bear Lake, *Shultz 4520* (UTC); E side of Bear Lake, *Shultz et al. 19824* (UTC); Eden Canyon, N of Laketown, *Shultz et al. 20290* (UTC); Deseret Land and Livestock Ranch, *Shultz et al. 20297* (UTC); Deseret Land and Livestock Ranch, *Thorne 3063* (UTC). Salt Lake Co.: Oquirrh Mtns, *Cottam 1446* (UT); above Jordan River, *Shultz 19678* (UTC); Camp Williams, *Shultz 19679* (UTC); mouth of Big Cottonwood Canyon, *Shultz & Shultz 7249* (UTC); Lambs Canyon, *Vickery 2638* (COLO, UT, UTC). San Juan Co.: Indian Canyon, 11 Sep 1954, *Flowers s.n.* (UT); road to Newspaper Rock, *Shultz & McReynolds 20173* (UTC); Kane Creek road, *Shultz & McReynolds 20179* (UTC); Grand Gulch Plateau, *Shultz et al. 9014* (UTC); La Sal Flat, *Willenthier 25* (RM). Sevier Co.: Willow Creek, 29 Aug 1962, *Jeffery s.n.* (UTC); Granite Ridge, 12 Sep 1961, *Nelson s.n.* (RM, UTC); Fishlake Mtns, *Shultz & Shultz 7400* (UTC). Tooele Co.: Site 22, *Long 580* (UTC); 2 mi N of Goldhill, *Shultz & Shultz 8163a* (UTC); Stansbury Mtns, *Taye 309* (UTC); Stansbury Mtns, *Taye 1262* (UTC); 3 mi W of Grantsville, *Ward & Ward 930* (UC). Uintah Co.: 11.2 km N of Maeser, *Barker 1982* (UTC); Vernal, *Fischer 63* (UTC); pipeline route, *Folks 249* (UTC); about 8 mi W of Vernal, along Hwy 40, *Neese 6789* (UTC). Washington Co.: along large wash on flat, *Christian 1121* (UTC); 7 mi S of Shivwits, 26 Aug 1956, *Ferguson s.n.* (UTC); Bull Valley Mtns, *Shultz & Shultz 7063* (UTC); between St. George and Beaver, *Tidestrom 33445* (RM). Wayne Co.: Henry Mtns, *Everitt 149* (COLO); near Loa, *McArthur U-44* (BRY, RM, UTC).—WASHINGTON: Asotin Co.: 5 mi E of Peola, *Daubenmire 60116* (RM). Benton Co.: McNary Dam, *Beetle 12771* (RM). Douglas Co.: E of Douglas, on Hwy 2, *Shultz 20249* (UTC); S of Chelan, *Shultz & McReynolds 20241* (UTC); E of Douglas, *Shultz & McReynolds 20250* (UTC); at edge of Lake Chelan, *Ward & Ward 853* (DS). Grant Co.: dry land near Moses Lake, *Schallert 7044* (MO). Klickitat Co.: High river bank at Bingen, *Suksdorf 2687* (DS, MO). Okanogan Co.: Brewster, *Beetle 12893* (RM); Nighthawk, 4 Oct 1911, *Jones s.n.* (UTC). Whitman Co.: Palouse Falls, *Meyer 1712* (MO, RM).—WYOMING: Albany Co.: Eagle Rock Rd, *Asplund 13* (RM); foothills above Centennial, *Bliss 404* (RM); Laramie Range, *Finzel 311* (RM); Platte Canyon, 4 Sep 1901, *Nelson s.n.* (MO); Laramie Plains, *Sharp 430* (RM); 20 mi S of Laramie, near Hwy 231, *Shultz et al. 6153* (UTC). Big Horn Co.: without locality, *Current 751* (RM). Carbon Co.: Natrona County line, *Asplund 6* (RM); Shirley Basin, *Current 471* (RM); without locality, *Nelson 1161* (RM). Converse Co.: Roush Farm, *Pfadt 202* (RM). Crook Co.: top of Devil's Tower, 21

Apr 1957, *Doody s.n.* (RM). Fremont Co.: Old Boysen Dam site, *Beetle 13200* (RM); Wind River Range, *Fisser 762* (RM); 0.5 mi S of Big Wind River bridge, 27 Aug 1956, *Palmer & Palmer s.n.* (MO); Crook's Gap in Green Mtns, *Porter 5571* (RM). Hot Springs Co.: N flank of Owl Creek Range, *Fisser 305* (RM); Grass Creek Basin, *Porter 6786* (RM). Natrona Co.: between Casper and Midwest, *Beetle 10252* (RM). Sublette Co.: Boulder Creek Flats, *Nelson 1111* (MO, RM); E of Pinedale, bank of New Fork River, *Shultz 19839* (UTC). Sweetwater Co.: Jim Bridger Coal Mine, 23 Sep 1980, *Barker s.n.* (UTC); 53 mi E of Farson, *Lang 111* (RM); along Black Fork River, *Lang 113* (RM); without locality, *Ownbey 1144* (UTC, RM); N edge of Rock Springs, *Porter & Porter 10099* (RM). Teton Co.: 2 mi S of Jackson Hole, *Beetle 12809* (RM); mesa of Yellowstone River, *Mearns 4863* (DS); Jackson Hole Wildlife Park, *Reed & Reed 948* (RM); Grand Teton Natl Park, *Reed & Reed 2560* (RM); Hoback Canyon, *Reed & Reed 3043* (RM); Grand Teton Natl Park, *Sabinske 23B* (RM). Uinta Co.: near Fort Bridger, *Leidy 61* (RM). Washakie Co.: 10 mi S of Tensleep, *Beetle 6127* (RM); W of Worland, *Nichols 555* (RM). Weston Co.: Bacon Creek, 25 Aug 1894, *Nelson s.n.* (RM). **Mexico.** BAJA CALIFORNIA: road between San Felipe and Ensenada, *Beetle M-188* (RM); San Carlos River, *Eastwood 12427* (CAS); La Rumorosa Graveyard, 4 Sep 1957, *Ferguson s.n.* (ARIZ, RM); 16 mi E of Ensenada, 5 Sep 1957, *Ferguson s.n.* (RM); 10 mi E of Ensenada, 5 Sep 1957, *Ferguson s.n.* (RM); Hechicera on Hwy 2, 1957, *Ferguson s.n.* (RM); Jacumba, 22 Jul 1922, *Fisher s.n.* (DS); Santo Domingo Canyon, *Howell 31067* (RM); SE of Ensenada, *Howell 31082* (CAS, RM); 2.5 mi S of La Rumorosa, *Raven 16826* (RM); Sierra San Pedro Martir, *Shultz & Shultz s.n.* (UTC); 2 mi S of La Rumorosa, *Thorne 57412* (UTC); 15 mi above Red Rock, *Ward & Ward 783* (DS); Santo Domingo River, *Ward & Ward 787* (RM).

Artemisia tridentata subsp. *tridentata* is the common sagebrush of deep, well-drained soils in the Great Basin of western North America, where it is often the dominant shrub of valleys and open grasslands. On drier sites and on well-drained soils of high plateaus or benches, it is replaced by *A. tridentata* subsp. *wyomingensis*. In deep soils of dry valley bottoms throughout the Great Basin, subsp. *tridentata* is conspicuous by its great height and wide inflorescences. It is common along roadways, fencerows, and other areas where moisture is more readily available through runoff or reduced competition. Sagebrush is often cleared by burning, herbicide spray, or the practice of "chaining," and is replaced by grasses (especially crested wheatgrass) suitable for livestock grazing (for a review of the literature, see Welch 2005).

I made no attempt to segregate the proposed variants within the subspecies, but there are geographic variants that are distinctive. *Artemisia tridentata* var. *angustifolia* was described from western Nevada and represents a narrow-leaved form that is common in dry sites (annual precipitation less than 40 mm). These xeromorphic populations occur in valley bottoms of Oregon, eastern California, western Nevada, Arizona, and New Mexico.

Tetraploid individuals are rare in subg. *Tridentatae* and tend to occur at higher elevations where one would normally find Wyoming or Mountain sagebrush. McArthur and others have informally called these tetraploid populations "upland sage," but no formal name has been applied.

9b. Artemisia tridentata subsp. **parishii** (A. Gray) H. M. Hall & Clements, Publ. Carnegie Inst. Wash. 326: 137. 1923. *Artemisia parishii* A. Gray, Proc. Amer. Acad. Arts 17: 220. 1882. *Artemisia tridentata* var. *parishii* (A. Gray) Jepson, Man. fl. pl. Calif. 1140. 1925. *Artemisia tridentata* f. *parishii* (A. Gray) Beetle, Rhodora 61: 83. 1959. *Seriphidium tridentatum* subsp. *parishii* (A. Gray) W. A. Weber, Phytologia 55: 8. 1984.—TYPE: U.S.A. California: Los Angeles Co., Newhall, 1881, *Parish & Parish 1065* (lectotype, here designated: GH!; isolectotypes: MO! NY, RSA! UC! US).

Medium-sized to tall shrubs, 10–20 (–30) dm tall; crowns rounded; vegetative branches interspersed among the flowering stems, with inflorescence branches appearing immersed in the elongated vegetative branches. Leaves 1.5–2.5 (–3.5) cm long, 0.1–0.3 cm wide, narrowly cuneate or lanceolate, usually 3-lobed, sometimes entire. Capitula 2–4 mm high, 1–2 mm wide, ovoid, usually nodding, sometimes erect. Inflorescences often leafy, broadly paniculate, 15–30 cm long, 2–6 cm wide; branches widely spreading, often drooping; leaves of flowering branches nearly as long as those of the vegetative stems. Florets 3–7. Cypselae hairy or glabrous. Chromosome number: 2n = 36 (Ward 1953). Fig. 31.

Common names. Parish sagebrush, Mohave sagebrush.

Phenology. Flowering mid-summer to late fall.

Distribution (Fig. 32). U.S.A.: California, Nevada, Utah; Mexico: Baja California; in loose sandy soils of valleys and foothills; 300–1800 m.

Additional Specimens Examined. **U.S.A.** California: Douglas Co.: 1.5 mi NE of Desert Station, *Lee 89* (UC). Inyo Co.: 26 mi S of Mohave, *Applegate 7000* (DS); head of Marble Canyon, *Munz 20174* (DS, RSA); 7 mi E of Lone Pine, *Shultz & Shultz 4623* (RM, UTC); Tuttle Cr drainage below Mount Whitney, *Shultz & Shultz 5013* (UTC); Owens Valley, *Wolf 2511* (DS, RSA). Kern Co.: S of Rosamont, *Wolf 2620* (DS, RSA, UC). Los Angeles Co.: Newhall, *Abrams 6363* (DS, MO, RM); Santa Clara River Valley, *Ewan 5296* (DS, RM); Antelope Valley, *Hall 10584* (UC); 2 km W of Rosamond, *Hall 10959* (RM, UC); 3 mi SW of Newhall, *Howell 27484* (CAS, RM, UT); Lancaster, *Hoffmann 28 Sep 1931* (CAS); Lancaster, *Jensen 3069* (UC); Newhall, *Munz 7802* (DS, POM); near New Hill, *Parish & Parish 1065* (MO); Rancho Santa Ana Botanic Garden, *Shultz & Shultz 5719* (UTC); 2 mi NW of Saugres, *Thompson 1425* (CAS, DS, UC). Mono Co.: Bridgeport, *Rose 6470* (UC). San Bernardino Co.: Adelanto Junction, *Reveal 1175* (DS, RSA, UTC). Ventura Co.: Santa Clara River, *Hall 20 Oct 1919* (UC).—Nevada: Lyon Co.: Sweetwater, *Beetle 12962* (RM). Mineral Co.: Montgomery Pass, *Shultz & Shultz 4600* (RM, UTC). Nye Co.: vicinity of Currant, *Bentley 1 May 1915* (DS).—Utah: Garfield Co.: 5 mi W of Escalante, Cave Cr Canyon, *Shultz 20277* (UTC); 6.6 mi SW of Circleville along Hwy 86, *Suttkus 75-27-2* (UTC). San Juan Co.: McCracken Mesa, *Van Cott V-198* (UTC). Washington Co.: E side of Pine Valley Mtns, *Shultz 17779* (UTC); Anderson Junction, *Turner & Turner 68-184* (UTC). **Mexico.** Baja California: 2.5 mi W of San Carlos Hot Springs, *Harbison 20419* (RM); Valle Trinidad, *Shultz et al. 5735* (UTC), *Shultz et al. 5747* (UTC).

Artemisia tridentata subsp. *parishii* is found in coastal ranges in southern California and Baja California, and inland to areas south of the Great Basin. It has been distinguished traditionally by the presence of drooping flowering branches and hairy cypselae. These characteristics occur on the type specimen, but only sporadically in populations throughout the warm desert regions of southern California, Nevada, and Utah. I define the subspecies as having long leaves and long vegetative branches that are strictly erect. This treatment expands the earlier circumscription for subsp. *parishii* (Shultz 1993) to include populations from the southern Sonoran and Mojave deserts, Owens Valley, and Colorado Plateau.

Morphologically, subsp. *parishii* is closest to subsp. *tridentata* in appearance. The leaves are long and narrow as is typical for subsp. *tridentata*, and for many years I thought the taxon was restricted to coastal California. Comparisons of populations from California (subsp. *parishii*) and Nevada (subsp. *tridentata*) grown in a common garden (Shultz 1991a; Shultz et al. 1991) reveal differences in physiology as well as in morphology.

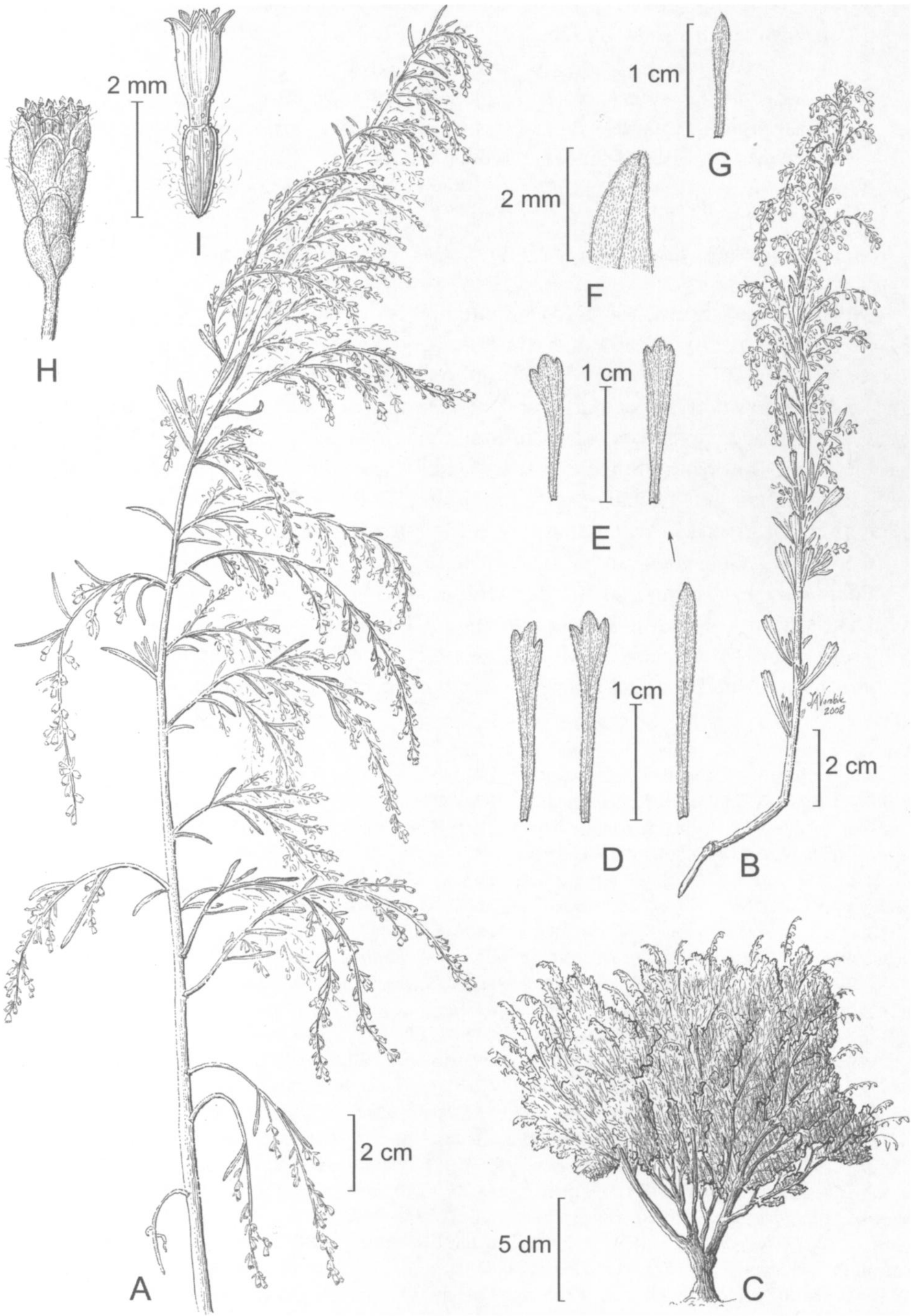

FIG. 32. *Artemisia tridentata* subsp. *parishii*. A. Flowering branch. B. Inflorescence branch. C. Habit. D. Ephemeral leaves. E. Persistent leaves. F. Detail of leaf tip. G. Inflorescence leaf. H. Capitulum. I. Floret and cypsela. (Based on: A. *Hall s.n.*, 20 Oct 1919; B, D, E, G, *Shultz & Shultz 4600*; F, *Shultz & Shultz 5719*; H, I, Stark *4525*.)

9c. Artemisia tridentata subsp. **vaseyana** (Rydberg) Beetle, Rhodora 61: 83. 1959. *Artemisia vaseyana* Rydberg, N. Amer. Fl. 34: 283. 1916. *Artemisia tridentata* var. *vaseyana* (Rydberg) B. Boivin, Phytologia 23: 91. 1972. *Seriphidium vaseyanum* (Rydberg) W. A. Weber, Phytologia 58: 384. 1985.—TYPE: U.S.A. Washington: Cascade Mts. [from Mt. Cooper, above Lake Chelan], 1889, *G. Vasey 480* (holotype: NY!; isotype: GH!).

Artemisia tridentata var. *pauciflora* Winward & Goodrich, Great Basin Naturalist 45: 102. 1985.—TYPE: U.S.A. Utah: Utah Co., left fork of Hobble Creek, *S. Goodrich et al. 21492* (holotype: BRY!; isotypes: MO! UTC!).

Medium-sized shrubs, 4–8 (–15) dm tall, highly aromatic; crowns flat-topped; vegetative branches of nearly equal lengths; inflorescence branches conspicuously overtopping the vegetative branches. Leaves 12–35 mm long, 3–7 mm wide, broadly cuneate, shallowly 3-lobed to (rarely) irregularly toothed. Capitula 2–3 mm high, 1.5–3 mm wide, narrowly to broadly campanulate, erect. Inflorescences narrowly paniculate, 10–15 cm long, 2–6 cm wide; flowering branches usually widely spreading, rarely drooping, conspicuously overtopping the vegetative branches. Florets 3–9. Cypselae glabrous. Chromosome number: 2n = 18, 36 (McArthur et al. 1981; McArthur & Sanderson 1999). Fig. 33A–H.

Common name. Mountain big sagebrush.

Phenology. Flowering mid-summer to late fall.

Distribution (Fig. 34). Canada: British Columbia; U.S.A.: Arizona, California, Colorado, Idaho, Montana, New Mexico, North Dakota, Nevada, Oregon, Utah, Washington, Wyoming; usually in rocky soils, in montane meadows, sometimes in forested areas; 2000–2800 m.

ADDITIONAL SPECIMENS EXAMINED. **Canada.** BRITISH COLUMBIA: Osoyoos, *Beetle 13984* (RM). **U.S.A.** ARIZONA: Coconino Co.: Navajo Mtn, *Clute 93167* (RM). Mohave Co.: Dellenbaugh site, *Shultz 19589* (UTC).—CALIFORNIA: Alpine Co.:; without locality, *Genz 8910* (UTC); just W of Monitor Pass, *Howell 41010* (CAS)1.5 mi W of Ebbe, *Lee 1* (RM); 1.25 mi E of Woodfords, *Lee 87* (UC). El Dorado Co.: Eldorado Natl Forest, *Johannsen 82653* (RM); along Tahoe-Yosemite Trail, *Robbins 1396* (UC). Fresno Co.: S Fork of King's River, *Culbertson 4809* (MO); Mono Creek, *Thomas & Thomas 4653* (DS). Inyo Co.: E flank of Mt Whitney, *Beetle 12937* (UTC); Inyo Mtns, *Dedecker 2857* (CAS); Thorndike Camp, 12 Jun 1958, *Ferguson s.n.* (UTC); Mahogany Flats, 14 Jun 1958, *Ferguson s.n.* (UTC); White Mtns, 16 Jun 1958, *Ferguson s.n.* (UTC); Whitney Portal Rd, *Howell 40980* (CAS); head of Wyman Canyon, *Munz 21041* (RSA); Big Pine Creek, near Glacier Lodge, *Reveal 218* (UTC); below Mono Pass, on E side, *Robinson 141* (RSA); Telescope Peak, *Roos 2796* (RSA); Baldy Peak, *Roos 2803* (RSA); Mahogany Flats, *Roos 2805* (RSA); Wild Rose Canyon, *Roos & Roos 2807* (DS); E of Andrew Mtn, *Roos & Roos 6210* (CAS); White Mtns, 6 mi ENE of Big Pine, *Shultz 5025* (UTC); Rock Creek Lake, *Shultz 5688* (UTC); trail to Mt Whitney, *Shultz & Shultz 4605* (UTC, RM); White Mtns, above Westguard Pass, *Shultz & Shultz 5030* (UTC, RSA); Rock Creek Lake, *Shultz & Shultz 5687* (UTC); trail to Mono Pass, *Shultz & Shultz 5707* (UTC); 5 mi S of Lee Vining, along Hwy 395, *Shultz & Shultz 5712* (UTC); White Mtns, *Shultz et al. 19796* (UTC), *Shultz et al. 19797* (UTC), *Shultz et al. 19798* (UTC), *Shultz et al. 19799* (UTC), *Shultz et al. 19800* (UTC), *Shultz et al. 19806* (UTC), *Shultz et al. 19811* (UTC), *Wolf 2593* (DS), *Wolf 4203* (RM). Kern Co.: Tehachapi Peak, *Dudley 309* (DS); Harvey Mtn, *Robbins 2155* (UTC); 2 mi N of Weldon, *Vogelin 260* (UC); Tojun Range, *Twisselmann 4597* (CAS); Cuddy Canyon, *Wheeler 294* (DS). Lassen Co.: Harvey Mtn, *Robbins 2155* (UTC); Harvey Valley, *Robbins 2157* (UC); 41 mi N of Susanville, on Hwy 395, *Shultz & Shultz 8604* (UTC); Modoc Natl Forest, *Smith 1026* (RM). Los Angeles Co.: San Gabriel Mtns, *Ewan 9859* (GH). Merced Co.: 1.5 mi S of Piedra Azul Canyon, *Janeway 3665* (UTC). Modoc Co.: ca. 20 mi S of Tulelake, *Shultz & Shultz 8587* (UTC). Mono Co.: Mammoth Lakes, *Beetle 12935* (MO); Lee Vining Grade, *Hall 11713* (UC); Sweetwater Mtn, *Hardman 17525* (CAS); Mono Mills, *Keck 5021* (UTC); Sonora Pass Rd, *Keck 5028* (DS); Sagehen Meadow, *Reveal 217* (UTC); Flat Canyon, *Reveal 1174* (UTC RSA); Rock Creek Canyon, *Shultz & Shultz 5709* (UTC); 8 mi S of Bridgeport, *Shultz et al. 19781* (UTC); Warren Creek crossing, *Shultz et al. 19791* (UTC); Warren Creek, *Shultz et al. 19792* (UTC); Mt Lola, *Trowbridge 8095* (CAS); 3 mi W of Benton Range, *Wolf 2565*

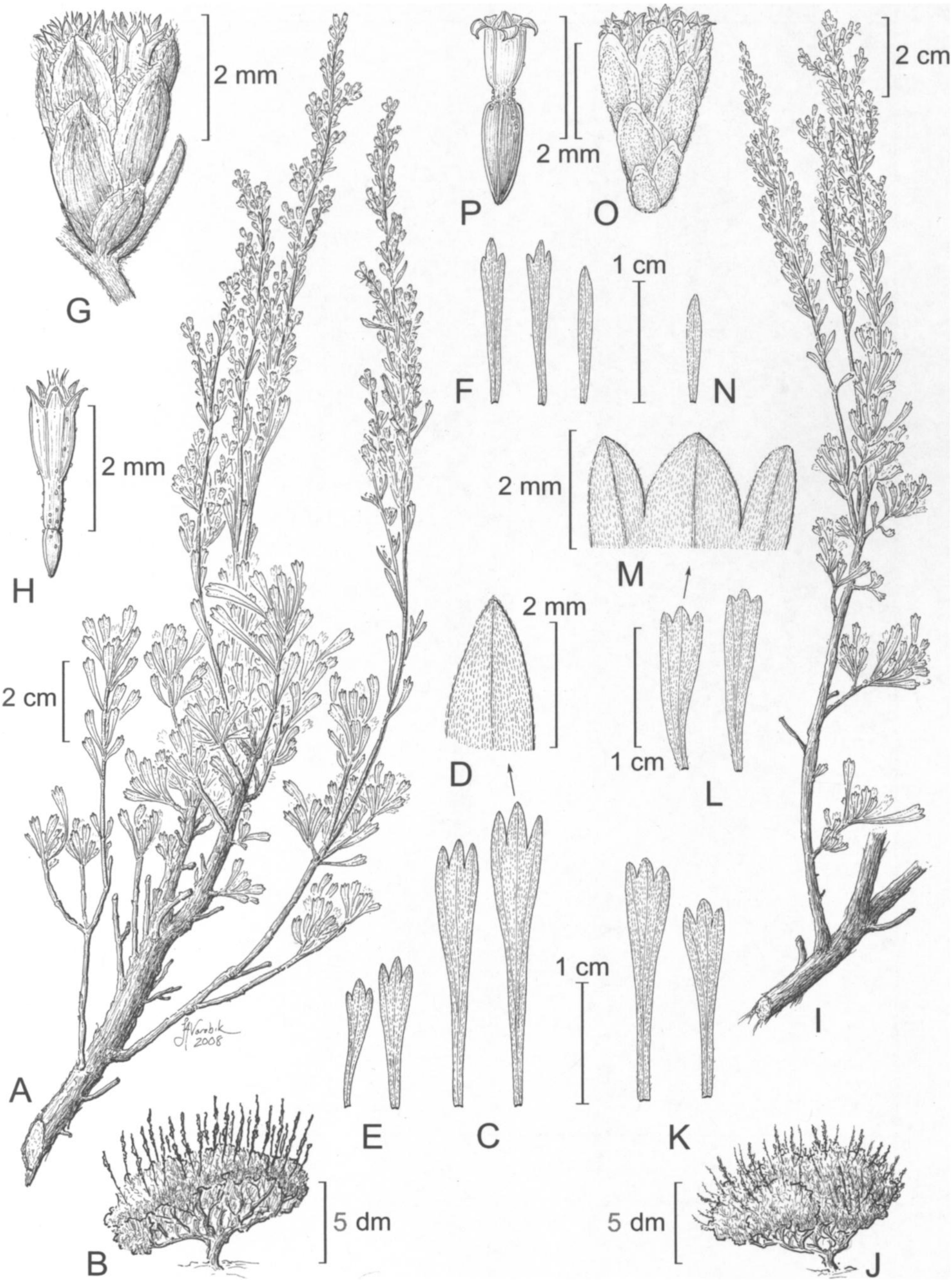

FIG. 33. *Artemisia tridentata*. A–H: *A. tridentata* subsp. *vaseyana*. A. Branch with leafy and flowering shoots. B. Habit. C. Ephemeral leaves. D. Detail of leaf tip. E. Persistent leaves. F. Inflorescence leaves. G. Capitulum. H. Floret. I–P: *A. tridentata* subsp. *wyomingensis*. I. Branch with leafy and flowering shoots. J. Habit. K. Ephemeral leaves. L. Persistent leaves. M. Detail of leaf tip. N. Inflorescence leaf. O. Capitulum. P. Floret and cypsela. (Based on: A–H, *Shultz 4509*; I, M, *Barker s.n.*, without date; G, J, K, L, N–P, *Shultz 9027*.)

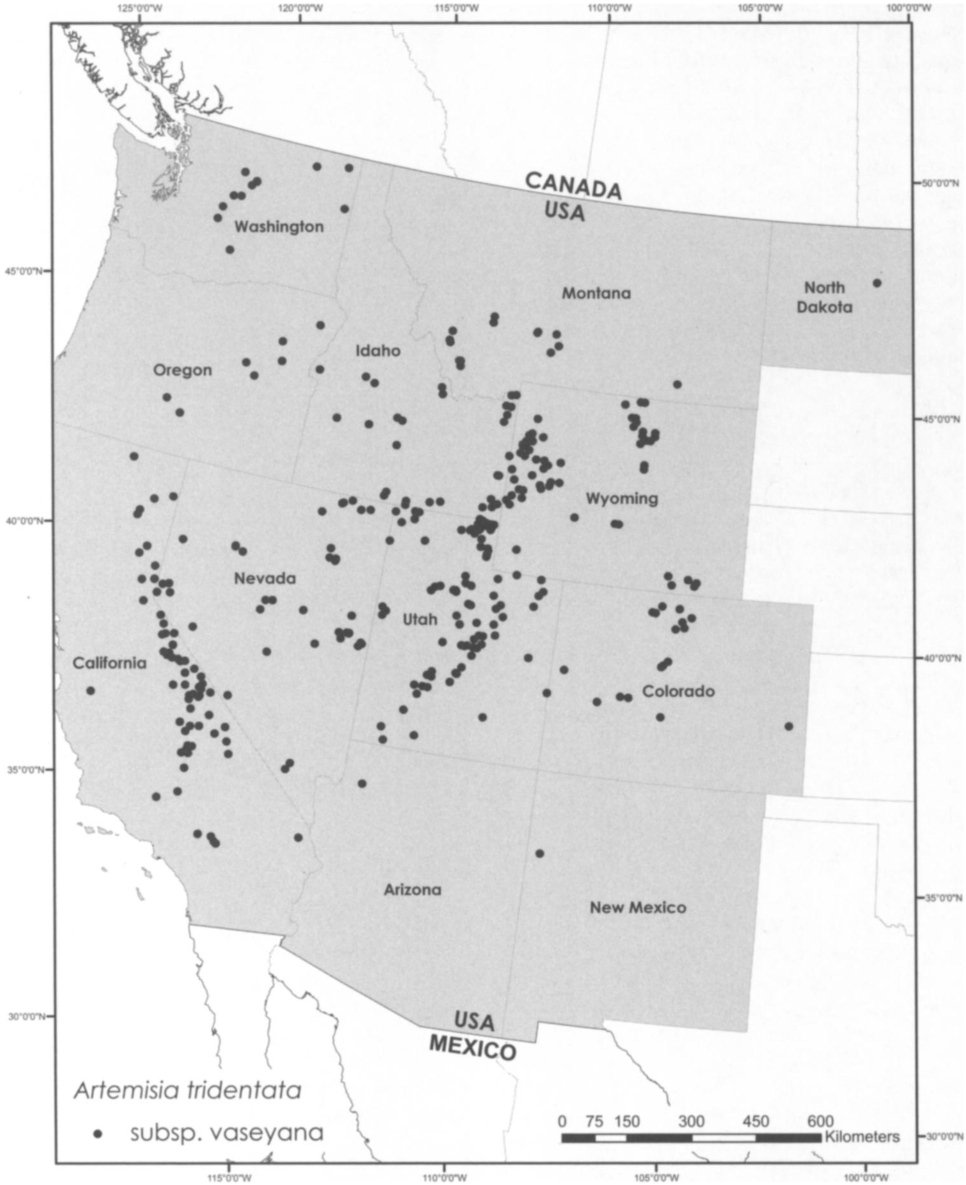

FIG. 34. Distribution of *Artemisia tridentata* subsp. *vaseyana*.

(CAS). Nevada Co.: Donner Lake, *Danner 192* (RM); Boca Dam, *Shultz & Shultz 10220* (UTC), *Shultz & Shultz 10221* (UTC); head of Sagehen Creek, *True & Howell 6029* (CAS). Placer Co.: Tahoe Natl Forest, 16 Jul 1934, *Bolt s.n.* (RM). Plumas Co.: Mt Ingalls, *Albertus 263* (UC); Feather River, *Barker 277* (CAS); Feather River Canyon E of Quincy, *Shultz & Garrison 20318* (UTC). San Bernardino Co.: Sugarloaf Mtn, *Balls 20199* (DS); Warner Hot Springs, Sep 1953, *Beetle s.n.* (CAS); Holcomb Valley, *Shultz & Thorne 4709* (UTC), *Shultz & Thorne 4710* (RSA, UTC); below Hitchcock Ranch, in Holcomb Valley, *Thorne et al. 53479* (UTC); near Boulder Bay, *Ward 978* (DS); Johnson Grade, *Wolf 4394* (RSA). Sierra Co.: 4 mi NE of Sierraville, *Lewis 541* (UC). Tulare Co.: ca. 40 km NE of Kernville, *Cronquist & Renner 12165* (UTC); Sequoia Natl Park, *Frost 7899* (UC);

between Church Dome and Black Mt, *Howell & True 48577* (CAS); Kennedy Meadow Campground, *Howell & True 43819* (CAS); Sequoia Natl Forest, *Lewis 18* (RM); southern Sierra Nevada Mtns, *Shultz & Shultz 5658* (UTC); SW edge of Monache Meadows, *Shultz & Shultz 5663* (UTC); 18 mi NW of hwy intersection, *Shultz & Shultz 5679* (UTC). Tuolumne Co.: W side of Tioga Pass, by reservoir, *Beetle 12943* (UTC); W slope of Sierra Nevada, *Wolf 5463* (RM). Ventura Co.: near lake in woods, *Balls 22205* (RM); Sespe Gorge, *Jepson 20205* (JEPS).—COLORADO: Archuleta Co.: ca. 15–25 mi N of Colorado/New Mexico border, on US Hwy 84, *Barkworth & Hoge 5098* (UTC). Clear Creek Co.: headwaters of Clear Creek, *Patterson 219* (MO). Douglas Co.: Torland, *Munz 3205* (POM). Eagle Co.: Derby Ranger Station, *Read R-167* (RM). Garfield Co.: Bar H-L Park, *Kane 419* (CS); Glenwood Springs, *Thomson RT58* (RM). Grand Co.: 15 mi NE of Kremmling, *Carpenter C-344* (RM); near Arapaho Forest, *Gierisch 1672* (RM); Gilsonite Ranger Station, *Gierisch 1677* (RM); Gilsonite Ranger Station, *McDougall 15* (RM); bluffs above N shore of Grand Lake, *Shultz & Shultz 10483* (UTC). Gunnison Co.: without locality, *Bryant 49* (CS); without locality, *Gierisch 2544* (CS). Jackson Co.: 5 mi SW of Walden, *Beetle 2351* (RM); 7.9 mi S of June State, *Johnson 60* (CS); near town of Coalmont, *Shultz & Shultz 5422* (COLO, UTC), *Shultz & Shultz 54224* (UTC). Kiowa Co.: Powder Wash, *Deming et al. 19-5* (UTC). Larimer Co.: Estes Park, *Cooper 116* (RM); North Park, *Osterhout 33* (RM); North Park, *Osterhout 1825* (RM); The Rustic, *Osterhout 4394* (RM); between Glacier and Mill Creek drainages, *Shultz 7155* (UTC); slopes of Palisade Mtn, *Woodson 1827* (MO). Mesa Co.: without locality, *Fechner 13424* (CS). Montrose Co.: 8 mi W of Montrose, *Rollins 1981* (RM); S rim of Grand Canyon, *Weber & Beck 16924* (UTC). Rio Blanc Co.: Yankee Gulch, *Allard & Walk 641* (CS). Routt Co.: 12 mi S of Oak Creek, *Blake 2340* (DS); Steamboat Springs, *Osterhout 1826* (RM). Saguache Co.: N Rock Cr, *Gierisch 1427* (RM). Summit Co.: Below summit, on mountain slope, *Beetle 12287* (UTC); Breckenridge, *Jones 738* (UTC), *Jones 11569* (MO); Ptarmigan Peak Trail, *Nelson 1224* (CS).—IDAHO: Bannock Co.: Mink Creek Canyon, *Lingenfelter 755* (UC). Bear Lake Co.: ca. 35 mi NE of Preston, *Bright 61-86* (UTC); Snowslide Canyon, Preuss Range, *Shultz & Shultz 8187* (UTC). Blaine Co.: along Alpine Creek, above Alturas Lake, *Cronquist 3755* (MO); N of Ketchum, on road to Stanley, *Shultz & Furlong 20165* (UTC); low hills S of Bellevue, *Shultz & McReynolds 19849* (UTC); 10 mi N of Ketchum, *Shultz & McReynolds 20163* (UTC). Bonneville Co.: Palisade Creek drainage, *Shultz & Shultz 7913* (UTC). Caribou Co.: E of Soda Springs, *Shultz 20190* (UTC), *Shultz 20192* (UTC). Cassia Co.: snow pocket NW of Indian Grove, *John 991* (UTC); Minidoka Forest, *McDonald MC-1365* (RM); City of Rocks, *Shultz & Shultz 8135* (UTC). Custer Co.: near Stanley, *Cronquist 3679* (MO); Challis Natl Forest, *Work 480* (RM). Elmore Co.: Boise Natl Forest, *MacFadden 25198* (CAS); 29 mi N of Mountain Home, *Shultz et al. 7473* (UTC). Franklin Co.: Franklin Basin, *Cottam et al. 15252* (UT). Fremont Co.: ca. 3 mi N of Ashton, *Shultz & Shultz 7933* (UTC); 1.5 mi S of Island Park, *Shultz & Shultz 7950* (UTC); near Mack's Inn, *Ward & Ward 903* (DS); SE of Henry's Lake, *Ward & Ward 909* (DS). Idaho Co.: Nez Perce, North Fork of Skookumchuck Creek, *Halvorson 183* (RM). Lemhi Co.: Gilmore divide, *Beetle 13934* (UTC). Oneida Co.: along road to Meadow Brook Ranch, *Shultz et al. 19649* (UTC); Curlew Valley Natl Grassland, *Shultz et al. 20156* (UTC). Twin Falls Co.: near Shoshone Forest Service Station, *Gierisch 820* (UTC). Valley Co.: N and above Fir Creek, *Lewis 2505* (UTC); Payette Natl Forest, *Martineau 149* (RM). Washington Co.: NE of Weiser, *Rosentreter 842* (SRP).—MONTANA: Beaverhead Co.: 20 mi N of Wisdom, *Beetle 2259* (UTC); 16 mi W of Dillon, *Beetle 12238* (UTC); 14 mi W of Dillon, *Beetle 12242* (UTC); 20 mi N of Wisdom, *Beetle 12259* (UTC); along Steele Creek, *Lesica 8830* (UTC). Flathead Co.: S of Big Prairie, 8 Sep 1939, *Bailey & Bailey s.n.* (UC). Gallatin Co.: Targhee Pass, *Beetle 12226* (UTC); Madison River, *Nelson & Nelson 6781* (UTC). Granite Co.: Drummond, *Booth 56909* (RM). Jefferson Co.: 2 mi NW of Boulder, *Beetle 12006* (UTC). Park Co.: 12 mi E of Livingston, *Shultz 11966* (UTC); Suksdorf's Gulch, *Suksdorf 970* (UTC). Rosebud Co.: 3 mi SW of Birney, 1 Aug 1957, *Bennett s.n.* (UC). Sweet Grass Co.: 14.5 mi S of Ringling area, *Beetle 12248* (UTC); Crazy Mtns, *Ramsden 1002* (UTC).—NEVADA: Clark Co.: Kyle Canyon, *Clokey & Anderson 8566* (UT, UTC). Douglas Co.: below Mt Rose, *Shultz & Shultz 8617* (UTC). Elko Co.: Humboldt Natl Forest, *Boyd & Leonard 106* (UTC); Coon Creek, *Holmgren 1885* (UTC); headwaters of Jack Creek, *Holmgren 1957* (UTC); end of Lamoille Canyon Rd, *Holmgren 2004* (UTC); Terrace Ranger Station, *Holmgren 2006* (UTC); ridge separating Mahue Canyon and Smith Canyon, *Holmgren 2029* (UTC); Lamoille Canyon, *Lewis 1884* (UTC); Jarbidge Mtns, *Lewis 1885* (UTC); Lamoille Canyon, *Lewis 2004* (UTC); 2 mi below Pole Creek Ranger Station, *Lewis 3742* (UTC); near Bear Creek pass, *Lewis & Lewis 3266* (UTC); Dolly Varden Mtns, *Pinzl 9293* (UTC); 8 mi SE of Lamoille, *Suttkus 67-36-6* (UTC). Esmeralda Co.: Mt Magruder, *Ferris 6648* (DS). Eureka Co.: near Pinto Summit, *Shultz & Shultz 8647* (UTC). Lander Co.: Austin Summit, *Genz 8963* (UTC); vicinity of Big Creek Canyon, *Goodner & Henning 1268* (UTC); E of Austin, *Ward & Ward 946* (UTC). Mineral Co.: Mount Grant Grade, *Train 4298* (UTC). Nye Co.: W Mid Valley, *Beatley 5494* (US); Big Cottonwood Canyon, *Johnson & Morgan 52* (UTC); W slope of White Pine Mtns, *Shultz & Shultz 4584* (RM, UTC). Ormsby Co.: E side of Lake Tahoe, *Smith 3661* (CAS). Pershing Co.: Buena Vista Camp, *Shultz & Shultz 10213.1* (UTC); Buena Vista Camp, above Unionville, *Shultz & Shultz 10218* (UTC), *Shultz & Shultz 10219* (UTC). Storey Co.: Gieger

Hill, *Shultz 19773* (UTC); Hwy 395, *Shultz et al. 19776* (UTC). Washoe Co.: Galena Creek, *Archer 5811* (MO); 1 mi N of Frank, *Nordstrom 984* (RM); summit of Mt Rose Hwy, *Rose 38285* (MO). White Pine Co.: Wheeler Peak Rd, *Lewis 2043* (UTC); 2 mi up Wheeler Peak Rd from Lehman Creek Campground, 27 Aug 1969, *Lewis s.n.* (UTC); E slope of Snake Range, *Shultz & Shultz 6297* (UTC); Schell Creek Range, *Tart & Howell 2707* (UTC), *Tart & Howell 2709* (UTC), *Tart & Howell 2711* (UTC); N of Wheeler Peak, *Tart & Howell 2712* (UTC); Schell Creek Range, *Tart & Howell 2713* (UTC); Kalamazoo Summit, *Tart & Howell 2724* (UTC); SW of Ely, *Tart & Howell 2725* (UTC).—New Mexico: Cibola Co.: Zunoi Canyon without locality, *Camazine 47* (COLO). Rio Arriba Co.: northern New Mexico, *Parry 133* (MO).—North Dakota: Billings Co.: upper part of butte, 19 Sep 1935, *Stevens s.n.* (GH).—Oregon: Baker Co.: Blue Mtns, *Ferris 951* (DS). Big Horn Co.: high ridges, *Irwin 9* (RM). Grant Co.: Blue Mtns, *Henderson 5547* (DS); Mt Ruth area, *Reid 265* (RM); 7 mi N of Seneca, *Ward 951* (DS). Lake Co.: Hwy 31, *Chambers & Tyrl 2427* (UTC); approx 17 mi N of Klamath Lake, *Shultz & Shultz 8586* (UTC). Union Co.: Mill Creek, *Sheldon 9020* (RM). Wallowa Co.: dry slopes near Ice Lake, *Peck 18580* (DS); 0.25 mi SW of Aneroid Lake, 22 Aug 1949, *Ward & Ward s.n.* (DS). County unknown: Wallowa Mtns, *Cusick 2486* (MO).—Utah: Beaver Co.: Tushar Mtns, *Taye 3282* (UTC), *Taye 3288* (UTC), *Taye 3654* (UTC). Box Elder Co.: summit of the Raft River Mtns, 25 Aug 1985, *Benson s.n.* (UTC); Raft River Mtns, *Shultz 4258* (UTC, RM); base of W slope of the Wellsville Mtns, *Shultz 5474* (UTC); N slope of the Raft River Mtns, *Shultz & Shultz 4254* (UTC), *Shultz & Shultz 4255* (UTC); Bald Mtn, *Shultz & Shultz 10207* (UTC); Black Pine Mtns, *Shultz et al. 19652.2* (UTC); SW Meadow Creek Butte, *Sommerville 2* (UTC); W slope of Grouse Creek Mtns, *Sommerville 14* (UTC). Cache Co.: around Tony Grove Lake, *Fitz 30* (UTC); ca. 8 mi E of Logan, *Johnson 350402* (UTC); foothills of Bear River Range, *Maguire 262* (UTC); 1 mi E of summit of Logan Canyon, *Maguire 5234* (UC), *Maguire 20121* (UTC); vicinity of summit of Logan Canyon, *Maguire 20131* (UTC); N Sinks area, *Maguire 20139* (UTC); Middle Sinks area, *Maguire 20142* (UTC); Beaver Basin area, *Maguire 20144* (UTC), *Maguire 20147* (UTC); Franklin Basin, *Maguire 20150* (GH, UTC); summit of Logan Canyon, *Maguire 21131* (MO); Logan Canyon, *Maguire 21605* (UC); 1 mi E of summit of Logan Canyon, *Maguire & Richards, Jr. 5234* (UTC); Logan Canyon, *Maguire & Stoddart 21665* (UTC); Bear River Range, *Maguire & Stoddart 21667* (UTC); 0.5 mi W of Franklin Basin Rd, *Maguire & Stoddart 21729* (UTC); W Hodges Pasture, 7 Aug 1934, *Passey s.n.* (UTC); Temple Fork turnoff, *Piep 04.075* (UTC); Tony Grove road, near turnoff to Lewis Turner Campground, *Piep 04.077* (UTC); Logan Canyon, *Piep 04.081* (UTC); 30 mi E of Logan, in Logan Canyon, *Piep & Mayne 99-017* (UTC); Green Canyon Nursery, *Shultz & Bilbrough 10043* (UTC); mouth of Green Canyon, *Shultz & Bilbrough 10046* (UTC); between Green Canyon and Logan Canyon, *Shultz & Olsen 9050* (UTC), *Shultz & Olsen 9051* (UTC), *Shultz & Olsen 9052* (UTC), *Shultz & Olsen 9053* (UTC); Malad Range, *Shultz & Shultz 8115* (UTC); Logan Canyon, S of Naomi Peak, *Shultz & Shultz 8203* (UTC), *Shultz & Shultz 8208* (UTC); slopes across from Spring Hollow, *Shultz 4439* (UTC); Wood Camp Hollow, Logan Canyon, *Shultz 4442* (UTC, RSA, MO), *Shultz 4444* (UTC); Amazon Hollow, *Shultz 4509* (UTC); Right-Hand Fork of Logan Canyon, *Shultz 10051* (UTC); mouth of Green Canyon, *Shultz 10276* (UTC); Franklin Basin, *Shultz 11558* (UTC); Bear River Range, Temple Fork Road, Mill Trace, *Shultz 19828* (UTC); Logan Canyon, *Shultz et al. 6507* (UTC); S face of Logan Peak, *Shultz et al. 7442.1* (MO, UTC); Logan Canyon, *Shultz et al. 19822* (UTC); Cart Hollow, *Tuhy 2291* (UTC); below Willow Springs, *Ward & Ward 926* (DS). Carbon Co.: 12.5 mi E of Soldier Summit, *Ibrahim 58* (UTC); First Water Canyon, *Lewis 7512* (UTC); Bob Wright area, *Lewis 7521* (UTC). Daggett Co.: Uinta Mtns, *Herman 4755* (MO); N slope of Uinta Mtns, *Richens 34* (UTC). Duchesne Co.: 17 km NW of Tabonia, *Cronquist et al. 12034* (UTC); 3.5 mi S of Tabonia, *Goodrich 20231* (UTC); near summit at Avintaquin Campground, *Shultz & Shultz 7303* (UTC), *Shultz & Shultz 7304* (UTC); ca. 1 mi from Fruitland, *Stockton 170* (UTC); 2 mi N of Indian Creek Pass, 29 Aug 1980, *Stockton s.n.* (MO, UTC). Emery Co.: middle of Long Point, *Lewis 7238* (UTC); Castle Valley, *Lewis 7642* (UTC); Huntington Canyon, *Lewis 7679* (UTC); E of Indian Creek, *Lewis & Lewis 7533* (UTC); head of Rock Canyon, *Lewis & Lewis 7544* (UTC); Scad Valley, *Lewis & Lewis 7774* (UTC). Garfield Co.: without locality, *Neese 9962* (RM). Grand Co.: ca. 12.5 mi NE of Mt Waas, *Franklin 2393* (UTC); near head of Post Canyon, *Graham 9938* (UTC, UC). Iron Co.: SW portion of the state, *Gierisch 268* (UTC). Juab Co.: Wasatch Range, *Goodrich 16469* (UTC); Trout Creek, *McMillan 1378* (UTC); Deep Creek Mtns, *Shultz 4364* (UTC); Deep Creek Mtns, *Shultz & Shultz 4364* (RM); along I-15, S of Nephi, *Shultz et al. 10152* (UTC). Kane Co.: Johnson Canyon, *Shultz & Shultz 9851* (UTC). Millard Co.: Pavant Mtns, *Shultz et al. 10163* (UTC). Morgan Co.: Deseret Land and Livestock Ranch, *Thorne 3110* (UTC). Piute Co.: Tushar Mtns, 22 Jul 1962, *Warnock s.n.* (UT). Rich Co.: ca. 3 mi SE of Monte Cristo Campground, *Johnson 440401 NW* (UTC); 1 mi E of Logan Canyon summit, *Maguire 5235* (UTC), *Maguire 20122* (UTC), *Maguire 20123* (UTC), *Maguire 20124* (UTC), *Maguire 20125* (UTC); 0.25 mi E of summit of Logan Canyon, *Maguire 20127* (UTC); 2 mi E of Logan Canyon summit, *Maguire & Richards, Jr. 5235* (UTC); E Shore of Bear Lake, *Piep 04.083* (UTC); Bear River Range, Logan Canyon, Sunrise Campground, *Shultz 19831* (UTC); E of Randolph, Old Canyon, Bear River Range, *Shultz & Peterson 20422* (UTC); E side of Bear Lake, *Shultz et al. 19825* (UTC); E side of Bear Lake, *Shultz et al. 20157* (UTC); Eden Canyon Rd, *Shultz et al. 20159* (UTC); 2 mi E of Laketown, *Shultz et al. 20160* (UTC); roadside at Deseret Land and Livestock Ranch, *Shultz et al. 20299* (UTC); benches E and S of Eden Canyon, north of Laketown, *Shultz et al. 20292* (UTC); Deseret Land and Livestock Ranch, *Shultz et al. 20301* (UTC); Laketown Canyon, *Thorne 3147* (UTC); 4 mi W of Garden City, *Ward & Ward 921* (DS); Deseret Land and Livestock Ranch, *Thorne 3061* (UTC). Salt Lake Co.: N base of Mt Olympus, *Cronquist & Neese 12052* (UTC); Cottonwood Canyon, 20 Aug 1972, *Epstein s.n.* (UT, UTC); Parley's Canyon, 10 Aug 1944, *Flowers s.n.* (UT); Wood Hollow Canyon, *Shultz 19758* (UTC); Transverse Mtns, Watts Road, *Shultz & Tart 19744* (UTC); Wood Hollow Canyon, *Shultz & Tart 19754* (UTC), *Shultz & Tart 19757* (UTC), *Shultz & Tart 19761* (UTC), *Shultz & Tart 19751* (UTC). Sanpete Co.: Ephraim Canyon, *Goodwin 41-AG-43* (RM); Wasatch Plateau, *Lewis 5629* (UTC); below mouth of Ephraim Canyon, *Lewis & Lewis 7470* (UTC). Sevier Co.: Fishlake Mtns, *Harris 27600* (MO); Upper Salina Creek, *Lewis 5794* (UTC); old reservoir site below Lost Lake, *Maguire 19980* (UTC); head of Second Creek in the Pavant Mtns, *Shultz et al. 10166* (UTC); hwy near Fish Lake, *Smith 15* (UTC); Tushar Mtns, 9 Jul 1961, *Warnock s.n.* (UT); Old Woman Plateau, *Welsh 22457* (UTC). Summit Co.: Red Mtn, *Neely et al. 2513* (UTC); ca. 2 mi SSW of Beaver View Campground, *Piep 04.053* (UTC). Tooele Co.: Site 24, *Long 601* (UTC); Hickman Pass, in E Hickman Canyon, *Taye 1280* (UTC). Uintah Co.: 2 mi NE of Lapoint, *Goodrich 18001* (UTC); Uinta Mtns, *Maguire 15590* (RM); Parks, *Maguire 17706* (UTC). Utah Co.: E of Strawberry Reservoir, *Beetle 13103* (RM); Diamond Fork, *Burke B-23* (RM); Mt Timpanogos, *Flowers 397* (UT); 2 mi SW of Santaquin, *Goodrich 16474* (UTC); Hobble Creek, *Goodrich et al. 21492* (BRY); Clear Creek, *Lewis 7653* (UTC); N of north relay tower, *Lewis 7661* (UTC); Wood Hollow Canyon, *Shultz & Tart 19747* (UTC). Wasatch Co.: between Strawberry and Soldier Creek Reservoirs, *Shultz & Shultz 7293* (MO, UTC). Washington Co.: 40 km and 56 deg. from St. George, *Goodrich & Monsen 22871* (UTC); Little Plain of Gooseberry Mesa, *Shultz & Shultz 98244* (UTC).—WASHINGTON: Chelan Co.: Leavenworth, *Beetle 12820* (UTC); 1 mi S of Cashmere, *Beetle 12843* (MO); N side of Cooper Mtn, *Beetle 12894* (UTC); old burn near the top of the SE side of Cooper Mtn, *Cronquist & Mastrogiuseppe 12171* (UTC); dry hillside along Columbia River, *Purer 7779* (MO); N side of Lake Chelan, *Ward & Ward 850* (DS). Douglas Co.: S of Chelan, *Shultz & McReynolds 20240* (UTC); Cooper Mtn, *Shultz & McReynolds 20242* (UTC), *Shultz & McReynolds 20244* (UTC). Ferry Co.: summit of Midnight Mtn, *Saufferer 319* (DS). Kittitas Co.: Frost Creek Trail, *Rummell 6* (RM); alpine slopes of Table Mtn, *Thompson 14248* (DS). Klickitat Co.: near JTS Ranch, *Baker 72* (MO). Spokane Co.: 8 mi W of Ione, *Kreager 416* (UTC); near Cheney, *Leiberg 945* (GH). Yakima Co.: Yakima region, *Brandegee 910* (UC).—WYOMING: Albany Co.: Laramie Range, *Aslamy 187* (RM); 1.5 mi NW of cemetery, *Current 456* (RM); Middle Crow Creek, *Feddema 3187* (RM); S of Laramie, 9 Sep 1919, *Hall s.n.* (UC); 5 mi E of Sybille Experiment Station, *Landon & Varcalli 1-18* (UTC); Laramie, *Nelson 8180* (MO, POM, RM, UTC); 0.5 mi E of Hwy 30 in Telephone Canyon, 1 Aug 1957, *Palmer & Palmer s.n.* (UTC); Laramie Range, *Porter 6867* (RM). Big Horn Co.: Big Horn Mtns, *Fonken & Nelson 749* (RM, UTC), *Nelson 785* (RM), *Nelson 6244* (RM), *Nelson 6520* (RM, MO); ca. 13 air mi ESE of Shell, *Nelson 6583* (RM, UTC); Big Horn Mtns, *Nelson 6608* (RM). Campbell Co.: Rozet, *Beetle 12139* (RM). Carbon Co.: Chalk Mtns, *Current 416* (RM); Battle Mtn, *Current 647* (RM), *Current 998* (RM). Fremont Co.: SE of Thermopolis, *Fisser 191* (RM); Wind River Range, *Fisser 770* (RM); SE edge of Trail Lake, at inlet of Torrey Creek, *Haines & Haines 5032* (UTC); Green Mtns, *Hartman 8429* (RM); Plot GM-3, *Holmgren & Boyle 16151* (UTC); E of the Wind River Mtns, *Shultz 20204* (UTC). Johnson Co.: Big Horn Mtns, *Ducholm 9161* (RM), *Fonken 494* (RM), *Nelson 5948* (RM). Lincoln Co.: canyon E of Afton, *Beetle 12297* (RM); N side of Clear Creek, 15 Aug 1970, *Bissell s.n.* (UTC); without locality, *Holmgren 16595* (COLO, UT, UTC); E of Gardiner River, *Mearns 4445* (DS); S end of Star Valley, *Porter 3809* (RM, UC); Salt River Range, *Shultz 751* (UTC); Salt River Range, near the Salt River Drainage, *Shultz 10838* (UTC); Allred Flat Campground, *Shultz 11551* (UTC); Grey's River drainage, *Shultz 20193* (UTC); S end of Star Valley, *Ward & Ward 919* (DS). Natrona Co.: Casper Mtns area, *Jozwik 334* (RM). Park Co.: Absaroka Mtns, *Evert 3125* (RM). Sheridan Co.: Big Horn Mtns, *Evers & Evers 114931* (RM), *Hartman 10175* (UTC), *Hartman 10176* (RM), *Hartman 10775* (RM). Sublette Co.: E of foothills, *Holmgren & Holmgren 9093* (RM); Tepee Ridge, *Lichvar 1081* (RM); Cora, *Marts 3* (WIS); Bare Mtn, *Shultz 389* (RM, UTC), *Shultz 390* (UTC); 0.8 mi S of bridge, Falls Creek, *Shultz 4463* (UTC); drainage above Fremont Lake, Wind River Mtns, *Shultz 19842* (UTC); E side of Fremont Lake, Wind River Mtns, *Shultz 19843* (UTC); 21 mi N of Cora, near Gypsum Springs, Pinedale District, *Shultz 19845* (UTC); ca. 1 mi W of Daniel Junction, *Shultz 20200* (UTC); W Gypsum Creek, *Soreng 1303* (RM). Teton Co.: Pilgrim Creek, *Beetle 11544* (UTC); Jackson Lake, *Beetle 12179* (MO); Pilgrim Creek, *Beetle 12185* (UTC); Junction of Hwy 89 and road to Labarge Creek, *Beetle 12303* (RM); Snow King Mtns, *Lichvar 419* (RM); Sheep Mtn, *Lichvar 758* (RM); Sportsmans Rd, *Lichvar 989* (RM); Snake River Canyon, *Marts 6* (WIS); Yellowstone Natl Park, *Oleson 107* (RM); Yellowstone Falls, *Rydberg 5202* (RM); meadow N of turnoff to Jenny Lake, *Shultz & Shultz 7956* (UTC); Blacktail Ponds Overlook, *Shultz 10103* (UTC); ca. 2 mi N of Jackson, on banks of sandstone, *Shultz 10832* (UTC); near Moran Junction, *Shultz 11557* (UTC); flats W of Blacktail Butte, *Shultz 11950* (UTC); Taggart Lake turnoff, *Shultz 11952* (UTC); E of Snake River, *Ward & Ward 913* (DS); E side of Snake River, *Ward & Ward 913* (RM), *Ward & Ward 916* (DS). Uinta Co.: near Fossil Butte Natl Monument, *Shultz 20209* (UTC). Washakie Co.: Big Horn Mtns, *Fonken 695* (RM), *Hartman 10555* (RM), *Nelson 5614* (RM), *Nelson 8156* (RM).

Artemisia tridentata subsp. *vaseyana* is the common sagebrush of montane habitats and is the most abundant of all the subspecies of *A. tridentata*. By some estimates, mountain sagebrush occupies an area of approximately 260,000 square kilometers (Beetle 1960). That estimate remains reasonably accurate today, even though sagebrush habitat has been affected by changes, largely through livestock grazing (removal of sagebrush by herbicide sprays), competition from introduced grasses, and die-off from a combination of insect damage and drought (for a review, see Welch 2005). While hybridization with other subspecies of *A. tridentata* (McArthur et al. 1979, 1988, 1998a) occurs where their ranges overlap, subsp. *vaseyana* usually grows at higher elevations than subsp. *wyomingensis* and subsp. *tridentata*, and is well differentiated by its broader leaves and flat-topped growth form.

Several variants have been discerned that may be the result of ecological specialization or hybridization. *Artemisia tridentata* var. *pauciflora* is an ecotypic variant of *A. tridentata* subsp. *vaseyana* that occurs in dry sites. This few-flowered variant (heads with six or fewer florets) is typically found on coarse, well-drained soils and south-facing slopes. In 2005, during my examination of plants at the presumed type locality for *A. vaseyana* above Lake Chelan in Washington, I observed plants with more than six flowers per head (*Shultz & McReynolds 20242*) as well as plants with fewer than six flowers per head (*Shultz & McReynolds 20244*), a variation that occasionally occurred within one inflorescence. The type specimen (*Vasey 480*) has more than six florets per head. *Artemisia tridentata* var. *angustifolia* is a narrow-leaved form that represents a xeromorphic extreme commonly found in dry sites in Oregon, California, and elsewhere. It is often identified as *A. tridentata* subsp. *vaseyana*, but I include the type of var. *angustifolia* in subsp. *tridentata* (p. 76). Subspecies *xericensis* is treated here as a nothotaxon; see p. 110.

Some informally described taxa are found in the ecological literature. An important hybrid complex, informally called "*bonnevillensis*" (Winward 2004), occurs on gravel shorelines near the northern limit of the ancient Pleistocene-era Lake Bonneville. It grows in sites intermediate to those occupied by subsp. *wyomingensis* and subsp. *vaseyana*. Studies by Garrison (2006) show that "bonnevillensis" populations differ morphologically from subsp. *wyomingensis*, subsp. *vaseyana*, and subsp. *tridentata*, but not by a consistent suite of characteristics. Garrison was unable to detect genetic differences among any of the subspecies, in spite of a morphometric analysis showing strong differentiation. The intermediacy of morphological characteristics are indicative of hybridization, but the patterns vary from one site to another, demonstrating possible stages of introgression that involve all three of the subspecies studied. The apparently stabilized hybrid populations produce fertile cypselae, and form large communities in northern Utah and southern Idaho. Inasmuch as "Bonneville sagebrush" provides habitat for sage grouse and pygmy rabbits, both of which are wildlife species of conservation concern, there are practical reasons for formally designating a nothotaxon (as has been done for subsp. ×*xericensis*; see p. 110). Since attempts to identify these variants genetically have not yet been successful, I treat them within subsp. *vaseyana* and defer to the manuscript in preparation by H. Garrison for further definition.

9d. Artemisia tridentata subsp. **wyomingensis** Beetle & A. M. Young, Rhodora 67: 405. 1965. *Artemisia tridentata* var. *wyomingensis* (Beetle & A. M. Young) S. L. Welsh, Great Basin Naturalist 43: 215. 1983. *Seriphidium tridentatum* subsp. *wyomingense* (Beetle & A. M. Young) W. A. Weber, Phytologia 55: 8. 1984. *Seriphidium tridentatum* var. *wyomingense* (Beetle & A. M. Young) Y. R. Ling in Hind, Jeffrey, and Pope, Advances in Compositae Systematics 288. 1995.—TYPE: U.S.A. Wyoming: N of Pinedale and 0.5 mi N of Daniel Junction, 20 Jul 1964, *A. L. Young 105* (holotype: RM!, photo: UTC!).

Low-growing to medium-sized shrubs, 2–5 (–15) dm tall; crowns uneven, rounded; vegetative branches stiffly spreading, interspersed among the old inflorescence branches that often persist for many years, giving older plants a "twiggy" appearance. Leaves (0.4–) 0.7–1.1 (–2) cm long, (0.1–) 0.2–0.3 cm wide, narrowly to broadly cuneate, deeply to shallowly 3-lobed, lobes rounded, the middle lobe often slightly longer than the lateral lobes and overlapping with them ("flared" at the apex). Capitula (1–) 1.5–2 mm high, 1.5–2 mm wide, narrowly campanulate, erect. Inflorescences 2–8 (–10) cm long, 2–6 cm wide, narrowly paniculate; branches mostly erect. Florets 4–8. Cypselae glabrous. Chromosome number: 2n = 36 (McArthur & Sanderson 1999). Figs. 7b, 33I–P.

Common name. Wyoming sagebrush.

Phenology. Flowering mid-summer to late fall.

Distribution (Fig. 35). U.S.A.: Arizona, California, Colorado, Idaho, Montana, New Mexico, Nevada, North Dakota, Oregon, Utah, Washington, Wyoming; in rocky or fine-grained soils, in cold desert basins to high plateaus, sometimes in foothills; 800–2200 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** ARIZONA: Apache Co.: without locality, *Beetle 12843a* (MO, UT). Mohave Co.: 1.8 mi SW of junction of Arkansas Ranch Rd and Tuweep-Nixon Rd, 25 Aug 1956, *Ferguson s.n.* (UTC); Hurricane Fault site, 25 Aug 1956, *Ferguson s.n.* (UTC); Little Tank-Wolf Hole, 26 Aug 1956, *Ferguson s.n.* (UTC); 1.2 mi N of Toroweep Point Campground, 25 Aug 1956, *Ferguson s.n.* (UTC); Mokiah Pass, 26 Aug 1956, *Ferguson s.n.* (UTC); 3.8 mi W of Nixon, 25 Aug 1956, *Ferguson s.n.* (UTC); 4.3 mi E of the Mount Trumbull school, 26 Aug 1956, *Ferguson s.n.* (UTC). Navajo Co.: 12 mi E of Kayenta, *Cutler 3194* (DS, MO).—CALIFORNIA: Inyo Co.: Owens Valley, *Shultz & Shultz 4602* (UTC); Owens Valley, *Shultz & Shultz 4602-a* (UTC). Lassen Co.: dry ridges, common, *Demaree 41518* (GH). Modoc Co.: Surprise Valley, *Willits 161* (DS, GH). Mono Co.: Adobe Valley, at Taylor Creek Rd, *Shultz et al. 19784* (UTC). Plumas Co.: between Quincy and Reno, ca. 2 mi W of Vinton, *Shultz & Garrison 20319* (UTC).—COLORADO: Delta Co.: Cedar Mesa, *Eggleston 14654* (GH). Garfield Co.: Long Ridge, *Nicholas 27* (CS). Jackson Co.: North Park, *Beetle 11625* (COLO), *Beetle 12199* (COLO); Lake John, *Johnson 887* (COLO); 5 mi N of Cowdry, *Lafferty 12* (COLO). Larimer Co.: Upper Laramie River, *Baker s.n.* (POM). Moffat Co.: 2 mi E of Utah border, *Shultz 4384* (UTC). Routt Co.: S of Oak Creek, *Beetle 11948* (COLO).—IDAHO: Bannock Co.: Pocatello, 26 Aug 1892, *Mulford s.n.* (MO). Blaine Co.: E of Fish Creek Reservoir, *Beetle 14132* (UTC). Clark Co.: 0.55 mi W of Dubois, *Passey & Hugie 57* (UTC). Gooding Co.: 0.5 W of Malad River, *Ward & Ward 892* (DS). Jefferson Co.: East Butte, *Shultz & Shultz 10259* (UTC); NE of East Butte, *Shultz et al. 10259* (UTC). Lemhi Co.: vicinity of Gilmore Summit, *Beetle 13946* (UTC). Lincoln Co.: 12 mi NE of Richfield, *Ward & Ward 893* (DS). Oneida Co.: Curlew Valley Grassland, *Shultz et al. 20152.1* (UTC), *Shultz et al. 20153* (UTC).—MONTANA: Broadwater Co.: Upper Missouri Valley, 27 Aug 1882, *Canby s.n.* (GH). Flathead Co.: Flathead Lake, *Cottam 175458* (UT). Garfield Co.: shore of Peck Lake, *Woodland 1188* (DS). Powder River Co.: 20 mi E of Ashland, *Beetle 14112* (RM).—NEBRASKA: Billings Co.: Southern edge of Kinley Plateau, 21 Aug 1992, *DiGiacomo & Leuszler s.n.* (UTC). Sioux Co.: Hat Creek Basin, 2 Aug 1889, *Webber s.n.* (MO).—NEVADA: Elko Co.: Toana Mtns, *Shultz & Shultz 8155a* (UTC); base of Copper Mtns, *Shultz & Shultz 10190* (UTC); W side of Pequop Mtns, *Shultz & Garrison 20332* (UTC); SW side of White Horse Pass, *Ward & Ward 936* (DS). Eureka Co.: just W of Dunphy, *Shultz & Shultz 10208a* (UTC); 5 mi N of Beowawe, *Shultz & Shultz 10250* (UTC). Humboldt Co.: dunes N of Winnemucca, *Shultz 7447* (UTC); 8 mi N of Rand, *Train 2593* (GH). Lander Co.: near mouth of Veatch Canyon, *Goodrich 6927* (UTC); Hickison summit, *Shultz & Shultz 8641* (UTC); E of Battle Mtn, *Shultz & Shultz 10209* (UTC). Pershing Co.: Buena Vista Valley, *Shultz & Shultz 10212* (UTC), *Shultz & Shultz 10212a* (UTC); 5.6 mi E of Sulphur, *Suttkus*

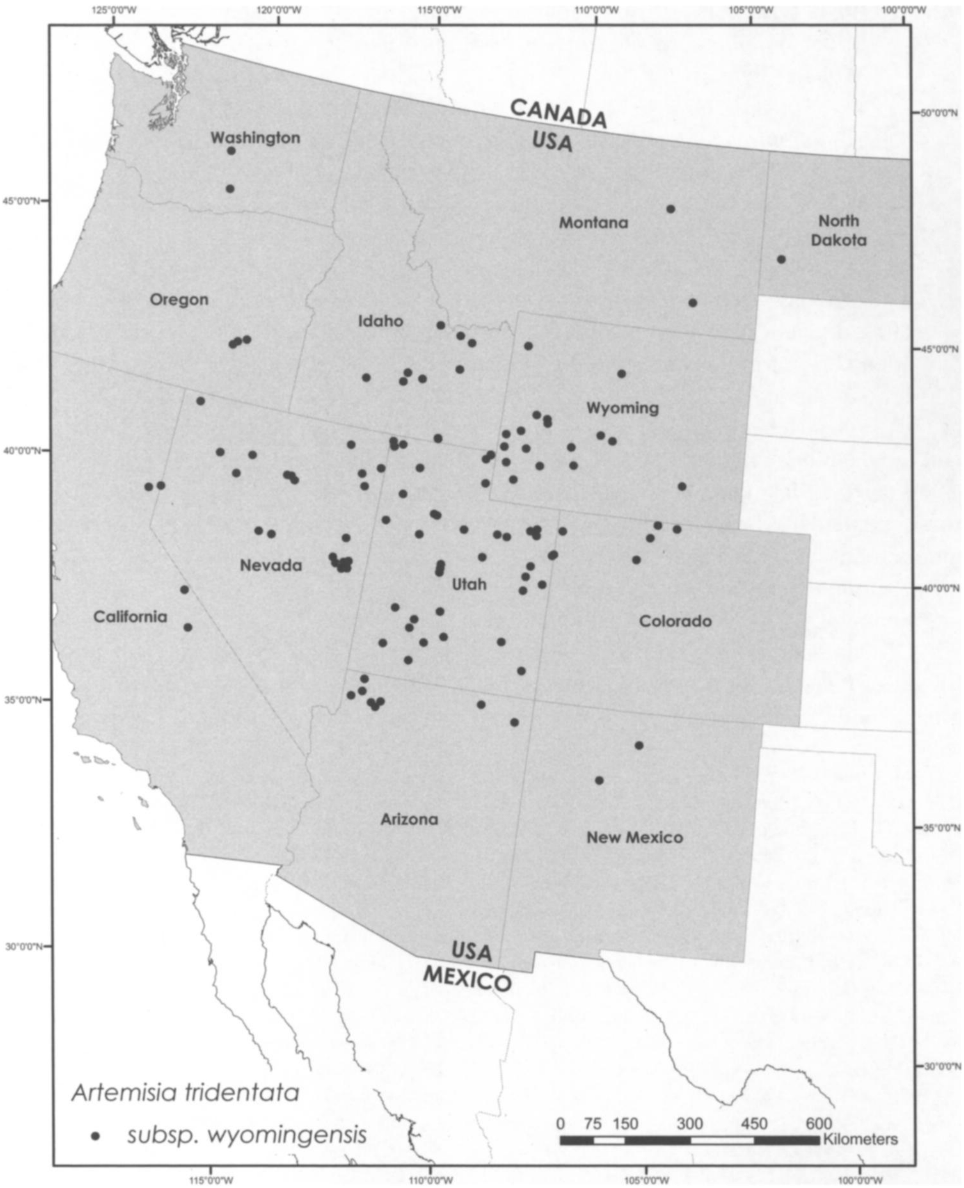

FIG. 35. Distribution of *Artemisia tridentata* subsp. *wyomingensis*.

67-33-5 (UTC). Washoe Co.: Red Rock junction, *Shultz & Shultz 8613* (UTC); W side of Swan Lake Reservoir, *Tiehm & Rogers 4781* (UTC). White Pine Co.: 20 mi S of McGill, *Beetle 13126* (GH); between the Schell Creek Range and the Egan Range, *Cronquist 12050* (UTC); 8 mi S of Ely, on Hwy 93, 20 Jul 1958, *Ryan s.n.* (UTC); Schell Creek Range, *Tart & Howell 2701* (UTC), *Tart & Howell 2703* (UTC), *Tart & Howell 2708* (UTC), *Tart & Howell 2718* (UTC), *Tart & Howell 2721* (UTC); Egan Range, *Tiehm & Nachlinger 12770* (UTC).—NEW MEXICO: Rio Arriba Co.: near Rosa, *Flowers 71* (UT). Sandoval Co.: La Ventana, 10 Jul 1959, *Hoffman s.n.* (MO).—OREGON: Harney Co.: ca. 12.4 mi SW of Princeton, *Acker 98* (UTC); ca. 12 mi SW of Princeton, *Acker 110* (UTC); 32.5 mi S of Burns, *Acker 111* (UTC); 3.3 mi N of Princeton, *Acker 120* (UTC); ca. 12 mi SW of Princeton, *Acker 124* (UTC); Squaw Butte Experiment Station, *Barkley 4710* (GH). Lake Co.: near Christmas Lake, *Leiberg 778* (GH); 6 mi S of French Glen, *Shultz 8580* (UTC).—UTAH: Beaver Co.: 6.5 hwy mi W of Milford, on Hwy 21, *Goodrich 18098* (UTC); Tushar Mtns, *Taye 3273* (UTC). Box Elder Co.: Raft River Mtns, 25 Aug 1985, *Benson s.n.* (UTC); Hogup Mtns, 23 May 1986, *Gilbert s.n.* (UTC); Dove Creek Pass, *Shultz & Shultz 8140* (UTC); base of Raft River Mtns, *Shultz & Shultz 10186* (UTC); 1 mi E of Meadow Creek Butte, *Sommerville 13* (UTC); 8 mi N of Grouse Creek, *Sommerville 49* (UTC); Grouse Creek, *Sommerville 50* (UTC). Carbon Co.: 10 mi NW of Helper, on state Hwy 191, *Shultz & Shultz 7306* (UTC). Duchesne Co.: 5 km S of Tabonia, *Cronquist et al. 12036* (UTC); 8 mi N of Duchesne, 11 Sep 1936, *Stoddart & Passey s.n.* (UTC). Garfield Co.: Dixie Natl Forest, 8 Sep 1961, *Folks s.n.* (UTC); Taylor Flat, *Shultz & Shultz 7347* (UTC); Orange Cliffs, *Shultz & Shultz 7359* (UTC); Boulder Mtn, *Shultz & Shultz 8056* (UTC); Orange Cliffs, *Shultz & Shultz 8155* (UTC). Grand Co.: on Castle Valley road, *Holmgren & Lewis 16327* (UTC); Hill Creek, on the E Tavaputs Plateau, *Peck 77* (UTC); Book Cliffs divide, *Shultz & Shultz 3812* (UTC). Iron Co.: ca. 10 mi W of Cedar City, *Shultz & Shultz 6210* (UTC); Escalante Desert, *Shultz et al. 10175* (UTC). Juab Co.: 15 mi NE of Scipio, *Goodrich 16397* (UTC); Mills Valley, *Goodrich 16448* (BRY, UTC); near Nephi, 17 Sep 1951, *Krajina s.n.* (GH); above Yuba Dam Reservoir, *Shultz et al. 10153* (NY, UTC); 1.5–2 mi S of Yuba Dam, *Shultz et al. 10158* (UTC). Kane Co.: along road to Navajo Mtn, *Atwood 3396* (BRY, UTC). Rich Co.: 0.5 mi E of Laketown, *Maguire 21720* (UTC); W side of Bear River Range, foothills W of Woodruff, *Shultz & Peterson 20431* (UTC); Eden Canyon Rd, *Shultz et al. 20158* (UTC); Eden Canyon, N of Laketown, *Shultz et al. 20291* (UTC). San Juan Co.: 4 air mi SW of Blanding, on W edge of White Mesa, *Shultz & Prigge 9027* (UTC). Sanpete Co.: S of Manti city garbage dump, *Lewis 6993* (UTC); Gunnison, *Ward 673* (MO). Sevier Co.: just N of Koosharen, *Shultz 6780* (UTC). Tooele Co.: Simpson Springs, Nov 2002, *Blonski s.n.* (UTC); W side of Great Salt Lake, *Garrett 5360* (GH, UT); Site 14, *Long 482* (UTC); 2 mi N of Goldhill, *Shultz & Shultz 8163* (UTC). Uintah Co.: along Ashley Creek, near mouth of Dry Fork, *Graham 7398* (MO, UTC); 5 mi W of Vernal, *Goodrich 18003* (BRY, UTC); 5.5 mi N of Lapoint, *Goodrich 22224* (UTC); E of the Walsh Knolls and W of the White River, *Shultz & Shultz 5141* (UTC); Walsh Knolls, *Shultz & Shultz 5418* (RM, UT, UTC), *Shultz & Shultz 5419* (UTC); 5 mi W of Vernal, on Hwy 40, *Shultz et al. 3786* (UTC), *Shultz et al. 3787* (UTC). Utah Co.: Mouth of Provo Canyon, *Passey & Hugie 22* (UTC). Washington Co.: near Leeds, *Eggleston 14829* (GH).—WASHINGTON: Kittitas Co.: 11 mi W of Vantage, *Ward & Ward 838* (DS). Spokane Co.: near Spokane, *Palmer 37847* (GH). Yakima Co.: 15 mi S of Toppenish, *Ward & Ward 836* (UC).—WYOMING: Albany Co.: Upper Laramie Plains, 2 Aug 1896, *Baker s.n.* (MO). Fremont Co.: Riverton, *Beetle 13191* (MO); South Pass, *Beetle 13194* (MO); Sweetwater Rd, *Haines 5585* (RM, UT, UTC); S of Dishpan Butte, *Haines & Haines 5441* (UTC); S of Riverton, 17 Aug 1950, *Palmer s.n.* (GH); E of the Wind River Mtns, *Shultz 20205* (UTC); S of Riverton, *Shultz 20206* (UTC). Lincoln Co.: Salt River Range, near the Salt River drainage, *Shultz 10839* (UTC); above Smith's Fork drainage, *Shultz & Shultz 2827* (UTC), *Shultz & Shultz 2828* (UTC). Sublette Co.: Fall Creek-Rand Rd, *Shultz 4464* (UTC); ca. 12 mi E of Pinedale, 0.5 mi W of Boulder, *Shultz 19841* (UTC); ca. 1 mi W of Daniel Junction, *Shultz 20199* (UTC). Sweetwater Co.: 19.2 km N of Jim Bridger coal mine, *Barker s.n.* (UTC); banks of Green River, *Boyle 1311* (UTC); Lucerne Valley, *Flowers 125* (UT); Lander cutoff, *Shultz 20202* (UTC), *Shultz 20203* (UTC). Teton Co.: Yellowstone Natl Park, *Churchill 570* (MO). Uinta Co.: S of entrance to Fossil Butte Natl Monument, *Shultz 19836* (UTC); near Fossil Butte Natl Monument, *Shultz 20210* (UTC). Washakie Co.: between Worland and Tensleep, *Porter & Porter 8216* (RM, RSA). Weston Co.: 2 mi N of Upton, *Beetle 12151* (MO).

Artemisia tridentata subsp. *wyomingensis* is the common sagebrush of rocky or fine-grained soils, from cold valley deserts to high plateaus in the Great Basin. This subspecies is an allopolyploid or autopolyploid, which may be derived either from the populations of subsp. *tridentata* with which it occurs or crosses with subsp. *vaseyana*. It can be distinguished from all the other subspecies of *A. tridentata* by its short, abruptly cuneate, vegetative leaves, which have an elongated central lobe that tends to overlap the lateral lobes. This subspecies is usually shorter than subsp. *tridentata*, and it has shorter and narrower flowering branches that are retained from year to year. Wyoming sagebrush may be increasing in abundance, in response to increased grazing pressure and drought, in the high valleys of the Great Basin. Populations of subsp. *wyomingensis* often co-occur with subsp. *tridentata*, but in microsites with finer-textured soil.

10. Artemisia pygmaea A. Gray, Proc. Amer. Acad. Arts 21: 413. 1886. *Seriphidium pygmaeum* (A. Gray) W. A. Weber, 55: 8. 1984.—TYPE: U.S.A. Nevada: near Eureka, Fish Creek, Aug 1885, *Brandegee s.n.* (holotype: GH!; isotype: UC).

Low-growing evergreen shrubs, 0.5–1 dm tall, slightly aromatic; crowns rounded or flat-topped; not root-sprouting, caudices coarsely woody. Stems pale to light brown, broadly branched with flowering branches stiffly erect, densely clothed with appressed foliage, glabrous to sparsely tomentose; bark gray. Leaves brittle, bright green, evergreen, rigid, attached singly (not fascicled), sessile; blades (1–) 3–8 mm long, 2–6 mm wide, oblong to ovate, pinnately deeply 3–7-lobed (nearly to the midribs), lobes divergent, to 1/3+ blade width, surfaces glabrous (some sparsely tomentose) and resinous. Capitula 4–5 mm high, 2–3 mm wide, turbinate, sessile. Phyllaries narrowly lanceolate, acute, green, margins broad, hyaline, glabrous or sparsely hairy. Inflorescences spicate, (1–) 2–3 cm long, 0.5–1 cm wide. Florets 2–6, all perfect and tubular; corollas 2.5–3 mm long, pale yellow, glandular; style branches apically fringed, recurved, exserted. Cypselae 0.8–1.5 (–2) mm long, glabrous, resinous. Pappus absent. Chromosome number: 2n = 18 (McArthur et al. 1981; McArthur & Sanderson 1999; Ward 1953); 2n = 36 (McArthur et al. 1981). Figs. 1a, 7h, 36.

Common name. Pygmy sage.

Phenology. Flowering late spring to fall.

Distribution (Fig. 37). U.S.A.: Arizona, Colorado, Nevada, New Mexico, Utah; in fine-textured soils of gypsum or shale; 1500–2000 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** ARIZONA: Coconino Co.: 2 mi S of Fredonia, *Darrow 3006* (CAS, UC); 3 mi SE of Fredonia, *Ripley & Barneby 8504* (CAS).—COLORADO: Montezuma Co.: N side of Cortez, *Anderson & Flemming 89* (UTC). Rio Blanco Co.: N of White River, on Colorado-Utah border, *Shultz & Shultz 5127* (RSA, UTC); N of the White River road access from Colorado, *Shultz & Shultz 5136* (COLO, UTC).—NEVADA: Elko Co.: Cobre, 1 Sep 1906, *Jones s.n.* (UTC); W of Pilot Mtn, 17 Jun 1939, *Lund s.n.* (UTC); S of Nine-Mile Well, 18 Sep 1938, *Passey s.n.* (GH, UTC); ca. 30 miles NW of Wendover, on road to Wells, *Shultz & Garrison 20315* (UTC); 32 mi W of Utah state line, *Shultz & Shultz 4335* (RSA, UTC). Eureka Co.: Fish Creek, Aug 1885, *Brandegee s.n.* (UC); S side of Lone Mountain, *Tiehm 6333* (CAS, UTC); 2 mi N of Fish Creek, *Ward 942* (DS, RM, UC); Fish Creek Valley, *Tiehm 6302* (UTC); 25.8 road mi W of Eureka, on Hwy 50, *Tiehm 8419* (UTC). Lincoln Co.: Pioche, 31 Aug 1912, *Jones s.n.* (DS, GH, RM); Lake Valley, *Tiehm 8380* (UTC). Nye Co.: White River Valley, *Shultz & Shultz 4560* (RSA, UTC), *Tiehm 6281* (UTC, CAS). White Pine Co.: 10 mi NW of Lund, *Goodrich 20080* (UTC); 17 mi S of Ely, *Maguire & Holmgren 25115* (UTC); 10 mi NE of Ely, 21 May 1957, *Ryan s.n.* (RM); Antelope Summit, 1 Aug 1958, *Ryan s.n.* (RM); Snake Range, *Tiehm 8397* (UTC); Egan Range, *Tiehm 8400* (UTC).—NEW MEXICO: McKinley Co.: N of Prewett, *Atwood 30823* (BRY, SRP).—UTAH: Beaver Co.: NE of Minersville, *Mutz 82-100* (BRY); 21 air mi SW of Milford, *Tiehm 6246* (CAS, UTC). Box Elder Co.: 2.5 mi E of Muddy Ranch, *Sommerville 40* (UTC). Carbon Co.: 12 mi E of Wellington, *Van Cott 108* (UTC). Duchesne Co.: Sowers Canyon, *Goodrich 4016* (COLO, UTC); 5 mi E of Duchesne, *Goodrich 4993* (RM, UT, UTC); lower Sowers Canyon, *Goodrich 5016* (UTC); Antelope Canyon, *Goodrich 14975* (BRY); W Tavaputs Plateau, *Goodrich 25392* (UTC); 8 mi SE of Duchesne, 18 Aug 1936, *Stoddart & Passey s.n.* (UC, UTC). Emery Co.: Page Flat, *Albee 2587* (UT), *Harris 916* (BRY); Muddy Creek Canyon, *Welsh 20451* (BRY). Garfield Co.: Circle Cliffs, *Harrison 1443* (BRY); 3.5 mi E of the mouth of Red Canyon, *Maguire 19081* (UC, UTC); Red Canyon, *Maguire 19549* (UC, UTC); Hunt Creek, *Welsh 14385* (BRY, UTC). Iron Co.: Hamblin Valley, *Kostler 1408* (BRY); Moenkopi shale, 6 May 1905, *Parry s.n.* (NY, UTC); without locality, fall 1953, *Parry s.n.* (UTC). Juab Co.: ca. 3 km S of Yuba Dam, *Cronquist et al. 12040* (UTC); Little Valley, *Goodrich 15281* (BRY); near center of section, Little Valley, *Goodrich 16377* (UTC); Yuba Dam, *Goodrich 16410* (BRY); 1.5–2 mi S of Yuba Dam, *Shultz et al. 10156* (UTC). Millard Co.: 9 mi N of Scipio, *Albee 1788* (UT); near Garrison, *Alder 84* (COLO, UT); Confusion Range, *Aitken 432* (UTC); Desert Range Experiment Station, *Beetle 13208* (RM), 24 Apr 1948, *Cook s.n.* (UTC), *Cottam 8098* (COLO, UT), 5 May 1905, *Cottam s.n.* (DS, US). Piute Co.: Piute Reservoir, *Neese 7150* (UTC). Sanpete Co.: near Gunnison, *Cottam 9386* (UT). Sevier Co.: Valley Mtns, *Welsh & Welsh 18209* (BRY). Tooele Co.: Vernon, *Jones 6413* (DS); 7 mi NE of Vernon, 4 May 1968,

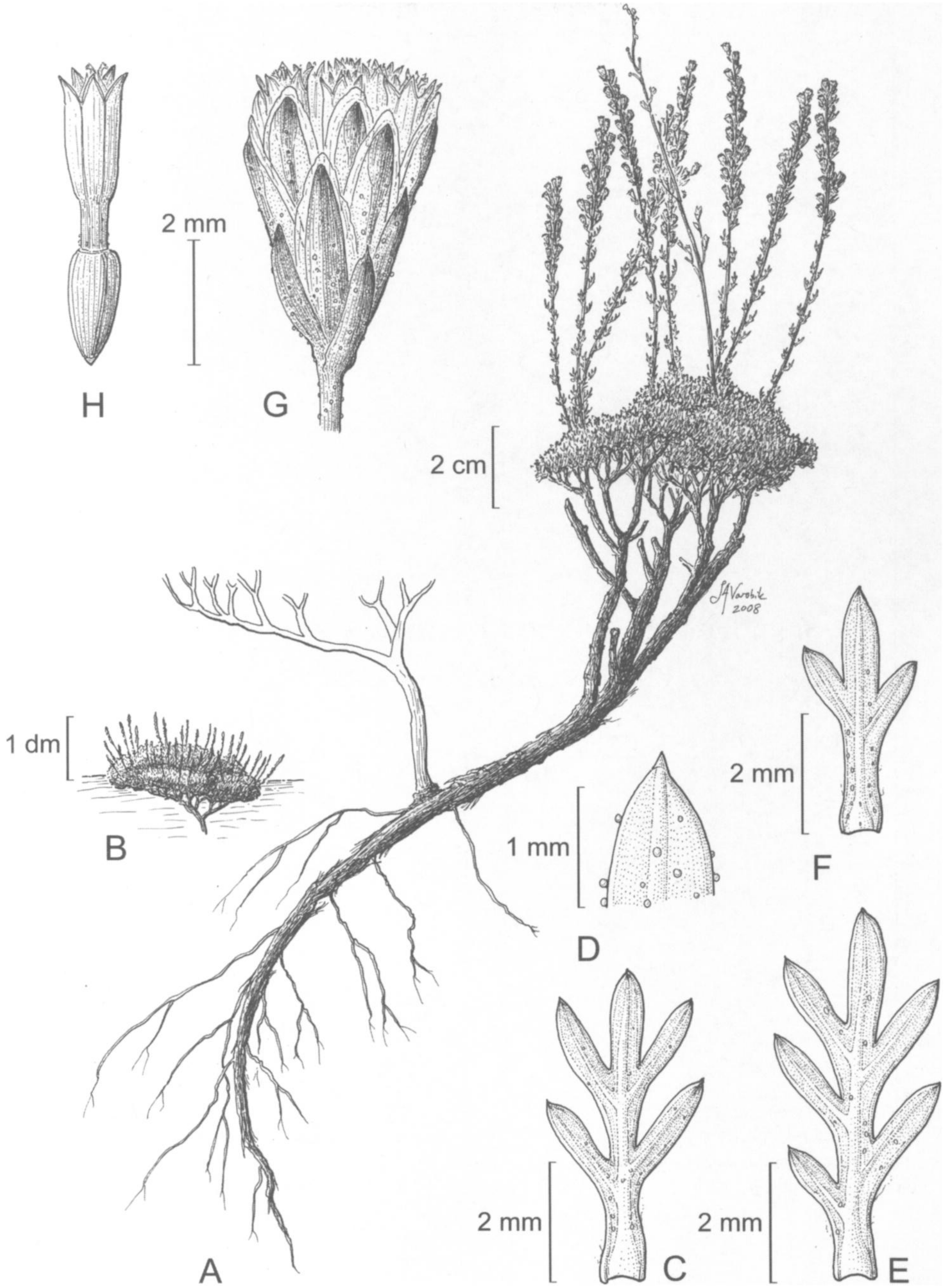

FIG. 36. *Artemisia pygmaea.* A. Habit. B. Habit. C. Leaf. D. Detail of leaf tip. E. Leaf. F. Inflorescence leaf. G. Capitulum. H. Floret and cypsela. (Based on: A, C, D–F, H, *Shultz et al. 10156*; G, *Tiehm 8397*.)

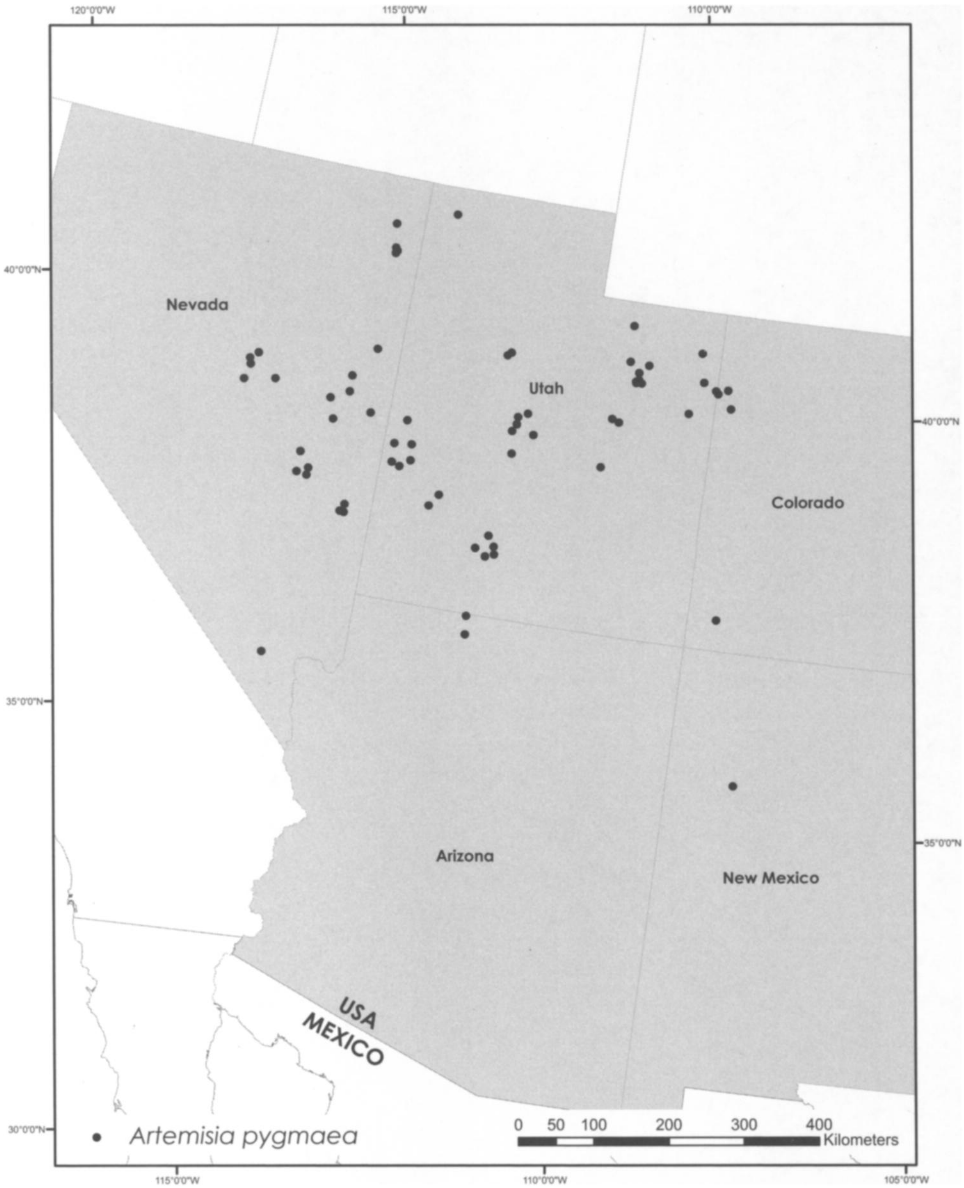

FIG. 37. Distribution of *Artemisia pygmaea.*

Telica s.n. (UTC). Uintah Co.: Hill Creek, 12 Sep 1960, *Bennett s.n.* (UTC); SW of Seep Ridge Rd, at Buck Canyon Road, *Peterson et al. 1394* (UTC); Klondike Canyon, *Shultz & Shultz 3832* (UTC); 7 mi NE of Bonanza, *Shultz & Shultz 5102* (COLO, RSA, UTC); 0.75 mi NE of Walsh Knolls, *Shultz & Shultz 5404* (UTC).

Artemisia pygmaea is a distinctive, faintly aromatic shrublet, often mistaken for something other than sagebrush. In early spring its stiff, bright green, deeply pinnatifid leaves cause it sometimes to be confused with *Leptodactylon pungens* (Torr.) Nutt. in the Polemoniaceae, but its narrow panicles and small capitula easily identify it as *Artemisia*. It differs from other members of the subgenus by its pinnatifid, bright green, and non-fascicled leaves. The molecular analysis by Watson et al. (2002) supports its phylogenetic alignment within subg. *Tridentatae*, and its shrubby growth form and homogamous flower heads align it morphologically with other members of the subgenus. The species is rare and restricted to shale barrens, accumulations of fine-textured calcareous colluvium, or welded ash tuffs. It is usually in sites surrounded by *Juniperus osteosperma* (Torr.) Little, but few other species are occur in the barren habitats where it is found.

The epithet refers to its short, "pygmy-like" growth form.

Artemisia sect. **Nebulosae** L. M. Shultz, sect. nov.—Type: *Artemisia californica* Lessing.
Artemisia [unranked] *Filifoliae* Rydberg, N. Amer. fl. 34: 257. 1916. *Artemisia* ser. *Filifoliae* (Rydberg) Y. R. Ling in Hind, Jeffrey & Pope, Advances in Compositae Systematics, 272. 1995.—Type: *Artemisia filifolia* Torrey.

A sect. Tridentatae differt capitulis heterogamis, foliis non fasciculatis.

Shrubs deciduous, mildly aromatic. Leaves not fasciculate, mostly deeply lobed (some entire) with filiform segments. Capitula heterogamous, arranged in narrow or broad panicles. Florets 0.8–2 mm long, pale yellow; marginal florets pistillate and fertile, or perfect and fertile (*A. filifolia*); central florets perfect and fertile, or functionally staminate with an abortive ovary (*A. filifolia*); style branches of marginal florets erect and with marginal stigmatic lines, of central florets spreading and apically fringed (but shriveled in *A. filifolia*). Cypselae 0.8–2 mm long, fusiform; pappus a rudimentary crown or absent (*A. filifolia*).

The name "*Nebulosae*" is chosen in reference to the still uncertain, or "nebulous," boundaries of the proposed section. It also alludes to the range of the three included species, which forms a geographic cloud-like "nebula" bordering the Intermountain Region, the core distribution for sect. *Tridentatae* (see Fig. 11). See p. 29 for discussion of sect. *Nebulosae*.

11. Artemisia californica Lessing, Linnaea 6: 523. 1831. *Crossostephium californicum* (Lessing) Rydberg, N. Amer. Fl. 34: 243. 1916.—Type: U.S.A. California: San Francisco [1816], *Chamisso s.n.* (holotype: HAL!; isotypes: GH!).

Artemisia fischeriana Besser, Nouv. Mém. Soc. Imp. Naturalistes Moscou 3: 21. 1834.—Type: U.S.A. California: San Francisco Bay, *Eschscholtz s.n.* (holotype: KW!).

Artemisia fischeriana var. *vegetior* Besser, Nouv. Mém. Soc. Imp. Naturalistes Moscou 3: 88. 1834.—Type: unknown.

Artemisia foliosa Nuttall, Trans. Amer. Philos. Soc., n.s., 7: 397. 1841. *Crossostephium foliosum* (Nuttall) Rydberg, N. Amer. Fl. 34: 243. 1916.—Type: U.S.A. California: Monterey [1834], *T. Nuttall s.n.* (holotype: PH!).

Artemisia abrotanoides Nuttall, Trans. Amer. Philos. Soc., n.s., 7: 399. 1841.—Type: U.S.A. California: near Santa Barbara, [1836], *T. Nuttall s.n.* (holotype: BM!).

Medium-sized to tall, erect, semi-deciduous shrubs (drought-deciduous, but evergreen during moist years), (2–) 15–25 dm tall, pungently aromatic; crowns rounded; sprouting from underground caudices. Stems relatively numerous, green or brown, coarsely branched, stout or slender, densely canescent to glabrate, bases brittle, woody; bark gray to gray-green. Leaves light gray-green, drought-deciduous (usually during early winter), pliable; blades 3–5 (–9) cm long, 0.5–2 cm wide, filiform or spatulate to obovate, deeply 3–5-lobed (rarely entire), lobes filiform, 0.5–1 (–2) mm wide, surfaces sparsely to densely hairy; margins revolute. Capitula 2–3 (–4) mm high, 2–4 (–5) mm wide, broadly campanulate or globose, nodding at maturity, pedunculate. Phyllaries in 3–4 series, broadly ovate, sparsely canescent. Inflorescences 6–20 cm long, 1–3 cm wide, narrowly paniculate; branches spreading. Marginal florets 6–10, pistillate, style branches with marginal stigmatic lines; central florets 18–25, perfect, style branches apically fringed, erect; corollas 0.8–1.2 mm long, pale yellow, glabrous. Cypselae 5-angled, 0.5–1.5 mm long, glabrous or glandular. Pappus present as rudimentary squamellae, forming a minute crown. Chromosome number: 2n = 18 (Keil et al. 1988). Fig. 38.

Common name. California sagebrush.

Phenology. Flowering early to late summer.

Distribution (Fig. 39). U.S.A.: California; Mexico: Baja California; in coastal scrub and dry foothills; 0–800 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** CALIFORNIA: Alameda Co.: upper Strawberry Canyon, Sugar Loaf, *Belshaw 229* (UC); S-facing slope above Poultry Experiment Station, *Belshaw 243* (UC); Berkeley Hills, *Chandler 740* (UC); Berkeley Hills, 16 Aug 1904, *Congdon s.n.* (UC); southeastern Redwood Ridge, *Constance 469* (UC); Berkeley, 1 Oct 1888, *Greene s.n.* (JEPS, UC); Arroyo Mocho, near Livermore, *Hoover 2727* (UC); Cedar Mountain, *Jepson 6218* (JEPS); Berkeley Hills, 14 Oct 1898, *Jepson s.n.* (JEPS); Berkeley Hills, Wildcat Canyon, *Lee 1233* (JEPS); Strawberry Canyon, Concord Quad, *Lundh 190* (UC); southern slopes of canyon, Botanical Garden B, *Rodin 273* (UC); above Tesla, Mt Hamilton Range, Corral Hollow, *Sharsmith 3401* (UC); 1 mi SE of Eden and Palomares Creek junction, Hayward, *Sindel 5* (UC); 0.5 mi N of extreme E end of Lake Chabot, Hayward Quad, *Sindel 7* (UC); 5 mi E of Castro Valley, *Sinnott et al. 530* (UTC). Contra Costa Co.: N road entrance to Mt Diablo State Park, *Bowerman 469* (UC); E flank of Donner Canyon, Mount Diablo, *Bowerman 1069* (UC); Mt Diablo State Park, *Crampton 5466* (UC); 1 mi NW of North Peak, Mt Diablo Quad, *Jensen 382* (UC); Las Trampas Ridge, *Jepson 6852a* (JEPS); Mount Diablo, 18 Oct 1898, *Jepson s.n.* (JEPS); Mt Wanda, Martinez, *Langston AL-90* (JEPS); 2 mi SW of Walnut Creek, 16 Jul 1912, *Taylor s.n.* (UC); Hampton Rd, 1.6 km S of Bear Creek Rd, *Yorks 366* (JEPS). Fresno Co.: near Cherry Hill, Panoche region, *Quibell 9358* (JEPS); Los Gatos Canyon, western Fresno County, *Twisselmann 12820* (JEPS, SBBG). Los Angeles Co.: vicinity of Mosquito Harbor, San Clemente Island, *Abrams & Wiggins 392* (UC); Cahuenga Pass, *Abrams 6374* (UC); Santa Monica Experiment Station, *Barber 284* (UC); Transverse Ranges, *Boyd & Raz 9850* (RSA); Ballona Slough, *Braunton 690* (UC); Peninsular Ranges, *David 19* (RSA); Santa Catalina Island, *Ewan 10806* (RSA); Rio Hondo River at Telegraph Rd, *Ewan 4009* (UC); Avalon, Santa Catalina Island, Public Utilities Canyon, *Fosberg 7157* (UC); Santa Catalina Island, 1 mile W of city of Avalon, *Henrickson 8132* (CHSC); near San Dimas Canyon Dam, *Horton 252* (UC); E of Saugus, Santa Susana Quad, *Johannsen 275* (UC); Santa Catalina Island, *McMinn 1299* (UC); San Clemente Island, W fork of Red Rock Canyon, *Moran 22688* (SD); San Bernardino Basin region, Cal Poly campus, 23 Feb 1948, *Mosbarger s.n.* (RSA); Transverse Ranges, *Munz 9440* (POM); E side of San Clemente Island, *Murbarger 1491* (UC); Sister Elsie Peak, *Peirson 245* (JEPS); near foot of Sister Elsie Peak trail, *Peirson 245* (UTC); Rd E of Avalon, Santa Catalina Island, *Pendleton 1373* (UC); 0.2 mi E of turn to Zuma Beach, US Hwy 1, *Raven & Thompson 13715* (JEPS); 2.7 mi N of Sunset Boulevard, Santa Monica Mtns, *Raven & Thompson 14727* (JEPS); NW end of campus, University of California-Los Angeles campus, Los Angeles, *Raven 11330* (JEPS); 2.6 m N of Sunset Boulevard, *Raven 13782* (JEPS); San Clemente Island, *Raven 17966* (SD, UC); Escondido Canyon, Triumfo Pass Quad, *Raymond 14* (UC); Pebbly Beach Rd, Catalina Island, *Reed 2811* (UC); Malibu, *Rose 46294* (UC); Transverse Ranges, *Ross & Porter 8433* (RSA); NW side of Elephant Hill, Pomona, Puente Hills, *Ross & Ross 5724* (UC); Lopez Canyon, N of Pacoma, *Schlising 3002* (CHSC); Rancho Santa Ana Botanic Garden, 14 Oct 1981, *Shultz s.n.* (UTC); N side of Verdugo Mtns, *Soza et al. 665* (RSA); Pat's Trail, San Clemente Island, *Trask 286* (UC); Palos Verdes Peninsula, S of Los Angeles, *Wallace & Wallace 2180* (RSA); Monrovia, Gold Hill, *Wallace 2157* (RSA); San Dimas, 1931, *Wheeler s.n.* (RSA); ca. 1 mi from junction with Wrigley, *Wolf 4207* (UC). Marin Co.: above Horseshoe Bay, Fort Baker, *Bacigalupi 2719* (UC); hills overlooking Fort Baker, *Bacigalupi 2749* (UC); Angel Island, 1 Oct 1888, *Brandegee s.n.* (UC); Tomales Point Rd, Point Reyes Peninsula, *Ewan 8071* (UC); W of Fairfax, *Jepson 9491* (JEPS); Honeymoon Beach Tomales Bay, *Schreiber 724* (UC). Merced Co.: Pecheco Pass summit, *Frazier 1* (UC). Monterey Co.: 1 mi NE of Elkhorn, San Juan Batista Quad, *Axelrod 597* (UC); Dolan Ridge, 13 Aug 1978, *Bickford s.n.* (UCSC); Del Monte, *Elmer 4048*

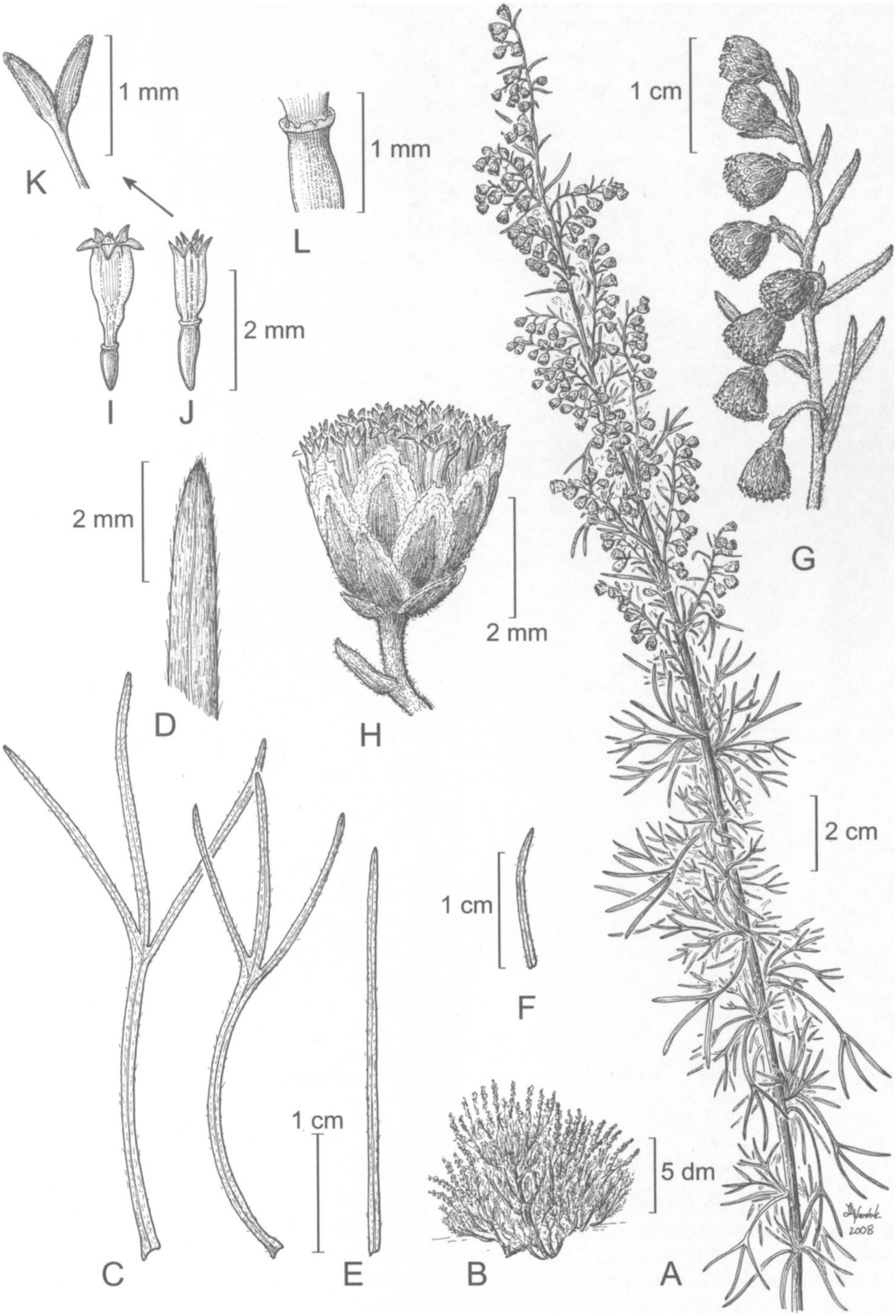

FIG. 38. *Artemisia californica*. A. Branch with leafy and flowering shoots. B. Habit. C. Leaves. D. Detail of leaf tip. E. Leaf. F. Inflorescence leaf. G. Distal portion of inflorescence branch. H. Capitulum, I. Disk floret with cypsela; note rudimentary, ring-like pappus. J. Marginal floret with cypsela; note ring-like pappus. K. Detail showing style branches. L. Detail of showing rudimentary pappus. (Based on: A, E–H, *Peirson 245*; C, D, *Ross, s.n.*, 2 Jan 1966; I–L, *Sinnott et al. 530*.)

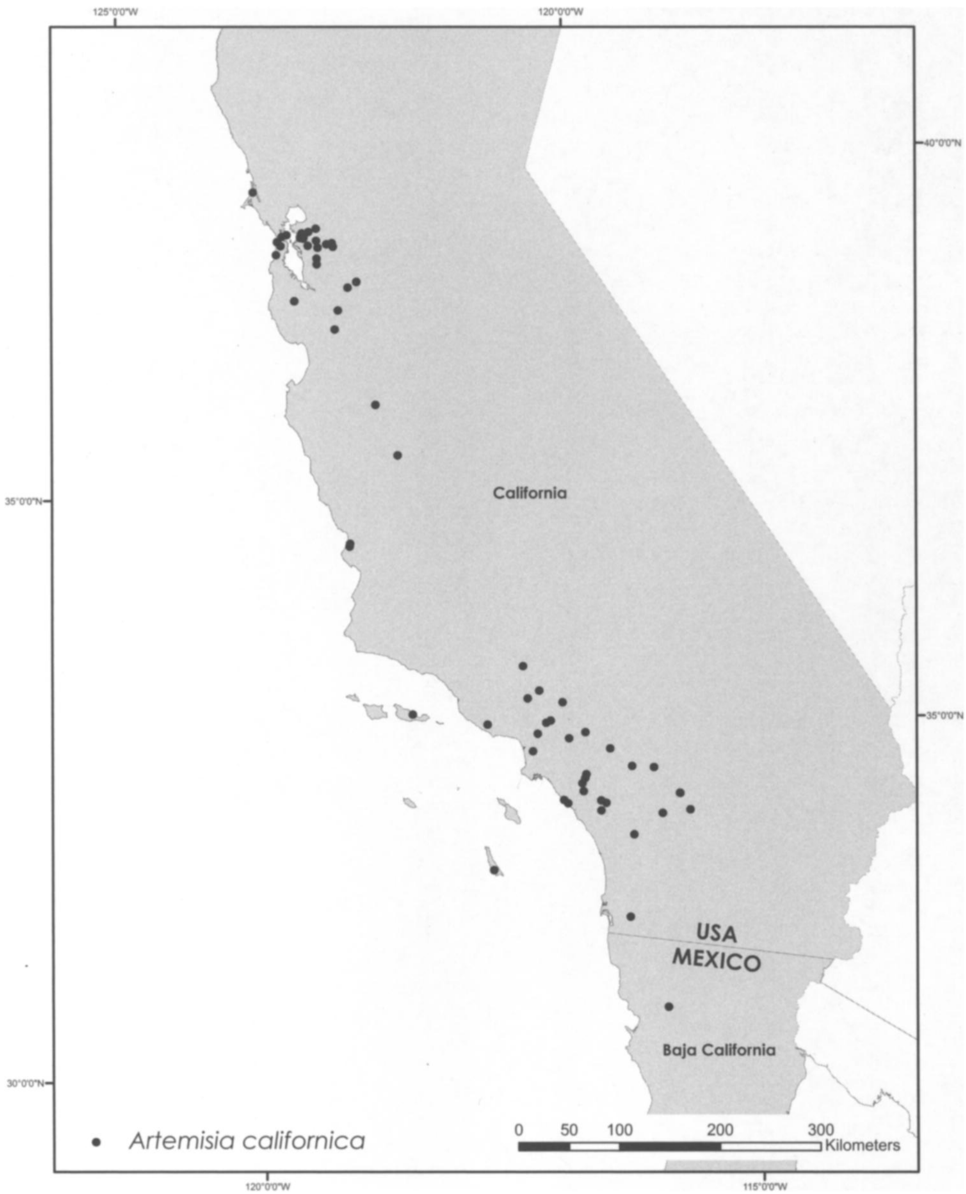

FIG. 39. Distribution of *Artemisia californica*.

(UC); Plot 55, Alberto School, King City Quad, *Graham 171* (UC); Pacific Grove, *Heller 7198* (UC); Plot 140, Semas, Mt Bradley Quad, *Hendrix 894* (UC); edge of dunes, Marina, *Hoover 11538* (UC); hill above Little Sur, Santa Lucia Mtns, *Jepson 2602* (JEPS); Monterey, Monterey Peninsula, *Parish 11580* (UC); on road to Gilroy-Prunedale, *Raven 2514* (UC); Pine Canyon, Salinas Quad, *Raymond 72* (UC); dry rocky place near Carmel, 11 Oct 1945, *Schallert s.n.* (UTC); 2.8 mi E of Leigh Ranch, Los Padres Natl Forest, *Simontacchi 670* (UC); on road to Watsonville, Monterey, *Wolf 3793* (UC). Napa Co.: hills due E of Yountville, *Raven 5180* (JEPS); 2.3 miles N of Monticello Rd on Atlas Peak Rd, *Ruygt 798* (JEPS). Orange Co.: San Joaquin Hills, W of Signal Peak, *Anderson 438439* (UC); Newport Bay, *Booth 223* (UC); Santa Ana Mtns, *Boughey 156* (UC); E end of Newport Bay, *Ewan 7710* (UC); El Toro Marine Base, *Gerhart 20* (UCSB); Santa Ana Mtns, *Mallory 63* (UCR), *Mallory 70*

(UCR); Siphon Reservoir, *Pitzer 311* (UCR); San Joaquin Hills, Crystal Cove State Park, *Pitzer 3373* (UCR); Sulfur Slide Hill in Santa Ana River canyon, *Reed 5640* (UCR); Blue Jay Campground, Los Pinos Peak, *Roberts, Jr. 807* (UCSB); Peninsular Ranges, *Shirokawa 36* (RSA); foothills S of Diamond Bar, *Shultz 4040* (UTC); Newport Beach, Corona del Mar, Corona Highlands, *Thompson 281965* (UC). Riverside Co.: Cabazon, Oct 1907, *Bailey s.n.* (UC); Snow Creek, *Balls & Everett 22755* (SD, UC); Agua Tibia Mtns, Pechanga Indian Reservation, *Banks 1146* (UCR); San Jacinto Mtns, Oasis de Los Osos, *Fellows 165* (UCR); San Jacinto Mtns/Sonoran (Colorado) Desert oasis, 6 Nov 1977, *Latting s.n.* (UCR); Colorado Desert, Cabazon, *Schellenger 44* (UC); Wilson Creek, San Jacinto Quad, *Van Fleet 5* (UC); western Colorado Desert/San Jacinto Mtns, *Zabriskie 548* (UCR); San Jacinto Mtns, Bautista Canyon, *Ziegler 244* (UCR); near Riverside, *Zumbro 365* (UC). San Bernardino Co.: Odessa Canyon, about 12 miles NE of Barstow, *Beach & Gould 200* (UC); Transverse Range, *Noyes 429* (RSA); San Bernardino Mtns, Yucaipa Valley, *Pitzer 303* (UCR); foothills at Loma Linda, 2 Jan 1966, *Ross s.n.* (UTC). San Diego Co.: 5 mi SE of San Clemente at San Onofre Nuclear Generating Station, *Henrickson 7064* (CHSC); Peninsular Ranges, *Hoffmaster 1141* (RSA); San Onofre Canyon, San Luis Rey Quad, *Jensen 163* (UC); 3 mi W of Jamul, *Shultz et al. 4761* (UTC); hills above Jamul, *Shultz et al. 4762* (MO, UC, UTC); SE slope Steward Mine, *Wheeler 8237* (RSA); between Alpine and 5 mi from Alpine, El Cajon, *Wiggins 2164* (UC). San Francisco Co.: near Laguna Honda, San Francisco, *Raven 8220* (JEPS); Laguna Honda, 11 Sep 1942, *Rose s.n.* (UTC); Point Lobos, near San Francisco, 10 Aug 1895, *Tidestrom s.n.* (UC). San Joaquin Co.: Ladd Mine, San Joaquin, *Wheeler 6995* (RSA). San Luis Obispo Co.: Plot 20, Reeds, Arroyo Grande Quad, *Carlson 196* (UC); Central Coast, atop Black Hill above Morro Bay, *Goeden 9* (UCR); Ragged Point, *Hoover 10005* (UC); mouth of Arroyo del la Cruz, *Jensen 48* (UCSC); 2.3 mi S along State Hwy 1, Monterey County line, *Raven 11289* (JEPS); San Luis Obispo, Sep 1906, *Unangst s.n.* (UC). San Mateo Co.: along Route 1, San Francisco City/County line, *Rossbach 616* (UC). Santa Barbara Co.: 1 mi SW of Zaca, Lompoc Quad, *Axelrod 122* (UC); vicinity of Smuggler's Cove, Santa Cruz Island, *Abrams & Wiggins 201* (UC); Santa Barbara Island, Channel Islands, *Abrams & Wiggins 299* (UC); Santa Cruz Island, *Balls & Blakley 23653* (UC); Goleta Point and University of California-Santa Barbara W Campus, *Boyce 135* (UCSB); along the Alamo Pintado Creek, *Breedlove 841* (UCSB); Pelican Bay, Santa Barbara Islands, *Clokey 5110* (UC, UCR); Prisoners Harbor, Santa Barbara Islands, Santa Cruz, *Clokey 5111* (UC, UCR); Ladies' Harbor, Santa Barbara Islands, *Clokey 5112* (UC); mesa near Santa Barbara, *Eastwood & Howell 145* (UC); 0.5 mi E of Summerland, Santa Barbara, *Embree 227* (UC); 0.75 mi SSW of Painted Cave, *Embree 377* (UC); Carpinteria Salt Marsh, *Ferren Jr. 1763* (UCSB); City of Solvang, *Frazier 5* (UC); SW of intersection of Storke Rd and El Cajon, *Gordon & Koehler 8062* (UCSB); Tunnel Rd, *Haller 1509D* (UCSB); Anacapa Island, 1 Jan 1901, *Hemphill s.n.* (UC); Toro Canyon Park, *Lavinger 033* (UCSB); 4 mi SE of Mt Solomon, Lompoc Quad, *Lee 288* (UC); San Miguel Island, *McMinn 2750* (UC); 2 mi NW of Wasioja, Santa Ynez Quad, *Peterson 178* (UC); Canyon back of Pelican Bay, Santa Cruz Island, *Williams 34* (UC); 4 mi S of Gary, Santa Barbara Natl Forest, Lompoc Quad, *Wilson 11* (UC); between Main Ranch and Prisoners Harbor, *Wolf 4140* (UC). Santa Clara Co.: 0.75 mi SSW of Tule Lake, Morgan Hill Quad, *Hendrix 727* (UC); Dry Creek, Plot 104, Mount Hamilton Quad, *Lundh 59* (UC); Black Mountain Rd, Santa Cruz Peninsula, *Randall 51* (JEPS); above Hall's Valley, Mount Hamilton, *Sharsmith 1345* (UC). Santa Cruz Co.: without locality, *Jones 2354* (UTC); Deer Ridge Farm, W-central California, *Pendleton 504* (UC). Sonoma Co.: State Hwy 1, 3.5 miles S of Fort Ross, *Crampton 2971* (UC). Ventura Co.: Pelican Bay, 2 Jul 1930, *Clokey s.n.* (UTC); along Stewart Canyon Rd, 20 Oct 1976, *Fairfax s.n.* (UCSB); Point Mugu, *Howell 3136* (JEPS); 2.5 mi NW of Ventura, *Jepson 20163* (JEPS); floodplain of Piru Creek, Blue Point, *Simontacchi 104* (UC); 2.5 mi N of Ojai, Santa Barbara Natl Forest, *Sowder 164* (UC); Sexton Canyon, Santa Paula Quad, *Sowder 300* (UC). **Mexico.** BAJA CALIFORNIA: 17 mi ENE of Ensenada, *Shultz & Shultz 6042* (UTC).

Artemisia californica is an important component of the coastal chaparral in southern California. Its threadlike leaves, green capitula, and *Salvia*-like odor distinguish it from any other shrub in California. *Artemisia nesiotica*, an endemic of the Channel Islands that has been considered a variant of *A. californica*, is distinct in size and form. Although I once included this species in subg. *Artemisia* for the treatment for the *Flora of North America* (Shultz 2006a), I now follow the molecular phylogeny of Watson et al. (2002) in assigning *A. californica* to the same clade as other species of subg. *Tridentatae*.

The possible relationship of *A. californica* to *A. chinensis* L. (sometimes included in *Crossostephium*) of southeastern Asia and the Philippines was noted by Torrey and Gray (1841) and Rydberg (1916) on the basis of ribbing of the cypselae, a characteristic also found in the Hawaiian *A. australis* Less., and the presence of a rudimentary pappus, a characteristic found in the Hawaiian *A. kauaiensis* (Skottsb.) Skottsb. (Shultz 1990).

12. Artemisia filifolia Torrey, Ann. Lyceum Nat. Hist. New York 2: 211. 1827. *Oligosporus filifolius* (Torrey) Poljakov, Trudy Inst. Bot. (Alma-Ata) 11: 170. 1961 [combination also proposed by W. A. Weber, 1984].—TYPE: U.S.A.: "arid plains of the Platte," [presumably eastern Colorado in 1820], *E. James s.n.* (holotype: NY!).

Artemisia plattensis Nuttall, Trans. Amer. Philos. Soc., n.s., 7: 397. 1841.—TYPE: U.S.A.: "upper plains of the Platte River" [presumably Nebraska, 1834], *T. Nuttall s.n.* (lectotype, here designated: PH!; isolectotype: GH!).

Medium-sized to tall, semi-deciduous shrubs, 6–18 dm tall, faintly aromatic; crowns rounded; not root-sprouting. Stems green or gray-green, curved, wandlike, usually slender, sometimes stout and stunted in harsh habitats, glabrous or sparsely hairy; bark gray. Leaves gray-green, deciduous or evergreen, pliable, (1.5–) 2–4 (–6) cm long, 0.1–0.9 mm wide, mostly entire and linear, or deeply 3-lobed, if 3-lobed, then the leaves to 2.5 cm wide but still with filiform lobes less than 1 mm wide, apices acute, surfaces glabrous or sparsely hairy. Capitula 1–1.5 (–2) mm high, 1.5–2 mm wide, globose, usually nodding, mostly sessile. Phyllaries ovate, margins scarious, inconspicuous, densely hairy. Inflorescences narrowly paniculate, 8–17 cm long, 2–4 (–5) cm wide; branches erect to somewhat recurved. Marginal florets 1–4, perfect, style branches with marginal stigmatic lines; central florets 3–6, functionally staminate (ovary aborted), style branches withered (abortive), erect; corollas 1–1.5 mm long, pale yellow, glabrous. Cypselae 0.2–0.5 mm long, oblong, distally incurved-falcate and oblique, glabrous, obscurely nerved. Pappus absent. Chromosome number: 2n = 18 (McArthur & Pope 1979). Fig. 40.

Common name. Sand sage.

Phenology. Flowering late summer to early winter.

Distribution (Fig. 41). U.S.A.: Arizona, Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas, Utah, Wyoming; in sandy soils, in open prairies and on dunes; 500–2000 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** ARIZONA: W side of Cockscomb, *Atwood & Kaneko 03384* (UTC); Coconino Co.: 3 mi S of Fredonia, 6 Aug 1957, *Beetle s.n.* (UTC). La Paz Co.: Billings, *Jones 4569* (UTC). Mohave Co.: Grand Canyon-Parashant National Monument, Black Canyon, *Atwood 27891* (UTC).—COLORADO: Arapaho Co.: Aurora, *King & Garvey 12691* (MO). Baca Co.: 3.5 mi S of Campo, *Mooers 919* (UTC); 23 mi S of Walsh, *Stephens & Brooks 21799* (KANU); vicinity of Wilson Ranch, 27 mi S of Pritchett, 6 Aug 1948, *Weber s.n.* (UTC). Bent Co.: 0.5 mi E of Prowers, *Stephens & Brooks 21977* (KANU). Cheyenne Co.: 19.6 mi W of Cheyenne Wells, *Miller et al. 6683* (UTC); 7.5 mi E of Kit Carson, *Stephens 62629* (KANU). Crowley Co.: 9.5 mi N of Ordway, *Stephens 62725* (KANU). Denver Co.: along the Platte River, *Jones 662* (UTC), *Jones s.n.* (UTC). Kiowa Co.: 3 mi SW of Haswell, *Stephens 62748* (KANU). Kit Carson Co.: 17.5 mi N of Burlington, *Stephens 62585* (KANU). Lincoln Co.: CO 94 2.2 mi W of the Cheyenne County line, *Freeman & Morse 16404* (KANU). Logan Co.: 3 mi SE of Sterling, *Stephens 5221* (KANU). Morgan Co.: country road, *Walter & Walter 8385* (MO). Phillips Co.: 5 mi S of Holyoke, *Stephens & Brooks 24063* (KANU). Pueblo Co.: 2 mi N of Pinon, *King & Garvey 12698* (MO). Washington Co.: 1 mi S of Otis, *Stephens 62539* (KANU). Weld Co.: river bench and hills above S Platte River, 17 Aug 1940, *Ewan s.n.* (UTC); 12 mi N of Stoneham, *McGregor 24538* (KANU); NW of Riverside Reservoir, *Robbins 897* (UTC). Yuma Co.: 2 mi S of Beecher Island, *Stephens 4927* (KANU).—KANSAS: Barber Co.: near Medicine Lodge, *Palmer 41838* (MO); 6 mi S of Sun City, *Wagenknecht 3174* (KANU). Clark Co.: 14 mi N of Ashland, *Stephens 84309* (KANU). Comanche Co.: 1 mi W of Protection, *Wagenknecht 4663* (KANU). Finney Co.: 0.5 mi S and 6 mi E of Garden City, *Richards 3058* (KANU). Ford Co.: 2 mi S of Dodge City, *Brooks 6411* (KANU). Gove Co.: 12 mi S of Gove, *McGregor 13656*

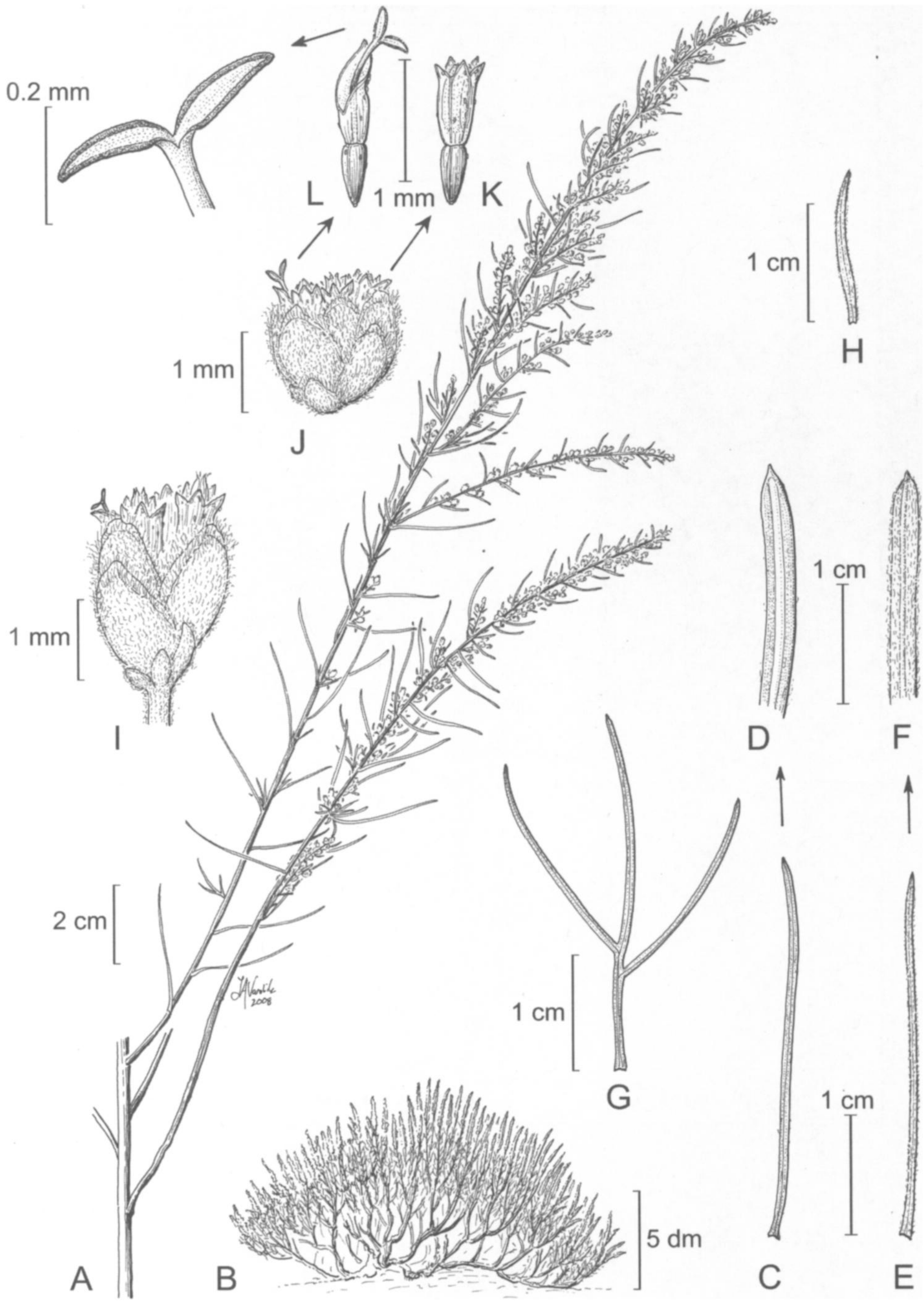

FIG. 40. *Artemisia filifolia*. A. Branch with flowering shoots. B. Habit. C. Leaf. D. Detail of leaf tip. E. Leaf. F. Detail of leaf tip. G. Leaf. H. Inflorescence leaf. I. Capitulum J. Capitulum, showing exserted style branches of a marginal floret. K. Perfect disk floret and cypsela. L. Pistillate floret, with ray-like ligule, and cypsela; detail showing style branches lacking fringe. (Based on: A, C, D, H, J, K, *Shultz & Shultz 8995*; E, F, *Atwood 27891*; G, I, *Nelson 8636*.)

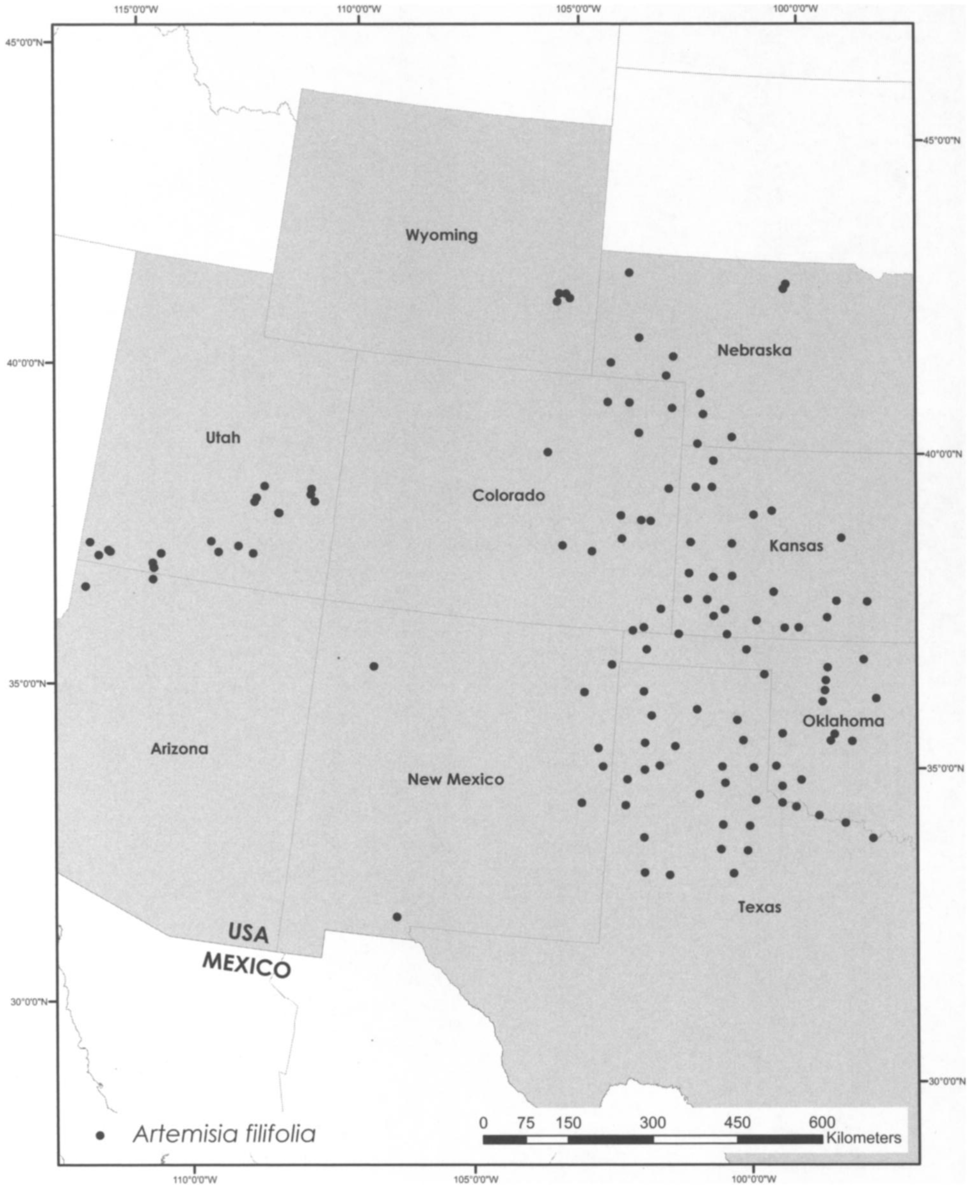

FIG. 41. Distribution of *Artemisia filifolia*.

(KANU). Grant Co.: 11 mi S and 1 mi E of Ulysses, *Stephens 64892* (KANU). Gray Co.: 2 mi E of Charlestown, *McGregor 3988* (KANU). Greeley Co.: 16 mi N and 7 mi E of Tribune, *McGregor 24460* (KANU). Hamilton Co.: 0.4 mi S and 2.5 mi E of Syracuse, *Richards 2991* (KANU). Haskell Co.: 1 mi S and 3.5 mi W of Satanta, *Stephens 87563* (KANU). Kearney Co.: 10 mi W of Lakin, *Brooks 3086* (MO). Kearny Co.: 3 mi SW of Lakin, *Stephens 84108* (KANU). Kingman Co.: 7 mi W of Kingman, *Stephens 2837* (KANU). Meade Co.: 8 mi S and 2 mi W of Meade, *Stephens 63005* (KANU). Morton Co.: E city limits Elkhart, *Richards 2980* (KANU). Pratt Co.: 6 mi E of Pratt, *Stephens 84751* (KANU). Rawlins Co.: 13 mi N and 1 mi E of McDonald, *Hauser & Brooks 2832* (KANU). Scott Co.: 14 mi N and 1 mi W of Scott City, *Stephens 57138* (KANU). Seward Co.: 14.5 mi N and 3 mi E of Liberal, *Stephens 84198* (KANU). Sherman Co.: 7 mi S and 3 mi W of Goodland, *McGregor 24478*

(KANU). Stanton Co.: 3.5 mi N of Johnson, *Stephens 84130* (KANU). Stevens Co.: 14 mi W of Moscow, *Stephens & Meyer 57496* (KANU). Thomas Co.: 1 mi S of Brewster, *McGregor 24648* (KANU). Trego Co.: 16.5 mi S of Collyer, *Stephens 2739* (KANU). Wallace Co.: without locality, *Snow s.n.* (KANU). Wichita Co.: without locality, 24 Aug 1912, *Agrelius & Agrelius s.n.* (KANU).—MONTANA: Chase Co.: SE of Enders, *Tolstead 411425* (MO). Sioux Co.: Monroe Canyon, Sep 1901, *Baker s.n.* (MO).—NEBRASKA: Banner Co.: 11 mi W of Morrill County line, *Richardson 1587* (KANU). Brown Co.: ca. 8 mi N of Johnstown, *Freeman 1261* (KANU). Chase Co.: 6 mi N of Imperial, *Stephens 50241* (KANU). Deuel Co.: 18 mi of E Chappell, *Stephens & Brooks 16028* (KANU). Dundy Co.: 5 mi N of Parks, *McGregor 18841* (KANU). Garden Co.: 4 mi N of Oshkosh, *Stephens & Brooks 24835* (KANU). Hitchcock Co.: 2.5 mi E of Trenton, *Stephens 62318* (KANU). Kimball Co.: 6 mi W of Kimball, *McGregor 24533* (KANU). Morrill Co.: 14 mi S and 2 mi W of Bridgeport, *Stephens & Brooks 16084* (KANU). Perkins Co.: 3 mi N of Grant, *Stephens 50207* (KANU). Sioux Co.: 22 mi S of Agate, *Stephens & Brooks 16169* (KANU).—NEW MEXICO: Curry Co.: 10 mi S of Broadview, *Stephens 79989* (KANU). De Baca Co.: 4 mi E of Fort Sumner, *Stephens & Brooks 25718* (KANU). Dona Ana Co.: cinder cones 6 mi W of La Mesa, *Fosberg 54028* (UTC). Harding Co.: 9 mi S of Bueyeros, *Stephens 75653* (KANU). Quay Co.: Nara Visa, 26 Oct 1910, *Fisher s.n.* (MO); 5 mi N of San Jon, *Stephens 75767* (KANU). Roosevelt Co.: 4.5 mi S and 2 mi W of Floyd, *Stephens 75902* (KANU). San Juan Co.: Chaco Canyon Natl Park, *Kass 1481* (UTC). Sandoval Co.: 13 mi SE of San Ysidro on Hwy 44, *Higgins 10474* (UTC). Torrance Co.: Clines Corners, *Wagner & Duke 4438* (MO). Union Co.: 12 mi S of Clayton, *Stephens 75595* (KANU).—OKLAHOMA: Alfalfa Co.: Kegelman Air Force Base, *Johnson & Proctor KEG0117* (OKL). Beaver Co.: 2 mi N of Beaver, *McGregor 35146* (KANU). Beckham Co.: North Fork of the Red River, *Eskew 1512* (OKL). Blaine Co.: just E of Okeene, *Smith 406* (OKL). Caddo Co.: near Hinton, at bottom of Devil's Canyon, *Stevens & 919* (OKLA). Canadian Co.: near Methodist camp, *Ray et al. 1012* (OKL); Methodist Canyon area, *Taylor & Taylor 20928* (KANU). Cimarron Co.: 3 mi N of Kenton, *Rogers 5433* (OKL). Comanche Co.: Wichita Mtns Wildlife Refuge, *Magrath 15827* (OCLA). Cotton Co.: 5 mi S of Randlett, *Hoagland 0420* (OKL). Custer Co.: 6 mi S and 4 mi E of Weatherford, *Reinke 324* (KANU); SW of South Canadian River, E of Thomas, *Seigler 10688* (OKL). Dewey Co.: Hwy 281 N, 1.5 mi S of intersection of Hwys 281 and 60, *Clarke 84* (CS); 0.5 mi N of Taloga, *Stephens 27204* (KANU). Greer Co.: Sandy Sanders Wildlife Management Area, *Hoagland 0049* (OKL). Harmon Co.: 1 mi E of McQueen, *Stephens 20796* (KANU). Harper Co.: along Hwy 183, between Buffalo and Woodward, *Nelson & Nelson 5278* (OKL). Jackson Co.: Hwy 6 at Red River, *Benesh & Hoagland E466* (OKL); 1 mi S and 8 mi E of Blair, *Stephens 27334* (KANU). Jefferson Co.: Red River at US Hwy 81 bridge, *Benesh et al. E564* (OKL). Kingfisher Co.: 1 mi N and 2 mi W of Dover, *Byers 87* (OKLA); 16 mi W of Hennessey, *Stephens 76627* (KANU). Major Co.: ca. 2 mi W of Bouse Junction, *Buthod AB-5167* (OKL); 7 mi N of Chester, *Stephens 27152* (KANU). Roger Mills Co.: 3.5 mi S and 4 mi W of Cheyenne, *Freeman & Morse 17626* (KANU); Antelope Hills, *Nelson et al. 5339* (OKL). Texas Co.: 7 mi SW of Elkhart, *Stephens 73825* (KANU). Tillman Co.: 7 mi E of Hwy 70 from jct with Hwy 183 near Davidson, *Hoagland et al. BLM0425* (OKL). Washita Co.: N on Hwy 54, *Hoagland & Gray 0320* (OKL). Woods Co.: N side of Cimarron River and W of Hwy 281, *Barclay w38-7* (TULS); 2.5 mi S of Waynoka, *McGregor 39241* (KANU). Woodward Co.: 5 mi S of Supply, *Nelson et al. 5300* (OKLA).—TEXAS: Bailey Co.: 18 mi S of Muleshoe, *Stephens 73122* (KANU). Briscoe Co.: 10.5 mi NW of Silverton, *Stephens 72289* (KANU). Carson Co.: 3 mi NW of Skelleytown, *Stephens & Brooks 17344* (KANU). Childress Co.: 8 mi N of Childress, *Stephens 80887* (KANU). Collingsworth Co.: 2 mi N and 0.5 mi W of Wellington, *Stephens 80947* (KANU); 2–3 mi S of Salt Fork of Red River, *Tharp & Miller 51-309* (UTC). Cottle Co.: 7 mi W of Paducah, *Stephens 80680* (KANU). Dallam Co.: 3.5 mi N of Dalhart, *Stephens 73675* (KANU). Deaf Smith Co.: 4.5 mi S and 22 mi W of Hereford, *Stephens 73281* (KANU). Dickens Co.: 10 mi N of Dickens, *Stephens 72450* (KANU). Donley Co.: 14.5 mi N of Clarendon, *Stephens 71986* (KANU). Gaines Co.: near Seagraves, *Correll & Johnston 24203* (MO). Hall Co.: 4.5 mi E of Lesley, *Stephens 72088* (KANU). Hartley Co.: 1.5 mi N of Channing, *Stephens 73534* (KANU). Hemphill Co.: Canadian River prairies, Aug 1900, *Eggert s.n.* (MO). Hockley Co.: 3.5 mi N and 5 mi W of Whitharral, *Stephens 72991* (KANU). Howard Co.: Big Spring, *Palmer 13057* (MO). Hutchinson Co.: 3 mi S of Stinnett, *Stephens & Brooks 25414* (KANU). Kent Co.: 1.5 mi W of Jayton, *Stephens 72664* (KANU). King Co.: 0.25 mi S of Guthrie, *Stephens 72529* (KANU). Lamb Co.: 3 mi N of Fieldton, *Stephens 80362* (KANU). Lipscomb Co.: 7.5 mi E of Follett, *Stephens 75141* (KANU). Lynn Co.: 10.5 mi W of Tahoka, *Stephens 72927* (KANU). Motley Co.: 19 mi N of Matador, *Stephens 72362* (KANU). Nolan Co.: between Colorado and Brazos rivers, 4 Aug 1934, *Barkley s.n.* (MO). Oldham Co.: 21 mi NE of Vega, *Stephens 73462* (KANU). Parmer Co.: 11 mi S of Friona, *Stephens 73221* (KANU). Potter Co.: 21 mi NW of Amarillo, *Stephens 76226* (KANU). Randall Co.: Buffalo Lake Wildlife Refuge, *Higgins 11342* (UTC). Roberts Co.: 2 mi NE of Miami, *Stephens 37411* (KANU). Runnels Co.: Ballinger, *Palmer 10331* (MO). Terry Co.: 14 mi SE of Brownfield, *Stephens 72857* (KANU). Val Verde Co.: near Del Rio, *Palmer 11087* (MO). Wheeler Co.: 1.5 mi W of Kellerville, *Stephens 76503* (KANU). Wilbarger Co.: 5 mi E of Odell, *Stephens 20701* (KANU).—UTAH: Emery Co.: San Rafael

Desert, near Keg Spring, *Bryan & Redd 9-1* (UTC); San Rafael, *Stanton s.n.* (UTC). Garfield Co.: Capitol Reef Natl Park, *Camp 16* (UTC); Hole-in-the-Rock road, *Shultz 20281* (UTC); near Hite, *Shultz & Shultz 8905* (UTC, MO). Grand Co.: between Balanced Rock and Courthouse, *Shaw 3056* (UTC); along Potash Rd Scenic Drive, *Stockton 161* (UTC). Kane Co.: Vermilion Cliff, *Fertig 22290* (UTC); 8 mi N of Kanab, 20 Jun 1940, *Maguire s.n.* (UTC); Hole-in-the Rock road, *Shultz 20280* (UTC); Johnson Canyon, *Shultz & Shultz 9842* (UTC). San Juan Co.: W slope of Comb Ridge, 27 Aug 1953, *Harrison s.n.* (UTC); S of Montezuma Creek in sandy soil, *Lyngholm & Smith 10* (UTC); Forgotten Canyon, *Shultz & Shultz 8995* (UTC); Spanish Valley, *Shultz & McReynolds 20176* (UTC); N of Mexican Water, *Smith 102* (UTC). Washington Co.: near Rockville, *Higgins 20890* (MO); 20 mi N of Hanksville, 3 Oct 1941, *Jansen s.n.* (UTC); 15 mi W of Zion Natl Park, 4 Aug 1934, *Maguire & Richards, Jr. s.n.* (UTC); off hwy, *Neely & Chambers 2047* (UTC); E side of the Pine Valley Mtns, *Shultz 4832* (MO, UTC); near base of Canaan Mtn, *Shultz & Anderson 5386* (UTC); SE benches of the Bull Valley Mtns, *Shultz & Shultz 7737* (UTC); Red Cliffs Recreation Area, *Shultz & Shultz 9814* (UTC). Wayne Co.: Capital Wash, 1 Jul 1940, *Maguire s.n.* (UTC); 3.3 mi S of Emery County line, *Shultz & Shultz 6978* (UTC); near Hans Flat Ranger Station, *Shultz & Shultz 7375* (UTC); Orange Cliffs of the Glen Canyon Natl Recreation Area, *Shultz & Shultz 7385* (UTC).—WYOMING: Goshen Co.: 7 mi W of Fort Laramie, *Stephens 70875* (KANU). Laramie Co.: Uva, *Nelson 8636* (UTC), 3 Sep 1901, *Nelson s.n.* (UTC). Platte Co.: 7.5 mi W of Guernsey, *Stephens 70819* (KANU).

Artemisia filifolia is one of the most easily distinguished of the shrubby taxa of *Artemisia*. Its filiform leaves, graceful wandlike branches, faintly aromatic foliage, and tiny flowering heads distinguish it from other members of subg. *Tridentatae*. Sand sage occurs in loose sandy soils, often with *Salvia dorrii* (Kellogg) Abrams and species of *Yucca* L. and *Opuntia* Mill.

I place this species in subg. *Tridentatae* based on a molecular phylogeny proposed by Watson et al. (2002). Riggins and Seigler (2006) also align the species in a broadly defined North American/Beringian clade, which encompasses sect. *Tridentatae*, *Sphaeromeria*, *Picrothamnus*, and a number of Alaskan species of *Artemisia*. My earlier treatment placed this species within subg. *Dracunculus* (Shultz 2006a).

13. Artemisia nesiotica P. H. Raven, Aliso 5: 341. 1963. *Crossostephium insulare* Rydberg, N. Amer. Fl. 34: 244. 1916, non *Artemisia insularis* Kitamura, 1936. *Artemisia californica* var. *insularis* (Rydberg) Munz, Man. S. Calif. bot. 575. 1935.—TYPE: U.S.A. California: San Clemente Island, Pot's Trail, Jun 1903, *B. Trask 286* (holotype: NY!; isotype: US!).

Low-growing or prostrate evergreen shrubs, 1–5 dm tall, mildly aromatic; crowns rounded; sprouting from underground caudices. Stems numerous, gray, ascending or prostrate, stiff and coarsely (broadly) spreading, densely canescent, bases woody and brittle; bark pale gray. Leaves dull green, evergreen, pliable, 3–6 cm long, 1–4 cm wide (or ca. 1.5 mm wide if entire), attached singly, palmately or pinnately 3–5 lobed, lobes 1.2–3 mm wide; blades linear-oblong, stiff (but not brittle), surfaces gray-hairy, sparsely to densely canescent, the adaxial surface tending to be dark green and less pubescent than the abaxial surface, margins not revolute. Capitula 3–4 mm high, 3–4.5 mm wide, broadly campanulate, usually erect, sometimes nodding. Phyllaries broadly ovate, densely hairy. Inflorescences sparsely leafy, 10–25 cm long, 2–5 (–7) cm wide. Marginal florets 10–15, pistillate, style branches with marginal stigmatic lines; central florets 20–40, perfect, style branches apically fringed, erect; corollas 1.2–2.0 mm long, glandular. Cypselae ca. 0.5 mm long, light brown, 5-ribbed, resinous. Pappus rudimentary, coroniform. Chromosome number unknown. Fig. 42.

Common name. Island sagebrush.

Phenology. Flowering late summer to early winter.

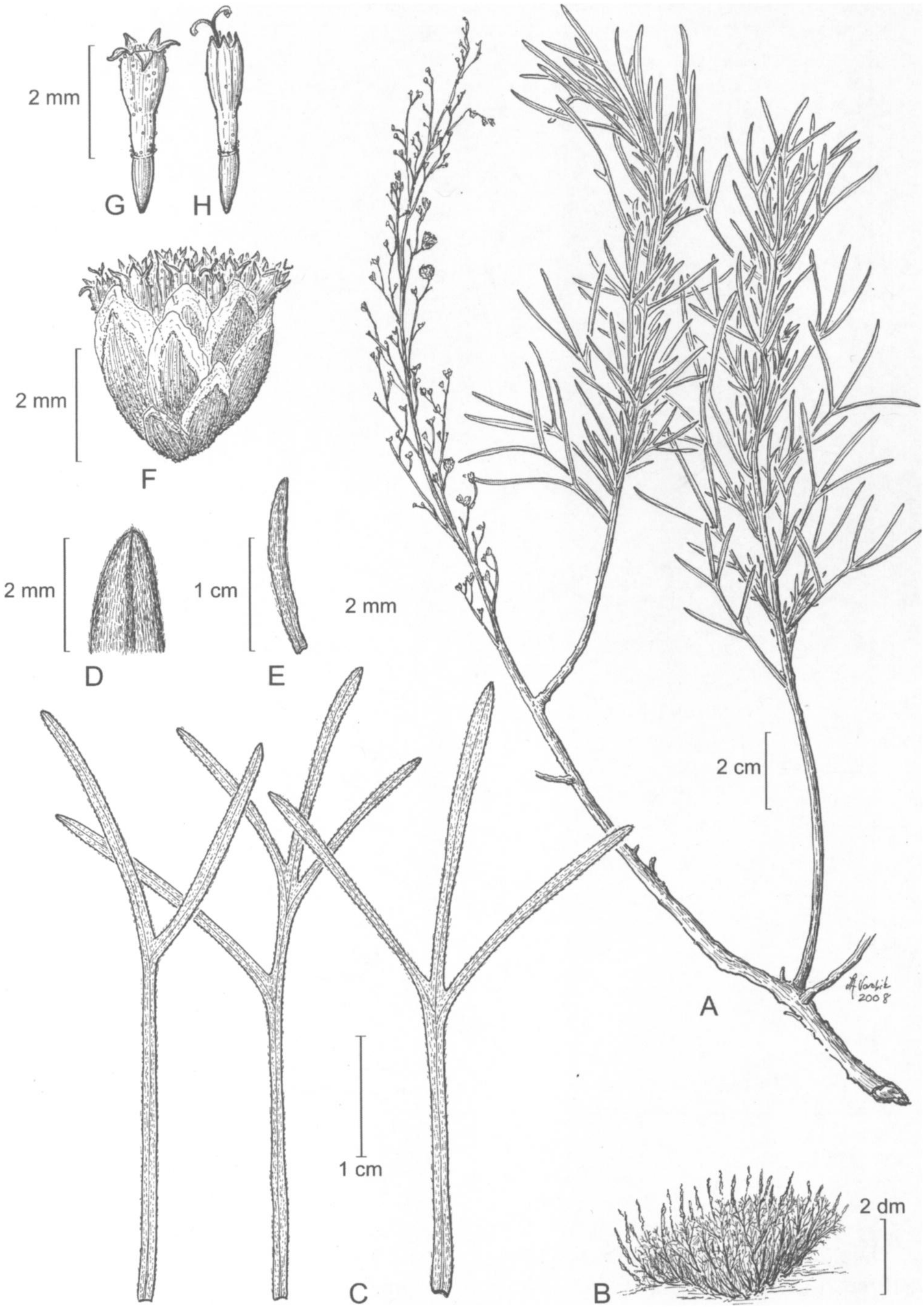

FIG. 42. *Artemisia nesiotica*. A. Branch with leafy and flowering shoots. B. Habit. C. Leaves. D. Detail of leaf tip. E. Inflorescence leaf. F. Capitulum. G, H. Florets; note rudimentary (ring-like) pappus. (Based on *Junak 705*.)

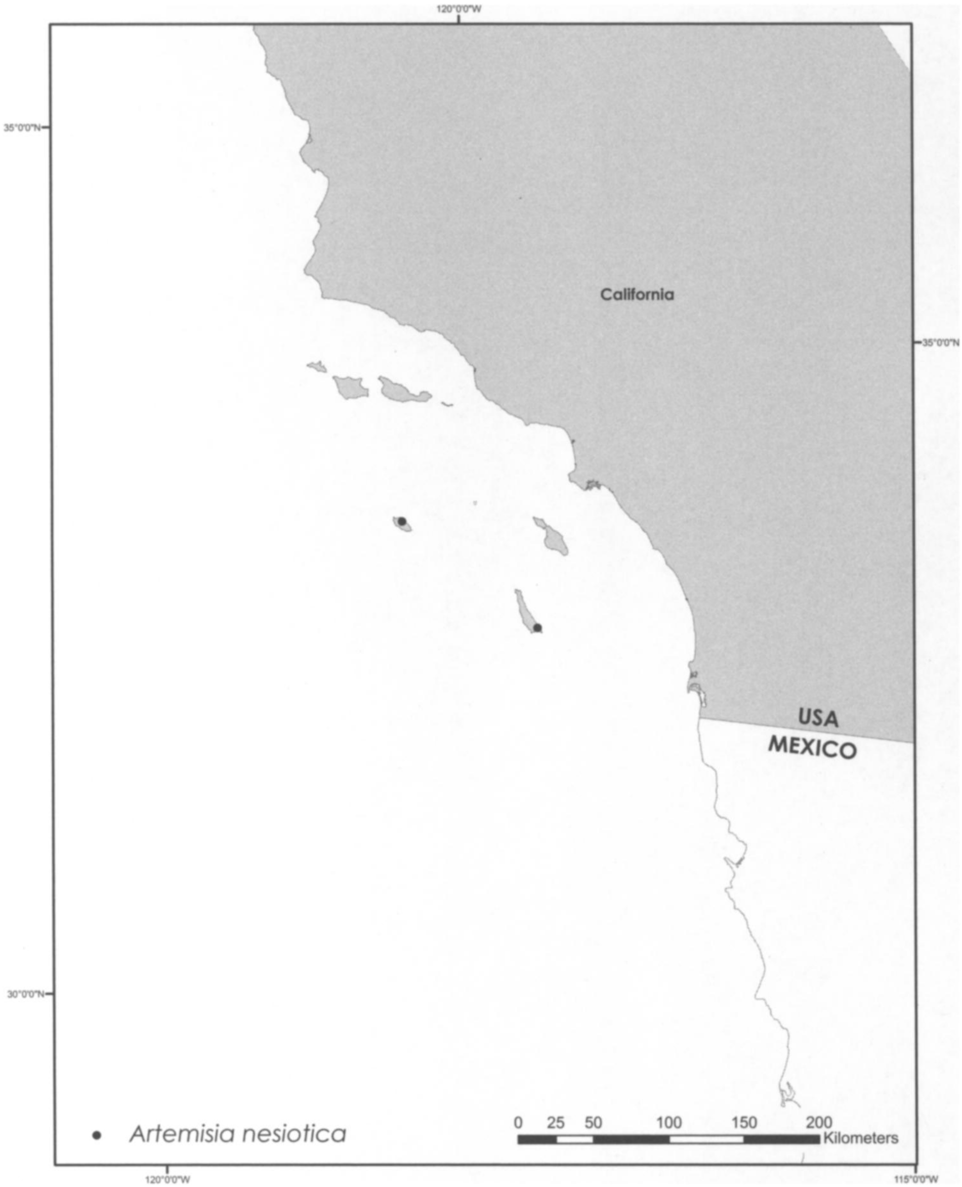

FIG. 43. Distribution of *Artemisia nesiotica*.

Distribution (Fig. 43). U.S.A.: endemic to San Nicolas Island, San Clemente Island, and Santa Catalina Island of the California Channel Islands; on rocky slopes and fog-shrouded hillsides; 0–100 m.

ADDITIONAL SPECIMENS EXAMINED. **U.S.A.** CALIFORNIA: Ventura Co.: San Clemente Island, 17 Sep 1894, *Brandegee s.n.* (UC); Santa Catalina Island, *Foreman et al. 89* (UC); Santa Catalina Island, NE coast, *Junak 705* (JEPS); Santa Catalina Island, S end of island, with cactus, *Murbarger 127* (UC); San Nicolas Island, *Trask 71a* (MO).

Artemisia nesiotica is endemic to the Channel Islands of California. It was originally described as a member of the genus *Crossostephium* by Rydberg (1916) and subsequently treated as a variety of *A. californica* by Munz (1935). The phylogeny, based on a comparison of ITS sequences (Riggins & Seigler 2006), shows a well-supported clade uniting *A. californica* and *A. nesiotica*. *Artemisia nesiotica* is well distinguished from *A. californica* by its shorter stature, wider leaf lobes, and larger capitula. There is no evidence of hybridization on the islands where the two species co-occur. Reports of *A. nesiotica* on the mainland of California are based on cultivated specimens found in botanical gardens.

Hybrid Taxa

The following are designated here as nothotaxa.

Artemisia ×argilosa Beetle [pro sp.], Rhodora 61: 84. 1959. *Seriphidium argilosum* (Beetle) K. Bremer & Humphries, Bull. Nat. Hist. Mus. London, Bot. 23: 188. 1993.—Type: U.S.A. Colorado: Jackson Co., "Coal Montana" mine site, *A. Beetle 12872* (holotype: RM!).—Chromosome number: 2n = 36 (McArthur et al. 1981).

Winward (2004) believes this species to be the result of hybridization between *A. cana* subsp. *viscidula* and *A. tripartita*. The plants have the growth form and floral morphology of *A. cana*, but differ in having deeply and irregularly divided leaves. *Artemisia ×argilosa* forms an isolated population that shows no signs of introgressing with surrounding plants of *A. cana* with which it grows. *Artemisia tripartita* subsp. *rupicola* occurs to the north, but there are no populations of subsp. *rupicola* or subsp. *tripartita* in the vicinity of Coalmont. *Artemisia ×argilosa* (named for its occurrence on argillic clay soil) is an anomalous hybrid known only from the type locality.

Additional Specimens Examined. **U.S.A.** Colorado: Jackson Co.: near town of Coalmont, *Shultz & Shultz 5421* (UTC); near Coalmont, *Shultz & Shultz 5430* (RSA, UTC).

Artemisia arbuscula subsp. **×longicaulis** Winward & McArthur [pro subsp.], Great Basin Naturalist 55: 152. 1995.—Type: U.S.A. Nevada: Pershing Co., Toulon exit along Interstate 80, 1053 m, 21 Aug 1986, *S. Sanderson & E. D. McArthur 1593* (holotype: BRY!; isotypes: RENO, UTC!).—Chromosome number: 2n = 54 (Winward & McArthur 1995; McArthur & Sanderson 1999).

The hexaploid *A. arbuscula* subsp. *×longicaulis* was described as an alloploid hybrid involving tetraploid *A. tridentata* subsp. *wyomingensis* and diploid *A. arbuscula* subsp. *longiloba* (Winward & McArthur 1995), a conclusion with which I concur. It has characteristics of both parents but is a low-growing shrub with sessile floral heads, characteristics that align it morphologically with *A. arbuscula* subsp. *arbuscula*. Specimens from western Nevada are identified routinely as small-headed representatives of *A. arbuscula*.

Additional Specimens Examined. **U.S.A.** Nevada: Pershing Co.: 4 mi N of Toulon, *McArthur & McArthur 1683* (SSLP); hills NW of Reno, just E of the California state line, *Shultz & Garrison 20324* (UTC).

Artemisia tridentata subsp. **×xericensis** Winward ex Rosentreter & R. G. Kelsey [pro subsp.], J. Range Managem. 44: 334. 1991.—TYPE: U.S.A. Idaho: Washington Co., T13N, R5W, Sec. 35, 16 km NE of Weiser near Mann Creek road, on moderately deep clay loam soils, 914 m, Oct 1987, *R. Rosentreter & A. DeBolt 842* (holotype: SRP; isotypes: CIC, UTC!).—Chromosome number: 2n = 36 (Mahalovich & McArthur 2004).

Winward originally proposed subsp. ×*xericensis* as a hybrid between *A. tridentata* subsp. *vaseyana* and subsp. *tridentata* (Rosentreter & Kelsey 1991). The plants have characteristics intermediate in morphology between the two subspecies, but they will usually key to subsp. *tridentata*. *Artemisia tridentata* subsp. ×*xericensis* has the irregular crown of subsp. *tridentata* and the broader leaf of subsp. *vaseyana*, but can be distinguished, in part, by the typical blue UV fluorescence of the latter. The plants grow on drier and warmer soils than are found in much of the range for subsp. *vaseyana*, and the extent of this "dryland" variant of mountain sagebrush may extend through much of south-central Idaho. Identification of this hybrid is difficult, and specimens of this hybrid are most likely filed as *A. tridentata* subsp. *tridentata* in herbaria.

EXCLUDED NAMES

The circumscription of *Artemisia* subg. *Tridentatae* is expanded in this treatment to include woody taxa formerly thought to belong to other subgenera. Recent studies by Riggins (Riggins & Seigler 2006; Riggins 2008) suggest that several other taxa, especially suffrutescent species now assigned to other subgenera of *Artemisia* and to *Sphaeromeria*, may warrant inclusion in the subg. *Tridentatae*, but the data are not conclusive. Because notable morphological differences separate the following taxa from members of subg. *Tridentatae,* the species listed below are excluded from my circumscription of the subgenus.

Artemisia papposa S. F. Blake & Cronquist, Leafl. W. Bot. 6: 43, plate 1. 1950.—TYPE: U.S.A. Idaho: Owyhee Co., *Maguire & Holmgren 26312* (holotype: WS!; isotype: UTC!).

Artemisia pedatifida Nuttall, Trans. Amer. Philos. Soc., n.s. 7: 399. 1841.—TYPE: U.S.A. Idaho: "arid plains of Lewis [Snake] River," *T. Nuttall s.n.* (holotype: GH!).

Artemisia porteri Cronquist, Madroño 11: 145. 1951.—TYPE: U.S.A. Wyoming: Fremont Co., ca. 40 mi SE of Riverton, 6 Jul 1949, *C. L. Porter 4969* (holotype: RM!; isotypes: CAS, DAO, GH! NY! PH, UTC! WTU, WU).

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NUMERICAL LIST OF TAXA

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2b. *A. cana* subsp. *bolanderi*
2c. *A. cana* subsp. *viscidula*
3a. *A. tripartita* subsp. *tripartita*
3b. *A. tripartita* subsp. *rupicola*
4. *A. rigida*
5a. *A. arbuscula* subsp. *arbuscula*
5b. *A. arbuscula* subsp. *longiloba*
5c. *A. arbuscula* subsp. *thermopola*
6. *A. nova*
7. *A. rothrockii*
8. *A. spiciformis*
9a. *A. tridentata* subsp. *tridentata*
9b. *A. tridentata* subsp. *parishii*
9c. *A. tridentata* subsp. *vaseyana*
9d. *A. tridentata* subsp. *wyomingensis*
10. *A. pygmaea*
11. *A. californica*
12. *A. filifolia*
13. *A. nesiotica*

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Photo: Leila M. Shultz

Cold-desert habitat typical for members of *Artemisia* sect. *Tridentatae*: *A. cana* subsp. *viscidula* (Mountain silver sagebrush), the dull gray-leaved shrub in drainages, and *A. tridentata* subsp. *vaseyana* (Mountain big sagebrush), the silver green shrub on margins. (Photo from Sublette Co., Wyoming.)

Photo: Leila M. Shultz

Warm desert valley dominated by *Artemisia filifolia* (sand sage), a representative of *Artemisia* sect. *Nebulosae,* in the Mohave Desert ecoregion. (Photo from Washington Co., Utah.)