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A review of *Sedum* section *Gormania* (Crassulaceae) in western North America

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Abstract

Sedum section *Gormania* was restricted to Oregon, Nevada and California in the western United States. After extensive field work from 2011 to 2016, we revised 17 members of the group using floral and vegetative characters, resulting in the acceptance of four new taxa in California. A serpentine endemic from the mountains of western Tehama County was recognized as *S. rubiginosum*. It was separated from *S. kiersteadiae* by its dense rosettes, overlapping stem leaves and non-apiculate corolla. A serpentine endemic from low elevation canyons in Del Norte County was described as *S. patens*. It was distinguished from *S. laxum* by its white spreading petals and yellow anthers. A plant of high elevation, serpentine and non-serpentine sites in Siskiyou County was circumscribed as *S. marmorense*; it differed from *S. oregonense* in its sepals and inflorescence with a thick granular waxy deposit, and leaves in dense rosettes. *Sedum paradisum* was segregated from *S. obtusatum*, raised to species level, and divided into two subspecies. Plants of the northern Sierra Nevada were newly defined as *S. paradisum* subsp. *subroseum*, separable with nodding young flowering shoots and a disjunct range in Butte, Plumas and Sierra counties. *Sedum flavidum* and *Sedum eastwoodiae* were removed from *S. laxum sensu stricto*, and raised to species rank, based on floral characters. We clarified the concept of *S. obtusatum* subsp. *retusum*, and restored it to the rank of species as *S. sanhedrinum*; it was restricted to Glenn, Lake, Mendocino, and Tehama counties, California. *Sedum flavidum* and *S. oregonense* as defined here showed more morphological variation than previously understood. Finally, we remarked on hybridization and cleistogamy observed in the field.

Introduction

Sedum Linnaeus (1753: 430) sect. *Gormania* (Britton in Britton & Rose 1903: 29) Clausen (1942: 29) consists of succulent plants with horizontal rhizomes or short, decumbent stems, conspicuous rosettes at the time of flowering, and petals that are fused at the base. As the section was defined by Clausen (1942, 1975) and Denton (1982), it was endemic to the California Floristic Province (Jepson eFlora 2017) except for *S. oregonense* (Watson 1882: 373) Peck (1941: 361), which grows on volcanic substrates in the Cascade Range as far north as Mount Hood, Oregon. The section was studied by Clausen (1942, 1975), and its classification was further refined by Denton (1982) as a result of her studies of flavonoid chemistry, chromosome numbers, interfertility, and hybridization (Denton 1979a, 1979b; Denton & Kerwin 1980) as well as her observations of morphology in the field and greenhouse (Denton 1982). Denton's taxonomic conclusions were summarized in the Jepson Manual for California (Denton 1993; Boyd & Denton 2012).

As field botanists worked with *Sedum* populations unknown to Clausen and Denton, they found problems with the earlier treatments. Similar plants from the same area were often identified as belonging to two or more species, certain supposedly rare plants were encountered frequently, and some plants had combinations of traits that did not match any published descriptions.

Consulting herbarium specimens did little to address these problems. The characteristic colors of the living foliage and flowers were lost when dried, and were rarely noted on herbarium labels (Moran 2009). The succulent foliage was difficult to dry, and the plants sometimes sprouted out of the side of the plant press unless the tissue was treated by freezing, boiling, or microwaving before pressing. Another difficulty was that the dried plants became brittle, losing parts when handled, thus many herbarium collections were fragmented over time.

With prompting and funding from the Shasta-Trinity National Forest, a field-based study of *Sedum* section *Gormania* was initiated in 2011 and continued through 2016. The study was based on traits of live plants, even though some of these traits could not be easily assessed on dried specimens. Here we report on morphological variation found during this study and the taxonomic conclusions drawn from the patterns of variation.

While this study was underway, genetic research on *Sedum* subgenus *Gormania* suggested that *S. oreganum* Nuttall (in Torrey & Gray 1840: 559) was phylogenetically basal to the *Sedum* section *Gormania* clade and that the highly variable *S. spathulifolium* Hooker (1832: 227) arose within the clade (Van Susteren 2015). We restricted our revision to *Sedum* section *Gormania sensu* Clausen (1975) because we did not study those two species as we did the others in the section. Molecular work based on Eurasian taxa also raised questions about the placement of North American taxa within *Sedum* (Nikulin *et al*. 2016), and requires further analysis of western hemisphere representatives.

Methods

In the summers of 2011 to 2016, cooperators for this project (listed in the acknowledgments) visited approximately 170 populations of *Sedum* section *Gormania* in the field in Oregon and California. We visited type localities of all previously published taxa in the group where localities were precise. The type localities were vague for *S. sanhedrinum* Berger (1930: 451) and *S. laxum* (Britton in Britton & Rose 1903: 29) Berger (1930: 451) subsp. *laxum*, so we sampled populations nearby. Additional sites were selected with advice from botanists familiar with the plants and the area, and by examining databased herbarium records (Consortium of California Herbaria 2017). We examined on-line images of some specimens, including types, at F, G, GH, K, LE, MO, NY, ORE, PH, RM, US, and YU. We also borrowed types and chromosome vouchers, or examined specimens from the following herbaria: BH, BM, CAS, CU, DS, F, GH, JEPS, MO, NY, ORE, OSC, POM, RSA, SBBG, SD, STNF, UC, UCR, UCSB, US, YM, WILLU, WS, and WTU. In addition, we examined or donated specimens to several public agency herbaria in California, not listed in Index Herbariorum, such as the collections of the Mendocino National Forest in Willows (abbreviated as "MNF"), and the Six Rivers National Forest in Eureka ("SRNF"). A number of our loans were chosen after examining taxonomic and chromosome literature (Hollingshead 1942; Clausen 1942, 1975; Clausen & Uhl 1944; Denton 1979b, 1982).

To supplement the available herbarium vouchers, we gathered over 170 specimens, each consisting of one to several flowering stalk(s), usually with a group of sterile rosettes. In each case, the bulk of the clonally spreading plant was left alive in the field. Over 12,000 photographs were taken of living plants in the field and fresh plants over gray cards. Selected traits were recorded from up to 5 fresh collections per population, often in the field so that fragile parts, as well as ephemeral shapes and colors, were captured as data (Table 1). Plants that lacked fully developed flowers when collected were planted in pots and grown out to anthesis. Potted *Sedum* were grown in outdoor private gardens or in the greenhouses of Oregon State University in Corvallis. Herbarium specimens were prepared by freezing or microwaving the plants before pressing and drying. Microwaves damage genetic material (Sagripanti *et al*. 1987), so we recommend freezing. Many of our collection labels indicated which technique was used. Herbarium specimens were supplemented with photographs and descriptive notes.

TABLE 1. Traits measured for the PCoA.

Trait	Type	Details
Rosette internode	measurement	mm
Rosette leaf color	qualitative	
Rosette leaf shape	qualitative	
Rosette leaf tip notched	yes/no	
Rosette leaf length	measurement	mm
Rosette leaf width	measurement	mm
Rosette leaf length/width	calculated	
Stem leaf color	qualitative	strongly glaucous, weakly glaucous, green, red
Stem leaf spreading or ascending	qualitative	
Stem leaf base auriculate	yes/no	
Stem leaf base decurrent	yes/no	
Stem leaf length	measurement	mm
Stem leaf width	measurement	mm
Stem leaf length/width	calculated	
Stem leaf length/rosette leaf length	calculated	
Inflorescence nodding in bud	yes/no	
Inflorescence type	qualitative	
Inflorescence glaucous	yes/no	
Inflorescence granular-waxy	yes/no	
Inflorescence length	measurement	cm
Inflorescence length/width	calculated	
Branch length/inflorescence length	calculated	

...Continued on next page

TABLE 1. (Continued)

Trait	Type	Details
Plant height	measurement	cm
Inflorescence length/plant height	calculated	
Sepals granular-waxy	yes/no	
Calyx lobe length	measurement	mm
Calyx lobe tip shape	qualitative	obtuse, acute, narrowly acute, acuminate
Petal length	measurement	mm
Sepal lobe length/petal length	calculated	
Petal spread at anthesis	qualitative	0–30°, 90°, other
Petal color (upper half)	qualitative	white, cream, yellow, pink, red, other
Petal color (lower half)	qualitative	white, cream, yellow, pink, red, other
Petal midrib	qualitative	white, cream, yellow, pink, red, green
Anther color (young)	qualitative	yellow, brown, pink/red, purple, black, other
Anther color (old)	qualitative	yellow, brown, pink/red, purple, black, other

Live sterile shoots were sent to the National Forest Genetic Electrophoresis Laboratory (NFGEL) to determine chromosome numbers by flow cytometry of leaf material. Where possible we gathered this material from populations used by Denton (1979b) for her chromosome counts.

Our initial data matrix used samples and characters with minimal missing data prior to statistical analysis. Nonetheless, variations in population size and phenology meant not all data fields were captured at each collecting site. The data matrix consisted of 40 characters and 575 samples. Samples or characters missing more than 10% of the data were omitted from the production data set. Quality control steps were performed in R (R Core Team 2016). Quality filtering resulted in a production data set consisting of 35 characters and 212 samples. Our final sample sizes for the principal coordinates analysis (PCoA) were provided in Table 2.

TABLE 2. Sample size in the PcoA. Populations of *Sedum moranii* were too small to sample.

Taxa	*n* =	Taxa	*n* =
Sedum albomarginatum	1	*Sedum oblanceolatum*	3
Sedum citrinum	9	*Sedum obtusatum*	8
Sedum eastwoodiae	1	*Sedum oregonense*	24
Sedum flavidum	27	*Sedum paradisum* subsp. *paradisum*	46
Sedum kiersteadiae	44	*Sedum paradisum* subsp. *subroseum*	7
Sedum laxum subsp. *heckneri*	3	*Sedum patens*	3
Sedum laxum subsp. *laxum*	15	*Sedum rubiginosum*	9
Sedum marmorense	5	*Sedum sanhedrinum*	7
Total			212

Multidimensional relationships among the samples were visualized using ordination. Multidimensionality was provided by the 35 characters recorded for each sample. Ordination attempted to reduce this multidimensionality into a smaller number of dimensions that captured the greatest amount of variation within the dataset. We employed principal coordinates analysis as our method of ordination (McCune *et al*. 2002). The PCoA began with calculation of a matrix of morphometric distances that were subjected to eigen analysis. Eigen vectors were used to visualize the multivariate relationships among samples.

To ensure that each character contributed equally to the ordination, the traits were centered and scaled. Centering consisted of subtracting each character's mean from each value while scaling consisted of dividing each character value by the character's standard deviation. This resulted in a data matrix where each character had a mean of zero and its dispersion was in units of standard deviations. Scaling was performed using the R function base::scale() (R Core Team 2016). From this scaled and centered data matrix a Euclidean distance matrix was calculated using the R function stats::dist() (R Core Team 2016). Euclidean distance employed the Pythagorean Theorem applied to *n* dimensions to

describe relationships among the samples (McCune *et al*. 2002). Principal coordinates analysis was performed on this matrix of Euclidian distances using the R function stats::cmdscale() (R Core Team 2016). A "spider" graph was created from the ordination using the function vegan::ordispider() (Oksanen *et al*. 2016). The plot of the ordination was created with vegan::ordiplot() (Oksanen *et al*. 2016). Each figure was generated by first subsetting the data to the desired taxa, then scaling, centering, and ordinating the subset. Each figure should be interpreted as a separate ordination.

Ecological zones, or ecoregions, were useful in summarizing the distribution of species. These were assigned using the published ecoregion map for Oregon (Meyers *et al*. 2015), with the understanding that their Siskiyou ecoregion in southwestern Oregon is a northern extension of the Klamath Ranges of California. For taxa in California we followed the geographic subdivisions of Baldwin *et al*. (2012), but with necessary revisions to the boundaries of the Cascade Range and Klamath Ranges, as explained in Lindstrand III *et al*. (2016) and revised on-line in the Jepson eFlora (2017). For convenience, we referred to both the California and Oregon geographic zones as ecoregions.

Cleistogamy observations were made in the field and on recently collected living material under a dissecting microscope, when late flowering shoots and the final flowers of the season were available.

Results

Morphological traits:—Seventeen taxa were recognized based on groups of populations that shared similar morphology and could be distinguished from other taxa. Geographically cohesive taxa were preferred; if disjunct populations could not be distinguished morphologically they were not recognized taxonomically.

Establishing a taxonomy of *Sedum* section *Gormania* based on morphology was complicated by phenology, within-population variation, hybridization, and problems of terminology. Observations and clarification of these issues are reported here.

Rosettes:—Most taxa, e.g., *Sedum flavidum* (Denton 1978: 233) B.L.Wilson & Zika (raised to species rank in this paper), *S. rubiginosum* Zika & B.L.Wilson (described in this paper), and *S. sanhedrinum*, had a very condensed growth form with short internodes; thus the leaves were closely spaced on the crowded rosettes (Fig. 1). Plants exposed to full sun tended to have dense rosettes in most species, except *S. citrinum* Zika (2014: 112), *S. kiersteadiae* (B.L.Wilson & R.E.Brainerd in Wilson *et al*. 2014: 9), and *S. oregonense*. These three taxa typically had loose, open, rosettes with elongated easily visible internodes and widely spaced leaves (Fig. 2). Some interpretation was needed to use this feature in the field, due to variation in growth form imposed by different substrates and microsites. There was variation in leaf spacing along single shoots. Many species occasionally showed well-spaced leaves on sterile shoots when growing in deep or shaded crevices or when sheltered from direct sun between adjacent rocks on a talus slope (Fig. 3).

FIGURE 1. Dense rosettes on vegetative shoots, without visible internodes between the leaves, were found in most species. A. *Sedum flavidum*, Trinity Co., California (*Zika 26646 & Brainerd*). B. *Sedum laxum* subsp. *laxum,* Del Norte Co., California (*Zika 25927*). C. *Sedum oblanceolatum*, Jackson Co., Oregon (*Zika 25636 & Lang*). D–E. *Sedum rubiginosum,* Tehama Co., California. D. Wild plant (*Zika 26238*). E. Cultivated plant (*Wilson & Coberly CWG-10*). F. *Sedum sanhedrinum*, Mendocino Co., California (*Zika 26629 & Brainerd*).

Rosette leaf shape:—Usually rosette leaves were obovate to obcordate, but oblanceolate leaves predominated in *Sedum albomarginatum* Clausen (1975: 424) and *S. oblanceolatum* Clausen (1975: 404). In most populations, notched leaf tips were common. However, in *S. sanhedrinum* and *S. rubiginosum,* leaf tips were often obtuse to acute and generally not notched. The margins of the rosette leaves were usually entire and thick, save *S. moranii* Clausen (1942: 40), which regularly had thin eroded margins visible at 10×.

Stem leaves:—Flowering shoots produce a series of leaves here called stem leaves. These were termed "bracts" in the California flora (Boyd & Denton 2012), although we restrict that term to the greatly reduced foliage within the inflorescence (as defined in Hickman 1993). Stem leaves withered and fell off, sometimes before anthesis, as the water

they stored was used in the reproductive effort (Fig. 4). As a result, few herbarium specimens showed intact stem leaves. Collectors should endeavor to gather material in early flowering stages to preserve the characteristic stem leaf shapes.

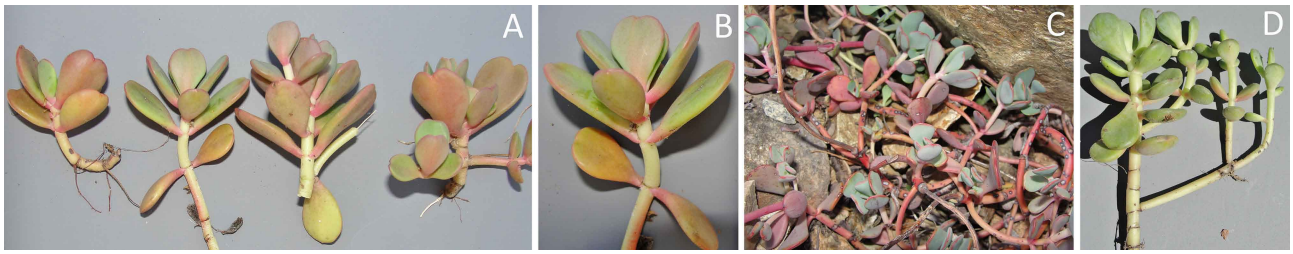

FIGURE 2. In full sun, loose open rosettes, with easily visible internodes, were characteristic of sterile shoots for three species. A–B. *Sedum citrinum*, Del Norte Co., California (*Zika 26185*). C. *Sedum kiersteadiae*, diffuse habit with numerous stolons typical of this species and the next, Siskiyou Co., California (*Zika 26289*). D. *Sedum oregonense*, Clackamas Co., Oregon (*Zika 25964*).

In most taxa, stem leaves were truncate-based and consistently longer than wide. Common shapes were elliptic, oblong, oblanceolate, obovate or broadly obovate (Fig. 5). In general, stem leaves differed in shape from the rosette leaves. However, *Sedum albomarginatum* and *S. oblanceolatum* had relatively narrow rosette leaves that were similar in shape to the usually oblanceolate stem leaves. *Sedum paradisum* (Denton 1978: 236) Denton ex B. L. Wilson (raised to species rank in this paper) and *S. sanhedrinum* were unusual in that the stem leaves were elongated and scarcely reduced distally, so that relatively large leaves subtended the lower flowering branches.

FIGURE 3. Species typically with dense rosettes in full sun occasionally formed loose rosettes in sheltered microsites, often associated with shade, talus, or protected crevices. A–B. *Sedum patens* vegetative shoots, Del Norte Co., California. A. Typical dense form (*Zika 26987*). B. Loose form (*Zika 26609 & Brainerd*). C–D. *Sedum paradisum* subsp. *subroseum*, Sierra Co., California (*Zika 26279*). C. Typical dense form. D. Loose form.

Suborbicular stem leaves predominated in *Sedum laxum* subsp. *heckneri* (Peck 1937: 121) Clausen (1942: 39), *S. eastwoodiae* (Britton in Britton & Rose 1903: 31) Berger (1930: 451), and in some populations of *S. flavidum* and *S. oregonense*. Suborbicular leaf bases were often slightly curved and sometimes clasped the stem with small auriculate lobes (*Sedum flavidum*), or clasped the stem strongly (*S. laxum* subsp. *heckneri*). There was always some variation in stem leaf shape across populations and on individual stems (Fig. 6). In *S. flavidum* there was also variation from year to year, with suborbicular stem leaves nearly absent some years, when stem leaves longer than wide predominated. We observed this both on cultivated specimens and in wild populations. For example, several wild populations of *S. flavidum* from Blue Point on the northwest slope of Dubakella Mountain, Trinity County, California, had mostly suborbicular, slightly clasping leaves in June 2012, but mostly oblong, truncate-based leaves in June 2014. This phenotypic phenomenon needs field study across several years to determine if stem leaf shape, at least in *S. flavidum*, responds to snowpack, soil moisture availability, early growing season precipitation, late frosts, or other environmental influences.

Some plants of *Sedum laxum* subsp. *laxum* and, rarely, *S. patens* Zika (described in this paper), had decurrent stem leaf bases (Fig. 7). This character was difficult to assess on dried specimens when the stem leaves had fallen, because ridges or scars on the dried stems were difficult to interpret.

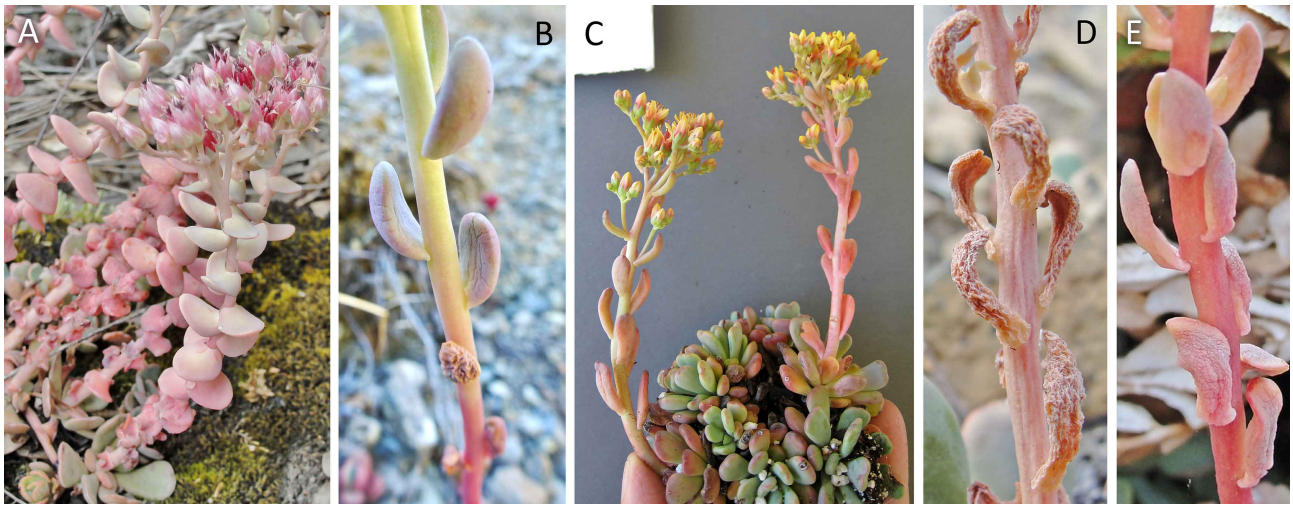

FIGURE 4. Water stored in the stem leaves appeared to be used in the reproductive effort. Stem leaves withered as flowering progressed. Proximal stem leaves shriveled before those near the inflorescence. A. *Sedum laxum* subsp. *heckneri*, Siskiyou Co., California; proximal stem leaves withered, distal still plump (*Zika 25640*). B. *Sedum patens*, Del Norte Co., California; proximal stem leaves shriveling during anthesis (*Zika 26608 & Brainerd*). C–D. *Sedum rubiginosum*, Tehama Co., California. C. Turgid stem leaves at the initiation of flowering (*Wilson & Coberly CWG-10*). D. Shriveled stem leaves at late anthesis (*Zika 26234*). E. *Sedum sanhedrinum*, Tehama Co., proximal stem leaves withering first (*Zika 25970*).

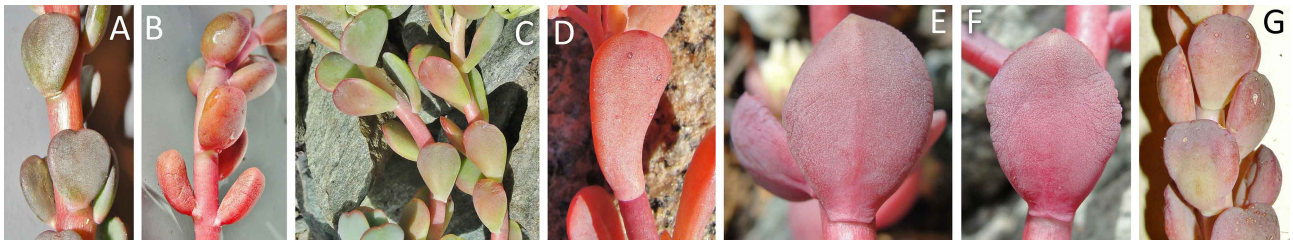

FIGURE 5. Stem leaves longer than wide, with a truncated base, were typical of most species of *Sedum* section *Gormania*. The stem leaves were commonly broadly obovate to elliptic or oblong, and were flattened or nearly cylindrical. A. *Sedum citrinum*, Del Norte Co., California (*Zika 26185*). B. *Sedum laxum* subsp. *laxum*, Del Norte Co. (*Zika 25927*). C. *Sedum oblanceolatum* × *oregonense*, Siskiyou Co., California (*Zika 25647B*). D. *Sedum obtusatum*, Nevada Co., California (*Zika 26271*). E–F. *Sedum oregonense*, Josephine Co., Oregon (*Zika 25657*). G. *Sedum sanhedrinum*, Lake Co., California (*Zika 26639 & Brainerd*).

FIGURE 6. Suborbicular stem leaves were typically found in *Sedum laxum* subsp. *heckneri, S. eastwoodiae,* in many populations of *S. flavidum*, and in scattered populations of *S. oregonense.* The leaf base was often slightly clasping on suborbicular stem leaves. Stem leaf shape varied across populations, growing seasons, and on individual stems. A–C. *Sedum flavidum.* A–B. Trinity Co., California (*Zika 25922 & J.K. Nelson*). C. Humboldt Co., California (*Wilson, Otting, & Darington CWG-118*). D. *Sedum laxum* subsp. *heckneri*, Jackson Co., Oregon (*Zika 11199*). E–G. *Sedum oregonense.* E–F. Clackamas Co., Oregon (*Zika 25964*). G. Del Norte Co., California (*Zika 25928*).

Inflorescences:—The inflorescence was a cyme. The flowering stem terminated in a centrally placed flower that was the first to bloom. Just below the central flower originated additional branches, sometimes very short, terminating in a flower. Each branch or series of short branches formed a cincinnus, sometimes forming scorpioid cymes. In

many species side branches formed at multiple nodes along the flowering axis below the central flower, producing a panicle-like cyme. The length and disposition of the lateral branches were uniform and characteristic for some species, and variable in others. The most common inflorescence shapes were dense and capitate, loose and flat-topped with elongated lower branches, and cylindrical.

FIGURE 7. Stem leaf bases were decurrent in some individuals of *Sedum laxum* subsp. *laxum*. A–D. Josephine Co., Oregon. A–C. *Zika 25655*. D. *Zika 26209*.

Flower size:—Using absolute measurements of flower parts to distinguish among taxa was complicated because flower size varied. The central flower, the first to bloom, was largest (Fig. 8). Flowers on the branches originating under the terminal flower bloomed next and were slightly smaller. Flowers at the tips of the circinni were small and did not always open.

FIGURE 8. The central basal flower in a cyme was the largest and opened first. A. *Sedum albomarginatum*, Plumas Co., California (*Zika 25865*). B. *Sedum citrinum*, Del Norte Co., California (*Zika 26201*). C. *Sedum laxum* subsp. *laxum*, Del Norte Co. (*Zika 25927*). D. *Sedum paradisum* subsp. *paradisum*, Shasta Co., California (*Lindstrand III & Van Susteren NSR-01*). E. *Sedum patens*, Del Norte Co. (*Zika 26609 & Brainerd*).

Sepals:—Sepals (Fig. 9), measured at anthesis, were relatively short (mostly about 25–33% as long as the petals) in most species, including *Sedum laxum* and its close relatives (*S. eastwoodiae, S. flavidum*), as well as in the species with narrow, spreading petals (*S. citrinum, S. patens,* and *S. kiersteadiae*). Sepals were relatively long (mostly (40–)50–70(–80)% as long as the petals) in *S. obtusatum* Gray (1868: 342)*, S. paradisum,* and *S. sanhedrinum*. In *S. oregonense,* the ratio of sepal to petal length varied from population to population and was usually 30–60% of the petal length. In all species the sepals elongated as the petals wilted after anthesis (Fig. 9C), presumably protecting the developing follicles.

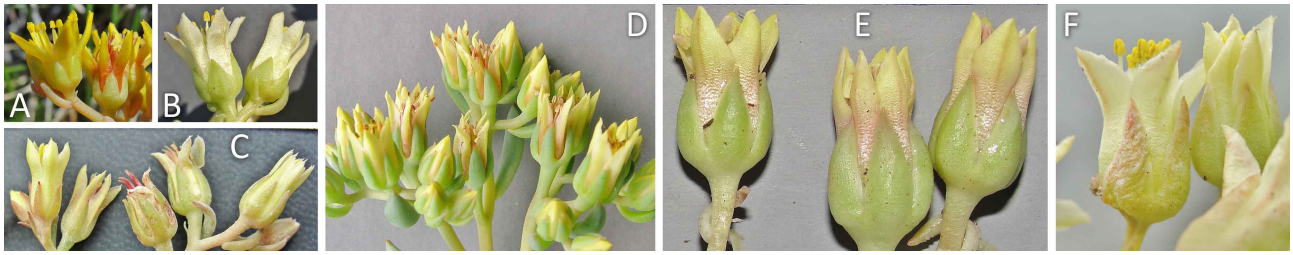

FIGURE 9. The sepals were short compared to the length of fresh petals in most species. In all species the sepals elongated after anthesis, as the petals wilted. A–C. Relatively short sepals in early anthesis. A. *Sedum citrinum*, Del Norte Co., California (*Zika 26193*). B. *Sedum oregonense*, Jackson Co., Oregon (*Zika 25666 & Wilson*). C. Sepals elongating post-anthesis, *Sedum oblanceolatum*, Siskiyou Co., California (*Zika 25650A*). D–F. Relatively long sepals in early anthesis. D–E. *Sedum paradisum* subsp. *paradisum*. D. Shasta Co., California (*Lindstrand III & Van Susteren NSR-8*). E. Trinity Co., California (*Zika 25920 & J.K. Nelson*). F. *Sedum paradisum* subsp. *subroseum*, Sierra Co., California (*Zika 26279*).

Petal shape:—Denton (1982) used the terms attenuate or sharply acute to define the petal tips of *Sedum laxum* and *S. moranii*, though they might more precisely be called acuminate with a tendency to roll inwards near the tip (Fig. 10). The petal tips were erect or straight, essentially parallel, or only slightly spreading from the axis of the flower. In the other species, the distal half of the petals was narrow (*S. kiersteadiae* or *S. citrinum*, Fig. 11), somewhat narrowed (e.g. some *S. flavidum*, Fig. 12), or broad (e.g. *S. obtusatum,* most *S. oregonense,* Fig. 13). As seen in Figure 12, there was considerable variation among individuals within a population of *S. flavidum*, but the narrow or wide petal extremes were seldom seen.

FIGURE 10. The petal tips erect and acuminate, essentially parallel to the floral axis. A–D. *Sedum laxum* subsp. *laxum.* A–B. Curry Co., Oregon (*Wilson & Otting CWG-240*). C–D. Josephine Co., Oregon (*Zika 25655*). E. *Sedum moranii*, Josephine Co. (*Zika 25631*).

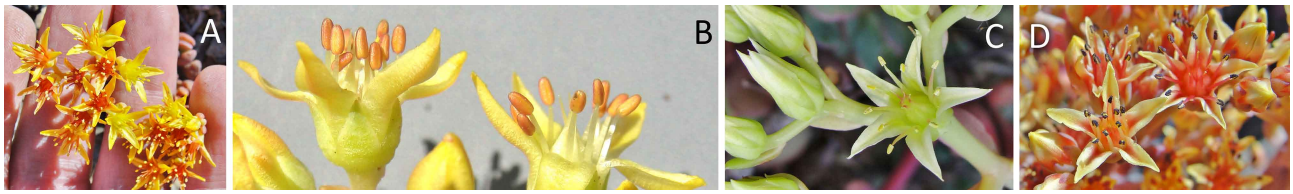

FIGURE 11. Petal tips narrow in the distal half; the petals strongly spreading to slightly reflexed. A. *Sedum citrinum*, Del Norte Co., California (*Zika 26620 & Brainerd*). B. *Sedum kiersteadiae*, Trinity Co., California (*Zika 26294*). C. *Sedum patens*, Del Norte Co. (*Zika 26609 & Brainerd*). D. *Sedum rubiginosum*, Tehama Co., California (*Zika 25522 & J.K. Nelson*).

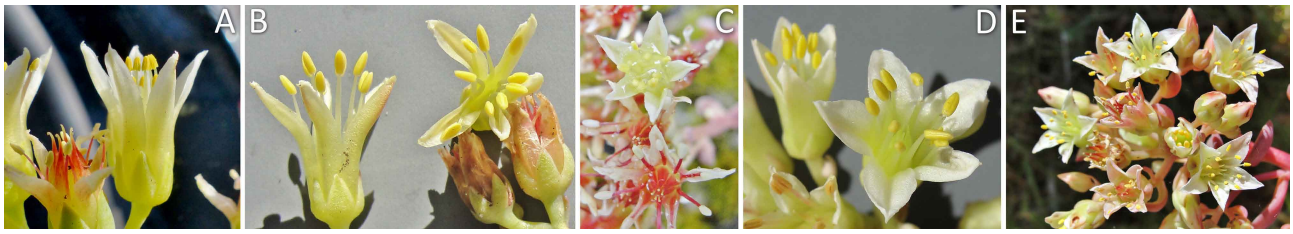

FIGURE 12. Variation in the width of the distal half of the petal in *Sedum flavidum*. A. Narrow-petaled extreme, Humboldt Co., California (*Wilson 18112*). B–D. Variation within a population, Trinity Co. (*Zika 25922 & J.K. Nelson*). B. Narrow-petaled extreme. C. Slightly narrowed petals. D. Typical broad petals. E. Slightly narrowed petals, Trinity Co., California (*CWG-102a*).

FIGURE 13. Distal half of the petals broad and ascending. A. *Sedum flavidum,* Trinity Co., California (*J.K. Nelson JKN-12-2*). B. *Sedum obtusatum*, Nevada Co., California (*Zika 26271*). C. *Sedum oregonense*, Del Norte Co., California (*Otting CWG-122*). D. *Sedum paradisum* subsp. *subroseum*, Plumas Co., California (*Wilson, Janeway & Zika CWG-14*).

Petal spread:—Each *Sedum* taxon had a characteristic degree to which the distal half of the petals spread or curved from the floral axis. In *S. laxum, S. moranii*, and *S. sanhedrinum,* the petals were typically erect or nearly so (Fig. 10). The narrow floral opening meant visiting insect pollinators forced their way into the flower to gather nectar at the base. In *S. eastwoodiae, S. flavidum, S. obtusatum, S. oregonense,* and *S. paradisum,* the petal tips spread to about 30(–45)° from the floral axis (Fig. 13). In *S. citrinum, S. kiersteadiae, S. patens* and *S. rubiginosum*, the petals spread to about 90°, or were slightly reflexed (Fig. 11). Plants grown in the greenhouse often had more divergent petals than was typical for wild individuals of the same species (Fig. 14).

FIGURE 14. Cultivated individuals often had petals more widely spreading than in the wild. A–B. *Sedum flavidum* corollas, Humboldt Co., California (*Brainerd & Otting CWG-103*). A. Ascending petals, wild plants. B. Spreading petals, cultivated plants. C–D. *Sedum laxum* subsp. *laxum* corollas, Del Norte Co., California. C. Erect petals, wild plants (*Brainerd & Otting CWG-107*). D. Ascending petals, cultivated plants (*Brainerd & Otting CWG-104*). E–F. *Sedum sanhedrinum* corollas, Tehama Co., California. E. Erect petals, wild plants (*Zika 26244*). F. Ascending petals, cultivated plants, Tehama Co. (*J.K. Nelson JKN-2*).

Petal color:—In many taxa, petals became red or pink after anthesis, as did the carpels and filaments (Fig. 15). Then those structures often faded to white or tan. In many plants with reddening petals, the petal base and/or midrib was pink or red from the early bud stage. Petals did not redden in *Sedum oblanceolatum* and most populations of *S. oregonense*. Yellow-flowered taxa kept in the greenhouse often produced paler flowers than in the field; sometimes pink-flowered species produced entirely white petals in cultivation (Fig. 16). In addition, we noted considerable year to year differences in the flower color of wild populations of *S. laxum* subsp. *laxum* in Del Norte County, California, where the same population was much pinker in some years, and much paler in other years. It would be interesting to know how and why these variations were produced, as flower color often was a useful character in identifying wild populations.

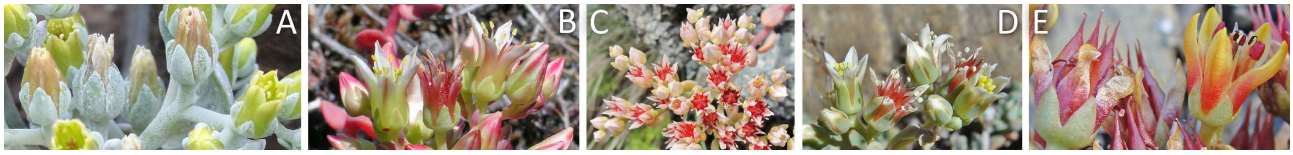

FIGURE 15. The color of the petals, anthers, filaments, and carpels often changed after anthesis. A. *Sedum albomarginatum*, after anthesis petals turned orange-brown; Butte Co., California (*Zika 25867*). B. *Sedum flavidum*, buds deep pink especially along the keel, faded to white at anthesis, then aged to a uniform deep pink; Humboldt Co., California (*Wilson, Otting, & Darington CWG-118*). C. *Sedum laxum* subsp. *laxum*, after anthesis green carpels turned dark red, red anthers turned white; Del Norte Co., California (*Zika 25936*). D. *Sedum paradisum* subsp. *subroseum*, after anthesis green carpels turned dark red, yellow anthers turned white; Plumas Co., California (*Wilson, Zika & Janeway CWG-15*). E. *Sedum rubiginosum*, after anthesis red-based yellow petals turned pallid; Tehama Co., California (*Zika 26234*).

FIGURE 16. Some taxa occasionally produced paler flowers in cultivation. A–B. *Sedum laxum* subsp. *laxum.* A. Pink petals, wild plants, Del Norte Co., California (*Zika 25927*). B. Fresh white petals with faint pink background, turning darker pink with age, cultivated, from Josephine Co., Oregon (*Zika 25487*). C–D. *Sedum paradisum* subsp. *paradisum*, Shasta Co., California. C. Yellowish petals, fading pinkish-orange, wild plants (*Zika 25924*). D. White petals, cultivated (*Lindstrand III & Van Susteren NSR-07*).

Anther color:—A few taxa produced anthers of more than one color in a population, including *Sedum kiersteadiae, S. paradisum* subsp. *paradisum,* and *S. rubiginosum*. Most individuals and most taxa produced anthers of a consistent color, a useful feature in the field. Fresh anthers, at or just before anthesis, were yellow, orange, rust-colored, dark red, or rarely light purple, depending on the species. In general, yellow or orange anthers usually turned brown with age, but varied to white, yellow, pink, red, orange, gray, or black. Rust-colored, red, or purple anthers usually turned black, less commonly white. At anthesis, yellow pollen may hide the anther color. In the herbarium the original color of dried anthers usually could not be assessed, and should be noted as part of the label data. Fresh anthers were papillose at 25×.

Chromosome numbers:—DNA content and ploidy of cells could not be determined by flow cytometry of live leaves. Samples produced multiple, inconsistent peaks within single runs. When multiple samples from a single individual were run, results were not consistent. DNA content of populations previously reported as diploid and hexaploid (Denton 1979b) were not distinguished. The inconsistency was probably caused by secondary compounds in the leaves.

In Table 3 we summarized known chromosome counts for species in *Sedum* section *Gormania*. Variable counts were found only in *S. oregonense,* which was tetraploid, hexaploid, or rarely diploid.

TABLE 3. Chromosome vouchers for *Sedum* section *Gormania*, arranged alphabetically by species, state and county. *2n* = chromosome number reported by Denton (1979b) and Denton & Kerwin (1980) for Denton collections, or by Clausen (1942) and Hollingshead (1942) for Clausen collections.

County in California (or Oregon)	*2n* =	Voucher	Determination by Clausen (1942), Hollingshead (1942), or Denton (1979b)	Accepted name in this paper
Sedum albomarginatum				
Plumas	30	*Denton 3853* WTU	*S. albomarginatum*	*S. albomarginatum*
Plumas	30	*Denton 3861* WTU	*S. albomarginatum*	*S. albomarginatum*
Plumas	30	*Denton 4060* WTU	*S. albomarginatum*	*S. albomarginatum*
Plumas	30	*Uhl 965A & Hutchison* JEPS	*S. albomarginatum*	*S. albomarginatum*
Plumas	30	*Uhl 968 & Hutchison* JEPS	*S. albomarginatum*	*S. albomarginatum*
Sedum eastwoodiae				
Mendocino	60	*Denton 3940* WTU (cited as *Denton 4940* in error by Denton 1979b)	*S. laxum* subsp. *eastwoodiae*	*S. eastwoodiae*
Mendocino	60	*Denton 4099* OSC, WTU	*S. laxum* subsp. *eastwoodiae*	*S. eastwoodiae*
Sedum flavidum				
Glenn	60	*Uhl 970* BH	*S. obtusatum* subsp. *retusum*	*S. flavidum*
Glenn	60	*Denton 3941* OSC, WTU	*S. obtusatum* subsp. *retusum*	*S. flavidum*
Humboldt	60	*Hutchison 2013* [= *Uhl 932*] JEPS	*S. laxum* subsp. *heckneri*	*S. flavidum*
Trinity	60	*Denton 3949* OSC, WTU	*S. laxum* subsp. *flavidum*	*S. flavidum*
Trinity	60	*Denton 3953* NY, WTU	*S. laxum* subsp. *flavidum* (type)	*S. flavidum*
Trinity	60	*Denton 4066* WTU	*S. laxum* subsp. *flavidum*	*S. flavidum*
Sedum kiersteadiae				
Siskiyou	30	*Clausen 4952, Trapido & Cook* BH, NY	*S. obtusatum* subsp. *boreale* (type)	*S. kiersteadiae*
Siskiyou	30	*Denton 4140* WTU	*S. obtusatum* subsp. *obtusatum*	*S. kiersteadiae*
Trinity	30	*Denton 4096* WTU	*S. obtusatum* subsp. *obtusatum*	*S. kiersteadiae*
Trinity	30	*Denton 4111* WTU	*S. obtusatum* subsp. *obtusatum*	*S. kiersteadiae*
Trinity	30	*Denton 4139* WTU	*S. obtusatum* subsp. *obtusatum*	*S. kiersteadiae*
Sedum laxum* subsp. *heckneri				
Humboldt	30	*Denton 3974* WTU	*S. laxum* subsp. *heckneri*	*S. laxum* subsp. *heckneri*
Humboldt	30	*Denton 3975* WTU	*S. laxum* subsp. *heckneri*	*S. laxum* subsp. *heckneri*
Humboldt	30	*Denton 3976* WTU	*S. laxum* subsp. *heckneri*	*S. laxum* subsp. *heckneri*
? Mendocino (probable locality error)	30	*Goodspeed 28.3* BH	*S. laxum* subsp. *retusum*	*S. laxum* subsp. *heckneri*
Siskiyou	30	*Denton 4014* OSC, WTU	*S. laxum* subsp. *heckneri*	*S. laxum* subsp. *heckneri*
Siskiyou	30	*Denton 4016* WTU	*S. laxum* subsp. *heckneri*	*S. laxum* subsp. *heckneri*
Siskiyou	30	*Hutchison 2036* JEPS	*S. laxum* subsp. *heckneri*	*S. laxum* subsp. *heckneri*

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TABLE 3. (Continued)

County in California (or Oregon)	*2n* =	Voucher	Determination by Clausen (1942), Hollingshead (1942), or Denton (1979b)	Accepted name in this paper
Sedum laxum* subsp. *laxum				
Del Norte	30	*Clausen C4941 & Trapido* WTU	*S. laxum* subsp. *latifolium*	*S. laxum* subsp. *laxum*
Del Norte	30	*Uhl 956* BH	*S. laxum* subsp. *latifolium*	*S. laxum* subsp. *laxum*
Del Norte	30	*Denton 3991* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Del Norte	30	*Denton 4001* NY, OSC, WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Del Norte	30	*Denton 4002* OSC, WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Del Norte	30	*Denton 4074* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Curry (Oregon)	30	*Denton 3021* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Curry	30	*Denton 3691* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Curry	30	*Denton 4003* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Curry	30	*Denton 4004* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Curry	30	*Denton 4005* OSC, WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Curry	30	*Denton 4006* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine (Oregon)	30	*Hutchison 2074* (= *Uhl 952*) BH	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Clausen 5015 & Trapido* BH (3 sheets)	*S. laxum* intermediate between subsp. *perplexum* and subsp. *typicum*	*S. laxum* subsp. *laxum*
Josephine	30	*Clausen C5018 & Trapido* BH	*S. laxum* subsp. *typicum*	*S. laxum* subsp. *laxum*
Josephine	30	*Denton 3982* OSC, WTU (cited in error as *Denton 3892* by Denton 1979b)	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Denton 3986* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Denton 3993* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Denton 4008* OSC, WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Denton 4009* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Denton 4010* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Denton 4057* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Denton 4076* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Denton 4081* WTU	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Hutchison 2063* (= *Uhl 946* BH, SD; = UC Botanical Garden 61.893)	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Josephine	30	*Hutchison 2076* (= *Uhl 953*) BH, DS	*S. laxum* subsp. *laxum*	*S. laxum* subsp. *laxum*
Sedum moranii				
Josephine (Oregon)	30	*Hutchison 2067* (= *Uhl 948*) BH, SD	*S. moranii*	*S. moranii*
Josephine	30	*Denton 4007* OSC, WTU	*S. moranii*	*S. moranii*
Josephine	30	*Denton 4054* WTU	*S. moranii*	*S. moranii*

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TABLE 3. (Continued)

County in California (or Oregon)	*2n* =	Voucher	Determination by Clausen (1942), Hollingshead (1942), or Denton (1979b)	Accepted name in this paper
Sedum oblanceolatum				
Jackson (Oregon)	30	*Denton 4110* OSC, WTU	*S. oblanceolatum*	*S. oblanceolatum*
Sedum obtusatum				
Mariposa	30	*Clausen 4801 & Trapido* BH (2 sheets)	*S. obtusatum* subsp. *typicum*	*S. obtusatum*
Mariposa	30	*Clausen 4823 & Trapido* BH (2 sheets)	*S. obtusatum* subsp. *typicum*	*S. obtusatum*
Mono	30	*Denton 3921* OSC, WTU	*S. obtusatum* subsp. *obtusatum*	*S. obtusatum*
Mono	30	*Denton 3923* OSC, WTU	*S. obtusatum* subsp. *obtusatum*	*S. obtusatum*
Mono	30	*Denton 3930* OSC, WTU	*S. obtusatum* subsp. *obtusatum*	*S. obtusatum*
Nevada	30	*Uhl 960* BH	*S. obtusatum*	*S. obtusatum*
Nevada/Placer	30	*Denton 3917* OSC, WTU	*S. obtusatum* subsp. *obtusatum*	*S. obtusatum*
Placer	30	*Uhl 961* BH	*S. obtusatum*	*S. obtusatum*
Placer	30	*Denton 3909* WTU	*S. obtusatum* subsp. *obtusatum*	*S. obtusatum*
Placer	30	*Denton 3919* WTU	*S. obtusatum* subsp. *obtusatum*	*S. obtusatum*
Tuolumne	30	*Clausen 4810 & Trapido* BH (3 sheets)	*S. obtusatum* subsp. *typicum*	*S. obtusatum*
Tuolumne	30	*Denton 3933* WTU	*S. obtusatum* subsp. *obtusatum*	*S. obtusatum*
Tuolumne	30	*Denton 3937* OSC, WTU	*S. obtusatum* subsp. *obtusatum*	*S. obtusatum*
Sedum oregonense				
Del Norte	90	*Denton 3987* OSC, WTU	*S. oregonense*	*S. oregonense*
Siskiyou	90	*Denton 3990* WTU	*S. oregonense*	*S. oregonense*
Trinity	60	*Denton 3961* WTU	*S. obtusatum* subsp. *retusum*	*S. oregonense*
Trinity	60	*Denton 3967* HSC, OSC, WTU	*S. obtusatum* subsp. *retusum*	*S. oregonense*
Trinity	60	*Denton 3968* WTU	*S. obtusatum* subsp. *retusum*	*S. oregonense*
Curry (Oregon)	90	*Denton 4000* WTU	*S. oregonense*	*S. oregonense*
Jackson (Oregon)	90	*Denton 3842* WTU	*S. oregonense*	*S. oregonense*
Jackson	90	*Denton 4011* WTU	*S. oregonense*	*S. oregonense*
Jackson	60	*Denton 4025* HSC, OSC, WTU	*S. obtusatum subsp. retusum*	*S. oregonense*
Jackson	90	*Denton 4030* WTU	*S. oregonense*	*S. oregonense*
Jackson	30	*Denton 4048* OSC, WTU	*S. laxum* subsp. *laxum*	*S. oregonense*
Jackson	90	*Denton 4049* WTU	*S. oregonense*	*S. oregonense*
Jackson	60	*Denton 4101* WTU	*S. obtusatum* subsp. *retusum*	*S. oregonense*
Josephine (Oregon)	90	*Denton 2754* WTU	*S. oregonense*	*S. oregonense*
Josephine	90	*Denton 3977* OSC, WTU	*S. oregonense*	*S. oregonense*
Josephine	90	*Denton 3979* OSC, WTU	*S. oregonense*	*S. oregonense*
Josephine	90	*Denton 3994* OSC, WTU	*S. oregonense*	*S. oregonense*
Klamath (Oregon)	90	*Clausen 4996 & Trapido* BH (3 sheets)	*S. oregonense*	*S. oregonense*
Klamath	c. 90	*Clausen 5006 & Trapido* BH (2 sheets)	*S. oregonense*	*S. oregonense*
Klamath	90	*Denton 4031* WTU	*S. oregonense*	*S. oregonense*

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TABLE 3. (Continued)

County in California (or Oregon)	*2n* =	Voucher	Determination by Clausen (1942), Hollingshead (1942), or Denton (1979b)	Accepted name in this paper
Sedum oblanceolatum				
Linn (Oregon)	90	*Denton 3704* WTU	*S. oregonense*	*S. oregonense*
Linn	90	*Denton 4032* OSC, WTU	*S. oregonense*	*S. oregonense*
Linn	90	*Denton 4034* WTU	*S. oregonense*	*S. oregonense*
Linn	90	*Denton 4035* WTU	*S. oregonense*	*S. oregonense*
Wasco (Oregon)	90	*Denton 4041* WTU	*S. oregonense*	*S. oregonense*
Sedum paradisum* subsp. *paradisum				
Trinity	30	*Denton 4097* NY, OSC, WTU	*S. obtusatum* subsp. *paradisum* (type)	*S. paradisum* subsp. *paradisum*
Trinity	30	*Denton 4098* WTU	*S. obtusatum* subsp. *paradisum*	*S. paradisum* subsp. *paradisum*
Sedum paradisum* subsp. *subroseum				
Plumas	30	*Uhl 962* BH	*S. obtusatum* subsp. *boreale*	*S. paradisum* subsp. *subroseum*
Plumas	30	*Denton 3878* OSC, WTU	*S. obtusatum* subsp. *boreale*	*S. paradisum* subsp. *subroseum*
Plumas	30	*Denton 3884* WTU	*S. obtusatum* subsp. *boreale*	*S. paradisum* subsp. *subroseum*
Sierra	30	*Denton 3899* OSC, WTU	*S. obtusatum* subsp. *boreale*	*S. paradisum* subsp. *subroseum*

We were unable to locate four chromosome vouchers for *Sedum laxum* that Denton (1979b) reported were deposited at WTU, and appear to be lost. In each case we found other Denton vouchers that document the identity of the population, and in some cases were also chromosome vouchers. The missing vouchers were *Denton 4075* (same site and taxon as *Denton 4001*), *Denton 4095* (same site and taxon as *Denton 4009*), *Denton 4100* (same site and taxon as *Denton 4125*), and *Denton 4067* (same site and taxon as *Denton 3975*), all at WTU.

One irregularity in the chromosome results was a specimen said to be *Sedum eastwoodiae* from Mendocino County. It was cited by Clausen (1942) as: "A plant from Mendocino Co., Calif., no. 28.3 in University of California gardens, sent by Professor T. H. Goodspeed and cultivated at Ithaca, New York, has a *2n* number of 30. In the small rosette-leaves and flowers, this seems near to *S. obtusatum*, but in that species the corolla is yellow and the inflorescence is not so dense, also the leaves are not retuse." The voucher (BH81412) is labeled: "Petals erect, keeled, only slightly divergent, white with pink median strip dorsally... Cultivated in greenhouse. Source: Professor T. H. Goodspeed, University of California, from Mendocino Co., California]... [pressed] 22 June 1944." This specimen was originally labeled as *S. laxum* subsp. *retusum* by Clausen, but later annotated to subsp. *eastwoodiae* by Clausen in 1977, and by Denton in 1980. All verified chromosome vouchers for *S. eastwoodiae* are *2n* = 60 (Denton 1979b; Table 3). The Goodspeed specimen was *2n* = 30, consistent with *S. laxum* subsp. *heckneri,* and was atypically large for *S. eastwoodiae*, with a stem 30 cm tall, sepals 4–5 mm long, and petals 8–9 mm long with acuminate, not acute tips. Morphologically, this was a good match for *S. laxum* subsp. *heckneri*, with clasping stem leaves scarcely longer than wide, and an ample inflorescence 7 × 8 cm. However, the Mendocino County location was unexplained, and we believe this was a geographic error for a more northerly location. In Table 3 this chromosome voucher was entered as *S. laxum* subsp. *heckneri* under Mendocino County, with a question mark, to indicate our uncertainty about the provenance.

Principal coordinates analysis:—Our principal coordinates analysis (PCoA) was based on data collected for characters in Table 1. For some taxa it did not show much separation, such as the similar species *Sedum flavidum* and *S. oregonense* (Fig. 17).

When we compared four taxa with narrow spreading petals, *Sedum citrinum, S. kiersteadiae, S. patens*, and *S. rubiginosum*, the PCoA provided strong support for their status as distinct species (Fig. 18).

A comparison of *Sedum albomarginatum* and *S. oblanceolatum* showed differences in Figure 19, despite their

obvious morphological similarities, such as a granular-waxy indument, as well as oblanceolate rosette leaves which gradually transitioned into very similar stem leaves. In the same graphic we compared the two subspecies of *S. laxum*. Their flowers were similar, with pink erect acuminate petals. In Figure 19 they resolved well into two discrete clusters. Flower color and petal shape distinguished *S. flavidum* from both subspecies of *S. laxum* in the PCoA. *Sedum eastwoodiae* was well separated from *S. flavidum* and *S. laxum* subsp. laxum in this analysis, but clustered with *S. laxum* subsp. *heckneri*, although the two were allopatric and differed in their petal shape, flower and stem size. *Sedum obtusatum* formed a discrete cluster on the graph, and was disjunct from the other taxa in Figure 19.

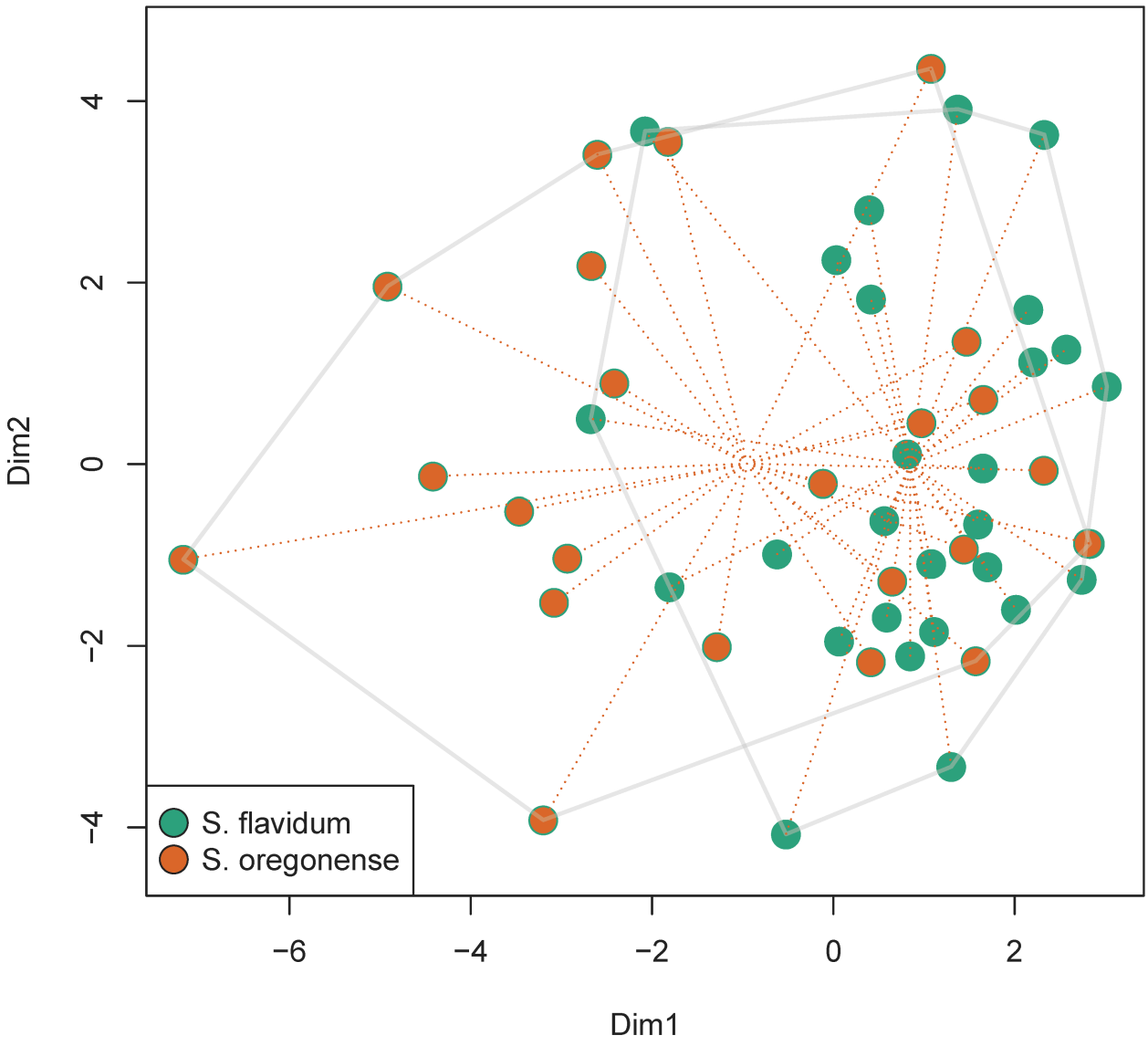

FIGURE 17. *Sedum flavidum* and *S. oregonense*; principal coordinates analysis of a matrix of Euclidean distances. These two species, although with different ranges, habitats, and different leaf densities on the sterile rosettes, did not separate in the PCoA.

Sedum marmorense Otting & R.E. Brainerd (described in this paper) graphed separately from the other taxa (Fig. 20). *Sedum sanhedrinum* overlapped with *S. paradisum* in the same comparison, although the angle of their petal tips differed. *Sedum paradisum* subsp. *subroseum* B.L. Wilson & Zika (described in this paper) did not separate clearly from *S. paradisum* subsp. *paradisum* in this analysis, despite differences in the emerging inflorescences and allopatric ranges.

Cleistogamy:—Flower size varied with location in the *Sedum* analyzed, with the first, central flower of the cyme being the largest (Fig. 8). The last flowers to bloom were small and often did not open, presumably precluding insect-mediated pollination. During this study we observed the transfer of pollen from the anthers to the stigma of unopened flowers in four taxa, late in the flowering season. In some, the ovules and ovaries appeared to be expanding. Our observations of apparent cleistogamy included *S. obtusatum, S. sanhedrinum, S. paradisum* subsp. *subroseum* and *S.*

rubiginosum. A comparative study of the seed production in selfing and outcrossing flowers of wild plants would be a welcome follow-up on these observations.

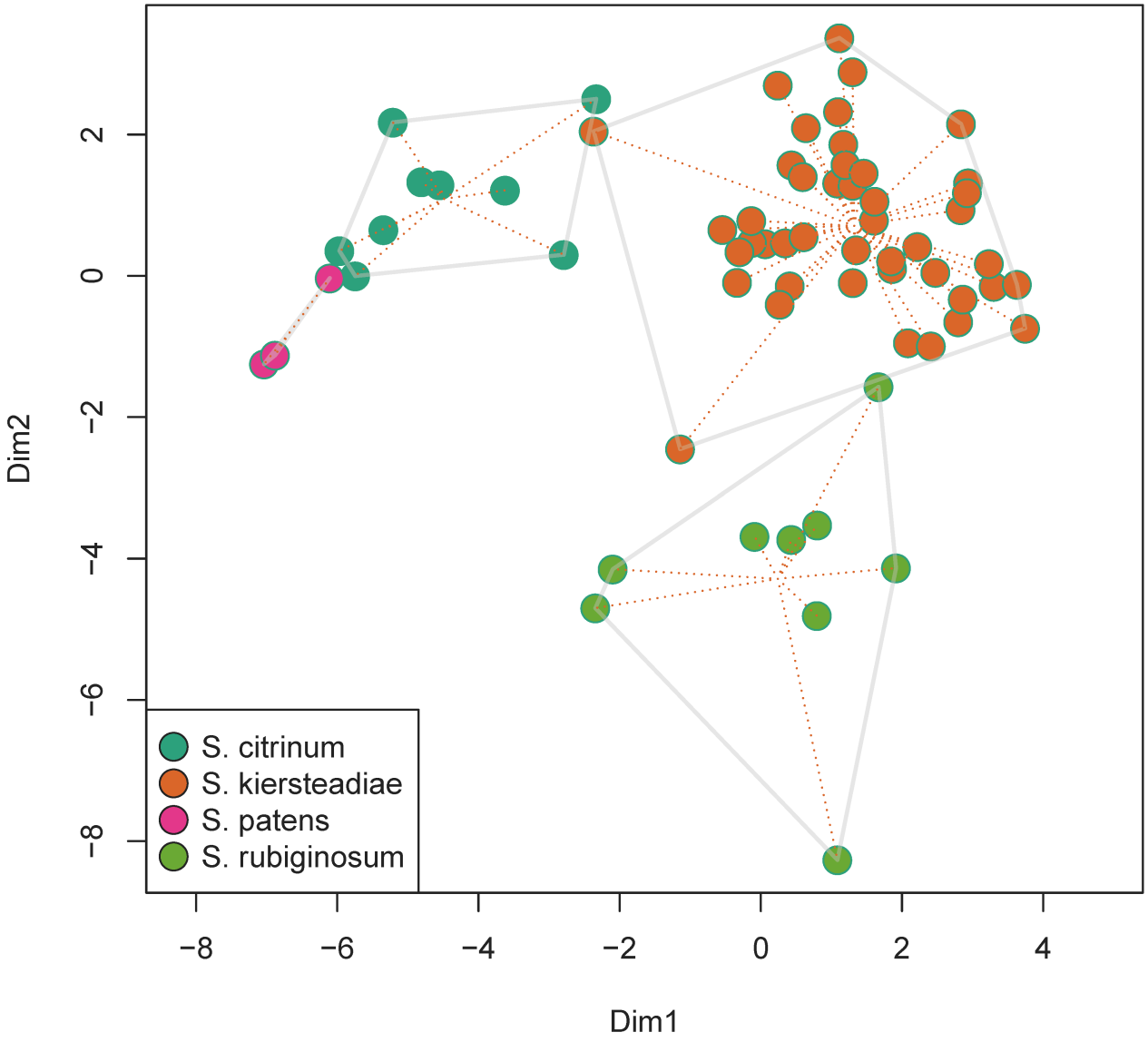

FIGURE 18. *Sedum citrinum, S. kiersteadiae, S. patens*, and *S. rubiginosum*, principal coordinates analysis of a matrix of Euclidean distances. These four species shared narrow spreading petals, but separated well in the key and in the PCoA analysis, on petal color, rosette density, and inflorescence shape.

Discussion

Principal coordinates analysis:—Our PCoA demonstrated separation for some taxa, and less for others. In a few instances we elected to supplement the PCoA data with our photographic data as well as a nuanced understanding of the morphological variation. For example, the PCoA merged the similar species *Sedum flavidum* and *S. oregonense* (Fig. 17). Nonetheless we can reliably separate these species in the field, based on the morphology of the vegetative shoots. *Sedum flavidum* has dense rosettes; *S. oregonense* has loose rosettes. Occasional plants in a population can vary in this character, depending on exposure, and this, plus the inherent variation both species exhibit in stem leaf shape, muddies the water in the numerical analysis. We can also separate the pair on ecological grounds, with *S. flavidum* generally found at lower elevations, in more heavily forested sites, more often on serpentine, and further south than *S. oregonense.*

In Figure 20, the PCoA did not clearly differentiate between *Sedum paradisum* and *S. sanhedrinum*. Yet we found that the two were separable in the field using the angle of the petals at anthesis. *Sedum sanhedrinum* had essentially

erect petals, while they were ascending in *S. paradisum* and the similar *S. obtusatum*. All of the taxa in Figure 20 were allopatric. Our PCoA might have provided more support for our taxonomic concepts with more data, but *S. marmorense* and *S. sanhedrinum* were rare and our samples were small. We summarized our taxonomic arguments below, in the discussions for each taxon, and in the key to species.

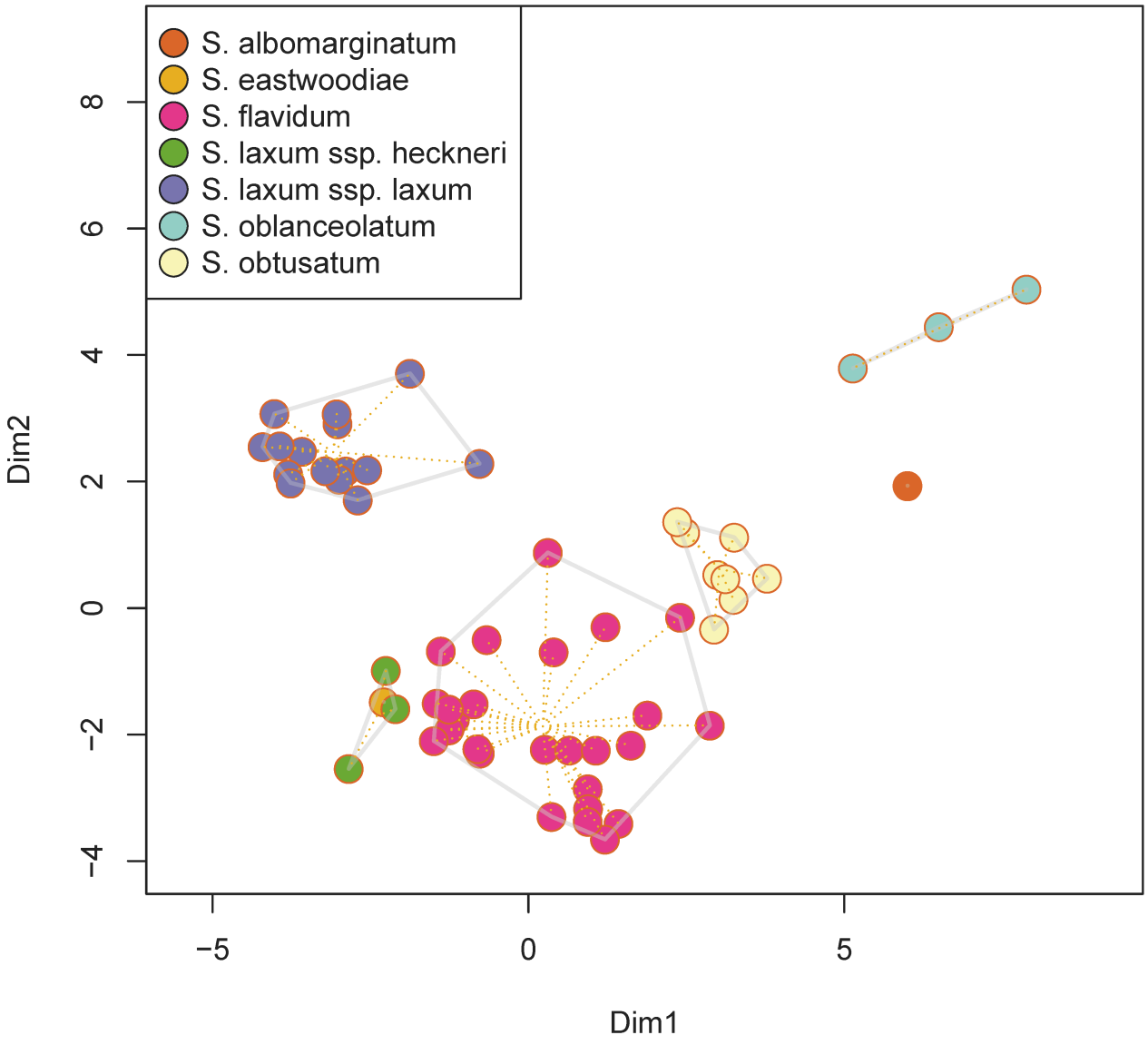

FIGURE 19. *Sedum albomarginatum*, *S. eastwoodiae, S. flavidum, S. laxum* subsp. *heckneri*, *S. laxum* subsp. *laxum*, *S. oblanceolatum*, and *S. obtusatum*, principal coordinates analysis of a matrix of Euclidean distances. The two subspecies of *S. laxum* had nearly identical flowers, with acuminate erect pink petals, but were separable on stem leaf characters in the key and in the PCoA. *Sedum albomarginatum* and *S. oblanceolatum* were quite similar in leaf shape and granular waxy indument, but divided on floral characters in the PCoA. Based on flower color and petal shape, *Sedum flavidum* clearly separates from the *S. laxum* subspp. in this analysis. Differences in petal shape and flower size, as well as disjunct ranges, were not revealed in the PCoA comparison of *S. eastwoodiae* and *S. laxum* subsp. *heckneri*.

Taxonomy:—It was difficult to parse morphological variation in *Sedum* section *Gormania* into neat, mutually exclusive species categories (Hey 2001; Yoon 2009) because of the biology of the plants, which lived on isolated rock outcrops and rocky forest openings. Habitats and populations were slightly to strongly isolated from each other. Seeds in this group were small, unwinged, smooth, and not adhesive; they lacked obvious adaptations for long-distance dispersal. Seed dispersers and pollinators surely moved genes from outcrop to outcrop along a ridgetop, but getting genes to the next ridge was probably a rare event. Thus populations tended to diverge genetically over both long and short distances, as reported by DeChaine & Martin (2005) for *S. lanceolatum* Torrey (1827: 205).

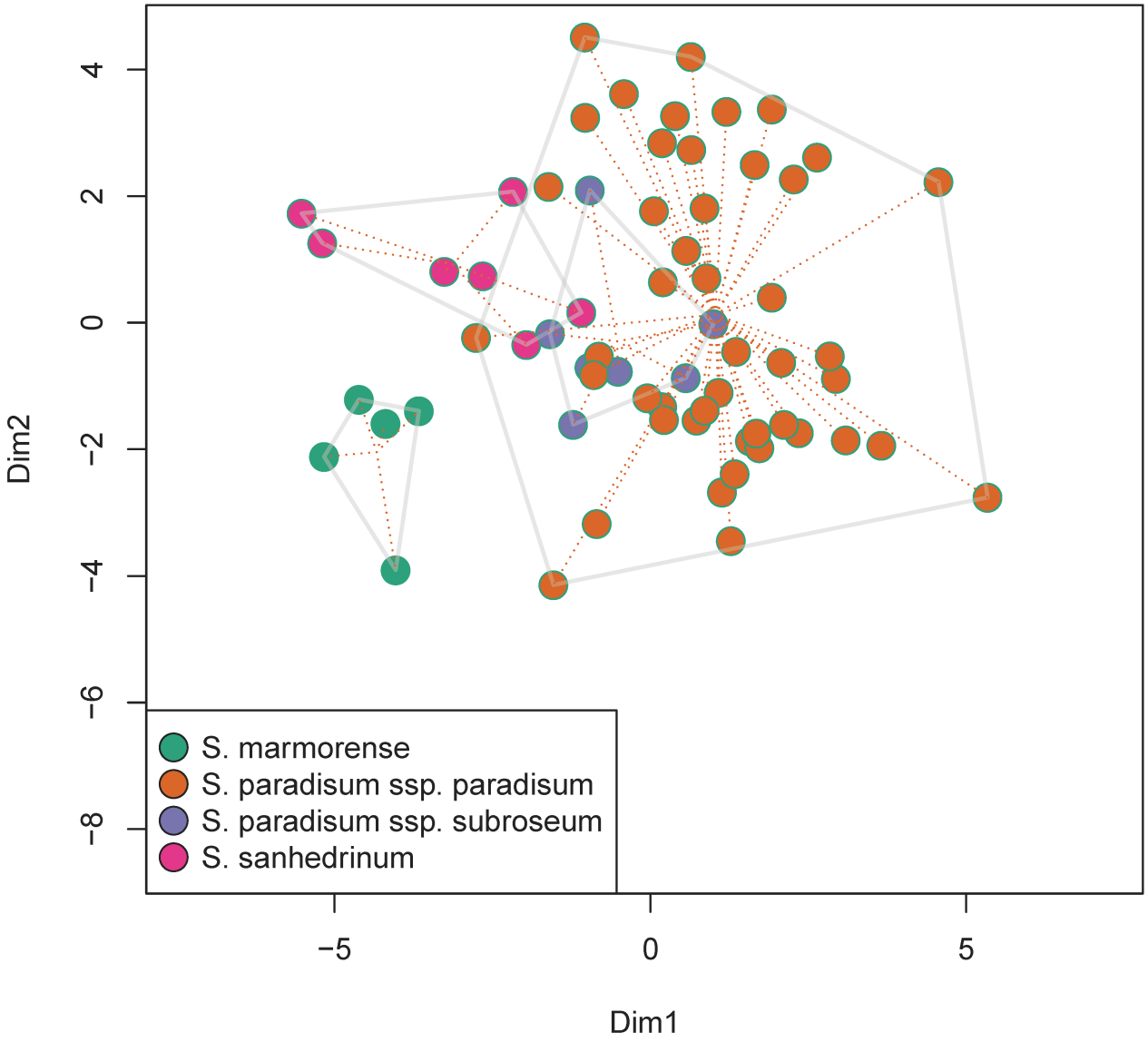

FIGURE 20. *Sedum marmorense, S. paradisum* subsp. *paradisum, S. paradisum* subsp. *subroseum,* and *S. sanhedrinum,* principal coordinates analysis of a matrix of Euclidean distances. Only *S. marmorense* was clearly separable with this statistical tool. *Sedum sanhedrinum* differed from the other three taxa in its erect petals.

While their fragmented habitat drove *Sedum* section *Gormania* populations apart, hybridization occasionally brought them together. Most suitable sites were home to only one species (Clausen 1975, Denton 1979a, Zika 1992), but a few sites had two or more species. Possible hybrids were observed at four localities (Table 4). In the greenhouse, experimental hybrids formed by parents with the same chromosome number were generally fertile, and even those with parents of different chromosome numbers were partially fertile (Denton 1979b, 't Hart 1997). Evolution in *Sedum* section *Gormania* may be reticulate. We know hybridization gave rise to other *Sedum* taxa, for example in the *S. rupestre* Linnaeus (1753: 431) complex in *Sedum* section *Sedum* ('t Hart *et al*. 1993).

We detected 17 groups of populations with consistent morphology, groups that were treated here as taxa. These were organized into 15 species, two of them with subspecies. All taxa were included in the identification key. Their diagnostic characteristics, distribution, and synonymy were explained below (see Taxonomic Treatment). Four new taxa were described in detail. The other taxa were briefly diagnosed.

Alliances within *Sedum* section *Gormania*:—In Table 5 we provided an outline of six informal groupings of species, possibly series, within *Sedum* section *Gormania*. This was based on the morphological similarities and differences captured in our photographic record of live plants, our field work, and also the PCoA analysis. We considered this a provisional classification for several reasons. We suspected some reticulate relationships and possible past

hybridizations, that were not easily placed in a linear classification. Extensive greenhouse hybridizations conducted by Denton (1979b) were done prior to the elucidation of 6 taxa. Finally, we had no independent molecular data to support our groups.

TABLE 4. Locations in California where putative hybrid *Sedum* section *Gormania* were observed, with the potential parental species present. Three potential parental species occurred at Canyon Creek.

Location	California County	Putative parental taxon	Putative parental taxon	Comment (Voucher)
Copper Butte	Siskiyou	*S. oblanceolatum*	*S. oregonense*	Parents common, hybrid rare (*Zika 25647B, 25649, 25650B*)
Swede Creek	Trinity	*S. paradisum* subsp. *paradisum*	*S. flavidum*	*S. flavidum* declined over 40 years, now extirpated (*Wilson et al. CWG-05*)
Underwood Mountain quarry	Trinity	*S. paradisum* subsp. *paradisum*	*S. flavidum*	(*Brainerd & Otting CWG-102b*) *S. spathulifolium* also present
Canyon Creek	Trinity	*S. paradisum* subsp. *paradisum*	*S. oregonense*	*S. kiersteadiae* also present

Despite those caveats, some taxa were grouped with confidence. In Table 5 *Sedum moranii* was uniquely glandular, and had erose rosette leaf margins, separating it from all other taxa. We placed it in its own group. It also had the smallest known range of any of the species in the section. The *S. albomarginatum* group was comprised of two taxa, united by their similar oblanceolate rosette and stem leaves, as well as their granular-waxy indument, and similar floral structure. The *S. citrinum* group had three members, defined by their yellow acute petals that are narrow distally and strongly spreading, and a tolerance of serpentine substrates. A group of three species centered on *S. obtusatum* was characterized by relatively long sepals at anthesis, ascending to erect white to yellow petals, and a tendency towards relatively long upper stem leaves. The *S. laxum* group, with three taxa, was delimited by the narrow acuminate pink or white petals, these either erect or strongly spreading, and stem leaves sometimes clasping or decurrent. Our final group, based on *S. oregonense*, had acute ascending petals, and relatively short sepals at anthesis. This assemblage was less coherent than the other five groups, and membership was less straightforward. The obvious floral similarities between *S. eastwoodiae* and *S. laxum*, such as the identical color of the petals and anthers, led others to include *S. eastwoodiae* as a subspecies of *S. laxum*. However, in our view, its acute ascending petals were representative of the *S. oregonense* group, not the *S. laxum* group. Its floral morphology and tetraploid chromosome level may indicate a hybrid ancestry for *S. eastwoodiae*, with one parent diploid *S. laxum.* The suborbicular stem leaves of *S. eastwoodiae* were also found in *S. flavidum* (Table 6). Similarly, some populations of *S. flavidum* can look much like *S. oregonense,* and the two species share ascending acute petals and yellow anthers, so we believe *S. flavidum* is better aligned there than with *S. laxum*, where previous workers placed it as a subspecies. The similar floral morphology of *S. oregonense* and *S. flavidum* may indicate shared ancestry, and the two clustered together closely in the PCoA. The three reported chromosome levels for *S. oregonense* were unique for section *Gormania*. Finally, *S. marmorense* shared a number of general morphological similarities in foliage and floral structure with *S. oregonense*, so we grouped it there. However, its unusual waxy-granular indument may be a relic of past hybridization with a present or ancestral member of the *S. albomarginatum* group.

The Klamath Ranges were the only ecoregion with representatives of all six groupings in Table 5, and all three known ploidy levels in Table 3. This suggests the Klamath area was possibly a refugium, or a zone of ancestral origins for section *Gormania*. In either case, presumably the various taxa or groups of taxa diverged and dispersed from there.

Cleistogamy:—Cleistogamy was reported in some species in Crassulaceae, such as *Sempervivum* section *Jovibarba* de Candolle (1828: 413, Günthart 1902: 61) and small-flowered species such as *Crassula aquatica* (Linnaeus 1753: 128) Schönland (1890: 37, Berger 1930). In *Sedum* section *Gormania,* all tested taxa were self-compatible to a greater or lesser extent (Denton 1979b); therefore, the cleistogamous flowers probably contributed to overall seed production. A combination of chasmogamous and cleistogamous flowers on a single plant are known from a number of unrelated species, such as *Impatiens capensis* Meerburgh (1775: pl. 10, Waller 1984), *Viola pubescens* Aiton (1789: 290, Culley 2000a), *V. canadensis* Linnaeus (1753: 936, Culley 2000b), and *Collomia grandiflora* Douglas ex Lindley (in Edwards 1828: pl. 1166, Lord & Eckard 1984).

TABLE 5. Informal groupings of species within *Sedum* section *Gormania*, based on morphology. Range follows the ecoregions in Jepson eFlora (2017) and Meyers *et al*. (2015). CaRH = High Cascade Range in California. Casc = Cascade Range in Oregon. CR = Coast Range in Oregon. KR = Klamath Ranges of California and Oregon (for convenience here including the Siskiyous ecoregion of southwestern Oregon as delimited in Meyers *et al*. 2015). NCoRH = High North Coast Ranges in California. NCoRO = Outer North Coast Ranges in California. SNH = High Sierra Nevada in California and Nevada.

	***Sedum* section *Gormania* groups**					
	S. albomarginatum Group	*S. citrinum* Group	*S. laxum* Group	*S. moranii* Group	*S. obtusatum* Group	*S. oregonense* Group
Taxa	*S. albomarginatum* *S. oblanceolatum*	*S. citrinum* *S. kiersteadiae* *S. rubiginosum*	*S. laxum* subsp. *heckneri* subsp. *laxum* *S. patens*	*S. moranii*	*S. obtusatum* *S. paradisum* subsp. *paradisum* subsp. *subroseum* *S. sanhedrinum*	*S. eastwoodiae* *S. flavidum* *S. marmorense* *S. oregonense*
Character						
Glandular inflorescence	no	no	no	yes	no	no
Granular-waxy inflorescence	yes	no	no	no	no	yes or no
Rosette leaves and stem leaves oblanceolate	yes	no	no	no	no	no
Stem leaves suborbicular	no	no	yes or no	no	no	yes or no
Stem leaves decurrent	no	no	yes or no	no	no	no
Sepals relatively short at anthesis	yes	yes	no	no	no	yes
Petal angle at anthesis	ascending	spreading	erect or spreading	erect	erect or ascending	ascending
Petal shape	broad, acute	narrow, acute	narrow, acuminate	narrow, acuminate	broad, acute	broad, acute
Primary petal color	white, yellow	yellow	pink, white	yellow	white, yellow, pink	white, yellow, pink
Anther color	Yellow	yellow, orange, red	yellow, red	yellow	yellow, orange, red	yellow, red
Range (States)	KR, SNH (OR, CA)	KR, CaRH (CA)	CR, KR, NCoRO, (CA, OR)	KR (OR)	KR, NCoRH, SNH (CA, NV)	Casc, KR, NCoRH, NCoRO (CA, OR)

Sedum are drought-adapted succulents that produce copious nectar to attract pollinators (Berger 1930). It would be useful to know if environmental factors such as water supply (e.g., available snow-melt and precipitation) affected nectar production or the proportion of flowers that remain closed, and if this in turn had consequences for seed production and recruitment. Reproductive studies may be needed when assessing the long-term potential threats posed by extended droughts, changing precipitation patterns, and variation in the snowpack, temperature, and length of the growing season in the mountains of California and Oregon.

Rarity and conservation:—Some taxa, such as *Sedum oregonense* and *S. obtusatum*, had hundreds of large populations widely distributed at moderate to high elevations, and seemed to face no current threats. At the other extreme, taxa like *S. eastwoodiae, S. marmorense, S. moranii, S. patens*, and *S. rubiginosum* were known from few populations, and had small total ranges within a single county (suggesting poor dispersal capabilities or strong habitat gradients). For these species, events like road-widening, a poorly-placed quarry, herbicides, an introduced pest, or

depredations by horticultural collectors could quickly extirpate populations. Changes in temperature, precipitation, snow cover, drought frequency or duration could potentially affect the reproduction of *Sedum* taxa in the next 50 years, especially in the drier interior ranges. Although many colonies were on remote slopes, they were vulnerable, and we considered those species in the most need of conservation attention. Of those five taxa, *Sedum eastwoodiae* and *S. moranii* were already tracked by state or federal organizations in recognition of a limited distribution and perceived threats. Slightly more numerous, but still with a small range and warranting concern, were *S. albomarginatum, S. citrinum, S. oblanceolatum, S. paradisum* subsp. *subroseum*, and *S. sanhedrinum*. Populations of *S. flavidum, S. kiersteadiae, S. laxum* subsp. *heckneri,* subsp. *laxum,* and *S. paradisum* subsp. *paradisum* seemed numerous and stable, but some populations disappeared in the last few decades, thus a periodic census or some form of monitoring recruitment would be appropriate for each. In this report, precise latitude and longitude were omitted to shield small populations from collecting pressure.

Taxonomic Treatment

We examined or annotated all specimens cited, unless noted.

1. *Sedum albomarginatum* Clausen (1975: 424). Figs. 8A, 15A, 21

Type:—UNITED STATES. California: Plumas Co., Serpentine Canyon, East Branch of North Fork of Feather River, 855 m, 6 June 1963, *R. T. Clausen 63169* (holotype, BH; isotype, *R. T. Clausen 63172* BH).

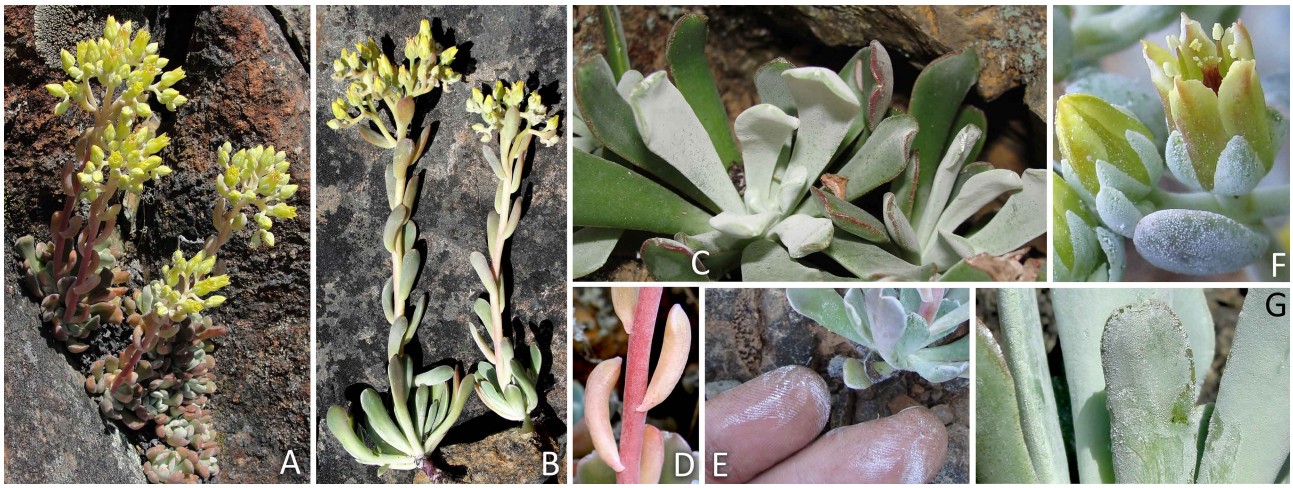

FIGURE 21. *Sedum albomarginatum*. A. Habit. B. Two flowering stems, the oblanceolate rosette leaves and stem leaves were similar in length and outline, the stem leaves were consistently elongated proximally and distally. C. Rosette leaves, fresh ones waxy, older weathered ones green. D. Stem leaves, showing truncated base. E–G. Dense white granular wax coating on fresh leaves, bracts and sepals, easily rubbed off on fingers. F. Flower and bud, showing erect pale yellow petals, white granular wax coating was dense on fresh sepals and bracts, sparse on corolla. G. Densely white granular waxy rosette leaves. A–D, G. Plumas Co., California (*Zika 25865*). E–F. Butte Co., California (*Zika 25867*).

Clausen, when preparing his type, provided different collection numbers for his replicates. Nonetheless, he indicated on his labels that he considered Clausen 63172 (BH) to be an isotype collection of *Sedum albomarginatum*, and that Clausen 63169 (BH) was the holotype. Both sheets were hand-labeled by Clausen, and collected at the same site on the same day, so we agree with Clausen that they represent one gathering of the type material, even with different collection numbers. Some additional live replicates were also gathered and used in his greenhouse studies, but these did not survive long in cultivation (Clausen 1975).

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Butte County:** Feather River Canyon, 9 June 1961, *Hutchison 2101* (JEPS); same site, 15 May 2012, *Zika 25867* (WTU). **Plumas County:** Feather River Canyon, 19 June 1963, *Clausen 63178* (BH); same site, 9 June 1961, *Hutchison 2126* (JEPS, K internet image); E Branch of N Fork of Feather River, 6 June 1967, *Hutchison 7333* (JEPS); canyon of the N Fork of Feather River, 915 m, 8 June 1943, *Youngs s.n.* [= *Clausen C43-55*] (BH, ex herb. Clausen); same site, collected living 9 June 1961, pressed 14 June

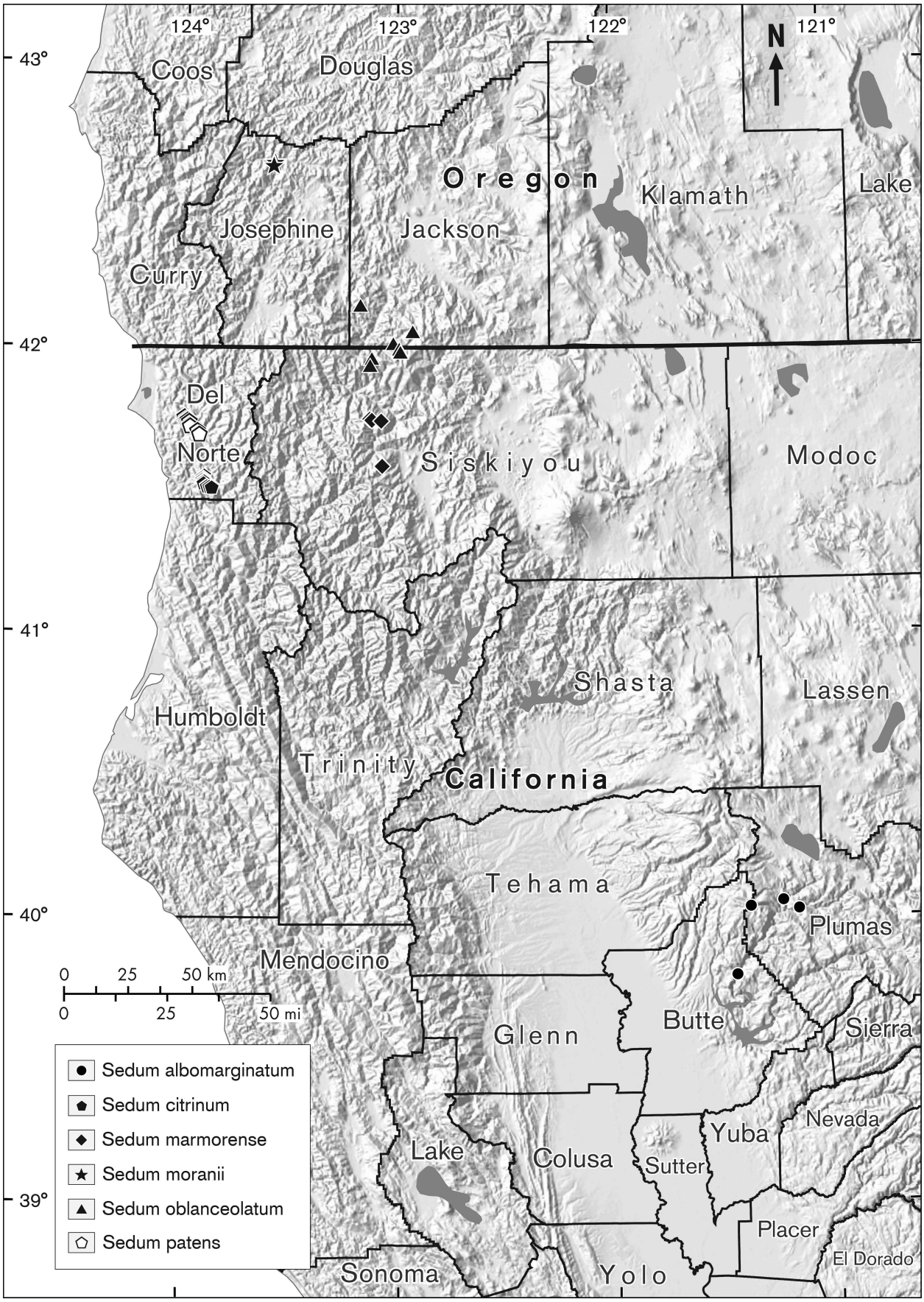

FIGURE 22. Distribution of *Sedum albomarginatum, S. citrinum, S. marmorense, S. moranii, S. oblanceolatum*, and *S. patens*, based on verified herbarium specimens.

1961, *Hutchison 2122* (F, JEPS, K internet image, NY, RSA); Feather River Canyon, N side of E Branch of N Fork, 26 June 1961, *Uhl 965a & Hutchison* (JEPS); same site, 26 June 1961, *Uhl 968 & Hutchison* (JEPS); N Fork Feather River, Serpentine Canyon, 853 m, 13 June 1976, *Denton 3853* (WTU); same site, 22 April 1977, *Denton 4060* (WTU); N Fork Feather River, 750 m, 13 June 1976, *Denton 3861* (WTU); same site, 15 May 2012, *Zika 25865* (JEPS, WTU); divide between Yellow Creek and Caribou Canyon, 1455 m, 6 August 2011, *Wilson et al. CWG-16* (OSC).

Distribution and ecology:—*Sedum albomarginatum* was restricted to Butte and Plumas counties in California, along the drainage of the North Fork of the Feather River and its tributaries (Fig. 22), where it grew on strongly serpentine bedrock, except for a northern population on a metasedimentary substrate. Recorded elevations ranged from 480–1740 m, in the northern High Sierra Nevada ecoregion (Jepson eFlora 2017). *Sedum albomarginatum* was rare, with a limited distribution and few populations, although some of the populations were large.

Notes:—*Sedum albomarginatum* (Fig. 21) had oblanceolate rosette and stem leaves with a thick and granular waxy indument that rubbed off easily when the plant was handled. The leaves rarely had white margins. The inflorescence branches and sepals were also granular-waxy, and the outer surface of the petals could also bear a few granules of wax early in the season. The sepals were about half as long as the petals, and the petal tips were ascending. At the start of flowering the petals were a clear pale yellow (Fig. 8A), with a pale or slightly darkened midvein, fading to orange-brown (Fig. 15A). The fresh anthers were yellow, aging to white or brown.

Sedum oblanceolatum was a closely related species (Table 5) from the Siskiyou Mountains in the Klamath Ranges ecoregion of California and adjacent Oregon (Meyers *et al*. 2015, Jepson eFlora 2017). It was similar to *S. albomarginatum* in that both had thick granular waxy deposits early in the growing season, and that the oblanceolate rosette leaves gradually transitioned to the similarly-shaped stem leaves. The two species were disjunct by 250 km (Fig. 22), and differed in flower color. *Sedum oblanceolatum* had consistently white corollas, proportionately narrower leaves, and often smaller plants. The leaves of both taxa quickly lost their wax to weathering unless sheltered by a rock overhang.

Sedum marmorense also had a thick waxy coating on leaves, inflorescence branches, sepals and sometimes on the pale yellow flowers, but its rosette and stem leaves were proportionally broader, and it grows in the Klamath Ranges ecoregion of Siskiyou County, California, 200 km northwest of *S. albomarginatum* (Fig. 22).

Clausen (1975: 429–433) reported a pungent odor to the flowers, and nocturnal moth visitors, based on the observations of Paul Hutchison.

2. *Sedum citrinum* Zika (2014: 112). Figs. 2A–B, 5A, 8B, 9A, 11A, 23, 24A.

Type:—UNITED STATES. California: Del Norte Co., ridge N of South Red Mountain, 1050 m, 9 June 2013, *P. F. Zika 26185* (holotype, WTU; isotypes, BH, CAS, GH, MO, OSC, RSA, UC, US).

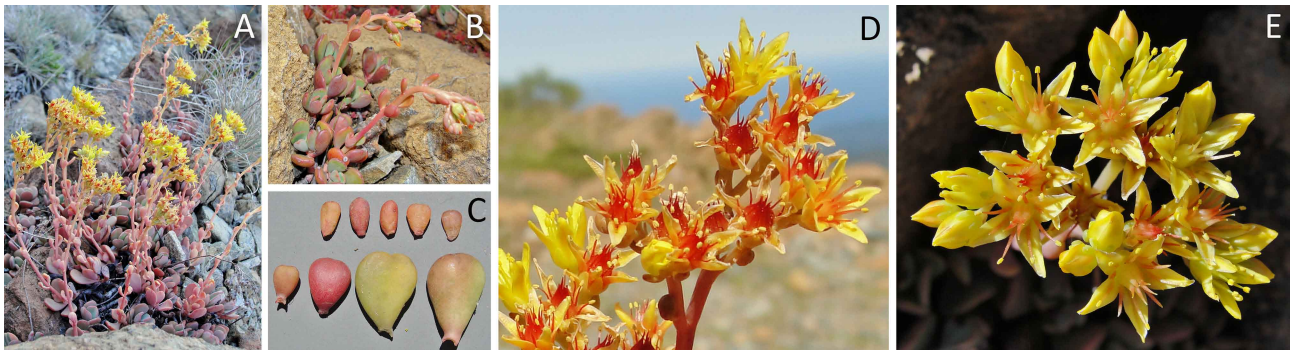

FIGURE 23. *Sedum citrinum*, Del Norte Co., California. A. Habit (*Zika 26611 & Brainerd*). B. Inflorescence nodded in bud, rosettes were loose (*Zika 26193*). C. Rosette leaves, lower row; stem leaves, upper row (*Zika 25930*). D–E. Deep yellow flowers with spreading narrow petals, yellow anthers faded white. D. *Zika 26619 & Brainerd*. E. *Zika 26620 & Brainerd*.

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Del Norte County:** near Red Mountain lookout, 1220 m, 26 June 1979, *Overton & Butler 6664* (HSC); N of South Red Mountain, 1050 m, 24 June 2012, *Zika 25930* (HSC, JEPS, SBBG, UCR); same site, 9 June 2014, *Zika 26611 & Brainerd* (OSC, WTU); NNW of South Red

Mountain, 1210 m, 24 June 2012, *Zika 25931* (DAV, MO, NY, US); same site, 9 June 2013, *Zika 26193* (BH, CAS, WTU); NW of South Red Mountain, 1235 m, 9 June 2013, *Zika 26201* (BH, CAS, RSA, WTU); N of Red Mountain, 1190 m, 10 June 2014, *Zika 26619 & Brainerd* (WTU); Turwar Creek drainage, NNW of Red Mountain Lookout, 1235 m, 10 June 2014, *Zika 26615 & Brainerd* (HSC, RSA, US); same site, 940 m, 10 June 2014, *Zika 26620 & Brainerd* (OSC, WTU).

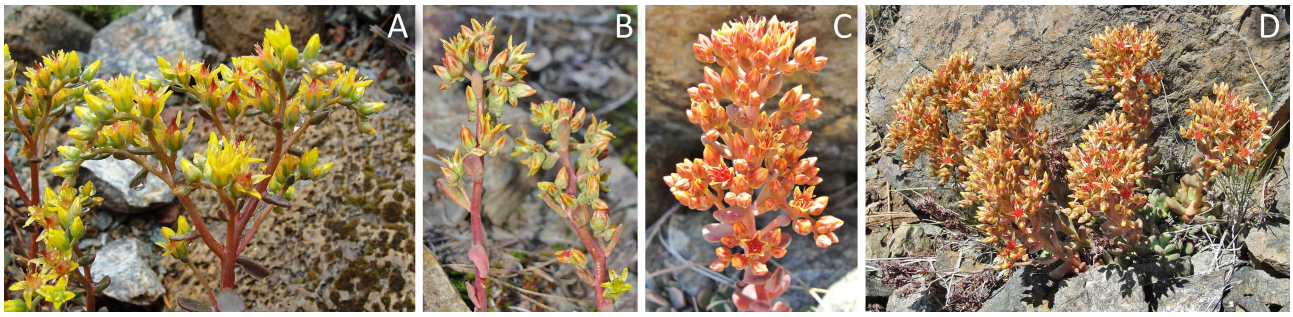

FIGURE 24. Inflorescence comparison between *Sedum citrinum*, *S. kiersteadiae*, and *S. rubiginosum*. All three species with narrow spreading yellow petals. A. *Sedum citrinum*, inflorescence with elongated lower branches, flat-topped, Del Norte Co., California (*Zika 25930*). B. *Sedum kiersteadiae*, cylindrical and loose inflorescence, individual flowers easily seen, Shasta Co., California (*Zika 26294*). C–D. *Sedum rubiginosum*, cylindrical and dense inflorescence, individual flowers less easily distinguished, Tehama Co., California (*Zika 25522 & J.K. Nelson*).

Distribution and ecology:—*Sedum citrinum* was endemic to gently sloping ultramafic outcrops and meadows at elevations of 940–1275 m in southern Del Norte County, California, where it was recorded from a few populations within an area of fifteen square km near South Red Mountain (Fig. 22), in the western Klamath Ranges ecoregion (Jepson eFlora 2017). Its ecology was summarized in Zika (2014).

Notes:—*Sedum citrinum* (Fig. 23) had thick obovate rosette leaves and thick oblong to elliptic or obovate stem leaves (Fig. 5A). The sepals were relatively short (Fig. 9A). The petals were deep yellow, narrow, and strongly spreading, often to 90° from the flower axis (Figs. 8B, 11A). Fresh anthers were yellow, aging to yellow, white, brown, or orange. The inflorescences were flat-topped or rounded, with elongate lower branches, not columnar or cylindrical as in the closely related species *S. kiersteadiae* and *S. rubiginosum* (Fig. 24). The three taxa were allopatric.

Sedum citrinum was similar to the recently described *S. kiersteadiae*, a more widespread species of the Cascade Range Highlands and Klamath Ranges ecoregions (Jepson eFlora 2017), from Siskiyou County, south to Trinity and Shasta counties (Fig. 25, Wilson *et al*. 2014). Both had narrow, widely spreading, yellow petals and vegetative shoots with well-spaced leaves in open rosettes. *Sedum citrinum* differed from *S. kiersteadiae* in inflorescence shape and also in flower color, which was paler in *S. kiersteadiae. Sedum citrinum* was also similar to *S. rubiginosum* of Tehama County, California. The latter was restricted to the extreme southern tip of the Klamath Ranges ecoregion, 150 km southeast of *S. citrinum* (Fig. 25), and had dense rosettes with larger, columnar inflorescences with more numerous and more densely crowded flowers.

3. *Sedum eastwoodiae* (Britton in Britton & Rose 1903: 31) Berger (1930: 451). Figs. 26–27.

Gormania eastwoodiae Britton in Britton & Rose (1903: 31). *Cotyledon mendocinoana* Fedde in Schumann & Fedde (1904: 828). *Sedum laxum* (Britton in Britton & Rose 1903: 29) Berger (1930: 451) subsp. *eastwoodiae* (Britton) Clausen (1975: 398). *Sedum laxum* (Britton) A.Berger var. *eastwoodiae* (Britton) Ohba (2007: 889).

Type:—UNITED STATES. California: northern Mendocino Co., Red Mountain, August 1902, *A. Eastwood s.n.* (lectotype, designated by Clausen [1942: 39], CAS; isolectotype, NY).

Britton (in Britton & Rose 1903) listed only one gathering of *Gormania eastwoodiae*, neither noting the location of replicates nor choosing one as a holotype. Clausen (1942) in effect lectotypified the CAS material as the holotype, and it was superior to the isotype at NY. His lectotype choice was probably influenced by correspondence at NY with Eastwood, dated 30 August 1903, which showed that the CAS collection was seen by Britton and then returned to Eastwood at CAS.

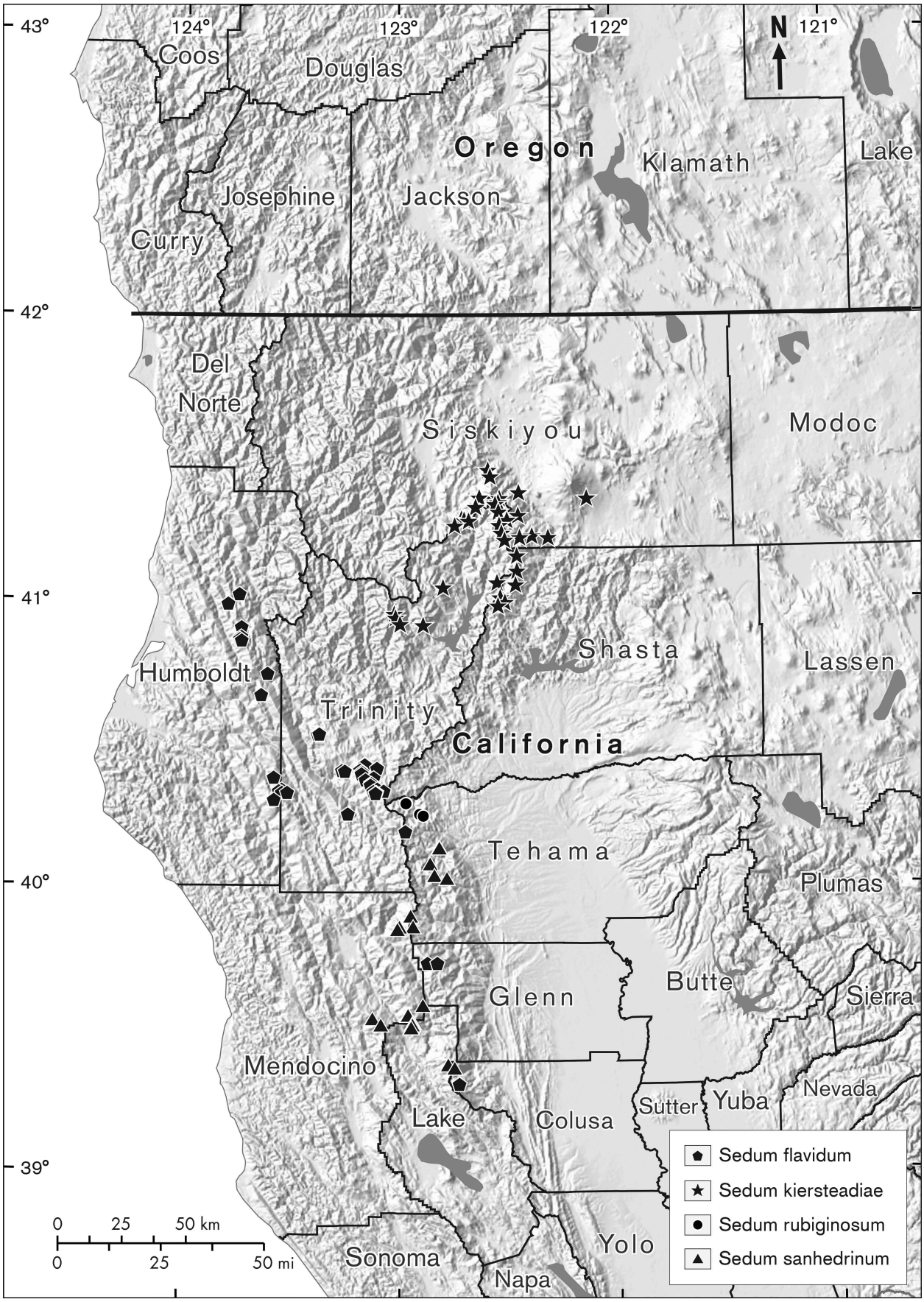

FIGURE 25. Distribution of *Sedum flavidum, S. kiersteadiae, S. rubiginosum*, and *S. sanhedrinum*, based on verified herbarium specimens.

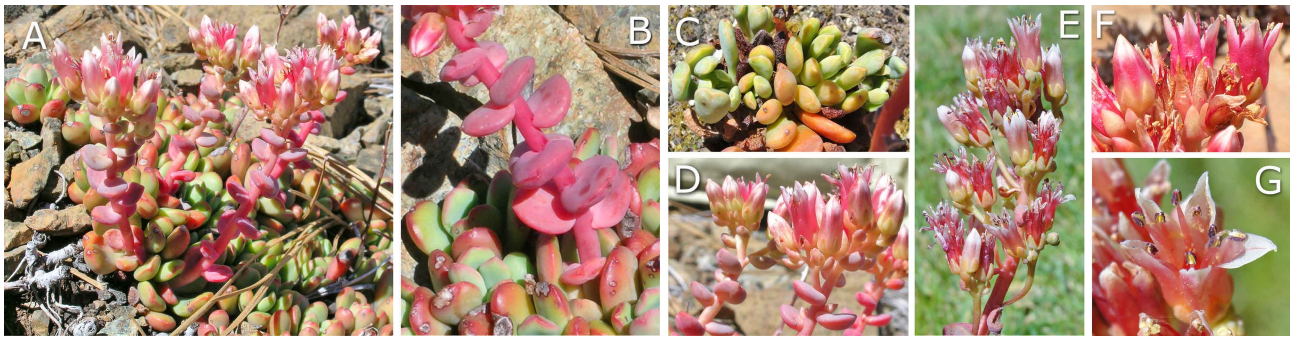

FIGURE 26. *Sedum eastwoodiae*, Mendocino Co., California (*Wilson & Otting CWG-117*). A. Habit, generally short plants with small leaves. B. Stem leaves, suborbicular, slightly glaucous, slightly clasping at base. C. Dense rosette leaves. D. Typical dense flat-topped inflorescences. E. Columnar inflorescence in cultivation. F. Flowers in the wild, ascending petals with acute tips, relatively short sepals, acute- to blunt-tipped. G. Flower in cultivation, petal tips broad, acute, spreading more than typical in wild plants.

TABLE 6. Selected traits of *Sedum* in *S. laxum*, *S. flavidum,* and *S. eastwoodiae.* Chromosome counts from Denton (1979b). In taxa with suborbicular leaves, some leaves on an individual plant, sometimes all leaves on a few plants, were elliptic to oblong.

Trait	*S. flavidum*	*S. eastwoodiae*	*S. laxum* subsp. *heckneri*	*S. laxum* subsp. *laxum*
Chromosome number	*2n* = 60	*2n* = 60	*2n* = 30	*2n* = 30
Stem leaves	suborbicular	suborbicular	suborbicular	oblong
Sepal shape	acute	acute	acuminate	acuminate
Petal color	white, pale yellow	pink with white edges	pink with white edges	pink with white edges
Petal tips	acute to obtuse	acute	acuminate	acuminate
Petal spread	ascending	ascending	erect	erect
Anther color	yellow, aging brown	dark red, aging black	dark red, aging black	dark red, aging black

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Mendocino County:** Red Mountain, 1097 m, 14 July 1962, *Hutchison 909* (JEPS, SD); same site, 1175 m, 14 July 1962, *Hutchison 911* (JEPS, RSA); same site, 1070 m, 14 July 1970, *Clausen 70-68* (BH), and *Clausen 70-69* (BH); same site, 1045 m, 18 July 1970, *Clausen 70-84* (BH); same site, 1110 m, 19 June 1976, *Denton 3940* (WTU); same site, 1025 m, 24 June 1977, *Denton 4099* (OSC, WTU); same site, 1240 m, 3 July 2012, *Wilson & Otting CWG-117* (OSC).

Distribution and ecology:—A narrow endemic on rocky serpentine slopes of Red Mountain and adjacent Little Red Mountain in Mendocino County, California, in the Outer North Coast Ranges ecoregion (Jepson eFlora 2017), at elevations of 600–1240 m (Fig. 27).

Notes:—*Sedum eastwoodiae* (Fig. 26) flowering stems were short, and the plants formed extensive mats of sterile rosettes. The rosette leaves were acute to obtuse, rarely notched. Stem leaves were suborbicular and slightly clasping. The sepals were relatively short; the petals ascending, bright pink, sometimes broadly edged with white, and had acute tips. The fresh anthers were dark red, aging black.

Sedum eastwoodiae was often treated as a subspecies of *S. laxum* (e.g., Denton 1982), and the two species had similar bright pink flowers and dark red anthers. However, *S. laxum* had more acuminate and stiffly erect petal tips. *Sedum eastwoodiae* had suborbicular stem leaves resembling those of *S. flavidum* and *S. laxum* subsp. *heckneri*, though the stem leaves of the latter were often larger. *Sedum eastwoodiae* shared with *S. flavidum* acute, slightly spreading petals, and a tetraploid chromosome count. The pallid flowers of *S. flavidum* were relatively shorter and wider than the pink flowers of *S. eastwoodiae*. The morphology of *S. eastwoodiae, S. flavidum,* and *S. laxum* were compared in Table 6.

Sedum eastwoodiae was identified as a candidate for federal endangered species status on 15 December 1980 (Federal Register Volume 45, page 82479). A listing petition was denied on 18 September 2014 by the United States Fish and Wildlife Service (Federal Register Volume 79, pages 56029–56040).

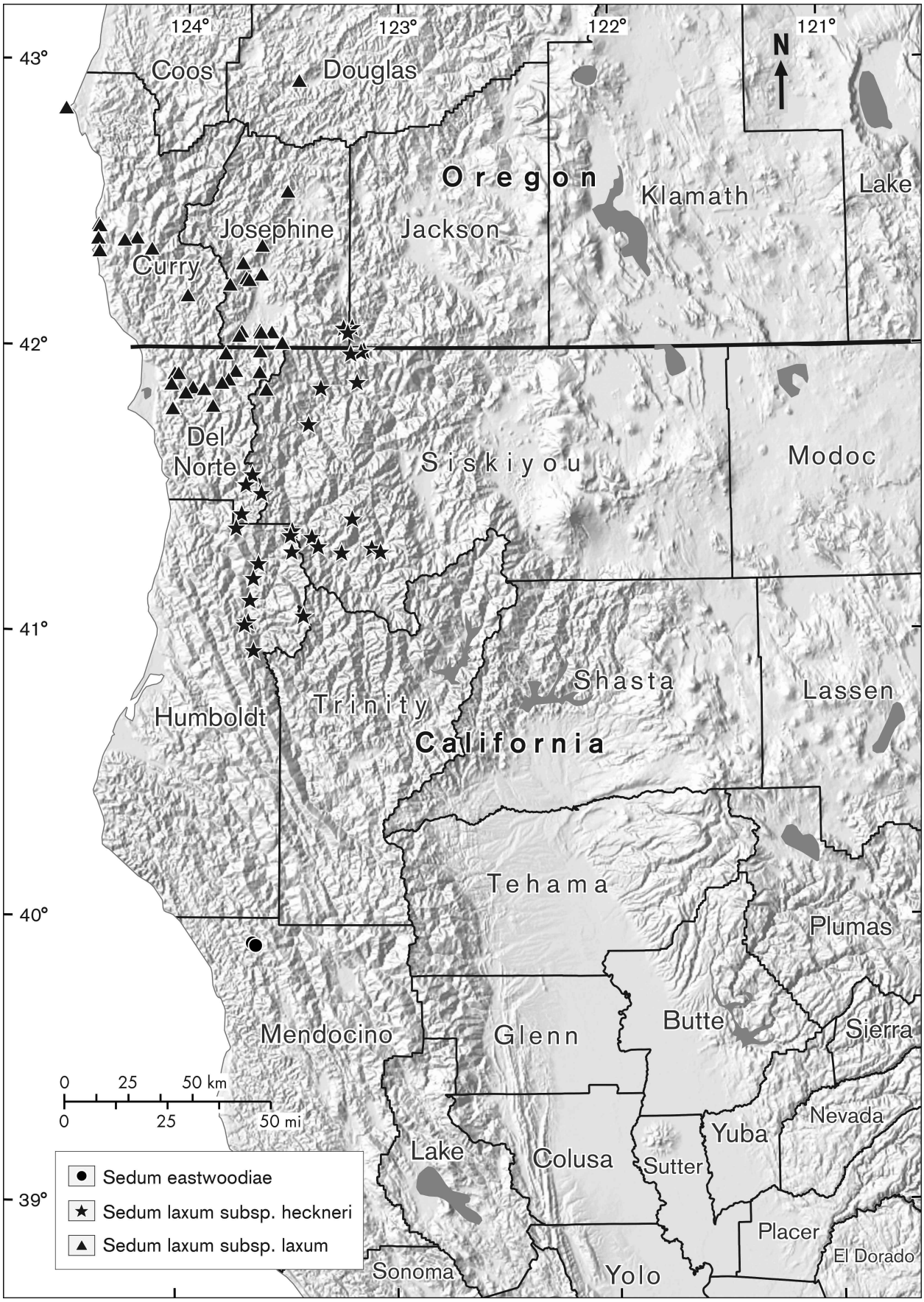

FIGURE 27. Distribution of the pink-flowered taxa *Sedum eastwoodiae, S. laxum* subsp. *heckneri*, and *S. laxum* subsp. *laxum*, based on verified herbarium specimens.

4. *Sedum flavidum* (Denton 1978: 233) B.L. Wilson & Zika, *comb. nov., stat. nov*. Figs. 1A, 6A–C, 12, 13A, 14A–B, 15B, 28.

Sedum laxum (Britton in Britton & Rose 1903: 29) Berger (1930: 451) subsp. *flavidum* Denton (1978: 233) (basionym). *Sedum laxum* (Britton) A.Berger var. *flavidum* (Denton) Ohba (2007: 889).

Type:—UNITED STATES. California: Trinity Co., 4.5 miles NE of Forest Glen along Post Creek, 914 m, 23 June 1976, *M. F. Denton 3953* (holotype, WTU; isotype, NY).

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Colusa County:** Mendocino National Forest, W of Upper Letts Lake, 1480 m, 24 June 2013, *Elliott 13* (CHSC, KANU, MICH); same site, 12 June 2014, *Zika 26643 & Brainerd* (SD, OSC, WTU); WSW of Upper Letts Lake, 1480 m, 12 June 2014, *Zika 26642 & Brainerd* (WTU); W of Big Spring picnic area, 1480 m, 1 July 2012, *Wilson & Otting CWG-114* (JEPS, RSA, WTU). **Glenn County:** SE of Mendocino Pass, 1798 m, 23 June 1961, *Uhl 970* (BH); Black Butte, 31 miles E of Covelo, 2134 m, 20 June 1976, *Denton 3941* (OSC, WTU); SE of Plaskett Meadows Campground, 1880 m, 2 July 2012, *Wilson & Otting CWG-115* (KANU, MO, US, WTU); road to Black Butte Lookout, 2155 m, 2 July 2012, *Wilson & Otting CWG-116* (OSC, WTU). **Humboldt County:** Grouse Mountain, 1524 m, 25 July 1933, *Tracy 12899* (UC [2 sheets]); near Sims Mountain, 430 m, 15 July 1980, *Newton 1549* (UC, WTU); same site, 17 July 2013, *Darington 13-SM* (HSC, JEPS, SBBG); Pilot Creek Quadrangle, 300 m, 15 July 1980, *M. Baker 2941* (UC, WTU); near Red Mountain, 11 July 1980, *M. Baker 2769* (UC); Lacks Creek area on Pine Ridge Road, 1032 m, 9 June 2012, *Brainerd & Otting CWG-103* (OSC, WTU); Titlow Hill Road above junction with Route 299, E of Arcata, 23 June 1990, *Chambers 5511* (OSC); Lassics Botanical Area, 26 July 2012, *L.D. Hoover LDH-1* (OSC); Horse Mountain, S of Berry Summit, 21 May 1961, *Hutchison 2013* [= *Uhl 932*] (JEPS); Horse Mountain, 1435 m, 9 July 1947, *Tracy 17865* (UC); same site, 4 July 2012, *Wilson, Otting, & Darington CWG-118* (GH, HSC, MO, WTU); Supply Creek, Hoopa, 730 m, 4 July 2012, *Wilson, Otting & Darington CWG-120* (OSC); G-O Road, 1465 m, 20 June 2014, *B.L. Wilson 18112* (OSC); Klamath River, 1.4 miles S of Siskiyou County line, 150 m, 10 July 1961, *Roderick 61.989* (JEPS); Highway 299, 595 m, 29 June 2013, *Wilson et al. CWG-238* (RSA). **Trinity County:** Post Creek, 885 m, 13 June 1951, *Moran 3484* (BH, CAS, UC); Klamath Mountains, North Post Creek, 885 m, 13 June 1963, *Clausen 63199* (BH); same site, 17 June 1963, *Clausen 63200* (BH); same site, 18 June 1963, *Clausen 63202* (BH, GH); Post Creek, 915 m, 22 June 1976, *Denton 3949* (OSC, WTU); Post Creek, 853 m, 23 April 1977, *Denton 4066* (WTU); same site, 19 June 2011, *Wilson & Coberly CWG-07* (OSC, UCR, WTU); Salt Creek, 945 m, 13 June 1951, *Moran 3483* (BH, CAS); same site, 13 June 1963, *Clausen 63195* (BH); same site, 19 June 1963, *Clausen 63197* (BH); E of Mud Springs, 1 July 1979, *Baker 608* (CAS); S of Peanut, 945 m, 25 June 1980, *Denton 4189* (WTU); Blue Point, 8 June 2012, *J.K. Nelson JKN-12-2* (CHSC, HSC); Bule Gulch, 917 m, 19 June 2011, *Wilson & Coberly CWG-06* (CAS, JEPS); N of Hackney Spring, 1375 m, 19 June 2011, *Wilson, Coberly & J.K. Nelson CWG-08* (KANU, MO, NY); road to Hell-to-Find Lake, 1295 m, 19 June 2011, *Wilson, Coberly & J.K. Nelson CWG-09* (DAV, RSA, US); W of Wildwood, 945 m, 13 June 1937, *Wolf 8799* (OSC); ENE of Limedyke Mountain, 1200 m, 22 June 2012, *Zika 25922 & J.K. Nelson* (DAV, HSC, WTU); NE of Red Mountain, 1260 m, 12 June 2014, *Zika 26646 & Brainerd* (WTU).

Distribution and ecology:—*Sedum flavidum* populations ranged in elevation from 231–1707 m. The species was variable in floral and stem leaf characters. Some of the variation was roughly correlated with three geographic areas in California (Fig. 25). A cluster of populations occurred in southern and eastern Trinity County, usually on serpentine substrates in the Klamath Ranges ecoregion. Closer to the coast were the western-most populations in Humboldt and southwestern Trinity counties. These plants were in the outer North Coast Ranges and the High North Coast Range ecoregions (Jepson eFlora 2017). Disjunct southern populations occurred in Glenn and Colusa counties, in the High North Coast Ranges ecoregion. We could not separate those populations in the PCoA analysis, and did not provide them with different taxonomic ranks here. Nonetheless, we felt they deserved further study, especially in the western and southern extremes of the range.

Notes:—*Sedum flavidum* (Fig. 28) had obtuse to notched dense rosette leaves. The stem leaves were typically small, suborbicular and slightly auriculate, but sometimes were elliptic to oblong. The stem leaves were flattened, planoconvex, or saddle-shaped, and varied in aspect, usually spreading, but occasionally ascending or slightly reflexed. The sepals were short relative to the petals. The petals of wild plants were usually ascending, and usually broad in the distal half (Fig. 12), obtuse to acute, white to pale yellow, sometimes red or pink along the midrib, occasionally also near the base, senescing white or pink to red, at least towards the base. The fresh anthers were yellow, aging white, pink, or brown.

FIGURE 28. A comparison of *Sedum flavidum* populations from three portions of its range. **Top row**, A–E. Northwestern portion of range, Humboldt Co., California (*Wilson, Otting, & Darington CWG-118*). A. Dense rosettes formed a mat. B–C. Inflorescences with white petals, yellow anthers. B. Stem leaves about as wide as long. C. Stem leaves longer than wide. D. Variant of corolla color, petals with pink midvein in bud and pinkish blush in bloom, more pronounced as the flowers faded. E. Typical corolla color, ascending white petals, distal half slightly narrowed, yellow anthers. **Center row**, F–L. Central portion of range, including the type locality, Trinity Co., California. F. Dense rosettes (*Zika 25922 & J.K. Nelson*). G–J. Variation in stem leaf shape. G. Rosette and flowering stem (*Wilson, Coberly & J.K. Nelson CWG-08*). G–H. Stem leaves longer than wide, truncated at base. H. (*Zika 26646 & Brainerd*). I. Stem leaves broadest above the middle, clasping at base, somewhat reflexed, type locality (*Wilson & Coberly CWG-07*). J. Stem leaves suborbicular, clasping at base (*Zika 25922 & J.K. Nelson*). K. Variant of corolla color, petals pale yellow-orange, fading pinkish (*Zika 26646 & Brainerd*). L. Typical flowers, broad ascending white petals, yellow anthers (*Zika 25922 & J.K. Nelson*). **Bottom row**, M–R. Southern portion of range, Colusa Co., California. M. Dense rosettes (*Zika 26642*). N. Flowering stems, stem leaves suborbicular (*Wilson & Otting CWG-114*). O. Stem leaves elliptic, truncated at base, planoconvex (*Zika 26642*). P. Stem leaf suborbicular, ± planar (*Zika 26642*). Q. Variant of corolla color, petals white with dark pink midveins in bud, faded pink, petal tips broad and ascending (*Zika 26642*). R. Typical flowers, broad ascending white petals, yellow anthers (*Zika 26642*).

We treated *Sedum flavidum* as different at the species level from the subspecies of *S. laxum*. They differed in ploidy level; $2n = 30$ in *S. laxum* and $2n = 60$ in *S. flavidum* (Table 6). *Sedum flavidum* corollas were white or pale yellow, with yellow anthers, while in *S. laxum* the fresh anthers were dark red, and the flowers were pink, or primarily pink with white margins (Table 6), though cultivated plants sometimes produced nearly white flowers (Fig. 16B). *Sedum flavidum* also differed in its blunter sepals, and had more acute and ascending petals (Denton 1979b). The suborbicular stem leaves of *S. flavidum* resembled those of *S. laxum* subsp. *heckneri* but tended to be smaller and ascending to spreading, less commonly reflexed. Also, elliptic to oblong stem leaves occur in *S. flavidum* populations in Colusa, Glenn, and southern Trinity counties; in *S. laxum* subsp. *heckneri,* the proportionately longer stem leaves are known only from a few plants in the Applegate River drainage.

Denton (1978) described *Sedum laxum* subsp. *flavidum* and placed it within *S. laxum* on the strength of leaf flavonoids, similar glaucous leaf surfaces, rosette leaf shape, rosette density, petal length to width ratio, and stigma diameter (Denton 1982). However, Denton & Kerwin (1980) identified their flavonoid voucher (*Denton 4048*) as *S. laxum* subsp. *laxum*; we annotated it to diploid *S. oregonense*. In addition, the flavonoids said to unite the subspecies of *S. laxum* (3,7-disubstituted kaempferol, laricytrin, and an unidentified flavone) were not restricted to this group, but were also found in *S. moranii, S. oblanceolatum,* and some populations of *S. oregonense.* Neither *S. moranii* nor *S. oblanceolatum* were closely related to *S. flavidum* (Table 5). Similarly, we found the morphological characters used by

Denton (1982) did not uniquely define *S. laxum*, but were shared with additional species. The petal length/width ratio of *S. flavidum* was shared with *S. oregonense*, and the rosette characters were similar in *S. obtusatum*.

Three populations in Colusa and Glenn counties, California, resembled *Sedum flavidum* populations near the type locality in having ascending, acute, white petals (sometimes marked with pink), proportionately short sepals, and suborbicular to oblong stem leaves. These plants were disjunct from the main range of *S. flavidum* as currently defined, and grew fairly close to *S. sanhedrinum* populations. They should be studied further.

Although the two were allopatric, *Sedum flavidum* was sometimes difficult to distinguish from *S. oregonense* morphologically, and their flowers were similar. Ecologically, *S. flavidum* was found at lower and more forested elevations, and further south. Many populations of *S. flavidum* had suborbicular slightly clasping stem leaves, at least some years, while this was uncommon to rare in *S. oregonense*. The two differed in the density and aspect of their vegetative shoots. *Sedum flavidum* had compact rosettes on short lateral shoots when growing in sunny exposed situations, sometimes forming dense mats of nearly uniform leaves (Fig. 1A). *Sedum oregonense* had loose rosettes with obvious internodes, on numerous elongate lateral shoots or stolons when growing in sunny exposed microsites (Fig. 2D).

5. Sedum kiersteadiae B.L.Wilson & R.E.Brainerd in Wilson *et al*. (2014: 9). Figs. 2C, 11B, 24B, 29

Type:—UNITED STATES. California: Shasta County, NE of Slate Mountain, 1372 m, 15 June 2012, *Lindstrand III & Van Susteren NSR-17* (holotype, OSC; isotypes, CAS, CHSC, DAV, HSC, MO, NY, RSA, UC, WTU).

Sedum obtusatum Gray (1868: 342) subsp. *boreale* Clausen (1942: 32). *Sedum obtusatum* A.Gray var. *boreale* (R.T.Clausen) Ohba (2007: 889).

Type:—UNITED STATES. California: Siskiyou County, Mount Shasta, E side of Mud Creek Canyon, 1707 m, 26 July 1940, *R. T. Clausen 4952, W. B. Cooke & H. Trapido* (holotype, BH; isotypes, BH, DS, NY).

Not *Sedum boreale* Günthart (1902: 49).

The type specimen of *Sedum obtusatum* subsp. *boreale* (*Clausen 4952 et al.*) was interpreted different ways. It was collected from Mud Creek on Mount Shasta in the southern Cascade Range, a location somewhat disjunct from other *Sedum* populations. The taxon was originally described as having pale to deep yellow, somewhat spreading petals, and associated with specimens collected further west (Clausen 1942). We interpreted at least one of the paratype specimens cited (*J. T. Howell 13450* (CAS), from Siskiyou County, California, Salmon-Trinity Alps, Caribou Basin, 25 July 1937) as *S. oregonense*. Later, Clausen (1975) and Denton (1982) applied the name *S. obtusatum* subsp. *boreale* to plants of the northern Sierra Nevada that had relatively large mats of dense rosettes and wide, apically obtuse, white petals that were pink at the base and senesce pink throughout, plants that we considered to be *S. paradisum* subsp. *subroseum*. We interpreted *Clausen 4952 et al.* and other plants recently collected from the canyon of the type locality (*Colberg MEC-1, Cooke 15459*) as belonging to *S. kiersteadiae*.

FIGURE 29. *Sedum kiersteadiae*. A. Habit, long easily visible internodes on sterile shoots; Trinity Co., California (*Zika 25680 & Wilson*). B. Stem leaves, Siskiyou Co., California (*Zika 25905 & J.K. Nelson*). C. Rosette leaves, lower row; stem leaves, upper row; Siskiyou Co. (*Zika 26289*). D. Columnar inflorescence at anthesis. E. Nodding inflorescence before anthesis. F–G. Pale yellow flowers, anthers dull red, petals spreading to slightly reflexed, the upper half narrow. D–G. Trinity Co. (*Zika 26294*). H–I. Variant of corolla color, flowers with reddish buds, midveins, and petal bases, anthers dull red, Siskiyou Co. (*Wilson, J.K. Nelson & Posey CWG-19*).

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Shasta County:** N of Sanford Pass, 1402 m, 15 June 2012, *Lindstrand III & Van Susteren NSR-15* (DAV, HSC, V); upper Slate Creek watershed, 1280 m, 15 June 2012, *Lindstrand III NSR-18* (CAS, JEPS, MO, NY, RSA). **Siskiyou County:** Mount Eddy, 29 June 1913,

Smith 433 (CAS); Mount Shasta, Mud Creek, 1740 m, 7 August 2011, *Colberg MEC-1* (MO, RSA); Mud Creek Canyon, 1981 m, 22 August 2013, *Cooke 15459* (OSC); road to Mount Eddy, 1270 m, 5 June 1978, *Denton 4140* (WTU); Mount Bradley, 1693 m, 12 July 2011, *Lindstrand III & Van Susteren NSR-09* (BH, F, GH, NY, US); Grey Rock Lake, 1775 m, 20 July 2011, *Lindstrand III & Van Susteren NSR-11* (CAS, CHSC, DAV, HSC, MO, NY, RSA, UBC, UC, WTU); Rattlesnake Hill, 1700 m, 20 July 2011, *Lindstrand III & Van Susteren NSR-12* (BH, GH); Mount Eddy Trail, 2135 m, 29 July 2011, *Van Susteren JVS-1* (CAS, JEPS); Little Castle Lake, 1815 m, 30 July 2011, *Van Susteren JVS-2* (DAV, HSC); road to Kangaroo Lake, 1495 m, 9 August 2011, *Wilson, J.K. Nelson & Posey CWG-18* (F, JEPS, RENO, US); W of Kangaroo Lake, 2015 m, 9 August 2011, *Wilson, J.K. Nelson & Posey CWG-19* (CAS, MO, NY); Shasta-Trinity National Forest, SSE of Crater Lake, 1760 m, 31 July 2011, *Zika 25680 & Wilson* (F, RENO, UBC, US, WTU); NW of Deadfall Lakes, 2100 m, 31 July 2011, *Zika & Wilson 25683* (CAS, JEPS, OSC, US, WTU); South Fork Willow Creek, 1125 m, 21 June 2012, *Zika 25901 & J.K. Nelson* (DAV, MO, NY, RSA); WNW of Gumboot Lake, 1960 m, 28 June 2013, *Zika 26289* (CHSC, HSC, UCR); ENE of Gazelle Mountain, 1630 m, 21 June 2012, *Zika 25905 & J.K. Nelson* (CAS, WTU). **Siskiyou/Trinity county line:** Mount Eddy, 2010 m, 7 August 2011, *Colberg MEC-2* (CHSC, STNF, WS); W of Toad Lake, 2120 m, 31 July 2011, *J.K. Nelson JKN-1* (GH, KANU). **Trinity County:** N of Trinity Center, 1525 m, 16 June 1977, *Denton 4096* (WTU); NW of Mount Eddy, 2255 m, 12 August 1967, *Heckard 1665* (JEPS); near Mount Eddy, 2040 m, 5 June 1978, *Denton 4139* (WTU); trail to Canyon Creek Lakes, 1430 m, 23 June 2011, *Stubbs et al. RS-27* (UC, WTU); Canyon Creek Wilderness, 4 July 2014, 1890 m, *Otting 3822* (HSC, MO, SOC); above Deadfall Lakes, 2300 m, 29 July 1977, *Denton 4111* (WTU); WSW of Deadfall Lakes, 1980 m, 31 July 2011, *Zika 25687 & Wilson* (US, WTU); Little Boulder Lake Trail, 1890 m, 28 August 2011, *Erwin SE-1* (MO, NY, RSA); Shasta-Trinity National Forest, Parks Creek Summit, 2100 m, 28 June 2013, *J.K. Nelson JKN-2013-1* (WS); Trinity Mountains, Grouse Lake, 1860 m, 20 July 2012, *Taylor 21285* (RSA, WTU); NNW of Picayune Lake, 1850 m, 31 July 2012, *Zika 25689* (MO, NY, OSC, WTU); NNW of Grey Rocks Peak, 1640 m, 28 June 2013, *Zika 26294* (CAS, JEPS, RSA).

Distribution and ecology:—Most populations were in the Klamath Ranges ecoregion along the border of Siskiyou County with Trinity and Shasta counties (Fig. 25). The northeastern-most colony was on Mount Shasta, in the high Cascade Range ecoregion (Jepson eFlora 2017). *Sedum kiersteadiae* preferred rock outcrops and rocky open forests, at elevations of 1145–2300 m. It grew on serpentine and volcanic substrates.

Notes:—*Sedum kiersteadiae* (Fig. 29) rosettes were relatively open, with most of the nodes well separated. The stem leaves were elliptic to obovate. The inflorescences were cylindrical. The sepals were half or less as long as the petals. The petals were yellow, often marked with red on the midrib or base, aging reddish, narrow, and acute, spreading about 90° from the flower axis at anthesis. The fresh anthers were usually rusty, dark orange, or red, senescing dark purple to black, less commonly yellow, senescing brown.

Sedum kiersteadiae was compared to the similar species *S. citrinum* and *S. rubiginosum* under *S. citrinum* (Fig. 24).

6. *Sedum laxum* (Britton in Britton & Rose 1903: 29) Berger (1930: 451)

Gormania laxa Britton in Britton & Rose (1903: 29). *Cotyledon brittoniana* Fedde in Schumann & Fedde (1904: 828). *Echeveria gormanii* Nelson & Macbride (1913: 476). *Sedum jepsonii* Butterfield (1936: 7).

Type:—UNITED STATES. Oregon: Josephine Co., Waldo, 4 June 1884, *Thomas Howell s.n.* (lectotype, designated by Clausen [1942: 37], NY; isolectotype, US).

Notes:—*Sedum laxum* plants were often relatively tall. Rosette leaves were fairly dense, and obovate, thin or thick, glaucous or green, and truncate to notched. Stem leaves were ascending and oblong or elliptic, crowded or not, sometimes thick, decurrent or not. Sepals were about a third or less as long as the petals. Petals were erect and bright pink with white margins (sometimes all white), slender, attenuate, usually erect. Anthers were dark red, aging black.

Sedum laxum was traditionally divided into as many as six generally allopatric subspecies. We recognized *S. laxum* subsp. *eastwoodiae,* and *S. laxum* subsp. *flavidum,* both tetraploid and with more obtuse petals, at the species level; see discussions under those taxa. We recognized as subspecies the diploids *S. laxum* subsp. *heckneri* with suborbicular, usually reflexed stem leaves, and *S. laxum* subsp. *laxum,* with stem leaves longer than wide, ascending, and sometimes thickened. Ranges of the two subspecies were discrete, with subsp. *heckneri* found east and south of subsp. *laxum*.

6a. *Sedum laxum* (Britton in Britton & Rose 1903: 29) Berger (1930: 451) **subsp. *heckneri*** (Peck 1937: 121) Clausen (1942: 39). Figs. 4A, 6D, 30

Sedum heckneri Peck (1937: 121). *Sedum laxum* (Britton) A.Berger var. *heckneri* (M.Peck) Ohba (2007: 889).

Type:—UNITED STATES. California: Siskiyou Co., [published in error in the protolog as Jackson Co., Oregon, see Clausen (1975: 391)], dry cliff along [Middle Fork] Applegate River, 4 miles above mouth of Carberry Creek, 26 June 1931, *M. E. Peck 16421* (holotype, WILLU).

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Del Norte County:** NW of Cedar Camp Spring, 1220 m, 8 June 1983, *Imper s.n.* (WTU); Six Rivers National Forest, S of Flint Valley, 1340 m, 27 July 1982, *Imper s.n.* (WTU); Six Rivers National Forest, N of Bluff Creek, 823 m, 30 July 1982, *Imper s.n.* (WTU). **Humboldt County:** S of Grizzly Camp, 1370 m, 5 September 1948, *Tracy 18190* (SD, UC, WTU); Klamath River, 305 m, June 1901, *Chandler 1439* (UC); S of Somes Bar, 21 June 1954, *Hitchcock 20219* (WS); Willow Creek Canyon, 305 m, 3 July 1944, *Tracy 17488* (UC); near Aikens Campground, 170 m, 25 June 1976, *Denton 3976* (WTU); SW of Hoopa, 260 m, 25 June 1976, *Denton 3974* (WTU); N of Hoopa, 240 m, 25 June 1976, *Denton 3975* (WTU); Salmon Summit, 1770 m, 30 July 1935, *Tracy 14363* (UC, WTU); Hoopa, 425 m, 4 July 2012, *Wilson, Otting & Darington CWG-119* (OSC, "SRNF," WTU); E of Weitchpec, 137 m, 29 June 2013, *Wilson et al. CWG-236* (HSC); road to E-Ne-Nuk Campground, 122 m, 29 June 2013, *Wilson et al. CWG-237* (JEPS). **Siskiyou County:** E of Forks of Salmon, 26 June 1937, *Eastwood & Howell 5056* (CAS); N Fork Salmon River, 675 m, 19 June 2014, *Wilson 18109 & Otting* (OSC); Whites Gulch, 770 m, 19 June 2014, *Wilson 18108 & Otting* (OSC); N of Clear Creek, 22 May 1961, *Hutchison 2036* (JEPS); near Upper Devils Peak, 1342 m, 7 August 1979, *Clifton 12757* (UC); SW of mouth of Carberry Creek, 700 m, 4 July 1976, *Denton 4014* (OSC, WTU); Middle Fork of Applegate River, 760 m, 5 August 1962, *Hutchison 958* (BH, SD); same site, 670 m, 4 July 1976, *Denton 4016* (WTU); same site, 670 m, 11 July 1991, *Kagan 7-11-91-01* (OSC); same site, 19 July 2011, *Zika 25641* (CAS, RSA); Slater Butte, 1067 m, 4 June 1947, *Detling 6120* (ORE); Salmon Mountains, N of Hancock Lake, 2105 m, 11 July 1969, *Oettinger 988* (RSA); Middle Fork of Applegate River, Whiskey Creek trail, 915 m, *Rolle s.n.* (OSC); Siskiyou Mountains, NW of Abney Butte, 675 m, 19 July 2011, *Zika 25640* (BH, HSC, SD, UCR); Antenna Ridge, 1305 m, 12 July 2014, *Otting 3841* (HSC, SOC, UBC, WTU). **OREGON. Jackson County:** Whiskey Peak, 1931, *Nye s.n.* (ORE); Upper China Gulch, May 1984, *Rolle s.n.* (OSC); Carberry Creek, Steve Fork, 790 m, 12 June 1991, *Zika 11199* (BH, OSC); Siskiyou Mountains, SE of Steve Peak, 830 m, 19 July 2011, *Zika 25653* (BH, CAS, OSC, RSA, UCR, WTU); E of Steve Peak, 780 m, 19 July 2011, *Zika 25652* (CAS, GH, MICH, RM, RSA, UC, WTU). **Josephine County:** above China Flat, 1095 m, August 1962, *Hutchison 956* (BH, JEPS); Slickrock Creek, 900 m, August 1962, *Hutchison 955* (JEPS); Wingdam Gulch, 1 August 1980, *Garcia 185* (OSC); Whiskey Peak, July 1932, *Nye 5* (ORE).

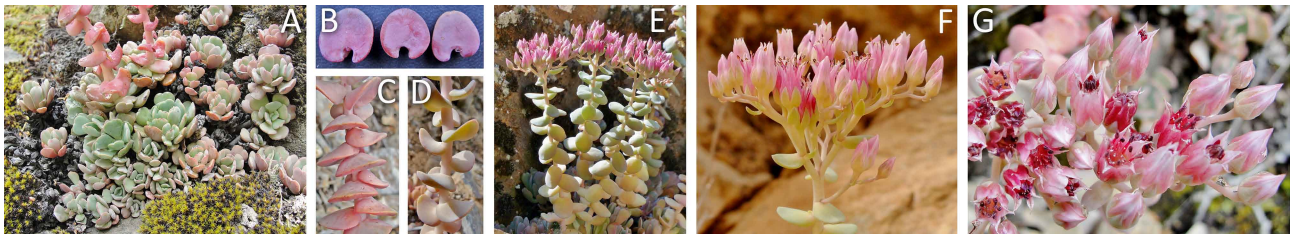

FIGURE 30. *Sedum laxum* subsp. *heckneri*. A. Dense rosettes, Siskiyou Co., California (*Zika 25640*). B–D. Stem leaves, clasping at base, nearly as long as wide, spreading, ascending, or descending. B, D. Jackson Co., Oregon (*Zika 25652*). C. Siskiyou Co. (*Wilson 18109 & Otting*). E. Habit, in flower. F. Flat-topped inflorescence, pink flowers. E–F. Siskiyou Co. (*Wilson 18108 & Otting*). G. Pink erect acuminate petals, dark red anthers, acuminate sepals; Siskiyou Co. (*Zika 25640*).

Distribution and ecology:—*Sedum laxum* subsp. *heckneri* (Fig. 27) ranged from Jackson County, Oregon, to Humboldt County, California, at lower elevations, in the Klamath Ranges ecoregion, and the northern edge of the Outer North Coast Ranges in California (Jepson eFlora 2017). Most populations were on rocky slopes, rubble, and cliffs, at elevations of 190–2104 m. Some colonies were on slopes with seasonal subsurface water flow. It was also found on roadcuts, which other *Sedum* section *Gormania* infrequently colonized. Some populations disappeared in recent years.

The chromosome voucher *Goodspeed s.n.* (BH 81412) cited by Clausen (1942), and in Table 3, had the morphology

and cytology of *Sedum laxum* subsp. *heckneri*, not *S. eastwoodiae*. The herbarium label location ("Mendocino Co.") appeared to be an error (see Results).

Notes:—*Sedum laxum* subsp. *heckneri* (Fig. 30) had blue-green or pinkish foliage. The stem leaves were usually suborbicular (rarely oblong), usually reflexed or spreading, with clasping, auriculate bases. The sides of the stem leaves were often planar, but were often oriented slightly downward, giving the whole leaf a saddle-like shape. A few plants in the Applegate River drainage rarely had oblong, somewhat reflexed stem leaves. The sepals were relatively short and often acuminate. The petals were acuminate and pink with white margins, and erect or nearly so at anthesis. The fresh anthers were red to dark red, senescing black.

The chromosome counts, flowers and inflorescences of *Sedum laxum* subsp. *heckneri* were identical to those of subsp. *laxum*. *S. laxum* subsp. *heckneri* was distinguished by reflexed, suborbicular, auriculate stem leaves. Stem leaves of subsp. *laxum* were elliptic to oblong, ascending to spreading, and truncate-based, not auriculate, though sometimes decurrent. The two subspecies of *S. laxum* were allopatric (Fig. 27).

Sedum laxum subsp. *heckneri* had acuminate slender erect petals 7–13 mm, and the stems were often elongate, (9)13–29 cm tall. In these characters it differed from *S. eastwoodiae*, which had relatively broader, more acute and ascending petals 4–9 mm, and stems 4–13 cm tall. The two were allopatric (Fig. 27) and had different ploidy levels (Table 3), though they shared similar-shaped stem leaves and pink flowers (Table 6). In addition to the differences emphasized in the key, the inflorescences of subsp. *heckneri,* in all but depauperate plants, were much larger than the inflorescences of *S. eastwoodiae*.

6b. Sedum laxum (Britton in Britton & Rose 1903: 29) Berger (1930: 451) **subsp. laxum**. Figs. 1B, 5B, 7, 8C, 10A–D, 14C–D, 15C, 16A–B, 31.

Sedum laxum (Britton) A.Berger subsp. *latifolium* Clausen (1942: 38). *Sedum laxum* (Britton) A.Berger var. *latifolium* (R.T.Clausen) Ohba (2007: 890).

Type:—UNITED STATES. California: Del Norte County, rocky slope along Smith River, 24 miles NE of Crescent City, 457 m, 24 July 1940, *R. T. Clausen 4941 & H. Trapido* (holotype, BH; isotypes, BH, NY).

Sedum laxum (Britton) A.Berger subsp. *perplexum* Clausen (1942: 36).

Type:—UNITED STATES. Oregon: [Curry County], cliff near [2 miles above] mouth of Rogue River, 8 July 1919, *M. E. Peck 8703* (holotype, BH; isotype, WILLU).

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Del Norte County:** Gasquet to Patricks, 27 June - 1 July 1922, *Abrams 8515* (POM), *Abrams 8516* (DS, WTU); Patrick Creek, 2 July 1936, *Eastwood & Howell 3646* (CAS); 10 miles NE of Crescent City, 12 July 1923, *Peirson 3958* (RSA); cultivated in greenhouse, source: Smith River 24 miles NE of Crescent City, 24 June 1944, *Clausen C4941* (WTU); 18 Mile Creek, 152 m, 5 July 1963, *Howe s.n.* (SD); Smith River at Stoney Creek, 107 m, 23 May 1972, *Wallace 1081 & DeBuhr* (RSA); Hiouchi Flat, 15 June 1951, *Moran 3486* (BH); E of Hiouchi, 80 m, 10 June 2012, *Brainerd & Otting CWG-104* (OSC, UCR); same site, 23 June 2012, *Zika 25927* (OSC, UCR, WTU); above Gasquet, 15 June 1951, *Moran 3487* (BH, CAS, UC); SW of Gasquet, *Denton 4002* (OSC, WTU); between Patricks Creek and Gasquet, 180 m, 22 June 2014, *Wilson 18122 & Otting* (OSC); Gasquet, 100 m, 24 June 2012, *Zika 25936* (NY, US); S of Idlewild, 17 June 1951, *Dress 3394* (BH); same site, 24 May 1961, *Hutchison 2081* (BH); Idlewild, 375 m, 10 June 2012, *Brainerd & Otting CWG-107* (DAV, HSC, KANU, RSA, STNF); between Crescent City and Oregon line, 29 June 1941, *Winblad s.n.* (CAS); Sanger Peak Road, 1615 m, 27 July 1949, *Whittaker SS264-S* (WS); Middle Fork Smith River, 365 m, 29 June 1976, *Denton 4001* (NY, OSC, WTU); ENE of Crescent City, 76 m, 24 April 1977, *Denton 4074* (WTU); SE of Cave Junction, 1135 m, 28 June 1976, *Denton 3991* (WTU); below Myrtle Creek, 60 m, 16 June 1937, *Wolf 8856* (RSA); same site, 10 July 1961, *Uhl 956* [= *Hutchison 2082*] (BH, JEPS); Oregon Mountain, 960 m, 15 June 1951, *Moran 3488* (UC); Gordon Mountain, 1250 m, 22 June 2014, *Wilson 18124 & Otting* (OSC). **Siskiyou County:** Siskiyou Mountains, WSW of Cyclone Gap, larvae of *Callophrys mossii*, Moss' elfin, Lepidoptera: Lycaenidae, feeding on flowers, 1615 m, 16 July 1974, *Emmel 512* (RSA). **OREGON. Curry County:** Snow Camp Forest Lookout, July 1951, *Vollmer & Beane 174* (DS); same site, 1 July 1976, *Denton 4006* (WTU); Vulcan Peak, 1106 m, 3 July 1973, *Denton 3021* (WTU); same site, 30 June 1976, *Denton 4003* (WTU); W of Vulcan Peak, 1160 m, 15 June 1975, *Denton 3691* (WTU); Pyramid Rock, 1220 m, 22 June 1936, *Thompson 12855* (BH, CAS, RSA, WILLU, WS, WTU); same site, 1 July 1976; *Denton 4005* (OSC, WTU); Hunter Creek Road, 565 m, 1 July 1976, *Denton 4004* (WTU); Gold Beach, 25 m, 1 July 2013, *Wilson & Otting CWG-240* (OSC, WTU). **Douglas County:** Beatty Creek Research Natural Area, 625 m, 28 May 1987, *Zika 10382* (OSC). **Josephine County:** Waldo, 7 July 1887, *T. Howell s.n.* (PH internet image); same site, 19 June 1932,

Applegate 7290 (DS); S of Waldo, 610 m, 1 August 1940, *Clausen 5018 & Trapido* (BH [3 sheets], DS); cultivated from same site, 25 July 1942, *Clausen C5018* (BH); near Waldo, 10 July 1961, Hutchison 2074 [= Uhl 952] (BH); Waldo Road, 590 m, 27 June 1976, *Denton 3982* (OSC, WTU); same site, 24 April 1977, *Denton 4076* (WTU); S of O'Brien, toll road to Gasquet, California, 10 July 1961, *Hutchison 2076* [= *Uhl 953*] (BH, DS); W of Selma, 505 m, 2 July 1976, *Denton 4010* (WTU); same site, 25 April 1977, *Denton 4081* (WTU); Rogue River above Galice, 230 m, 31 July 1940, *Clausen 5015 & Trapido* (BH [3 sheets]); same site, 23 May 1961, *Hutchison 2063* [= *Uhl 946*] (BH, SD); same site, 28 May 1963, *Clausen 63148* (BH); same site, 8 June 1963, *Clausen 63149* (BH); S of Galice, 325 m, 2 July 1976, *Denton 4008* (OSC, WTU); same site, 21 April 1977, *Denton 4057* (WTU); Wimer Road, 455 m, 5 July 1949, *Whittaker SS105-S* (WS); Eight Dollar Mountain, 17 June 1932, *Applegate s.n.* (DS); SW of Eight Dollar Mountain, 515 m, 9 June 2013, *Zika 26209* (GH, NY, OSC, WTU); ENE of Fiddler Mountain, 800 m, 20 July 2011, *Zika 25655* (CAS, F, GH, KANU, UCR, US, WTU); SSE of Cave Junction, 615 m, 27 June 1976, *Denton 3986* (WTU); en route to Babyfoot Lake, 600 m, 28 June 1976, *Denton 3993* (WTU); E edge of Kalmiopsis Wilderness, 1340 m, 30 July 1977, *Denton 4125* (WTU); SE of Serpentine Mountain Lookout, 1050 m, 2 July 1976, *Denton 4009* (WTU); N of Tennessee Mountain, 460 m, 2 July 2011, *Zika 25487* (CAS, WTU); same site, 20 July 2011, *Zika 25654* (HSC, KNFY, MO, OSC, UC); NNE of Buckhorn Mountain, 255 m, 3 June 2017, *Zika 28801* (WTU).

Distribution and ecology:—Inland mountains, river canyons, and coastal bluffs in Josephine and Curry counties, south to Del Norte and Siskiyou counties, California, usually on serpentine substrates in the Klamath Ranges (Jepson eFlora 2017). Habitats included rocky slopes, ridges, knolls, talus, and ledges, usually in full sun and on dry thin soils, at elevations of 45–1646 m. Populations of *Sedum laxum* subsp. *laxum* were found north and west of subsp. *heckneri* (Fig. 27).

Notes:—*Sedum laxum* subsp. *laxum* (Fig. 31) had stem leaves longer than wide, ascending, not clasping, thick or thin, decurrent or not, crowded or not. Rosette and stem leaves were flat or distinctly thickened, and varied in color from green and waxless to blue-green and thinly glaucous, or pink. The sepals were relatively short and often acuminate, but varied to acute. The petal tips were narrow, acuminate, erect or nearly so, and pink with white margins, rarely entirely white. The fresh anthers were dark red, rarely red orange, senescing black or white.

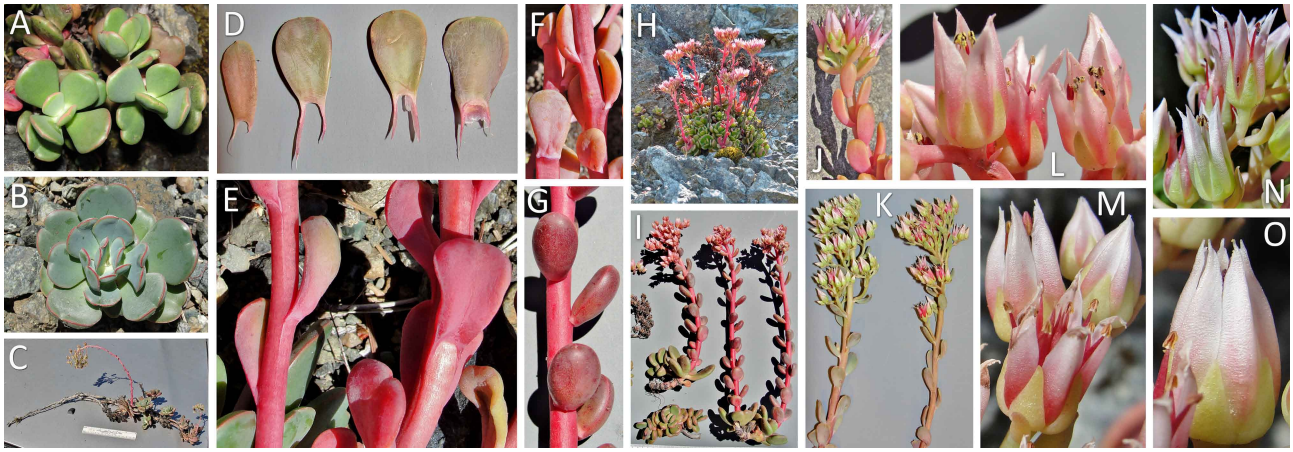

FIGURE 31. *Sedum laxum* subsp. *laxum*. A–C. Dense rosettes on sterile shoots. A. Relatively plump rosette leaves, green to faintly glaucous, corresponding to the type of *S. laxum* subsp. *latifolium*, Del Norte Co., California (*Zika 25927*). B–C. Relatively thin rosette leaves, moderately glaucous and blue-green, Josephine Co., Oregon (*Zika 25655*). C. Rhizomes and stolons to 40 cm, bearing rosettes. Scale 15 cm. D–G. Stem leaf variation. D–E. Typical stem leaves, longer than wide, thin, base decurrent. D. Gray stem leaves, Josephine Co. (*Zika 26209*). E. Red stem leaves, Josephine Co. (*Zika 25655*). F. Transitional stem leaves, thin, slightly decurrent at base, Del Norte Co. (*Brainerd & Otting CWG-107*). G. Plump stem leaves, truncated at base, corresponding to the type of *S. laxum* subsp. *latifolium,* Del Norte Co. (*Zika 25927*). H–K. Inflorescence variation. H–I. Flat-topped inflorescences. H. Low coastal plants, corresponding to the type of *S. laxum* subsp. *perplexum*; Curry Co., Oregon (*Wilson & Otting CWG-240*). I. Tall inland plants; Del Norte Co. (*Zika 25927*). J. Capitate inflorescence (*Brainerd & Otting CWG-107*). K. Cylindrical inflorescence, Josephine Co. (*Zika 26209*). L–O. Pink flowers, darkened with age, red anthers, erect petals with acuminate tips, elongate acuminate sepals; Del Norte Co. L. Dark pink flowers (*Zika 25927*). M–O. Pale pink flowers. M, O. Subapical mucro prominent and extended past the petal apex (*Zika 25936*). N. Narrow sepals (*Brainerd & Otting CWG-107*).

Plants treated here as *Sedum laxum* subsp. *laxum* were further subdivided into thick-leaved *S. laxum* subsp. *latifolium* of the Smith River drainage in northwest California, thin-leaved *S. laxum* subsp. *laxum* of inland mountains, and small *S. laxum* subsp. *perplexum* with crowded, slightly thickened stem leaves, at the coast (Fig. 27). These minor expressions were not worth separating, with many intermediate plants not easily placed.

Sedum laxum subsp. *latifolium* was submerged into *S. laxum* subsp. *laxum* by Denton (1979a, 1979b, 1982, 1993; Boyd & Denton 2012). Ohba (2007) resurrected the concept of subsp. *latifolium* (as var. *latifolium*). Following Clausen (1975: 394), Ohba (2009), commented that subsp. *latifolium* (as var. *latifolium*) was the "most robust" infraspecific taxon within *S. laxum*. Well-developed plants of *S. laxum* subsp. *latifolium* were robust compared to most members of *Sedum* section *Gormania*, but were not unusually large compared to *S. laxum* subsp. *laxum* and subsp. *heckneri*. We measured stem heights up to 48 cm for subsp. *laxum* from Josephine County, Oregon (*Zika 28801*), more robust than the maximum reported height of 40 cm for subsp. *latifolium* (as var. *latifolium*) provided by Ohba (2009). At their extremes, the strongly glaucous and somewhat flattened rosette leaves of *S. laxum* subsp. *laxum,* when fresh (Fig. 31B), were different from the green, nearly waxless, and plump fresh rosette leaves of subsp. *latifolium* (Figs. 1B, 31A), in the Smith River basin. However, we found both flat and plump rosette leaves on plants at the subsp. *latifolium* type locality in 2013. Similarly, plants of subsp. *laxum* from low elevation (255 m) along the Rogue River showed some green rosette leaves that were plump and as much as 5.5 mm thick, while other rosette leaves were relatively thin and more glaucous (*Zika 28801*). In the Smith River basin, subsp. *latifolium* stem leaf bases were usually truncate. However, a few were decurrent, such as *Wallace 1081 & DeBuhr* (RSA), and thus transitional to the concept of subsp. *laxum*. As we defined it, subsp. *laxum* populations most commonly had decurrent leaf bases outside the Smith River basin. But there were exceptions, and some plants or populations had stem leaf bases that were not decurrent, though usually decurrent leaves could be observed on other leaves or stems of the same plant, or on nearby plants. Again, the low elevation plants on the Rogue River (*Zika 28801*) were instructive, showing a mix. Decurrent or truncate stem leaf bases were present on different plants, as well as a number of intermediate forms.

Sedum laxum subsp. *perplexum* lived near the mouth of the Rogue River and south, close to the Oregon coast. The plants were small and erect, unlike typical plants of either *S. laxum* subsp. *latifolium* or *S. laxum* subsp. *laxum*. Their stem leaves were overlapping and usually not decurrent. The rosette and stem leaves were green and somewhat thickened, though not quite so plump as was typical of *S. laxum* subsp. *latifolium*. Short coastal plants were a morphological extreme, easily distinguished from robust inland *S. laxum* subsp. *laxum,* but size appeared to vary continually over the Siskiyou Mountains.

Although some populations within the *Sedum laxum* subsp. *laxum* complex were easily distinguished, many were intermediate between the named forms. Treating them all as a single taxon was appropriate.

7. *Sedum marmorense* Otting & R. E. Brainerd, *sp. nov*. Figs. 32 G–L, 33

Species Sedum oblanceolatum proxima sed differt foliis basalibus rosulatis obovatis, a Sedum oregonensis rosulis densissimis et inflorescentiis granularibus ceraceisque.

Type:—UNITED STATES. California: Siskiyou Co., Klamath Mountains, Marble Mountain Wilderness Area, Upper Wright Lake, 2295 m, 12 July 2013, *R. E. Brainerd 2180 & N. Otting* (holotype, OSC; isotypes, GH, NY, RSA, UC, WTU).

Rhizomes and stolons 1–6.5 cm long, 1.2–3.5 mm in diameter. Rosettes not numerous, 17–36 mm diameter, densely arranged, generally without visible internodes in exposed situations. Rosette leaves green or glaucous, but not granular waxy, often with red margins, aging red then orange, strongly flattened dorsiventrally, obovate, oblanceolate, or lanceolate, 6–24 × 3–11 mm, length to width ratio 1.3–2.8; base cuneate; tip retuse to rounded. Stem leaves ascending to slightly spreading, slightly to strongly glaucous, but not granular waxy, green, pink, or red; ovate, obovate, oblong, or occasionally lanceolate, 7–10 × 2–6 mm, length to width ratio 1.3–3.6, flattened, base truncate; tip acute to rounded or shallowly retuse. Fertile stems green, pink, or red, 4.4–15 cm, nodding in bud, erect in flower and fruit. Inflorescences (0.5–)1.4–6.0 × (0.5–)1.8–4.5 cm, length to width ratio 0.7–1.8, often globose to subglobose, occasionally more elongated, usually densely flowered, paniculate cymes. Proximal branches 3–7, ascending, (0.3–)1–2.8 cm, solitary at nodes; all branches with granular waxy flakes early in season. Inflorescence bracts resembling stem leaves but smaller, 4–9 × 1–3 mm, length to width ratio 2–4; bases truncate, tips (acute to) obtuse or rounded. Flowers 6–42 per inflorescence. Calyx green, with granular waxy flakes early in season, 3.5–5.2 × 2.7–4.3 mm; 32–69% as long as perianth; sepals fused basally for 0.5–1.5 mm, lobes 2.4–4.7 mm, acute, less often obtuse, the very tip rounded. Petals 5, 5.3–7.5 mm, 1.4–2.8 mm wide at midlength, fused at base for 0.9–2.5 mm, ascending at an angle of 5–20° from the floral axis at anthesis, white, cream, or light yellow, aging pale yellow or pink; midvein green, cream, or pale yellow,

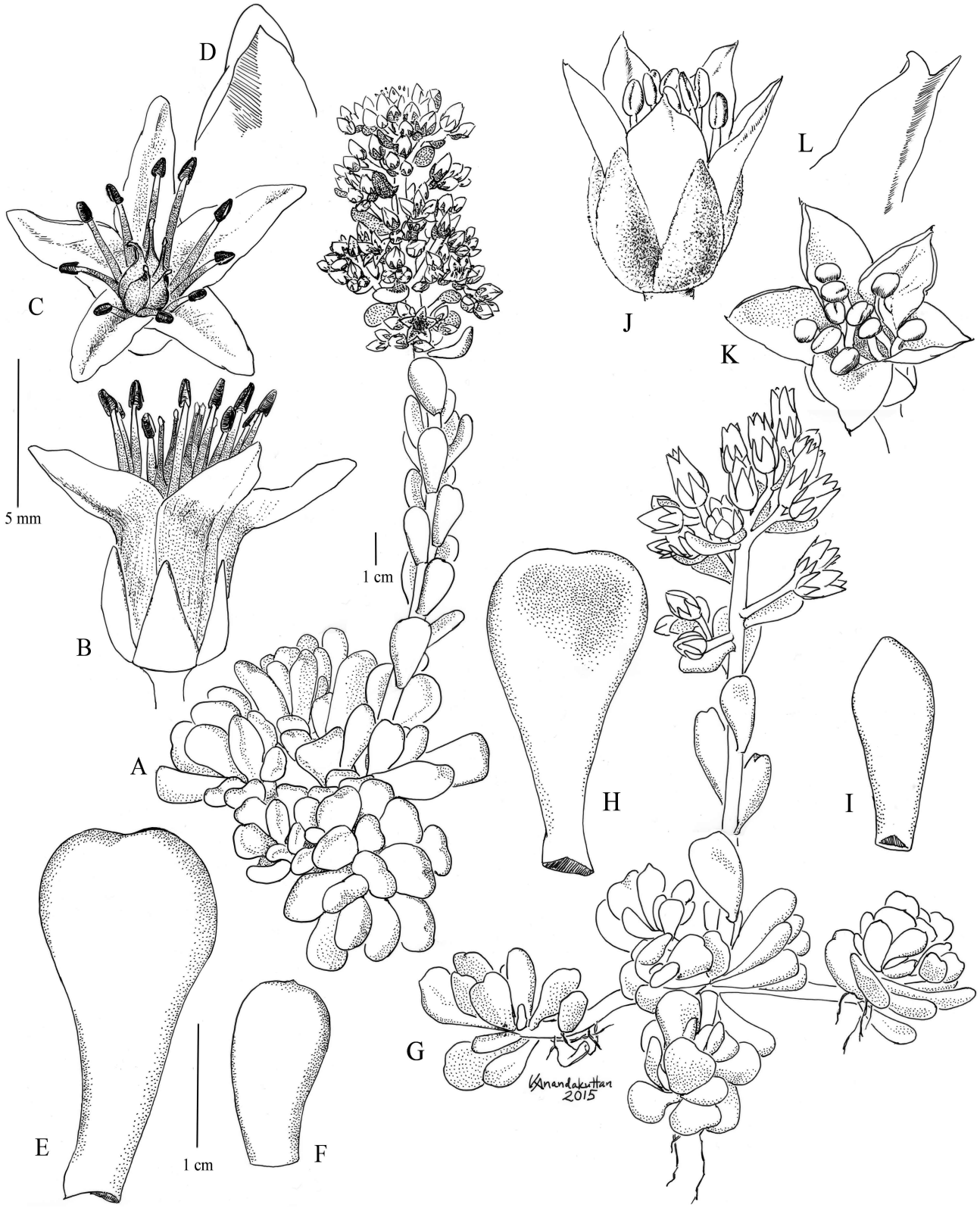

FIGURE 32. A–F. *Sedum rubiginosum*. A. Habit, showing dense rosettes, overlapping stem leaves, and cylindrical densely-flowered inflorescence. B. Flower, side view, showing spreading petals. C. Flower, top view, showing gradual taper to narrow petal tips. A–D. *Zika 25522 & J.K. Nelson*. E. Rosette leaf. F. Stem leaf. E–F. *Zika 26234.* **G–L. *Sedum marmorense***. G. Habit, showing stolons and dense rosettes. H. Rosette leaf. I. Stem leaf. G–I, K–L. (*Brainerd 2180 & Otting*). J. Flower, side view, showing granular wax on sepals and ascending petals (*Otting 3837*). K. Flower, top view, showing acute broad petal tips. L. Petal apex, showing projecting subapical mucro on right, and hooded petal tip on left.

often aging pink; apiculate, the mucro 0.1–0.3 mm. Stamens 10, shorter than the petals; filaments cream or yellow, often almost transparent, aging red; anthers 0.8–1 × 0.3–0.6 mm (when dried), yellow, aging red-orange or reddish-brown, papillose at 20×. Nectaries shallowly crescent-shaped, sunken in middle, yellow, 0.5–0.7 mm, 0.1 mm high. Ovaries 3.8–8.5 mm, erect, fused for 0.7–1.5 mm, maturing into 5 dark red-brown, erect follicles. Follicles 6.6–7.2 mm, with erect to slightly curved style remnant forming a narrow beak approximately 2 mm; bases fused for 0.8–1.5 mm. Seeds 12–31 per follicle, brown, narrowly elliptic, shiny, longitudinally striate, 0.7–1 × 0.15–0.3 mm (including stipe), stipe 0.05–0.1 mm.

Paratypes:—UNITED STATES. **CALIFORNIA. Siskiyou County:** Marble Mountains, 8 August 1939, *Howell 15141* (CAS, POM); Marble Mountains, NE of Red Mountain, 2345 m, 12 July 2013, *Brainerd 2185 & Otting* (OSC); Tom Martin Peak, 2023 m, 11 July 2014, *Otting 3837* (CAS, MO); Lake Mountain, 2080 m, 6 July 2014 m, *Otting 3831 & Brainerd* (OSC); Lake Mountain, 2034 m, 6 July 2014, *Otting 3832 & Brainerd* (CAS, JEPS, WTU).

FIGURE 33. *Sedum marmorense*. A–D. Habitat, Siskiyou Co., California. A, D. *Brainerd 2180 & Otting*. B: *Otting 3832 & Brainerd*. C: *Brainerd 2185 & Otting*. E. Two fertile shoots, yellow flowered. F. Two fertile shoots, erect and just about to flower, white flower buds. G. Dense rosettes, new growth slightly glaucous and whitened, but not granular waxy. H. Oblanceolate stem leaves on left, rosette leaves on right. I. Sheltered sterile shoot with loosely arranged leaves. J. Young nodding inflorescences, flower color not yet apparent. K. Obovate stem leaves, bases truncate. L. Flower buds, granular white wax on sepals, white-flowered form. M. Flowers, side view, ascending white petals, sepals not showing granular white wax, slightly more weathered than L. N. Flower, side view, ascending pale yellow petals, granular white wax on sepals of flower buds. O. Flower, top view, ascending pale yellow petals, granular white wax on sepals. E–O. *Brainerd 2180 & Otting*.

Distribution and ecology:—Endemic to a narrow zone 19 km long in the Marble Mountains, in the Klamath Ranges of Siskiyou Co., California (Fig. 22). We uncovered three extant populations, at elevations of 2023–2345 m, on broad flat stony crests to moderate slopes. Aspects varied from south to west to north. Flowering was observed in July, but this was following winters with very low snow cover. The sites were dry sunny cracks and crevices on rocky ridgelines, in low ledges or massive outcrops, as well as in soil pockets on a talus slope among boulders. The underlying bedrock was metasedimentary, metavolcanic, and ultramafic, according to geologists on the Klamath National Forest (Juan de la Fuente and Derek Beal, pers. comm.). Some common associates included: *Achillea*

millefolium L., *Arctostaphylos* sp., *Calamagrostis* sp., *Eriogonum umbellatum* Torr., *Festuca roemeri* (Pavlick) E.B. Alexeev, *Heuchera* sp., *Holodiscus discolor* (Pursh) Maxim., *Lomatium macrocarpum* (Hook. & Arn.) J.M. Coult. & Rose, *Myriopteris gracillima* (D.C. Eaton) J. Sm., *Penstemon deustus* Douglas ex Lindl., *Polystichum* sp., and *Pseudoroegneria spicata* (Pursh) Á. Löve.

Etymology:—*Sedum marmorense*, or Marble Mountains stonecrop, was named for the Marble Mountains and for the marble substrate on which it sometimes grows.

Notes:—*Sedum marmorense* (Fig. 32G–L) resembled *S. oregonense*, but the former has waxy granules on the calyces and inflorescence branches, and was a more delicate plant with looser rosettes. *Sedum marmorense* differed from *S. albomarginatum* and *S. oblanceolatum* in its relatively wide rosette and stem leaves (Fig. 33E–F), and in the relative difference in leaf shape and size between the rosettes and stems (Fig. 33H). *Sedum oblanceolatum* and *S. albomarginatum* had oblanceolate foliage that was quite similar on the stems and the rosettes (e.g., Fig. 21B). As with some farinose species of North American primrose (*Primula* Linnaeus 1753: 142), the waxy particles can melt away from specimens dried with heat, complicating identification.

8. ***Sedum moranii*** Clausen (1942: 40). Figs. 10E, 34

Cotyledon glandulifera Henderson (1930: 26). *Sedum glanduliferum* (L.F.Hend.) Peck (1941: 134). *Gormania glandulifera* (L.F.Hend.) Abrams (1944: 343).

Type:—UNITED STATES. Oregon: Josephine Co., along the trail, 3 miles below Almeda, Rogue River, 1 June 1928, *L. Leach 1599* (holotype, ORE; isotypes, ORE [2 sheets]).

Not: *Sedum glanduliferum* Gussone (1827: 519).

Additional specimens examined:—UNITED STATES. **OREGON. Josephine County:** Rogue River near Grave Creek, 275 m, 1 July 1976, *Denton 4007* (OSC, WTU); same site, 21 April 1977, *Denton 4054* (WTU); same site, 15 May 1977, *Fosback & Fosback s.n.* (OSC); same site, 16 June 1933, *Leach 4334* (ORE); same site, 23 May 1961, *Hutchison 2067* (BH, SD); same site, 23 May 1961, *Hutchison 2068* (BH, SD); same site, 23 May 1961, *Uhl 948* (SD); same site, 28 May 1963, *Clausen 63141* (BH); same site, 18 July 2011, *Zika 25631* (CAS, WTU); same site, 200 m, 1 July 2013, *Wilson & Otting CWG-241* (UC).

Distribution and ecology:—A narrow endemic and rare along the lower Rogue River at elevations of 200–300 m, in Josephine County, Oregon, on serpentine cliffs and outcrops (Fig. 22), in the Siskiyous ecoregion (Meyers *et al*. 2015). Extant populations were recorded from 2 km of the river corridor, making this the smallest known range of any member of the section. This was the only member of *Sedum* section *Gormania* endemic to Oregon.

Notes:—*Sedum moranii* (Fig. 34) rosette leaves were thin-edged and often erose-margined at 10× magnification. Stem leaves were oblong. The inflorescence was strongly glandular and clearly cymose, with 3 main branches. The petals were elongate, yellow, narrow distally, with acuminate erect tips. Glandular *S. moranii* was unique in section *Gormania* and easily identified. With its restricted range, atypical morphology, and diploid chromosome level, it may be relictual.

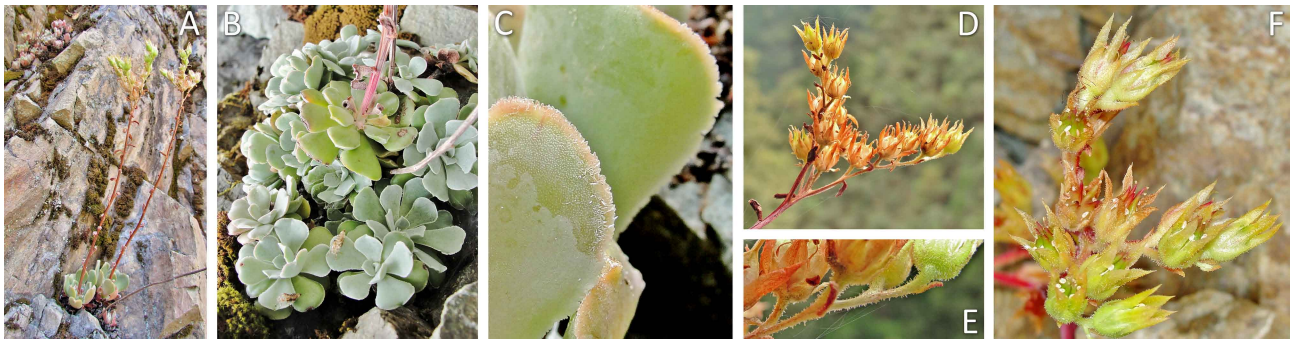

FIGURE 34. *Sedum moranii*, Josephine Co., Oregon. A. Habit (*Wilson & Otting CWG-241*). B–C. Dense sterile rosettes, blue-green leaves, slightly glaucous, with irregularly eroded margins. D–F. Dichotomous inflorescence, branches and sepals with prominent glands, petals yellow, erect, narrow and acuminate, anthers yellow, faded white. B–F. *Zika 25631*.

9. *Sedum oblanceolatum* Clausen (1975: 404). Figs. 1C, 9C, 35

Type:—UNITED STATES. Oregon: Jackson Co., road 0.8 km below Deadmans Point, ridge NW of Dutchman Peak, 1580 m, 8 July 1965, *R. T. Clausen 651034* (holotype, BH; isotypes, BH, US).

The type sheets bear a second collection, of fruiting material, that are not part of the type material. The fruiting stems were gathered at the type locality on 7 August 1965, and were numbered *Clausen 651034,* as were the flowering shoots of the type.

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Siskiyou County:** Applegate River drainage, N of Cook and Green Pass, 1370 m, 24 May 1987, *Denton 4335* (WTU); same site, 11 June 1991, *Zika & Mumblo 11198* (OSC); same site, 19 July 2011, *Zika 25650A* (CAS, HSC, RSA, UCR); Elliott Creek Road, 975 m, *Rolle s.n.* (OSC). **OREGON. Jackson County:** Tallowbox Lookout spur, 1310 m, 19 July 2012, *Joachims & Busby OR110-475* (OSC); near Dutchman Peak, 1525 m, 13 July 1950, *Whittaker 201* (BH, WS); same site, 28 July 1977, *Denton 4110* (OSC, WTU); W of Little Red Mountain, 1500 m, 3 June 1992, *Zika 11612* (OSC); near Kinney Mountain, 1220 m, 15 June 1984, *Rolle* (OSC); NW of Dutchman Peak, 1582 m, 3 July 1965, *Clausen 651013* (BH), *Clausen 651016* (BH); same site, 18 July 2011, *Zika 25636 & Lang* (GH, KNFY, UC, WTU); same site, 3 July 2014, *Otting 3813* (CAS, MO).

Distribution and ecology:—Limited to southern Jackson County, Oregon, in the Siskiyous ecoregion (Meyers *et al*. 2015), and the adjacent portion of Siskiyou County, California (Fig. 22), in the Klamath Ranges ecoregion (Jepson eFlora 2017). Its habitat was sunny xeric rock outcrops and, less commonly, thin-soiled rocky slopes, occasionally in partial or full shade of open forest canopy, at elevations of 975–1740 m. Substrates were diverse, including diorite, granite, phyllite-schist, schist, metavolcanics, metasedimentary rocks, as well as ultramafics such as serpentine, soapstone, and peridotite.

Notes:—*Sedum oblanceolatum* (Fig. 35) had oblanceolate rosette and stem leaves. The young leaves and inflorescences had a white granular and irregular waxy coating; the wax wore off with age. The inflorescence branches and sepals were also strongly glaucous, in addition to the granular wax, at least when young. The sepals were acute; the petals were white and relatively broad distally, acute, and ascending at anthesis. Fresh anthers were yellow. Similar *S. albomarginatum* differed in the color of its flowers (Fig. 21), a coarser habit, separate follicles in fruit, and its allopatric range (Fig. 22).

Hybrids:—Rare putative hybrids (*Zika 25647B, 25650B*), morphologically intermediate between two common putative parents at the site (*Sedum oblanceolatum, Zika 25650A; S. oregonense, Zika 25647A*), were recorded at Copper Butte, Siskiyou Co., California (Fig. 5C, Table 4).

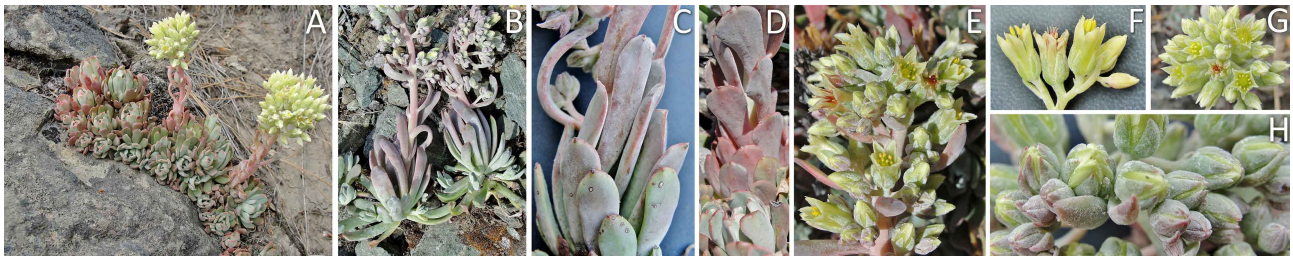

FIGURE 35. *Sedum oblanceolatum*. A. Habit, dense rosettes, type locality, Jackson Co., Oregon (*Zika 25636 & Lang*). B–C. Rosette leaves and stem leaves similar, oblanceolate, Siskiyou Co., California (*Zika 25650A*). D. Stem leaves of a putative hybrid in a mixed population of *S. oblanceolatum* and *S. oregonense*, Siskiyou Co. (*Zika 25649*). Stem leaves are ascending and overlapping, as in *S. oblanceolatum,* but relatively broad, as in *S. oregonense* at the site. E. *S. oblanceolatum,* dense inflorescence, varying from capitate to cylindrical. F–H. Flowers and buds, showing ascending white petals with acute tips, yellow anthers, and granular-waxy young sepals. F, H. *Zika 25650A*. G. *Zika 25636 & Lang*.

10. *Sedum obtusatum* Gray (1868: 342). Figs. 5D, 13B, 36

Gormania obtusata (A.Gray) Britton in Britton & Rose (1903: 29). *Cotyledon obtusata* (A.Gray) Fedde in Schumann & Fedde (1904: 827). *Echeveria obtusata* (A.Gray) Nelson & Macbride (1913: 476).

Type:—UNITED STATES. California. [Mariposa County], Mount Hoffmann, 3290 m, [24 June 1863], *W. H. Brewer 1678* (lectotype, designated by Clausen [1975: 371], GH; isolectotype, US).

Gormania burnhamii Britton in Britton & Rose (1903: 30, as "burnhami"). *Cotyledon burnhamii* (Britton) Fedde in Schumann & Fedde (1904: 827). *Sedum burnhamii* (Britton) Berger (1930: 451, as "burhamii").

Type:—UNITED STATES. California. Tuolumne County, from Lake Eleanor to Lake Vernon, along trail, 16 July 1894 [US sheet says 1884, in error], *S. H. Burnham s.n.* (lectotype, designated by Clausen [1942: 31], NY; isolectotypes, BH [2 sheets, one a fragment], POM, US [fragment]).

Gormania hallii Britton in Britton & Rose (1903: 29). *Cotyledon yosemitensis* Fedde in Schumann & Fedde (1904: 828). *Echeveria brittonii* Nelson & Macbride (1913: 476). *Sedum hallii* (Britton) Praeger (1921: 241). *Sedum obtusatum* A.Gray var. *hallii* (Britton) Smiley (1921: 213).

Type:—UNITED STATES. California: [Tuolumne Co.], Yosemite National Park, vicinity of Tuolumne Meadows, 2590–2895 m, July 1902, *H. M. Hall & E. B. Babcock 3545* (lectotype, designated by Clausen [1942: 31], NY; isolectotypes, DS, F, GH, MO, POM, RM internet image, UC, US [2 sheets, one a fragment]).

Sedum rubroglaucum Praeger (1919: 51).

Type:—UNITED STATES. California: [Mariposa Co.], Yosemite National Park, Four Mile Trail [formerly known as Short Trail] to Glacier Point, cracks in granite, ca. 7000 feet, 4 July 1940, *R. V. Moran 539* (neotype, designated by Zika [2015: 4], YM; isoneotype, UCSB). Illustrated as fig. 125 (Praeger 1921: 219).

Asa Gray (1868) listed three specimens when he described *Sedum obtusatum*, all mounted on one sheet at GH, and all syntypes. Two specimens were *Bolander 4960* and *Brewer 1920*, cited below. Clausen (1975: 371) typified the name by choosing the third specimen as the lectotype, *Brewer 1678* (GH), a gathering from Mount Hoffmann, which is a peak listed in modern references as 10771 feet (3283 m) in elevation, in Yosemite National Park. The specimen label says only: "Mount Hoffmann, 10800 feet [3292 m], Geological Survey of California, 1860–62, *W. H. Brewer 1678*" (GH42519). Amy Kasameyer (pers. comm., UC) found that Brewer had these additional notations in his collecting book for *1678*: "coll. 24 June 1863, Mount Hoffmann, the leaves of this seen abundant on the higher granite rocks, but flowers scarce, dull yellow."

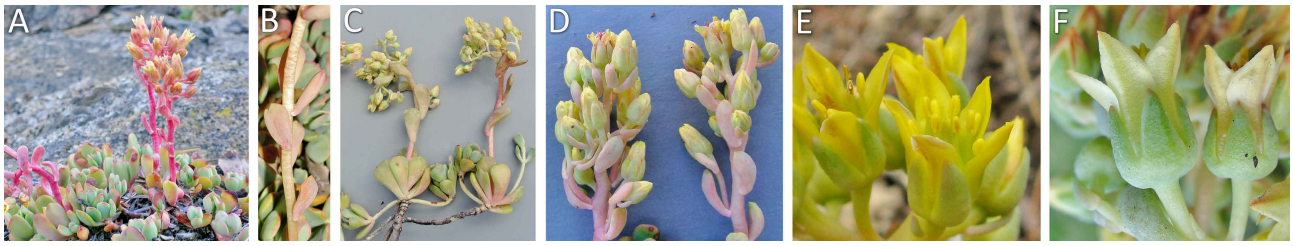

FIGURE 36. *Sedum obtusatum*. A. Habit, showing numerous dense rosettes, Nevada Co., California (*Wilson & Otting CWG-110*). B. Stem leaves, longer than wide, truncated bases, Sierra Co., California (*Zika 26267*). C. Young inflorescence axes bent, pre-anthesis, Nevada Co. (*Zika 26271*). D. Inflorescences cylindrical to capitate or flat-topped (*Wilson & Otting CWG-110*). E–F. Flowers. E. Typical bright yellow flowers, yellow anthers, elongated sepals, Mono Co., California (*Janeway 11160*). F. Pallid flowers, ascending petals with acute tips (*Zika 26271*).

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Alpine County:** East Blue Lake, 2470 m, 15 August 1933, *Wolf 5311* (CAS, DS, RSA [3 sheets]); Blue Lakes, 1 July 1961, *Hutchison 2141* (BH, SD); NE of Hermit Valley, 2225 m, 13 July 1956, *Everett & Balls 22145* (RSA, WS). **El Dorado County:** Angora Peak, 2530 m, 14 July 1913, *Smiley 40* (GH); Emerald Bay, Lake Tahoe, 4 June 1934, *Maguire, Maguire & Maguire 15168* (BH); above E shore Echo Lake, 2134 m, 25 July 1943, *Robbins 1320* (RSA); above Glen Alpine, 22 July 1950, *Moran 3449* (BH). **Fresno County:** Margaret Lakes area, 8 August 1954, *Quibell 4203* (OSC, RSA, WS); above Huntington Lake, 2316 m, 10 August 1963, *Howe s.n.* (SD); Wren Peak, 2865 m, 1 July 1990, *Shevock 11918 et al.* (CAS, RSA); Monarch Divide, SSW of Mount Harrington, 3000 m, 2 July 1990, *Ross 3042* (CAS, RSA). **Madera County:** Shuteye Mountain, 2470 m, 19 July 1914, *Smiley 569* (GH); canyonside below Shadow Lake, ca. 2500 m, 10 July 1977, *Moran 24301* (SD); Shadow Lake Trail 1 mile from Agnew Meadow, 2469 m, 18 July 1962, *Reveal & Reveal 429* (RSA, WTU). **Mariposa County:** Vernal Falls, on granite rocks, 14 July 1866, *H.N. Bolander 4960* (GH, K internet image, UC, US, YU internet image) (syntype); Yosemite National Park, SE slope of Mount Hoffmann, 2745 m, 7 July 1940, *Clausen 4823 & Trapido* (BH [2 sheets]); Yosemite National Park, above Nevada Falls, 1525 m, 4 July 1940, *Clausen 4801 & Trapido* (BH [2 sheets]); Yosemite National Park, top of Half Dome, 25 June 1942, *Roos 1748* (UCR); between Vernal and Nevada Falls, 1590 m, 24 June 1964, *Clausen 641018* (BH); same site, 1604 m,

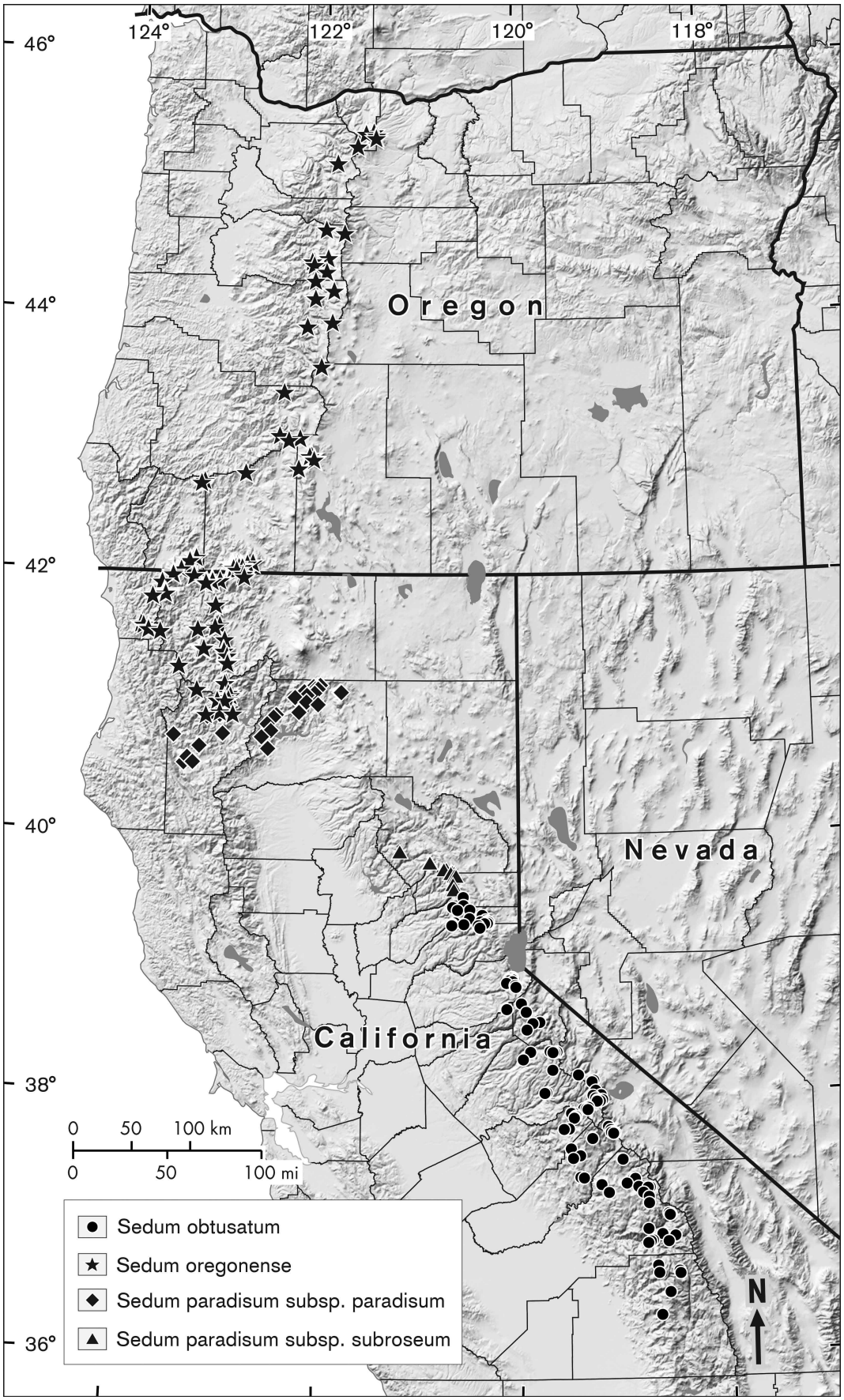

FIGURE 37. Distribution of *Sedum obtusatum, S. oregonense, S. paradisum* subsp. *paradisum, S. paradisum* subsp. *subroseum*, based on verified herbarium specimens.

24 June 1964, *Clausen 641019* (BH), *Clausen 641010* (BH); Yosemite National Park, NE of Wawona, 1970 m, 12 July 1964, *Clausen 641061* (BH), *Clausen 641060* (BH); W of Lake Tenaya, 2545 m, 16 June 2013, *Van Susteren JVS-13-5* (CHSC, TO). **Mono County:** Barney Lake, 2530 m, 21 July 1940, *Munz 16142* (RSA, WTU); E of Sonora Pass, 2590 m, 23 July 1932, *Pierson 10408* (RSA); E of Bennetville Mine Tunnel, 2990 m, 7 September 1967, *Chafin 23* (OSC, SD, WTU); Sonora Pass, E slopes 2605 m, 16 June 1976, *Denton 3921* (OSC, WTU); E of Tioga Pass, 2600 m, 17 June 1976, *Denton 3923* (OSC, WTU); near Tioga Pass, 2940 m, 17 June 1976, *Denton 3930* (OSC, WTU); trail on Green Creek, 2535 m, 25 June 2013, *Janeway 11160* (CAS, DAV, HSC, KANU). **Nevada County:** Yuba Pass, 1753 m, 28 May 1961, *Uhl 960* (BH); between Lake Spaulding and Highway 20, 1615 m, 15 July 1978, *Howe s.n.* (SD); above Donner Lake, toward Donner Pass, 7 August 1903, *Heller 7105* (BM, E *n.v.*, GH, K internet image; LE *n.v.*, PH *n.v.*, POM); N of Donner Pass, 2035 m, 29 June 2012, *Wilson & Otting CWG-110* (MO, US); road to Bowman Lake, 1640 m, 30 June 2012, *Wilson & Otting CWG-111* (NY, RENO, UBC, WTU); Discovery Trail, 1425 m, 30 June 2012, *Wilson & Otting CWG-112* (JEPS); SW of Summit Lake, 2210 m, 28 June 2013, *Zika 26271* (DAV, WTU). **Nevada/Placer County border:** Donner Pass, 2165 m, 15 June 1976, *Denton 3917* (OSC, WTU). **Placer County:** Donner Pass, 2165 m, 28 May 1961, *Uhl 961* (BH); Donner Lake, 1875 m, 15 June 1976, *Denton 3909* (WTU); Palisade Lake, 2105 m, 15 June 1976, *Denton 3919* (WTU). **Sierra County:** E of Keystone Mountain, 1890 m, 1 July 1994, *Ahart 7437* (JEPS); Jackson Meadows Reservoir, 1850 m, 28 June 2013, *Zika 26267* (OSC, WTU). **Tulare County:** Monarch Lakes Trail, 2590 m, 19 July 1951, *J.T. Howell 27978* (RSA); E slope Moses Mountain, 2700 m, 23 July 1982, *Shevock 9950* (RSA). **Tuolumne County:** peak near Sonora Pass, dry exposed rocks near summit, 12000 feet, 17 July 1863, *W.H. Brewer 1920* (GH, UC) (syntype); summit of hill south of Camp 127, 21 July 1863, *W.H. Brewer* (US internet image, YU internet image); Sonora Pass, 1980 m, 18 July 1938, *Wiggins 8945* (GH, RSA,WTU); same site, 2438 m, 3 July 1961, *Hutchison 2154* (BH, SD); same site, 1828 m, 2 July 1961, *Hutchison 2152* (BH); Yosemite National Park, Lambert Dome, 2621 m, 8 July 1940, *Clausen 4824 & Trapido* (BH [2 sheets]); same site, 2835 m, 8 July 1940, *Clausen 4832 & Trapido* (BH [2 sheets]), *Clausen 4832a & Trapido* (BH); Emigrant Lake, 2680 m, 12 August 1942, *Wiggins 10126* (WTU); W of Sonora Pass, 2925 m, 17 June 1966, *Wallace 623* (RSA); WSW of Sonora Pass, 12 August 2012, *Brainerd 2073 & Zika* (F); Yosemite National Park, W of Vernon Lake, 2040 m, 6 July 1940, *Clausen 4810 & Trapido* (BH [3 sheets]); Tuolumne Meadows, 2665 m, 17 June 1976, *Denton 3933* (WTU); Tioga Pass, 2240 m, 17 June 1976, *Denton 3937* (OSC, WTU). **NEVADA. Mineral County:** Aurora, 2285 m, 10 July 1929, *Wright s.n.* (SBBG); [county not specified], near Carson City, 1864, *Anderson 271* (GH fragment).

Distribution and ecology:—Distributed for 400 km in the northern, central, and southern high Sierra Nevada ecoregions (Jepson eFlora 2017), south of the Middle Yuba River in Sierra County, south to Tulare County, California, at elevations of 1450–3550 m (Fig. 37). Recent searches in central western Nevada failed to relocate the species (A. Tiehm, pers. com.)

Notes:—*Sedum obtusatum* (Fig. 36) had obovate, obtuse to retuse rosette leaves and elliptic to oblong or narrowly obovate stem leaves. The sepals were acute and relatively long, varying from (40–)50–75(–80)% as long as the petals. The petals were bright yellow to pale yellow, acute, relatively broad distally, and ascending at anthesis. The fresh anthers were yellow, aging brown or white.

Sedum obtusatum was most similar to *S. paradisum* subsp. *subroseum*, and the easiest way to separate them, besides geographic range, was the color of the flowers, which were always pale to deep yellow in *S. obtusatum,* and white fading to pink in *S. paradisum* subsp. *subroseum*. The latter was restricted to slopes north of the Middle Yuba River; *S. obtusatum* to the south of Middle Yuba River (Fig. 37). In the Sierra Nevada mountains south of Lake Tahoe, *S. obtusatum* was the only representative of section *Gormania*. The stem leaves were more uniformly elongate in *S. paradisum* than they were in *S. obtusatum*, which generally shows longer proximal stem leaves, and some reduction in the length of distal stem leaves. In addition, there was a tendency for the flowers of *S. paradisum* to be straight-sided in side view, below the spreading of the petals; *S. obtusatum* flowers often showed a slight constriction between the sepal apex and spreading petal tips, so that in side-view the flower was somewhat hourglass-shaped.

11. ***Sedum oregonense*** (Watson 1882: 373) Peck (1941: 361). Figs. 2D, 5E–F, 6E–G, 9B, 13C, 38

Cotyledon oregonensis Watson (1882: 373). *Gormania watsonii* Britton in Britton & Rose (1903: 29). *Echeveria watsonii* (Britton) Nelson & Macbride (1913: 476). *Sedum watsonii* (Britton) Tidestrom in Dayton (1927: 119, as "watsoni").

Type:—UNITED STATES. Oregon: [likely Hood River Co., on the E side of Barlow Pass in the White River drainage], northern Oregon, Cascade Mountains near Mount Hood, White River Hill, Barlow Pass, July 1880, *J. Howell & T. J. Howell s.n.* (lectotype, designated

by Clausen [1942: 35], GH; isolectotypes, DS, G ex herb. de Candolle internet image, LE internet image, ORE, US internet image, YU 69005 internet image).

The protolog said the type was collected in June 1880, but the type specimens were all labeled July 1880. The detailed locality data came from the duplicate at ORE, which was labeled in Thomas J. Howell's hand as an isotype. Several of the isotypes listed his brother Joseph Howell as a co-collector.

Additional specimens examined: CALIFORNIA. Del Norte County: Sanger Peak road, 1646 m, 1 July 1972, *Howe s.n.* (SD); E of Sanger Peak, 1585 m, 27 June 1976, *Denton 3987* (OSC, WTU); Bear Basin Butte, 1605 m, 5 July 2012, *Otting CWG-122* (JEPS, WTU); SE of Chimney Rock, 1400 m, 19 July 1950, *Tracy 19202* (UC); WSW of Sawtooth Mountain, 1300 m, 9 June 2013, *Zika 26205* (OSC, WTU); near Peak Eight, 1425 m, 24 June 2012, *Zika 25928* (HSC, JEPS, RSA); NW of Peak Eight, 1270 m, 10 June 2014, *Zika 26621 & Brainerd* (OSC, WTU). **Del Norte/Siskiyou county border:** Poker Flat, 26 June 1937, *Leach 4713* (ORE). **Siskiyou County:** Salmon Mountains, above Taylor Lake, 2165 m, 21 August 1939, *Carter 1467* (DS); Salmon-Trinity Alps Primitive Area, Caribou Lake, 2040 m, 27 July 1955, *Wiggins 13521* (DS, WS); Devils Punchbowl, 1525 m, 31 August 1963, *Wheeler 8322* (RSA); Red Buttes Wilderness, SW of Buck Peak, 1675 m, 11 August 2011, *Brainerd 1916* (OSC); Bolan Lake Road, 1455 m, 1 July 2012, *Roché CR-1* (OSC); Salmon Mountains, English Peak, 1768 m, 4 August 1969, *Thorne 63383 & Oettinger* (RSA); Salmon Mountains, Etna Pass, 1860 m, 11 July 2013, *Brainerd & Otting CWG-242* (CAS, CHSC, DAV); same site, 19 June 2014, *B.L. Wilson 18106* (WTU); Salmon Mountains, Russian Wilderness, S of Little Duck Lake, 2235 m, 8 July 2013, *Brainerd & Otting CWG-247* (MO, RENO, WTU); same site, 2210 m, 8 July 2013, *Brainerd & Otting CWG-248* (BH, MICH, OSC); E of Little Duck Lake, 2040 m, 8 July 2013, *Brainerd & Otting CWG-250* (F, GH, UBC); Siskiyou Mountains, Sterling Mountain, Soda Creek, 1770 m, 3 July 1934, *Wheeler 2847* (RSA); Copper Mountain, 1720 m, 27 June1976, *Denton 3990* (WTU); Siskiyou Mountains, WNW of Copper Butte, 1610 m, 19 July 2011, *Zika 25647A* (CAS, F, JEPS, RSA, UCR, WTU); Cook and Green Pass, 1735 m, 11 June 1991, *Zika 11197* (OSC); S of Cook and Green Pass, 1225 m, 13 July 2013, *Brainerd & Otting CWG-251* (OSC); E of Cook and Green Pass, 1400 m, 13 July 2013, *Brainerd & Otting CWG-252* (WTU); road to Big Meadow trailhead, 1915 m, 12 July 2013, *Brainerd 2190 & Otting* (OSC); Red Rock Mountain, 2185 m, 2 September 1974, *Mastrogiuseppe & Mastroguiseppe 172* (OSC); Siskiyou Wilderness, above Raspberry Lake, 1745 m, 28 August 2012, *Roché & Korfhage CR-2* (SOC); Siskiyou Wilderness, Preston Peak ridge, 2020 m, 28 August 2012, *Roché & Korfhage CR-3* (DAV). **Trinity County:** Trinity Alps, Salmon-Trinity Primitive Area, Sapphire Lake, 2286 m, 10 August 1954, *Kruckeberg 3737* (WS, WTU); N of Dedrick, 1340 m, 24 June 1976, *Denton 3961* (WTU); trail to Canyon Creek Lakes, 1340 m, 24 June 1976, *Denton 3967* (HSC, OSC, WTU); same trail, 1606 m, 24 June 1976, *Denton 3968* (WTU); Trinity Alps, N of Grizzly Lake, larvae of *Callophrys mossii* feeding on flowers, 1980 m, 26 July 1993, *Emmel 1279* (RSA). **OREGON. Clackamas County:** Mazama Lodge, 21 July 1927, *Leach 1281* (ORE); High Rock, 1475 m, 11 July 2012, *Zika 25964* (F, GH, HSC, KANU, MO). **Curry County:** en route to Babyfoot Lake Botanical Area, 1315 m, 29 June 1976, *Denton 4000* (WTU). **Deschutes County:** 21 miles SW of Bend, 2 September 1976, *Crosby 1036* (OSC); Deschutes National Forest, Sisters Road, 7 August 1931, *Henderson 13992* (ORE); Soda Creek, 15 July 1947, *Ireland 2659* (ORE). **Deschutes or Lane County:** W of North Sister, August 1957, *Van Vechter 151* (OSC). **Douglas County:** Cascade Range, Willamette National Forest, Rigdon Point proposed Research Natural Area, 1 August 1991, *Brainerd & Newhouse s.n.* (OSC); Huckleberry Mountain, 22 August 1978, *Christy 2388* (ORE); Bald Ridge, 22 July 1975, *Crosby 263* (OSC); Gooseberry Burn, Twin Lakes Trail, 10 July 1941, *Detling 4966* (ORE); Umpqua National Forest, S of Black Rock, 29 September 1993, *Fosback & Fosback 713* (OSC); Calapooya Range, E of Loletta Lakes, 1630 m, 12 August 2010, *Halse 8054* (RSA); Umpqua National Forest, 1920, *Ingram 1410* (OSC); Abbott Butte, 6 July 1899, *Leiberg 4261* (ORE); Black Rock Lookout, 23 July 1944, *Overlander s.n.* (OSC); Rogue-Umpqua Divide Wilderness, above Rocky Ridge Trail, 1835 m, 9 August 2012, *Roché & Korfhage RRR* (SOC). **Douglas or Jackson County:** Crater Lake Road, 12 August 1896, *Leiberg 2937* (ORE); near Abbott Butte, 21 June 1972, *Mitchell 67* (OSC). **Hood River County:** Mount Hood region, head of Bluegrass Ridge, 31 July 1927, *Thompson 3323* (DS, WILLU); same site, *Thompson* 3322 (WTU); same site, 6 August 1927, *English Jr. 864* (BH); Mount Hood National Forest, near Bottle Prairie, 21 July 1933, *Jones 4193* (POM, WTU [2 sheets]). **Jackson County:** Siskiyou Mountains, Pilot Rock, 18 June 1928, *Applegate 5520* (DS); Ragsdale Butte, 1370 m, 29 June 1939, *Hitchcock 5015 & Martin* (BH, GH, RSA, WS, WTU [2 sheets]); Mount Ashland, 19 July 1913, *Peck s.n.* (WILLU); same site, 28 July 1935, *Thompson 12365* (CAS, WILLU, WTU); same site, 5 July 1957, *Dennis 578* (OSC); same site, 10 June 1976, *Denton 3842* (WTU); same site, 4 July 1976, *Denton 4030* (WTU); W of Mount Ashland, 2010 m, 22 August 1976, *Denton 4049* (WTU); Observation Gap, 2135 m, 29 June 1977, *Denton 4101* (WTU); Big Red Mountain, 2040 m, 15 July 1950, *Whittaker SS-391* (WS); Rogue River National Forest, Grayback Mountain, 1745 m, 3 July 1976, *Denton 4011* (OSC, WTU); Deadmans Point,

1980 m, 28 July 1977, *Denton 4109* (WTU); W of Deadmans [Point], 1900 m, 4 July 1976, *Denton 4025* (HSC, OSC, WTU); Dutchman Peak, 2165 m, 28 July 1977, *Denton 4108* (WTU); E of Dutchman Peak, 1995 m, 22 August 1976, *Denton 4048* (OSC, WTU); same site, 28 July 1977, *Denton 4104* (WTU); N of Prospect, 21 June 1925, *Pendleton s.n.* (OSC); Cascade Mountains, July 1927, *Sherwood s.n.* (WILLU); WNW of Dutchman Peak, 1820 m, 30 July 2011, *Zika 25666 & Wilson* (CAS, DAV, HSC, KNFY, NY, OSC, SOC, WTU). **Jefferson County:** Brush Creek and Cabot Creek Canyons, 5 August 1959, *Swedberg 168* (OSC). **Jefferson or Linn County:** Mount Jefferson, Echo Lake, 19 July 1907, *Gorman 2783* (OSC). **Jefferson or Marion County:** divide west of Whitewater Creek, 20 August 1920, *Gorman 5097* (ORE). **Josephine County:** Siskiyou National Forest, near Babyfoot Lake Botanical Area, 1345 m, 29 June 1976, *Denton 3994* (OSC, WTU); WSW of King Mountain, 950 m, 20 July 2011, *Zika 25657* (NY, UC, WS, WTU); Klamath Mountains, King Mountain, 1500 m, 13 July 2013, *Brainerd & Otting CWG-243* (HSC, KANU, WTU); E of Tannen Lake, 29 July 1976, *Crosby 826* (OSC); near Bolan Lake, 20 July 1945, *Peck 23874* (WILLU); Bolan Mountain, 30 July 1976, *Crosby 837* (OSC); same site, 26 June 1976, *Denton 3977* (OSC, WTU); same site, 26 June 1976, *Denton 3979* (OSC, WTU); Bolan Lake, 1640 m, 26 June 1973, *Denton 2754* (WTU); Mount Elijah, 24 June 1949, *Detling 6494* (ORE); same site, 10 July 1949, *Whittaker SS-144* (WS); Lake Mountain Trail, 20 July 1950, *Detling 6722* (ORE); Grayback Mountain, 13 July 1930, *Henderson 12830 et al.* (ORE); near Wilderville, 26 May 1923, *Savage s.n.* (ORE). **Klamath County:** Crater Lake [National Park], 22 August 1896, *Gorman s.n.* (ORE); same site, 25 August 1902, *Cusick 2974* (ORE); same site, 30 August 1916, *Peck 4664* (OSC); same site, 30 August 1916, *Heller 12608* (BH, OSC); Crater Lake [National Park], Cathedral Cliff, 19 August 1896, *Gorman s.n.* (ORE, WILLU); Crater Lake [National Park], Vitae Falls, 1830 m, 21 July 1935, *Thompson 12248* (CAS, POM, WILLU, WTU); same site, 2010 m, 30 July 1943, *Clausen 4996 & Trapido* (BH [3 sheets]); same site, 2073 m, *Hutchison 948* (SD); [Crater Lake National Park], Garfield Peak, 11 August 1919, *Sweetser s.n.* (ORE); same site, 19 July 1935, *Applegate 9847* (WILLU); same site, 2285 m, 30 July 1940, *Clausen 5006 & Trapido* (BH [2 sheets]); same site, 5 July 1976, *Denton 4031* (WTU); Lakeview Mountain, 20 August 1926, *Anderson 318* (OSC); Union Creek, 21 June 1928, *Sipe s.n.* (OSC); Cowhorn, 27 July 1948, *Menefee 10* (OSC). **Lane County:** Linton Creek, 19 July 1926, *Anderson 316* (OSC); South Sister Peak, 26 June 1934, *Andrews s.n.* (ORE); Bohemia Mountain, 24 June 1924, *Constance s.n.* (ORE); same site, 17 September 1946, *Baker 3290* (OSC); Fairview Mountain, 28 September 1947, *Baker 5139* (OSC); O'Leary Mountain, 27 July 1938, *Detling 3417* (ORE); same site, 12 July 1965, *Clausen 651050* (BH); same site, 16 July 1965, *Clausen 651060* (BH, GH), *Clausen 651068* (BH); E of Deer Butte, 1192 m, 24 July 1965, *Clausen 651078* (BH), *Clausen 651080* (BH); same site, 12 August 1965, *Clausen 651172* (OSC); Moolak Mountain, 1 August 1941, *Detling 5084* (ORE); Tenas Lake, 23 July 1942, *Detling 5394* (ORE); Rebel Peak, 6 July 1951, *Detling 7008* (ORE); Bohemia Camp, 1 August 1936, *Gilkey & Powell s.n.* (OSC); Horsepasture Trail, 19 July 1936, *Henderson s.n.* (ORE); Willamette National Forest, Olallie Trail, 27 July 1938, *Ireland 1252* (ORE); NW of Benson Lake, 11 September 1948, *Ireland 2858* (ORE); Fairview Mountain, 27 May 1934, *King s.n.* (ORE); Horsepasture Mountain, 1 July 1914, *Peck 4666* (WILLU); N of Mink Lake, 1580 m, 22 July 1965, *Clausen 651073* (BH), *Clausen 651076* (BH); SE of French Mountain, 1390 m, 19 June 2016, *Zika 27948* (GH, OSC). **Linn County:** Willamette National Forest, N of junction Highway 126 and Belknap Springs Road, 6 July 1976, *Denton 4032* (OSC, WTU); E of junction Highways 126 and 20, 1145 m, 6 July 1976, *Denton 4034* (WTU); Carpenter Mountain, 23 July 1941, *Detling 5061* (ORE); Clear Lake, 29 June 1943, *Gilkey & Smith s.n.* (OSC); Cascade Range, Willamette National Forest, Bruno Meadows, 17 July 1998, *Halse 5432* (BH, OSC, RSA); road to Clear Lake, 24 July 1953, *Hitchcock 20077* (OSC); Deer Butte Trail, 1 July 1942, *Hopson s.n.* (OSC); Iron Mountain, 28 August 1960, *Mason 532* (OSC); same site, 1465 m, 2 August 1975, *Denton 3704* (WTU); same site, 6 July 1976, *Denton 4035* (WTU); S of Cone Peak, 1440 m, 6 July 2012, *Zika 25959* (RSA, UBC, WTU); Mount Jefferson, 14 August 1919, *Peck 9163* (WILLU); Nash Crater, 1949, *Roach s.n.* (OSC); W of junction of Routes 20 and 22, 10 May 1957, *Steward 7346* (OSC); Route 126, E of Route 20, 1100 m, 10 July 2012, *Zika 25962* (BH, CAS, DAV, JEPS). **Marion County:** Mount Jefferson, Jefferson Park, August 1933, *Leach 4436* (ORE); same site, 7 July 1927, *Evinger s.n.* (OSC); Santiam National Forest, head of Whitewater Creek, 10 September 1916, *Flory* (OSC); Mount Jefferson, Park Butte, 8 August 1933, *Leach 4437* (ORE); S of Breitenbush, 10 August 1935, *Peck 18779* (WILLU). **Wasco County:** Mount Hood National Forest, Bulo Point, 1435 m, 7 July 1976, *Denton 4041* (WTU).

Distribution and ecology:—*Sedum oregonense* grew in the Cascades and Siskiyous ecoregions of Oregon (Meyers *et al*. 2015), and the northern Klamath Ranges ecoregion of California (Jepson eFlora 2017). It was recorded from Mount Hood, Oregon, to northern Trinity County, California, a north-south distance of 500 km and the largest distribution of any member of *Sedum* section *Gormania* (Fig. 37). A common and wide-ranging species of ledges, stony ridgelines, and subalpine rocky meadows, it was capable of colonizing recent lava flows and roadcuts. *Sedum oregonense* was known from elevations of (760–)1067–2470 m in California. In Oregon the elevational range was

880–2300 m, where it occurred on the crest as well as the west slopes of the Cascade Range, within the Cascades ecoregion (Meyers *et al*. 2015). Bedrock substrates were varied, and according to herbarium labels included volcanics, granite, diorite, and schist. Unlike most taxa in section *Gormania*, *Sedum oregonense* did not seem limited by dispersal or recruitment difficulties over most of its range. For example, over time it successfully recolonized the Crater Lake area of the southern Oregon Cascades (Zika 2003) after the massive eruption of Mount Mazama 7700 years ago, estimated to have buried 13,000 square kilometers under 15 cm or more of ash and pumice (Williams 1942). Once established, *S. oregonense* often spreads vegetatively, and many populations were vigorous and large. In this way, ecologically, it was more like widespread western species such as *S. spathulifolium* and *S. oreganum*.

Notes:—*Sedum oregonense* (Fig. 38) was a variable taxon, in its cytology and morphology. Its characteristic habit was with numerous branching stolons, bearing loose rosettes with obovate, rounded to retuse leaves. The stem leaves were elliptic to oblong or obovate, and truncate at the base, or suborbicular and slightly clasping; some populations exhibited both forms of stem leaves. Inflorescence branches and the foliage were usually slightly glaucous. The inflorescences varied from flat-topped to capitate or cylindrical. The sepals were relatively short. The ascending acute petals were relatively broad distally, and usually white, but sometimes cream or pale yellow in the southern portion of the range. The corollas usually lacked pink or red color. The fresh anthers were yellow, generally becoming white or brown with age.

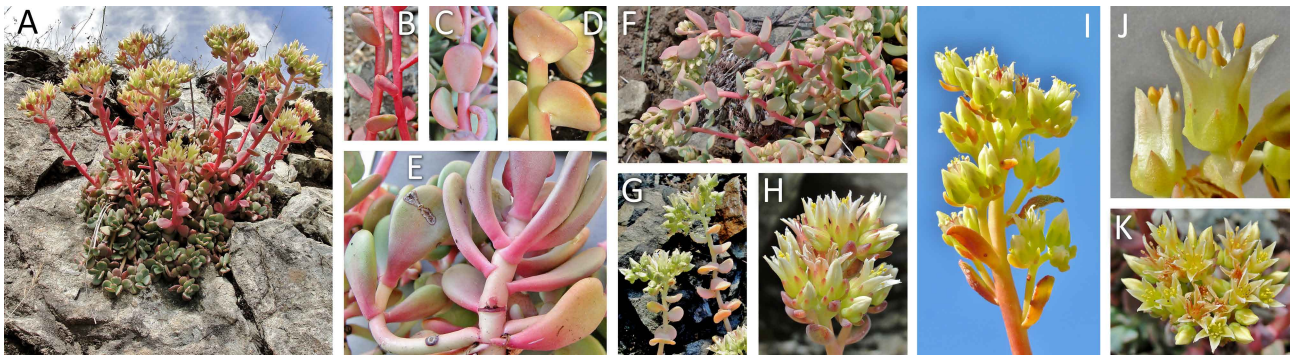

FIGURE 38. *Sedum oregonense*. A. Habit, with numerous branched sterile shoots, Josephine Co., Oregon (*Zika 25657*). B–D. Stem leaves, varied from much longer than wide to ± as long as wide, truncated or slightly clasping at base. Colors varied from red to pink, orange, purplish, green or gray. B. *Zika 25657*. C. Linn Co., Oregon (*Zika 25962*). D. Clackamas Co., Oregon (*Zika 25964*). E. Loose rosettes, with easily visible internodes between leaves of the sterile shoots, slightly glaucous, Del Norte Co., California (*Otting CWG-122*). F. Nodding or arching young inflorescences, pre-anthesis, Lane Co., Oregon (*Zika 27948*). G–I, K. Inflorescences, varied from flat-topped to capitate or cylindrical. J–K. Flowers, petals typically white, rarely pale yellow, petals ascending, anthers yellow, Josephine Co. G. Del Norte Co. (*Zika 25928*). H–I, K. Josephine Co. H, K. *Zika 25657*. I–J. *Brainerd & Otting CWG-243*.

Over most of the northern portion of its range *Sedum oregonense* was the only representative of *Sedum* section *Gormania.* The numerous loose rosettes, with easily observed internodes between the leaves, distinguished it from similar species in northern California, *S. flavidum* and *S. marmorense*.

Heteroploidy, different chromosome ploidy levels within a single taxon, was known within some *Sedum* species outside section *Gormania* (Uhl 1962), such as *S. lanceolatum, S. stenopetalum* Pursh (1814: 324), and *S. wrightii* A. Gray (1852: 76). Nonetheless, Denton (1982) divided most white-flowered *Sedum* by chromosome number into two taxa, tetraploid *S. obtusatum* subsp. *retusum,* sometimes with suborbicular stem leaves, and hexaploid *S. oregonense,* often with oblong stem leaves. Northwards in the Oregon Cascades, polyploids she considered *S. oregonense* had either suborbicular or oblong stem leaves (Denton 1982; this study). Denton studied populations along a 20 km transect between Mount Ashland and Dutchman Peak, in the Siskiyou Mountains of Jackson Co., Oregon. Her vouchers at WTU (Table 3) documented chromosome counts of $2n = 30$, 60, and 90 (Denton 1979b; Denton & Kerwin 1980). We revisited Denton's transect over four field seasons, and were unable to find consistent morphological characteristics to distinguish between the three chromosome races. Therefore, we treated all those populations as part of *S. oregonense* and considered the species a heteroploid. Denton and Kerwin (1980: 905) noted that the hexaploid and tetraploid populations were "morphologically most similar" though they placed them in different species. Even if it was considered appropriate to distinguish tetraploid and hexaploid *S. oregonense* taxonomically, the name *S. obtusatum* subsp. *retusum* was misapplied (see the nomenclatural notes for *S. sanhedrinum*).

In her monograph, Denton (1982) cited duplicates from Ragsdale Butte, Jackson Co. (*Hitchcock & Martin 5015*

WTU) as both *Sedum laxum* subsp. *laxum* and as *S. oregonense*. The specimens had the same habit and habitat, and did not differ in technical details of the foliage, stem leaves, or inflorescence, so we interpreted all replicates of that gathering as *S. oregonense*.

12. *Sedum paradisum* (Denton 1978: 236) Denton ex B. L. Wilson, *stat. nov*.

Sedum obtusatum Gray (1868: 342) subsp. *paradisum* Denton (1978: 236) (basionym). *Sedum obtusatum* A.Gray var. *paradisum* (Denton) Ohba (2007: 889).

Type:—UNITED STATES. California: Trinity County, Trinity National Forest, Salmon Trinity Alps Primitive Area, 4 miles N of trailhead on trail to Canyon Creek Lakes, or ca. 8 miles N of Dedrick, 1340 m, 17 June 1977, *M. F. Denton 4097* (holotype, WTU; isotype, NY).

Denton (1993: 534) inadvertently published *Sedum paradisum* at species rank as a nomen nudum; here we validate the name with reference to the basionym.

We treated *Sedum paradisum* as two geographic subspecies. Between their ranges lies Lassen Peak and a large area affected by its eruptions. Appropriate habitat for *Sedum* is limited in this area because most rock outcrops were recently exposed and excessively dry. We hypothesize that any *Sedum paradisum* once present in this area was killed by the eruptions of Lassen Peak in 1914, or in previous volcanic episodes dating back 27,000 years.

12a. *Sedum paradisum* (Denton 1978: 236) Denton ex B. L. Wilson subsp. ***paradisum***. Figs. 8D, 9D–E, 16C–D, 39.

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Shasta County:** Bollibokka Mountain, 1160 m, 15 June 2011, *Lindstrand III & Van Susteren LL-1* (OSC); South Fork Mountain, 975 m, 15 June 2011, *Lindstrand III & Van Susteren NSR-1* (HSC, JEPS, WTU); same site, 20 June 2011, *Lindstrand III LL-3* (HSC, OSC, UC, WTU); Bagley Mountain, 1320 m, 8 July 2011, *Lindstrand III & Van Susteren NSR-05* (BH, CAS, DAV, WS); Shoeinhorse Mountain, 1585 m, 8 July 2011, *Lindstrand III & Van Susteren NSR-06* (F, GH, HSC, WTU); Tombstone Mountain, 1495 m, 12 July 2011, *Lindstrand III & Van Susteren NSR-07* (KANU, MO, NY); Bald Mountain, 1370 m, 12 July 2011, *Lindstrand III & Van Susteren NSR-08* (CAS, JEPS, RENO, RSA, SOC, UBC, US, WS); W of Grizzly Peak, 1760 m, 14 July 2011, *Lindstrand III & Van Susteren NSR-09* (BH, F, GH, NY, US); ridgeline above headwaters of Fall Creek, 1220 m, 18 June 2012, *Lindstrand III & Van Susteren NSR-10* (DAV); above headwaters of Fall Creek, 1220 m, 18 June 2012, *Lindstrand III NSR-13* (WTU); Satin Peak, 1365 m, 6 July 2011, *Van Susteren & Youngblood NSR-03* (UBC, WTU); Beetle Butte, 1310 m, 7 July 2011, *Van Susteren & Youngblood NSR-04* (JEPS, US); Red Mountain, 1645 m, 6 July 2012, *Engstrom 1* (OSC); headwaters Little S Fork Dog Creek, 1035 m, 20 June 2012, *Lindstrand III NSR-11* (CAS, DAV, HSC, NY, RSA); Schell Mountain, 1340 m, 18 June 2012, *Lindstrand III NSR-16* (JEPS, UBC, US); SW of Sugarloaf Lookout, 1100 m, 5 July 2011, *Van Susteren NSR-02* (RENO, RSA, WTU); Hawkins Creek, 790 m, 17 June 2011, *Wilson et al. CWG-01* (BH, CAS, DAV, F, WTU); Deer Creek, 760 m, 17 June 2011, *Wilson et al. CWG-02* (GH, WTU); McCloud Reservoir dam, 815 m, 17 June 2011, *Wilson 16526 et al.* (NY); same site, 23 June 2012, *Zika 25924* (JEPS, WTU). **Trinity County:** Underwood Mountain Road, 1235 m, 7 June 2012, *Brainerd 2032 & Otting* (OSC, WTU); N of Dedrick, 1090 m, 17 June 1977, *Denton 4098* (WTU); Stuart Fork of Trinity River, 1980–2225 m, 25 July 1937, *J.T. Howell 13503* (GH); Butter Creek, 4 June 2012, *J.K. Nelson 12-1* (OSC); Canyon Creek Trail, 915 m, 1 July 1949, *Balls 13766* (RSA, WTU); same site, 29 June 2011, *Spooner et al. RS-28* (OSC, STNF, UC); same site, 23 June 2011, *Stubbs et al. RS-02*; same site, 23 June 2011, *Vollmann et al. RS-02* (GH, KNFY, OSC, STNF, WTU); Canyon Creek Wilderness, 1935 m, 4 July 2014, *Otting 3820* (NY, RSA, UBC); Hayfork Bally Lookout, 1780 m, 18 July 2011, *Vollmann & Stubbs RS-32* (OSC, WTU); Glennison Gap, 1150 m, 18 June 2011, *Wilson et al. CWG-03* (KANU); road to Hobo Gulch, 1175 m, 18 June 2011, *Wilson et al. CWG-04* (MO); NE of Friend Mountain, 1260 m, 22 June 2012, *Zika 25920 & J.K. Nelson* (CAS, HSC, OSC); SSE of Grassy Mountain, 1265 m, 22 June 2012, *Zika 25921 & J.K. Nelson* (RSA, WTU); Eagle Rock, 6 July 2011, *Stubbs RS-28b* (WTU); Trinity Alps Wilderness, 1720 m, 4 July 2014, *Otting 3816* (MO, "SRNF").

Distribution and ecology:—*Sedum paradisum* subsp. *paradisum* was endemic to Shasta and Trinity Counties, California, at elevations of (235–)1605–2005 m (Fig. 37). It favored rocky slopes, ridges, outcrops, and cliffs. The underlying bedrock was usually not serpentine. Its northern limit was within the redefined Klamath Ranges ecoregion (Baldwin *et al*. 2012, Lindstrand III *et al*. 2016, Jepson eFlora 2017). A single extant population (Red Mountain, *Engstrom s.n.*) was recorded from the Cascade Range Highlands ecoregion (Jepson eFlora 2017), near its border with

the Klamath Ranges ecoregion in Shasta Co., California, and may represent relatively recent colonization. This *Sedum* was considered rare (Nakamura & Nelson 2001), but in recent years was found on numerous rarely-visited peaks. It had a limited range and was uncommon, but not rare.

Notes:—*Sedum paradisum* subsp. *paradisum* (Fig. 39) had tight to moderately tight rosettes. The rosette leaves were often flat gray or lead-colored, sometimes with green or pinkish tones. Young fertile shoots typically remained erect and straight throughout development. The stem leaves were gray or pink to reddish, and were elliptic to oblong, relatively long, and did not significantly decrease in length near the inflorescence. The sepals were usually 50–80% as long as the petals. The petals were obtuse to acute and cream-colored to white or, especially in the western edge of the range, light yellow. They senesced to a pale dull orange or faint pink. The fresh anthers were yellow to light orange or pale red, aging to white, brown, or dark red.

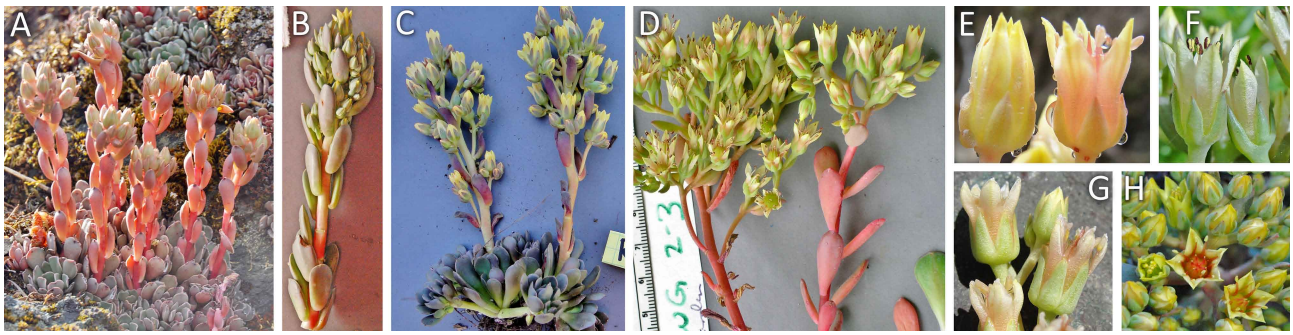

FIGURE 39. *Sedum paradisum* subsp. *paradisum*. A. Habit, showing dense rosettes, uniformly elongated stem leaves, the pre-flowering inflorescences erect, Trinity Co., California (*Wilson et al. CWG-03*). B–C. Cylindrical inflorescences, uniformly elongated stem leaves, Trinity Co. B. *Wilson et al. CWG-03*. C. *Spooner et al. RS-28*. D. Flat-topped inflorescence, Shasta Co., California (*Wilson et al. CWG-02*). E–H. Flowers. Sepals relatively long; variation in flower color, petals ascending, acute, pale yellow to white or orange-pink; anthers yellow, orange, or reddish. E. Trinity Co. (*Zika 25921 & J.K. Nelson*). F–H. Shasta Co. F. *Lindstrand III NSR–16*. G. *Zika 25924*. H. *Lindstrand III & Van Susteren NSR-01*.

The relatively long sepals and elongate upper stem leaves helped distinguish *Sedum paradisum* subsp. *paradisum* from *S. oregonense* and *S. flavidum*. The dull gray foliage, ascending petals, and erect young fertile shoots provided distinctions from *S. sanhedrinum*. The separation of taxa within *S. paradisum* is discussed under subsp. *subroseum*.

Hybrids:—Putative *Sedum paradisum* subsp. *paradisum* hybrids were found at two sites (Table 4). One was the mouth of Swede Creek near its confluence with the Trinity River. *Sedum paradisum* subsp. *paradisum* and some odd-looking putative hybrids were present (*Wilson et al. CWG-05*). *Sedum flavidum* occurred there in the past but declined and was ultimately lost from the site within the last 40 years (Darington, pers. obs.). At the highly disturbed Underwood Mountain quarry, *S. paradisum* subsp. *paradisum* was present with some atypical, possibly hybrid plants (*Brainerd & Otting CWG-102b*). Plants approaching *S. flavidum* also occurred in the quarry (Darington, pers. obs.). *Sedum paradisum* subsp. *paradisum, S. kiersteadiae,* and *S. oregonense* all occurred in the Canyon Creek drainage in northern Trinity County. Many plants there were difficult to identify. There was a considerable elevational and geological gradient, and related differences in phenology, which made it difficult to compare populations. We were not sure if some plants appear intermediate due to hybridization, unusual morphological variation, or if there are other factors. Answers will require repeated visits to the area in a single season, so populations can be examined at peak flowering times.

Possible hybrid specimens examined:—UNITED STATES. **CALIFORNIA. Trinity County:** Swede Creek, 355 m, 17 June 2011, *Wilson et al. CWG-05* (OSC); same site, 7 June 2012, *Brainerd & Otting CWG-101* (OSC); Underwood Mountain Road, 1235 m, 7 June 2012, *Brainerd & Otting CWG-102b* (OSC).

12b. *Sedum paradisum* (Denton 1978: 236) Denton ex B. L. Wilson subsp. ***subroseum*** B. L. Wilson & Zika, *subsp. nov*. Figs. 3C–D, 9F, 13D, 15D, 40A–F, 41.

Species nostra Sedum paradisum subsp. paradisum aemulans, differt axe inflorescentiae juvenili nutante, a Sedum obtusatum subsp. obtusatum floribus albis postea saepe pallide erubescentibus recedens.

Type:—UNITED STATES. California: Plumas County, dry serpentine ridgetop 1 air mile NE of Pilot Peak, 2005 m, 6 August 2011, *P. F. Zika 25721 & L. P. Janeway, B. L. Wilson* (holotype, WTU; isotypes, CAS, CHSC, OSC, UC).

FIGURE 40. A–F. *Sedum paradisum* subsp. *subroseum*. A. Habit, showing stolons and dense rosettes, and consistently elongated proximal and distal stem leaves (*Zika 26283*). B. Flower, side view, showing ascending petals and elongated sepals. C. Flower, top view, showing broad upper petal and acute tips. B–C, E–F. *Zika 26279*. D. Petal tip enlargement, showing subterminal mucro projecting on the right side, and the hooded petal tip on the left side (*Zika 26283*). E. Rosette leaf. F. Stem leaf, with truncated base; in the field the stem leaves were often a dull gray, but varied to green or pink. **G–M. *Sedum patens*.** G. Habit, showing loose rosettes, stem leaves longer than wide, and widely branched inflorescence. H. Flower, side view, showing spreading petals. I. Flower, top view, showing narrow gradually tapered upper half of petals, and acuminate tips. G–I. *Zika 26609 & Brainerd*. J. Enlargement of petal tip, showing subterminal mucro projecting on right, hooded petal tip on left (*Zika 26608 & Brainerd*). K. Dehisced follicles with attenuated apex. L. Rosette leaf. M. Stem leaf, with truncated base. K–M. *Zika 25935*.

Rhizomes and stolons to 18 cm long, 1.7–5.1 mm diameter; sterile leafy shoots often numerous. Rosettes 13–55 mm diameter. Rosette leaves usually dense, in shady situations sometimes loosely arranged with visible internodes, slightly glaucous, at least when young, green, grey-green, orange to red, or purple, strongly flattened dorsiventrally, obovate to oblanceolate, cuneate, 10–31 × 6–16 mm, 2–3.5 mm thick, apices obtuse or notched, less commonly truncate or acute. Stem leaves ascending, slightly glaucous, at least when young, and colored like the rosette leaves, 9–20 × 3–11 mm, 1.5–3.5 mm thick, flattened, truncate at base, narrowly oblong, oblong-oblanceolate, or obovate to oblanceolate, apices acute or obtuse. Fertile stems pink to reddish or orange (green), 6–21 cm tall, nodding or bent in bud, usually erect in flower and fruit. Inflorescences 2.5–13 × (1–)2–7 cm, narrowly cylindrical panicle-like cymes or flat-topped and corymbiform, subglobose if depauperate, with 4–10 branches, proximal branches ascending or spreading, 15–60 mm long, solitary at inflorescence nodes. Inflorescence bracts resembling stem leaves, but smaller, 2.5–18 × 1–8.5 mm, bases truncate, tips acute or blunt. Flowers (3–)10–49 per inflorescence, fresh flower diameter (5–)7–12 mm, flowers 5-merous, erect, calyx green, pink or brown, 3.6–6.4 × 3.7–6.1 mm, sepals fused basally 0.8–2.2 mm, free sepal tips 2.3–4.9 mm long, apex narrowly acute, acute or obtuse. Fresh petals fused at base 1.4–3.3 mm; petals 6.5–10.1 mm long, 2.7–3.9 mm wide at mid-length, creamy-white, white, or greenish-white, base often dull light pink, midvein pink to red (especially in bud), apices or bases often pink or red, especially with age. Fresh petal blade v-shaped or trough-shaped in cross section, broad, distal half ovate or widely deltoid, at half its length slightly spreading circa 30° from floral axis, apex sometimes apiculate with subterminal mucro 0–0.2 mm. Stamens 10, when fresh shorter to longer than petals, filaments greenish-white or white, aging red, fresh anthers narrowly elliptic or oblong to elliptic-oblong, 1.2–1.8 × 0.6–0.85 mm, yellow, aging white or less often gray, brown, orange, or blackish. Nectaries shallowly crescent-shaped, sunken in middle, white to dark yellow, 0.8–1.6 × 0.3–0.6 mm. Ovaries 4.0–6.3 mm, erect, fused 0.5–1.4 mm, maturing into 5 dark brown erect follicles, 4.2–6.7 mm, with erect to slightly curved style remnant forming a narrow beak 0.6–1.3 mm, follicles fused 1.1–2.0 mm at base, containing 19–24 seeds. Seeds medium brown, oblanceolate, shiny, striate, 1.1–1.35 × 0.4–0.5 mm, including stipe 0.05–0.25 mm.

Paratypes:—UNITED STATES. **CALIFORNIA. Butte County:** below Pilot Peak, on Quincy-Laporte Road, 1930 m, 6 August 2011, *Wilson 16817 & Janeway, Zika* (OSC, WTU). **Plumas County:** near La Porte, 915 m, 29 June 1968, *Ahart s.n.* (CAS); N side of Pilot Peak, 20 September 2011, *Ahart 17693* (WTU); Plumas-Eureka State Park, 1592 m, 28 May 1961, *Uhl 962* (BH); Eureka Peak, 1695 m, 31 July 1964, *Clausen 641125* (BH); W of Eureka State Park, 1660 m, 13 June 1976, *Denton 3878* (OSC, WTU); SSW of Graeagle, 1830 m, 14 June 1976, *Denton 3884* (WTU); Bucks Lake, summer 1975, *Griggs 310* (CAS); Lakes Basin area, 1980 m, 11 August 1950, *Weatherby 1510* (RSA); Little Jamison Creek, 1600 m, 27 July 1964, *Clausen 641107* (BH), *Clausen 641108* (BH), *Clausen 641110* (BH), *Clausen 641111* (BH), *Clausen 641114* (BH); Jamison Creek, 1700 m, 6 August 2011, *Wilson, Janeway & Zika CWG-14* (DAV, JEPS, RENO, RSA, WTU); Quincy-Laporte Road, 1930 m, 6 August 2011, *Wilson, Zika & Janeway CWG-15* (HSC, US); WNW of Mills Peak, 1885 m, 28 June 2013, *Zika 26283* (DAV, HSC, JEPS, UCR). **Sierra County:** NE of Gold Lake, 1990 m, 29 July 1964, *Clausen 641120* (BH, GH); Sierra Buttes, 29 July 1964, *Clausen 641127* (BH, GH)*, 641115* (BH, GH), *641116* (BH); same site, 14 June 1976, *Denton 3899* (OSC, WTU); E of La Porte, 1700 m, 28 July 1982, *Ahart 3700* (CAS); Packer Lake, 1940 m, 28 June 2013, *Zika 26279* (CAS, CHSC, RSA, SD).

Distribution and ecology:—Restricted to the Northern High Sierra Nevada ecoregion (Jepson eFlora 2017), California, north of the Middle Yuba River, at elevations of 915–2005 m (Fig. 37). Habitats included rocky slopes, ridgelines, and dry cliffs, in full sun to partial shade, on a variety of bedrock types including peridotite, andesite, and granite. Common associates included: *Abies magnifica* A. Murray bis, *Aconogonon phytolaccifolium* (Meisn. ex Small) Rydb., *Calochortus leichtlinii* Hook. f., *Cryptogramma acrostichoides* R. Br., *Eriogonum umbellatum* var. *nevadense* Gand., *E. ursinum* S. Watson var. *ursinum*, *Myriopteris gracillima*, *Pellaea bridgesii* Hook., *Penstemon deustus*, *P. newberryi* A. Gray, *Pinus contorta* Douglas ex Loudon*, P. jeffreyi* Balf., *P. lambertiana* Douglas, *Poa secunda* J. Presl, *Silene bernardina* S. Watson, and *Spiraea splendens* É.N. Baumann ex K. Koch.

Etymology:—*Sedum paradisum* subsp. *subroseum*, or Plumas stonecrop, was named for its flowers, which usually turned pinkish and with age gave the entire inflorescence a rosy appearance.

Notes:—*Sedum paradisum* subsp. *subroseum* (Figs. 40A–F, 41) differed from *S. paradisum* subsp. *paradisum* in its bent young inflorescence axis, slightly shorter sepals, more strongly red-tinted foliage, and its more eastern distribution in the Sierra Nevada range.

Sedum paradisum subsp. *subroseum* was separable from *S. obtusatum* in the Sierra Nevada by flower color; petals of *S. paradisum* subsp. *subroseum* were white while those of *S. obtusatum* were pale yellow to deep yellow. The two were allopatric. The southernmost known station of *S. paradisum* subsp. *subroseum* was at Sierra Butte, north of the Middle Yuba River, and the northernmost known station of *S. obtusatum* was near Jackson Meadows Reservoir, 11 km distant and south of the Middle Yuba River.

FIGURE 41. *Sedum paradisum* subsp. *subroseum*. A–D. Habitat. A. Plumas Co., California (*Zika 25721 Janeway & Wilson*). B. Sierra Co., California (*Zika 26279*). C–D. Plumas Co. (*Zika 26283*). E. Young inflorescences, nodding prior to anthesis on right, straightening as coming into flower on left; stem leaves elongated and overlapping proximally and distally; Plumas Co. (photo: Tim Hanson). F. Erect flowering shoots in full sun, Plumas Co. (*Zika 25721 Janeway & Wilson*). G–H. Lax growth form in partial shade on mossy ledges, sheltered vegetative shoots with loose rosettes; Sierra Co. (*Zika 26279*). I–J. Typical dense rosettes in full sun, showing variation in color, Plumas Co. (*Zika 25721 Janeway & Wilson*). K. Rosette leaves, bottom row; stem leaves, upper row; Sierra Co. (*Zika 26279*). L. Inflorescence, Plumas Co. (*Wilson, Janeway & Zika CWG-14*). M–P. Flowers, showing fresh anthers yellow to almost white, after dehiscence white or brownish, ascending petals white or pinkish, aged pink to dark pink, distal half of petal broad, acute. M. Green metallic bee visiting flowers, Plumas Co. (*Zika 26283*). N–O. Sierra Co. (*Zika 26279*). P. Two flowers and a bud, fresh anthers almost white, subapical mucro on petal tips, and as flower matured, sepals elongated, lower half of petals with deeper color; Plumas Co. (*Wilson, Zika & Janeway CWG-15*).

13. ***Sedum patens*** Zika, *sp. nov*. Figs. 3A–B, 4B, 8E, 11C, 40G–M, 42

Species insignis Sedum laxum eximie affinis sed petalis niveis apicibus patentibus necnon antheris luteis notabilis.

TYPE:—UNITED STATES. California: Del Norte County, SE of Bald Hill, 90 m, 9 June 2015, *P. F. Zika 27047* (holotype, WTU; isotypes, CAS, GH, MO, NY, OSC, RSA, UC).

Rhizomes and stolons to 35 cm long, 3.7–5.8 mm diameter; sterile leafy shoots 1–7. Rosettes 20–48 mm diameter. Rosette leaves mostly densely arranged without visible internodes, in shady or sheltered situations sometimes loosely arranged with visible internodes, only faintly glaucous, at least when young, green to gray-green, red, or purple, strongly flattened dorsiventrally, obovate to widely obovate, cuneate, 10–35 × 12–21 mm, 3–6 mm thick, apices obtuse, truncate or, more commonly, shallowly notched. Stem leaves ascending, slightly glaucous, at least when young, and colored like the rosette leaves, 11–15 × 7–11 mm, 2–3.5 mm thick, flattened, truncate at base, oblong–oblanceolate, obovate, or broadly obovate, apices obtuse. Fertile stems pink to reddish or green, 7–29 cm tall, nodding or bent in bud, usually erect or leaning in flower and fruit. Inflorescences 2.5–11.5 × 3–8 cm, flat–topped cymes with 3–12 branches, proximal branches ascending or spreading, 20–115 mm long, solitary at inflorescence nodes. Inflorescence bracts smaller and

narrower than stem leaves, 4–10 × 1–4 mm, bases truncate, tips acute. Flowers (10–)15–31 per inflorescence, fresh flower diameter 10–14 mm (6–7 mm before spreading), flowers 5–merous, erect, calyx green, 3.7–4.9 × 3.4–4.3 mm, sepals fused basally 0.7–1.1 mm, free sepal tips 2.6–3.5 mm long, apex narrowly acute to acuminate. Fresh petals fused at base 1.9–2.4 mm; petals 8.5–12.1 mm long, 2.4–2.8 mm wide at mid-length, white or greenish-white, and same color at base and on midvein, aging to dirty white. Fresh petal blade v-shaped or trough-shaped in cross section, relatively narrow, distal half oblong then gradually narrowing, narrowly deltoid, at half its length slightly to strongly spreading 45–90° from floral axis, apex apiculate with subterminal mucro 0.3–0.5 mm. Stamens 10, when fresh shorter than to equaling petals, filaments greenish-white or white, similar in color with age, fresh anthers oblong to lance-oblong, 1.2–1.9 × 0.5–0.7 mm, yellow, aging yellow, papillose at 20×. Nectaries shallowly crescent-shaped, sunken in middle, white, 0.6–1 × 0.3–0.4 mm. Ovaries 4.6–6.1 mm, erect, fused 1–1.3 mm, maturing into 5 dark brown erect follicles, 5–6 mm, with erect to slightly curved style remnant forming a narrow beak 0.9–1.5 mm, follicles fused 1 mm at base, containing 10–12 seeds. Seeds medium brown, oblanceolate, shiny, striate, 1–1.2 × 0.3 mm, including stipe 0.2 mm.

Paratypes:—UNITED STATES. **CALIFORNIA. Del Norte County:** South Fork Smith River, 120 m, 8 July 1950, *W.B. Cooke & V.G. Cooke s.n.* (UC); ENE of Bald Hill, 125 m, 24 June 2012, *Zika 25935* (OSC, WTU); same site, 9 June 2014, *Zika 26608 & Brainerd* (OSC, SD, WTU); SE of Bald Hill, 120 m, 9 June 2015, *Zika 27063* (RSA, WTU); SSE of Canthook Mountain, 180 m, 10 June 2014, *Zika 26623 & Brainerd* (DAV, MO, OSC, WTU); W of Canthook Mountain, 155 m, 9 June 2014, *Zika 26609 & Brainerd* (CAS, CHSC, OSC, WTU); same site, 9 June 2015, *Zika 27064* (CHSC, WTU); same site, 9 June 2015, *Zika 27065* (HSC, WTU); SSE of Craigs Creek Mountain, 100 m, 16 May 2015, *Zika 26987* (UCR, OSC); same site, 9 June 2015, *Zika 27060* (JEPS, WTU); same site 17 May 2015, *Zika 26999* (WTU).

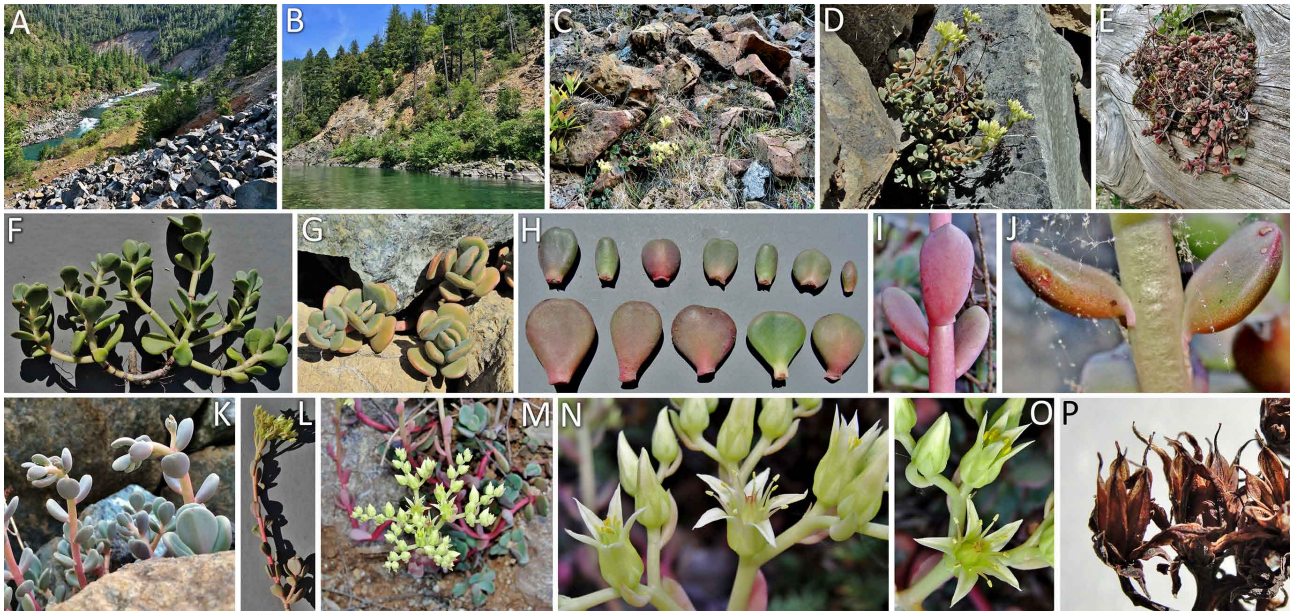

FIGURE 42. *Sedum patens*, Del Norte Co., California. A–E. Serpentine habitat. A. Talus (*Zika 26987*). B. Streambank ledges (*Zika 27063*). C. Type locality, rocky slope (*Zika 27047*). D. Talus (*Zika 27060*). E. On wood, in a knothole on a fallen tree on a talus slope (*Zika 26987*). F. Loose rosettes from a sheltered microsite (*Zika 27047*). G. Typical dense rosettes in sunny sites (*Zika 27060*). H. Rosette leaves, bottom row; stem leaves, upper row (*Zika 26987*). I. Typical stem leaves, bases truncated (*Zika 26609 & Brainerd*). J. Unusual stem leaves, bases decurrent (*Zika 26609 & Brainerd*). K. Nodding or arching inflorescences, pre-anthesis (*Zika 26987*). L–M. Flat-topped inflorescences. L. *Zika 27047*. M. *Zika 26609 & Brainerd*. N–O. Flowers, white acuminate narrow petals, spreading at maturity, anthers yellow (*Zika 26609 & Brainerd*). P. Dehisced follicles with attenuated apex (*Zika 26999*).

Distribution and ecology:—The documented distribution of *Sedum patens* was along the South Fork of the Smith River, in the Klamath Ranges of southern Del Norte County, California (Fig. 22). Populations varied from 90–200 m elevation, on dry or damp steep open rocky slopes, talus, and cliffs with a south, east or north aspect, on ultramafic soils or bedrock. Most plants were in full sun, but some were in sheltered crevices and in partial shade. One colony with numerous shoots was growing on wood, in a knothole on a large toppled tree on a steep slope (Fig. 42E). The northern-most populations were just south of and upslope from the coastal redwood association, dominated by *Sequoia sempervirens* (D. Don) Endl., in the canyon bottoms. Very little was known about *S. patens*, which was first

collected in 1950. A more complete assessment of its distribution awaits further field surveys in steep trail-less terrain. We noted seven populations, which varied in size from fewer than 50 plants to approximately 1000 individuals. Photos of plants in the adjacent Mill Creek drainage to the west, on or near state park land, also suggested *S. patens*, but no specimens were seen.

Some common associates included *Achillea millefolium*, *Adiantum aleuticum* (Rupr.) C.A. Paris, *Aspidotis densa* (Brack.) Lellinger, *Cerastium arvense* L., *Carex mendocinensis* Olney ex W. Boott, *Castilleja pruinosa* Fernald, *Chamaecyparis lawsoniana* (A. Murray) Parl., *Elymus glaucus* Buckley, *Erigeron foliosus* Nutt., *Eriophyllum lanatum* (Pursh) J. Forbes, *Festuca californica* Vasey, *F. roemeri* (Torr. & A. Gray) Greene var. *klamathensis* B.L. Wilson, *Frangula californica* (Eschsch.) A. Gray subsp. *occidentalis* (Greene) Kartesz & Gandhi, *Holodiscus discolor*, *Iris thompsonii* R.C. Foster, *Montia parvifolia* (Moc. ex DC.) Greene, *Poa piperi* Hitchc., *Polystichum imbricans* (D.C. Eaton) D.H. Wagner, *Pseudotsuga menziesii* (Mirb.) Franco, *Rhododendron occidentale* (Torr. & A. Gray) A. Gray, *Schedonorus arundinaceus* (Schreb.) Dumort., *Silene serpentinicola* T.W. Nelson & J.P. Nelson, *Tauschia glauca* (J.M. Coult. & Rose) Mathias & Constance, *Toxicodendron diversilobum* (Torr. & A. Gray) Greene, *Triteleia laxa* Benth., and *Whipplea modesta* Torr.

Etymology:—*Sedum patens*, or Smith River stonecrop, was named for the widely spreading petals.

Notes:—*Sedum patens* (Figs. 40G–M, 42) had narrow white acuminate petals and yellow anthers. In *Sedum* section *Gormania* only two taxa displayed occasional stem leaves with decurrent bases, *S. patens* and *S. laxum* subsp. *laxum*. In the Smith River basin and in coastal Oregon, *S. laxum* subsp. *laxum* often showed truncate leaf bases, while in Josephine County Oregon (and elsewhere), *S. laxum* subsp. *laxum* often displayed strongly decurrent leaf bases, sometimes completely lacking truncate stem leaf bases. Most plants of *S. patens* had truncate leaf bases, but the presence of some with decurrent bases (Fig. 42J) suggested an alliance with *S. laxum,* or possible hybridization. Both taxa share long narrow acuminate-tipped petals. *Sedum patens* was easily separated from *S. laxum* by the yellow anthers and spreading white petals; *S. laxum* subsp. *laxum* and subsp. *heckneri* had dark red anthers and erect, usually pink petals, occasionally whitish above or on the margins, and pink at the base or center.

In cultivation we noticed a pungent honey-like odor to the flowers, detectible from a few meters and persisting after dark, suggesting moth pollinators.

14. Sedum rubiginosum Zika & B. L. Wilson, *sp. nov*. Figs. 1D–E, 4C–D, 11D, 15E, 24C–D, 32A–F, 43

Differt haec species a Sedum kiersteadiae rosulis foliorum densis, floribus numerosioribus, sine vel reduci mucrone abaxiali subterminali, necnon foliis caulinis numerosis imbricatisque.

TYPE:—UNITED STATES. California: Tehama County, SE of Tedoc Mountain, 1490 m elevation, 5 July 2011, *P. F. Zika 25522 & J. K. Nelson* (holotype, WTU; isotypes, CAS, OSC).

Rhizomes and stolons to 30 cm long, 2–11 mm diameter; sterile leafy shoots not numerous, rosettes 14–120 mm diameter. Rosette leaves often densely arranged without visible internodes, glaucous, at least when young, green to gray, orange to red, or purple, strongly flattened dorsiventrally, oblanceolate, cuneate, 9–72 × 5.5–20.5 mm, 2.5–5.5 mm thick, apices obtuse, or truncate or shallowly notched, rarely acute. Stem leaves ascending, slightly glaucous, at least when young, and colored like the rosette leaves, 8.5–26 × 3–10 mm, flattened, truncate at base, narrowly oblong to oblanceolate, apices acute or obtuse. Fertile stems green to pink, reddish or orange, 6–28.5 cm tall, nodding or bent in bud, erect in flower and fruit. Inflorescences 4.5–18 × 2.5–6.5 cm, usually densely-flowered, narrowly cylindrical or ellipsoidal panicle-like cymes with 7–17 branches, proximal branches ascending-erect, 12–75 mm long, solitary at inflorescence nodes. Inflorescence bracts resembling stem leaves, but smaller, 4–18 × 1–9 mm, base truncate, tips acute or blunt. Flowers 26–152 per inflorescence, fresh flower diameter 8–12 mm, flowers 5-merous, erect or spreading, calyx green, brown, or red, 2.5–3.4 × 2.4–4.1 mm, sepals fused basally 0.7–1.4 mm, free sepal tips 1.6–2.4 mm long, apex acute to obtuse. Fresh petals fused at base 1.1–2.1 mm; petals 5.0–7.8 mm long, 1.9–3.2 mm wide at mid-length, pale to medium yellow, sometimes fading to white, midvein orange to red or pink (especially in bud), apices or bases often orange to pinkish or reddish, especially with age. Fresh petal blade v-shaped or trough-shaped in cross section, narrow, at half its length spreading 90° from floral axis, apex with or without a subterminal mucro, if present the mucro 0.05–0.15 mm. Stamens 10, when fresh shorter to longer than petals, filaments white to green or pale yellow, aging red, fresh anthers oblong, 1.1–1.45 × 0.5–0.65 mm, orange to dark red, aging red, orange, brown, or black, papillose at 20×. Nectaries shallowly crescent-shaped, sunken in middle, white to pale yellow, 0.5–1.2 × 0.1–0.3 mm. Ovaries 3.6–6(–7.3) mm, erect, fused 0.6–1.7 mm, maturing into 5 dark brown erect follicles, 5.2–9.2 mm, with erect to slightly

curved style remnant forming a narrow beak 1.2–3.5 mm, follicles fused 1.7–3.0 mm at base, containing 9–26 seeds. Seeds medium to dark brown, oblanceolate, shiny, striate, 0.8–1.3 × 0.3–0.5 mm, including stipe 0.05–0.2 mm.

Paratypes:—UNITED STATES. **CALIFORNIA. Tehama County:** N of Tedoc Gap, 1415 m, 19 June 2011, *Wilson & Coberly CWG-10* (JEPS); Tedoc Mountain,1450 m, 26 June 2013, *Zika 26234* (CHSC, JEPS, OSC); same site, 26 June 2013, *Zika 26238* (CAS, DAV, HSC, RSA, UCR); Little Red Mountain, 1355 m, 24 June 2014, *J.K. Nelson 2014-067 & Tate, Rainbow* (OSC, WTU).

Distribution and ecology:—Currently known from two population aggregates in northwestern Tehama County, California (Fig. 25), in the southern Klamath Ranges ecoregion (Jepson eFlora 2017). Found on gentle to steep rocky slopes, and talus, at southeast, west, northwest, and northeast aspects, in full sun or partial shade of widely scattered pines, on dry reddish peridotite bedrock exposures, at elevations of 1350–1500 m. Associates included *Arctostaphylos patula* Greene, *Aspidotis densa* (Brack.) Lellinger, *Calocedrus decurrens* (Torr.) Florin, *Elymus elymoides* (Raf.) Swezey, *Eriogonum libertini* Reveal, *E. nudum* Benth., *Eriophyllum lanatum, Galium bolanderi* A. Gray, *Garrya congdonii* Eastw., *Minuartia rosei* (Maguire & Barneby) McNeill, *Packera greenei* (A. Gray) W.A. Weber & A. Löve, *Phacelia corymbosa* Jeps., *Pinus jeffreyi, P. sabiniana* Douglas ex D. Don, *Pyrola picta* Sm., *Quercus vaccinifolia* Kellogg, *Streptanthus barbatus* S. Watson, and *S. tortuosus* Kellogg.

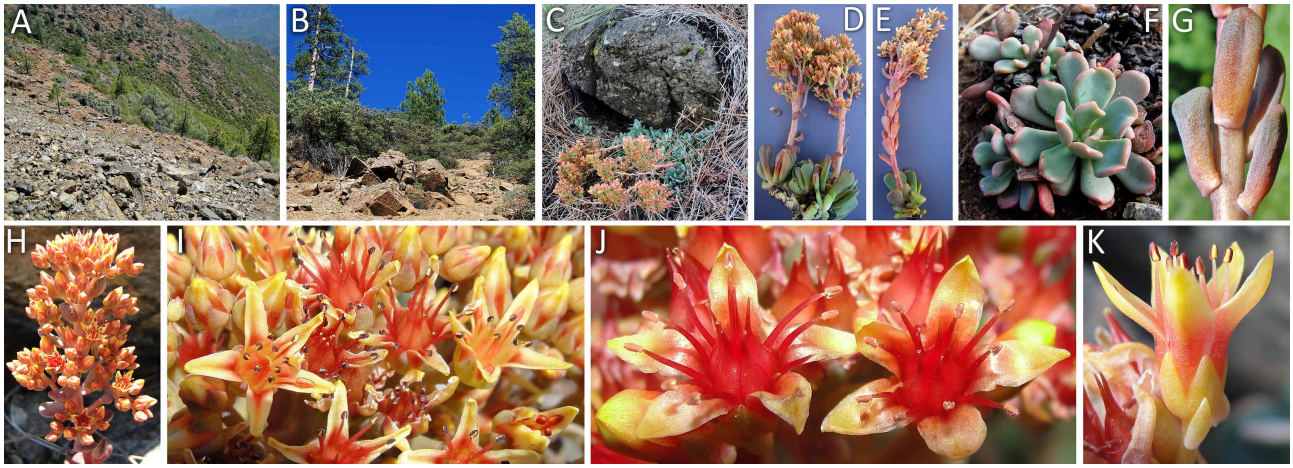

FIGURE 43. *Sedum rubiginosum*, Tehama Co., California. A–C. Habitat, rocky serpentine slopes. A. Photo: J.K. Nelson (*Zika 25522 & J.K. Nelson*). B. *Wilson & Coberly CWG-10*. C. *Zika 26238*. D–E. Flowering shoots (*Zika 25522 & J.K. Nelson*). F. Dense rosettes (*Zika 26234*). G. Oblong overlapping ascending stem leaves, faintly glaucous, with truncated bases (*Zika 26238*). H. Cylindrical inflorescence in early anthesis, flowers dense (*Zika 25522 & J.K. Nelson*). I–K. Flowers, petals narrow, acute, spreading, reddish towards base, anthers dark red. I. Typical narrow petals (*Zika 25522 & J.K. Nelson)*. J. Unusually broad petals (*Zika 26238*). K. Relatively short sepals (*Zika 26234*).

Etymology:—*Sedum rubiginosum*, or Tedoc stonecrop, was named for the reddish colors found in the fresh and aged petals, as well as the rusty red anthers.

Notes:—*Sedum rubiginosum* (Figs. 24, 32A–F, 43) shared many ecological and morphological characteristics of *S. kiersteadiae*. Both were found on serpentine soils and had a cylindrical inflorescence when well-developed, with red anthers, narrow yellow petals and pink to red colors at the base of the corolla, especially with age. *Sedum rubiginosum* had more robust growth when sheltered, denser rosettes, more stem leaves, and more flowers than *S. kiersteadiae*. *Sedum rubiginosum* was found well to the south of the known range of *S. kiersteadiae* (Fig. 25). Tedoc stonecrop occasionally produced cleistogamous flowers late in the flowering season.

15. *Sedum sanhedrinum* Berger (1930: 451). Figs. 1F, 4E, 5G, 14E–F, 44D, 45

Gormania retusa Rose in Britton & Rose (1903: 31). *Cotyledon retusa* (Rose) Fedde in Schumann & Fedde (1904: 828). *Sedum laxum* (Britton in Britton & Rose 1903: 29) Berger (1930: 451) subsp. *retusum* (Rose) Clausen (1942: 39). *Sedum obtusatum* Gray (1868: 342) subsp. *retusum* (Rose) Clausen (1975: 375).

Type:—UNITED STATES. California: Lake Co., Sanhedrin Mountains, 5000 feet [1525 m], 6 August 1902, *A. A. Heller s.n.* (lectotype, designated by Clausen [1942: 39], US; isolectotype, NY).

Not *Cotyledon retusa* (Lindley 1847: 306) Baker in Saunders (1869: sub. t. 64, no. 22).

Not *Sedum retusum* Hemsley (1880: 51).

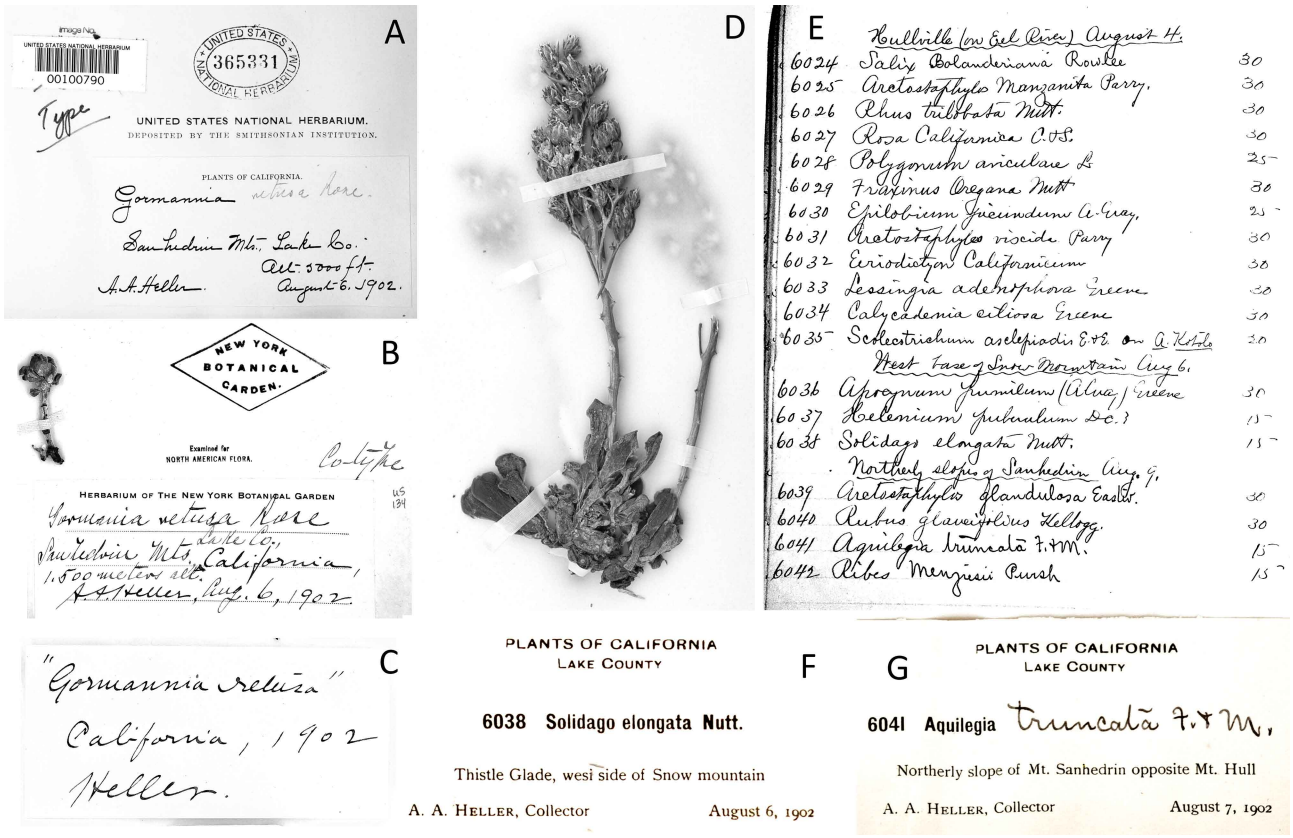

FIGURE 44. *Gormania retusa* type locality. A. Handwritten label of lectotype, Sanhedrin Mts., Lake Co., alt. 5000 feet, 6 August 1902, *A. A. Heller s.n.* (US). The label handwriting does not match Heller's handwriting in his collection notes. B. Handwritten isolectotype label at NY, in the handwriting of Nathaniel Britton (Amy Weiss pers. comm.). C. Label from inside the fragment packet, isolectotype (NY). D. Lectotype specimen (US), shadows showing where two inflorescences were once present. E. Heller's 1902 collecting book at WTU, with no listing for *Gormania* (or *Sedum*). 4 August, Hullville on Eel River (*Heller 6024–6035*). 6 August, West base of Snow Mountain (*Heller 6036–6038*). 9 August, Northerly slope of Sanhedrin (*Heller 6039–6042*). F. Printed label of *Heller 6038* (NY 2339077 ex herb. BKL), 6 August 1902, from low elevation at "Thistle Glade, west side of Snow Mountain". G. Printed label of *Heller 6041* (NY 2743052 ex herb. BKL), 7 August 1902, from "northerly slope of Mount Sanhedrin opposite Mt. Hull." There was no entry for 7 August 1902 in Heller's collection book, where he listed *6041* on 9 August. A, D. Images reproduced with permission, courtesy of United States National Herbarium, Smithsonian Institution. B–C, F–G. Images reproduced with permission, they belong to the C. V. Starr Virtual Herbarium of The New York Botanical Garden (http://sweetgum.nybg.org/science/vh/).

We were not certain where Amos Arthur Heller (1867–1944) collected the lectotype of *Gormania retusa* (*Sedum sanhedrinum*, Fig. 44), which was labeled "Lake Co., Sanhedrin Mountains, alt. 5000 feet [1524 m], 6 August 1902, *A. A. Heller s.n.*" (Fig. 44A). His bound collecting notebook for 1902, archived at WTU, did not have an entry for the type of *Gormania retusa*. His collecting trip in the vicinity of Sanhedrin Mountain was between 14 July and 11 August 1902 (*Heller 5855* to *Heller 6048*). His next collections were dated 18–20 August in Sonoma County (*Heller 6049–6056*). The *Gormania retusa* lectotype at US (Figs. 44A, D), and the isolectotype at NY (Figs. 44B–C), were dated 6 August, both in a handwriting that does not match the hand in Heller's notebook (Fig. 44E). There were three entries in Heller's book for 6 August (*Heller 6036–6038*), all from "Thistle Glade," on the west side of Snow Mountain (Fig. 44F). The exact location was uncertain, but likely along the lower drainage of Thistle Glade Creek, which drains the western flank of Snow Mountain, entirely within Lake Co., from 1850–5600 feet [564–1707 m] elevation. Because Heller's notebook (*Heller 6038,* Fig. 44E) clarified these collections [*Apocynum* Linnaeus (1753: 213)*, Helenium* Linnaeus (1753: 886)*,* and *Solidago* Linnaeus (1753: 878)] were from the "west base of Snow Mountain," this would be the wrong habitat and too low an elevation for *Sedum sanhedrinum*, which is known from 4600 feet [1402 m] and higher. A more appropriate habitat for *Sedum sanhedrinum* would be the "northerly slope of Mount Sanhedrin opposite Mt. Hull" where he collected *Aquilegia* Linnaeus (1753: 533; *Heller 6041*, Fig. 44G) on 7 August, and labeled it from Lake Co. His collecting book (Fig. 44E) lists *Heller 6041* on 9 August, not 7 August, adding some uncertainty. Most

of the northern slope of Mount Sanhedrin, N of the summit at Big Signal Peak, and at elevations above 1400 m, is in present day Mendocino Co., but was part of Lake Co. in Heller's day. Heller also gathered specimens in the Sanhedrin summit region earlier in his trip, on 20, 22, 24, and 28 July, but any of those dates created a larger discrepancy with the label data on the type of *G. retusa*.

In summary, we believe there were minor inconsistencies on the lectotype label for *Gormania retusa* at US. The handwriting on the US and NY types did not belong to Heller, and so it is understandable if some of the details were not a perfect match for Heller's notebook. It appears Heller was at low elevations on 6 August (Figs. 44E–F), but at suitable high elevations on either 7 or 9 August (Fig. 44E), perhaps the correct collection date for the type. All Heller's printed labels credited his collections to Lake Co. (Consortium of California Herbaria 2017), though some were in modern day Mendocino Co. The type locality may be the north slope of Mount Sanhedrin (Fig. 44G), at ca. 5000 feet [1524 m], and this was probably in modern Mendocino Co., not Lake Co. *Sedum sanhedrinum* was extant but uncommon on Mount Sanhedrin, along the ridge east of Big Signal Peak (Steven Darington, obs.; *Hutchison 913*). Finally, Heller's numbered gatherings in his collecting book indicated sets of 15–30, which Heller was offering for sale (at 5 cents each). The lack of a collection number on the type suggests that the stonecrop was uncommon in 1902, and so Heller did not gather it as a large set of replicates for sale.

Additional specimens examined:—UNITED STATES. **CALIFORNIA. Glenn County:** Bear Rock, 1510 m, 26 June 2013, *Wilson & Otting CWG-230* (OSC, WTU). **Lake County:** Snow Mountain, 1 July 1929, *Baker 3541* (UC); Mendocino National Forest, Forest Service Road M1, 1585 m, 14 July 1977, *Smith 9330 et al.* (RSA, WTU); W slope of Goat Mountain, 1490 m, *Dean 5042* (UCR); Hull Mountain, 1955 m, 26 June 2013, *Wilson & Otting CWG-231* (OSC, WTU); same site, 12 June 2014, *Zika 26639 & Brainerd* (OSC). **Mendocino County:** summit Mount Sanhedrin, 1885 m, 21 July 1962, *Hutchison 913* (BH, JEPS); ENE of Bald Mountain, larvae of *Parnassius smintheus* near [subsp.] *sternitzkyi* feeding on plants, 1860 m, 22 July 2001, *Emmel 1731* (UCR); Monkey Rock, 1920 m, 26 June 2013, *Wilson & Otting CWG-232* (HSC, JEPS); same site, 11 June 2014, *Zika 26637 & Brainerd* (CAS, CHSC, SBBG); NE of Eel River Work Station, 1485 m, 27 June 2013, *Wilson & Otting CWG-233* (DAV); same site, 11 June 2014, *Zika 26629 & Brainerd* (OSC, WTU); W of Little Baldy, 1415 m, 11 June 2014, *Zika 26633 & Brainerd* (OSC, WTU); Hull Mountain, 1890 m, 12 June 2014, *Zika 26638 & Brainerd* (WTU). **Tehama County:** South Yolla Bolly (Mount Linn), 2285 m, 16 July 1955, *Barbe 175* (UC [2 sheets]); South Yolla Bolly Peak, 14 July 1963, *Clausen 63206* (BH); South Yolla Bolly Mountains, Valentine Ridge, 18 June 1963, *Clausen 63212* (BH); same site, 18 June 1963, *Clausen 63212* (BH); same site, 30 June 1963, *Clausen 63209* (BH); same site, 3 August 1963, *Clausen 63208* (BH); same site, 14 August 1963, *Clausen 63400* (BH); Tomhead Lookout, 2040 m, 2 August 2011, *J.K. Nelson JKN-2* (JEPS, RSA); same site, 13 July 2012, *Zika 25970* (WTU); same site, 27 June 2013, *Zika 26244* (WTU); Government Flat, 1740 m, 27 June 2013, *Wilson & Otting CWG-234* (CAS, NY).

Distribution and ecology:—*Sedum sanhedrinum* was restricted to Glenn, Lake, Mendocino, and Tehama counties, California (Fig. 25). The populations ranged from the Yolla Bolly Mountains in the north to Goat Mountain in the south, all in the High North Coast Ranges ecoregion (Jepson eFlora 2017), at elevations of 1415–2286 m. Substrates included serpentine and schist. Habitats were rocky slopes, ridgelines, talus, boulder fields, and rocky creek banks, usually in dry to very dry sites, in full sun or, less commonly, in light shade.

Morphological notes:—*Sedum sanhedrinum* (Fig. 45) was often a stout plant with dense rosettes of acute to truncate leaves. The petals were erect or spreading about 10° from the floral axis, and pale to bright yellow, often with an apricot tinge near the base. It was apparently closely related to *S. paradisum* subsp. *paradisum*. Both had overlapping stem leaves, elongate towards and into the inflorescence. Both had relatively long sepals, dense rosettes, and similar variation in flower color. However, they were allopatric, with *S. paradisum* subsp. *paradisum* (Fig. 37) found northwest of *S. sanhedrinum* (Fig. 25). Living plants also differed in the angle of petals, which were ascending in *S. paradisum* and essentially erect in *S. sanhedrinum*. Early in the growing season, before the flowers opened, *S. sanhedrinum* flowering stems nodded, while they were erect in *S. paradisum* subsp. *paradisum*.

Nomenclatural notes:—Understanding *Sedum sanhedrinum* was difficult for several reasons. The name was published overseas, and was unknown to most California botanists. The type specimen was discolored and its stem leaves fell off (Fig. 44D), complicating its interpretation. Location information for the type specimen was vague. The name *S. obtusatum* subsp. *retusum,* founded on *S. sanhedrinum*, was employed broadly (Clausen 1975, Denton 1982), based on a description (Denton 1982) that did not fit plants collected at the type locality. Thus there were many specimens and literature reports of *S. obtusatum* subsp. *retusum* that we referred to more northern entities, especially *S. oregonense* and *S. kiersteadiae.*

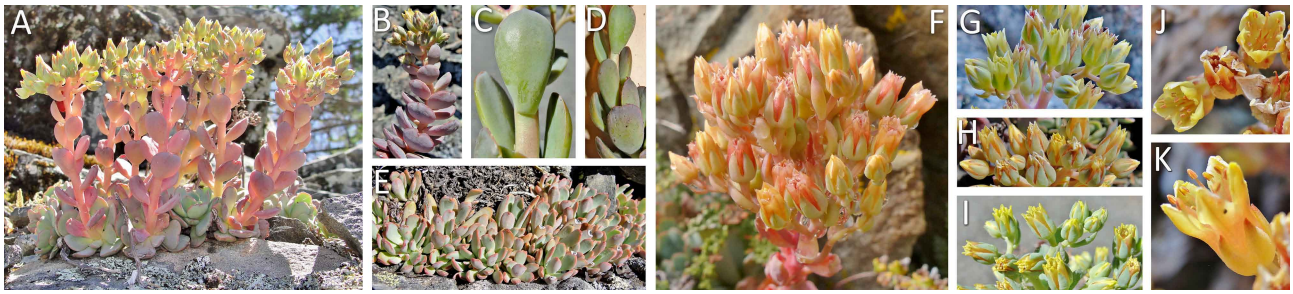

FIGURE 45. *Sedum sanhedrinum*. A. Habit, showing large rosette leaves and ascending stem leaves, Mendocino Co., California (*Zika 26629 & Brainerd*). B–D. Variation in stem leaves, spreading to ascending, broadly to narrowly obovate, bases truncated, slightly glaucous, green to purple or pink. B. *Zika 26629 & Brainerd*. C–D. Mendocino Co. (*Zika 26633 & Brainerd*). E. Dense and small rosette leaves, Tehama Co., California (*Zika 26244*). F. Capitate inflorescence, with dense flowers, Lake Co., California (*Wilson & Otting CWG-231*); inflorescences were also cylindrical (e.g., Fig. 45D, type) or flat-topped. G–K. Variation in flowers, corolla color pale yellow, orange-yellow, or bright yellow, faded to pink, orange-brown, pale brown, or yellow-brown, white or dull red; anthers yellow or, rarely, dull orange-red, faded to pink, reddish, white, or dull yellow; sepals elongated after anthesis. G. Tehama Co. (*Wilson & Otting CWG-234*). H. *Zika 26629 & Brainerd*. I. *Zika 26633 & Brainerd*. J–K. Petals erect, tips acute to blunt, Tehama Co. (*Zika 25970*).

The name *Sedum obtusatum* subsp. *retusum* was applied to plants with white or pale yellow petals, growing in the North Coast Range and Klamath ecoregions, north to the Siskiyou Mountains just north of the Oregon border (Denton 1979b, 1982, 1993; Denton & Kerwin 1980; Boyd & Denton 2012). Those plants were reported to have loose rosettes and to form extensive stoloniferous mats (Denton 1982). That appeared to be a misinterpretation. In our view, most specimens reported as *S. obtusatum* subsp. *retusum* (Denton 1982) were *S. oregonense*, which had loose rosettes, a spreading stoloniferous habit, and white flowers. Denton (1979b, 1982; Denton & Kerwin 1980) restricted her *S. oregonense* species concept to hexaploid plants. Based on chromosome counts, Denton interpreted tetraploid colonies as *S. obtusatum* subsp. *retusum*, but we considered them to be *S. oregonense* (Table 3). We revisited some of Denton's northern tetraploid populations and found no morphological markers to separate them from diploid or hexaploid *S. oregonense*.

Key to species of *Sedum* section *Gormania* in western North America

The key below was based on living material. It relied on characters that were difficult to observe on pressed dried material in a herbarium, such as inflorescence wax, flower colors, petal shape and angle, stem leaf attachment, and the density of sterile rosettes growing in sunny exposed situations. We suggest keying plants that retain some stem leaves, early in the flowering cycle.

1. Flowers and inflorescences stipitate-glandular; rosette leaf margins usually slightly eroded or irregular (10×); at elevations of 200–300 m along the Rogue River, southwestern Oregon ..... *S. moranii*
1- Flowers and inflorescences lacking glands; rosette leaf margins usually entire; range widespread in Oregon, California, and adjacent Nevada; at low to high elevations, including the Rogue River 2
2. Fresh petals at anthesis spreading strongly to (50–)90(–120)°; petals white or yellow (often marked with red) and relatively narrow 3
2- Fresh petals at anthesis erect or ascending [slightly spreading to 30(–45)°]; petals white, yellow, or pink, broad or narrow 6
3. Inflorescences flat-topped cymes on well-developed plants; fresh anthers deep yellow; petals lacking red at and before anthesis; in the Klamath Ranges of southern Del Norte County, California 4
3- Inflorescences cylindrical or elliptical, panicle-like, on well-developed plants; fresh anthers red, orange, or occasionally yellow; petals pale or medium yellow usually with red on midrib or base at or before anthesis; in the Klamath and Cascade Ranges of Tehama to southern Siskiyou counties, California 5
4. Petals deep yellow, 6–9 mm long; floral buds deep yellow with yellow or orange midvein; elevations of 940–1275 m ..... *S. citrinum*
4- Petals white, 8.5–12.1 mm long; floral buds white to greenish-white, with white or greenish midvein; elevations of 90–200 m ..... *S. patens*
5. Most rosettes loose with internodes easily visible; inflorescences loosely flowered with up to 54 flowers; petal tips commonly with subterminal mucro; stem leaves typically overlap 0–2 other stem leaves; on Mount Shasta, Cascade Range, and Klamath Ranges of adjacent portions of Shasta, Siskiyou and Trinity counties, California ..... *S. kiersteadiae*
5- Most rosettes dense with internodes obscured; inflorescences densely flowered, with up to 152 flowers; petal tips commonly with-

out subterminal mucro; stem leaves typically overlap 3–5 other stem leaves; southern tip of the Klamath Ranges, northwestern Tehama County, California ..... *S. rubiginosum*

6. Fresh petals primarily pink at or before anthesis, (margins occasionally white), erect or nearly so, spreading to 15(–30)° from the floral axis; anthers dark red; sepals usually ≤ 33% as long as petals 7

6- Fresh petals primarily white to yellow, sometimes dull pink basally at or before anthesis (margins white or yellow), erect or slightly spreading, to 45° from the floral axis; anthers yellow, orange, or red; sepals 20–80% as long as the petals 9

7. Stem leaves elliptic to oblong, not clasping or auriculate, base sometimes decurrent, often more than 2× as long as wide, ascending to somewhat spreading; on serpentine substrates; from Douglas County, Oregon, south to Del Norte and northern Siskiyou counties, California ..... *S. laxum* subsp. *laxum*

7- Stem leaves usually suborbicular (rarely oblong and more than 2× as long as wide), usually clasping or auriculate, never decurrent at base, widely spreading to ± reflexed; on serpentine or non-serpentine substrates; Jackson County, Oregon, south to Mendocino County, California 8

8. Petal tips narrow, often ± acuminate; petals 7–13 mm long; stem leaves spreading to ± reflexed; flowering shoots (9–)13–29 cm tall; from Applegate River drainage, Jackson County, Oregon, south to Hoopa area, Humboldt County, California ..... *S. laxum* subsp. *heckneri*

8- Petals tips broader, acute; petals 4–9 mm long; stem leaves spreading, not reflexed; flowering shoots 4–13 cm tall (Clausen 1975); range on and near Red Mountain, northern Mendocino County, California ..... *S. eastwoodiae*

9. Fresh anthers orange to dull brick red, or dark red 10

9- Fresh anthers yellow 11

10. Fresh petals primarily yellow, though usually with reddish midribs, sometimes with reddish bases; stem leaves truncate at base, never clasping or auriculate or decurrent; petal tips usually lacking subterminal abaxial mucro (occasionally with mucro to 0.05–0.15 mm); northwestern Tehama County, California, in the vicinity of Tedoc Mountain ..... *S. rubiginosum*

10- Fresh petals primarily white, though usually with pinkish midribs, sometimes with pinkish bases; stem leaves truncate or decurrent at base, or clasping or auriculate at base; petal tips usually with subterminal abaxial mucro; Humboldt, Del Norte, and Siskiyou counties, California, and southwestern Oregon ..... albino forms, go to lead 7

11. Sepals, inflorescences, and leaves with a thick layer of granular white wax leaving a residue on fingers when handled (the wax weathers away and is lost when microwaved, so easiest to see on fresh young flowering material) 12

11- Sepals, inflorescences, and leaves ± glaucous (thinly waxy) but without a thick layer of granular white deposits of wax 14

12. Rosette leaves usually obovate; rosette leaves dissimilar in shape from and more abruptly transitioning to stem leaves; Marble Mountains, Siskiyou County, California ..... *S. marmorense*

12- Rosette leaves usually oblanceolate; rosette leaves very similar in shape and gradually transitioning to stem leaves; absent in Marble Mountains 13

13. Rosette leaves usually more than 10 mm wide; petals pale yellow; mature fruits with carpels free to base; North Fork Feather River basin, west slope of the Sierra Nevada, Butte and Plumas counties, California ..... *S. albomarginatum*

13- Rosette leaves usually less than 10 mm wide; petals white or creamy-white; mature fruits with carpels fused slightly above base; Applegate River basin, Klamath Mountains (including Siskiyous), southern Oregon and northern California ..... *S. oblanceolatum*

14. Petals gradually tapered to narrow tip, often acuminate ..... *S. patens*

14- Petals more abruptly tapered to a wider tip, often acute to obtuse 15

15. Rosettes loose with internodes easily visible; petals white; Cascade Range of Oregon and Klamath Mountains of Oregon and California ..... *S. oregonense*

15- Rosettes dense with internodes obscure; petals white or yellow; California, including Klamath Mountains 16

16. Stem leaves usually suborbicular, base clasping to auriculate ..... *S. flavidum*

16- Stem leaves usually oblong to narrowly obovate, often more than twice as long as wide, base truncate 17

17. Sepals 20–33(–40)% as long as petals ..... *S. flavidum*

17- Sepals 40–80% as long as petals 18

18. Stem leaves not reduced upwards, large at base of stem and at base of inflorescence; fresh petals primarily white or creamy-white; foliage often dull gray, but varying to green or pink ..... *S. paradisum* subspecies 19

18- Stem leaves reduced upwards, larger at base of stem than at base of inflorescence; fresh petals primarily white or yellow; foliage often green or pink to red or orange 20

19. Free sepal lobes 2.3–4.9 mm; calyx 3.6–6.4 mm; developing inflorescences bent or nodding in bud, straightening for anthesis (some plants of cliffs ultimately bending to follow a light source); Sierra Nevada mountains of Plumas and Sierra counties, California ..... subsp. *subroseum*

19- Free sepal lobes 6–7 mm; calyx 6–8 mm; developing inflorescences erect in bud, straight for anthesis (some plants of cliffs ultimately bending to follow a light source); Cascade and Klamath Ranges of Shasta and Trinity counties, California ..... subsp. *paradisum*

20. Petals erect or nearly so; flowers ovate in lateral view, widest near base and evenly tapered to summit, not constricted to a "waist" near the apex of the sepals; High North Coast Ranges, California ..... *S. sanhedrinum*

20- Petals spreading to about 30° from floral axis; flowers often slightly hourglass-shaped in lateral view, widest near base and slightly constricted to a "waist" near the apex of the sepals, then slightly expanded distally; Sierra Nevada from Sierra County south, California ..... *S. obtusatum*

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