Camissonia brevipes (A. Gray) Raven subsp. *brevipes*, from a watercolor by Henry R. Mockel, made near Palm Springs, Riverside County, California; original in the Hunt Botanical Library, Pittsburgh. Reproduced by permission of Mr. Mockel and the Hunt Botanical Library.

BULLETIN OF THE UNITED STATES NATIONAL MUSEUM

CONTRIBUTIONS FROM THE UNITED STATES NATIONAL HERBARIUM

VOLUME 37, PART 5

A REVISION OF THE GENUS CAMISSONIA (ONAGRACEAE)

By PETER H. RAVEN

SMITHSONIAN INSTITUTION PRESS • CITY OF WASHINGTON • 1969

For sale by the Superintendent of Documents, U.S. Government Printing Office
Washington, D.C. 20402 - Price $1.75

A REVISION OF THE GENUS CAMISSONIA (ONAGRACEAE)

By Peter H. Raven

Introduction

Camissonia is one of the better characterized genera of Onagraceae' tribe Onagreae. This tribe consists of 11 genera, more than half of the total for the family. Included in it are some 215 species, comprising about a third of the Onagraceae. My most recent synopsis of the genera and tribes of the family was presented in 1964 (Brittonia 16: 276) and listed 12 genera of Onagreae. Subsequently, a detailed study of the then monotypic genera *Gongylocarpus* and *Burragea* (Carlquist and Raven, Amer. Journ. Bot. 53: 378–390. 1966) has led to the conclusion that they should be merged. I would now list the genera of the tribe Onagreae as follows: *Gongylocarpus* (including *Burragea*), *Camissonia, Gayophytum, Xylonagra, Oenothera, Stenosiphon, Hauya, Calylophus, Gaura, Clarkia, Heterogaura.*

I cannot agree with Munz (N. Amer. Fl. II. 5: 53. 1965) as to the desirability of separating *Hauya* as a tribe distinct from the rest of the Onagreae solely because these plants have stipules. This appears to be an unwarranted emphasis of a single characteristic which would lead to a less realistic portrayal of affinities within the family. Indeed, the evidence seems to indicate clearly that *Hauya* is more closely related to the other genera of tribe Onagreae with divided sporogenous tissue—*Calylophus, Gaura, Clarkia,* and *Heterogaura*—than these genera are to the remainder of the tribe. It scarcely seems credible that the division of the sporogenous tissue of the anthers into packets, separated by sterile tissue, is a characteristic that arose more than once in the evolution of this group, and the combination of evening opening of the flowers (in *Hauya, Calylophus hartwegii* sens. lat., and most species of *Gaura*) with a broad, open hypanthium can hardly be dismissed as mere coincidence.

My own work on the genus *Camissonia* was initiated in August 1957 and has occupied much of my time since that date. It is based on the rich collections of this genus in the herbarium of the United States National Museum and other herbaria (listed below), as well as on extensive field studies throughout the area of the group. The first part of this work was published in 1962—a revision of the group then known as *Oenothera* subg. *Chylismia* (Univ. Calif. Publ. Bot. 34: 1–122). Subsequently, I became convinced that the species recently included in *Oenothera* could better be grouped as three genera: *Camissonia*, *Calylophus*, and *Oenothera*. I explained the reasons for this decision to Dr. Philip A. Munz, and he requested that I publish this material in synoptical form so that he could adopt the new generic delimitations for his forthcoming treatment of the family (N. Amer. Fl. II. 5: 79. 1965). Setting aside my work on the present revision, I prepared a synopsis of the species and the sectional classification of *Camissonia*, making new combinations when names were available and in general presenting a bare outline of my views on the species in this group, but without detailed justification. I did not, however, publish any new species for which names at some level were not already available. I made this manuscript available to Dr. Munz and proceeded to get the material into print as soon as possible (Brittonia 16: 276–288. 1964).

Soon after the article appeared, Dr. Munz informed me that he had changed his mind and would not accept my concepts of the genera involved. He did, however, accept every proposition I made about species, subspecies, and sections, making some dozens of transfers of these taxa to *Oenothera* without comment on or justification for their new status. I would naturally have preferred to make these changes in rank in the present paper, where they could be fully discussed and justified in detail. I have attempted to do this herein, even when the changes in status have been made earlier.

Delimitation of *Camissonia*

In order to evaluate the position of *Camissonia*, it is necessary to review some of the material I presented in 1964. *Clarkia*, recognized as a distinct genus by all authors for more than 50 years, is distinguished from *Oenothera* (in the broad sense of Munz) by two characteristics only: its possession of divided sporogenous tissue in the anthers and by the basal attachment of these anthers. But similarly divided sporogenous tissue is found in *Hauya*, *Gaura*, *Heterogaura*, and in that portion of *Oenothera* treated by Munz as the subgenera *Calylophus* and *Salpingia* and by me as the genus *Calylophus*. All of these genera are likewise similar in stigma morphology (Raven, Brittonia 16: 278. 1964) and in their broad, relatively long hypanthia. The evidence that they are a coherent group, with clear interrelationships, appears unequivocal.

There are two other distinctive groups of genera in the tribe Onagreae. The first consists of *Oenothera* (in the relatively narrow sense) and *Stenosiphon*, separated most obviously by the indehiscent, 1-seeded fruits of the latter. In these two genera, the stigma is of a type unknown elsewhere in the family: 4-lobed, without any disc at the base and the lobes receptive all around. The second group consists of the genera *Gongylocarpus*, *Xylonagra*, *Gayophytum*, and *Camissonia*, all consisting of plants with a capitate or hemispherical stigma of a sort widespread in the rest of the family, as well as relatively short hypanthia and flowers that open primarily in the morning.

Looking at the pattern of variation in the tribe from this vantage point, it is possible to recognize three distinct groups, the relationships between which are not close. In spite of its highly specialized fruits, it seems clear that *Gongylocarpus* includes the most generalized species found in the tribe. It is the only genus of the tribe that retains the original basic chromosome number for the family, $n=11$. It is further clear that the sort of capitate or hemispherical stigma found in this genus and in *Xylonagra*, *Gayophytum*, and *Camissonia* is primitive in the tribe and probably in the family as a whole. One other genus of the tribe, *Hauya*, has a similar hemispherical stigma; but in *Hauya*, as we have seen, the sporogenous tissue in the anthers is divided into packets by sterile tissue. *Hauya* is generalized in a number of respects: chromosome number ($x=10$), habit (shrubs or trees to more than 30 m. tall), and possession of stipules. Thus *Hauya* must represent a relatively early offshoot of the phyletic line that also gave rise to *Calylophus*, to *Gaura*, to *Clarkia*, and to *Heterogaura*. One could scarcely imagine that these groups gained their identical anther morphology independently, and we have mentioned their similar floral morphology and biology. The relationships of the group comprising *Oenothera* and *Stenosiphon* are obscure, although is it clear that they belong in the tribe Onagreae. At some point the ancestors of these plants made the transition to an evening-opening habit, with the deep, narrow hypanthia and expanded stigmatic surface characteristic of moth-pollinated plants in many families.

What then is the rationale for retaining *Oenothera*, *Camissonia*, and *Calylophus* in a single genus, when these three groups differ absolutely in anther morphology and stigma morphology, and modally in floral biology? At best, this can be justified only on historical grounds; there are no transitions between these three groups, no species are intermediate, and no confusion of delimitation exists. The characters used to separate the universally recognized genera *Clarkia*, *Gayophytum*, *Stenosiphon*, *Gaura*, *Heterogaura*, and *Xylonagra* are of the same sort as those which separate *Oenothera*, *Camissonia*, and *Calylophus*, and the groups delimited are clearly as meaningful and coherent phenetically. Of even more crucial importance, the evidence that these three genera are each more closely related to other genera than they are to one another appears overwhelming; not a single fact has been adduced in opposition to this view. If our taxonomy is to show anything whatsoever about the relationships of plants, there appear to be only two possible courses of action. One would result in the grouping of all genera of the tribe Onagreae, except *Hauya* and *Gongylocarpus*, into a single genus; the other is the generic treatment adopted here.

Historical and Taxonomic Considerations

A historical review of generic concepts in the tribe Onagreae was presented in 1964 (Raven, Brittonia 16: 276–288) and will not be repeated here. Many aspects of the taxonomic history of particular species groups are given in the general remarks on the sections concerned. A few general points are, however, germane.

The genus *Camissonia*, as delimited in this treatment, was first outlined in my 1964 paper. Indeed, *Camissonia* is a somewhat unfamiliar name, *Sphaerostigma*, *Taraxia*, *Eulobus*, and *Chylismia* being more frequently employed at the generic level for some of its constituent groups. Very few combinations under *Camissonia* were made prior to 1964; nevertheless, this does clearly seem to be the oldest generic name applied to the complex in question, antedating *Sphaerostigma* by 17 years. Although the name *Sphaerostigma* is more familiar, it has never been used in the inclusive sense of *Camissonia* as applied in the present monograph, and nothing seems to be gained by conserving it or any other junior synonym over *Camissonia*.

Most species of *Camissonia* are endemic to the Western United States, with three reaching adjacent Western Canada, a number in the bordering states of Mexico, and one in Western South America, whence the first known species, *C. dentata*, was described by Cavanilles in 1795. The increasing tempo of exploration of California and adjacent regions throughout the 19th century led to the discovery of most of the species known today. The first more or less synoptical treatment was that of Sereno Watson in his "Revision of the extratropical North American species of the genus *Oenothera*" (Proc. Amer. Acad. 8: 573–618. 1873); Watson's work was reasonable and conservative as to species delimitation. In 1896, John Kunkel Small published a review of the species under the title, "*Oenothera* and its segregates," Bull. Torrey Cl. 23: 167–194. 1896. This was an exceedingly uncritical treatment at both specific and generic levels, replete with new combinations and hasty, superficial judgments. Starting six years later, Hector Léveillé confused the taxonomy of *Oenothera* and related groups to an unprecedented degree by publishing his "Monographie du Genre *Onothera* (1902–1913)." Léveillé was surely one of the most erratic taxonomic workers ever to publish a large amount of material, and it is unfortunate that he concentrated so much of his effort on *Oenothera*; his illustration of an annual member of the Polygonaceae, facing p. 167 of his Monographie, labeled "*Onothera gracilis* (Philippi) Lévl." is merely one example of his notoriously superficial work. Aven Nelson remarked about Léveillé's efforts in 1905 (Bot. Gaz. 40: 54. 1905), "It is extremely difficult to believe that his grouping of the specimens can stand, especially when one finds that the annotations do not harmonize with the final published list, and that the nomenclature of the illustrations in some instances does not coincide with that of the text."

Nelson did not help matters much in his review of *Sphaerostigma*, presented as "Contributions from the Rocky Mountain Herbarium. VI." (Bot. Gaz. 40: 54–63. 1905), for this was again a relatively uncritical listing of species which did not advance the understanding of the group to any marked degree. On the other hand, this paper did, for the first time, have the advantage of some knowledge of the plants in the field, and it probably represents an improvement over the efforts of Small and Léveillé, if not those of Watson.

In 1928, when P. A. Munz instituted his invaluable monographic series on *Oenothera*, there were probably few groups of plants in the United States for which the taxonomy was more confused. The conservative approach used in Munz' revisions of *Oenothera* subg. *Chylismia* (Amer. Journ. Bot. 15: 223–240. 1928), *Sphaerostigma* (Bot. Gaz. 85: 233–270. 1928), and *Taraxia* and *Eulobus* (Amer. Journ. Bot. 16: 246–257. 1929) brought a remarkable degree of order out of a tremendously confused situation. These three papers provided a sound basis for the accumulation of knowledge about the plants here treated as *Camissonia* which has served very well for some 40 years.

It is instructive to consider how and why the present revision differs from them. Munz recognized 32 species; the present paper includes 61. Both, coincidentally, recognize 29 major infraspecific taxa. Thus the number of species has nearly doubled in the 40 years. One obvious reason for this change has been the accumulation of additional herbarium material during the intervening years. In 1929 Munz had available 13 collections of the three species of sect. *Eulobus* endemic to Baja California; I have been able to study well over a hundred. That this has not been the primary reasons for the recognition of more species, however, is suggested by the fact that in this section, for all the accumulation of additional information, the taxonomy has remained unchanged.

A much more important reason for the recognition of more species now than in 1928–9 has been the accumulation of additional information. First has been chromosomal information so vital to an understanding of the polyploid complexes which sect. *Holostigma* and sect. *Camissonia* have proved to be. It is not surprising that some of the most dramatic inflations in species number have taken place in these groups, 4 species and 7 additional varieties in the former being recognized here as 14 species with 3 additional subspecies, and 2 species with 6 additional varieties in the latter being recognized here as 12 species with 4 additional subspecies. These changes have been made largely to accommodate the distinctive population systems that have been revealed by chromosomal information, although a few of the taxa recognized were unknown or uncollected in 1929. A second sort of information concerns the breeding systems of the plants concerned; thus series of populations consisting of relatively large-flowered, often self-incompatible individuals are routinely separated at present from their relatively small-flowered, autogamous relatives at the specific level, whereas in 1929 the biological significance of such distinctions was largely unknown to or not appreciated by taxonomists.

The most important changes in taxonomy in the past 40 years, however, have been philosophical. In 1929, degree of difference or similarity was the aspect of variation patterns stressed most in making taxonomic decisions. In 1968, the pattern itself was stressed, with discontinuities in the pattern of variation being emphasized as much as or in some instances even more than the degree of similarity between the two populations being compared. In 1929 relatively similar populations were often grouped as varieties of a single species regardless of whether they intergraded or remained completely distinct in nature. Very different plants were separated at the species level even if they intergraded completely and numerous intermediates were represented in the material being studied. The taxon here called *Camissonia pubens* was formerly considered a variety of *Oenothera contorta* (Munz, Bot. Gaz. 85: 254. 1928), even though no intermediates were found or expected; on the other hand, the taxa here called *Camissonia boothii* subsp. *desertorum* and subsp. *alyssoides*, being quite different, were considered to belong to distinct species, even though it was noted that the former "grades . . . insensibly . . ." (Munz, Bot. Gaz. 85: 246. 1928) into the latter. Neither treatment reflects more information about the systems of populations being classified, or is "better"; rather, each is in accordance with the taxonomic spirit of the times in which it was constructed. As usual, one must turn to the presentation of data on which the taxonomy is based to learn anything about the pattern of variation that underlies the taxonomy; the mere recognition of taxa conveys only a strictly limited amount of information about the organisms being classified. Either sort of taxonomic philosophy might be used to construct a useful classification if the facts on which it was based were correct and well ordered; neither could be so used if the facts were incorrect or poorly aligned with one another. In the final analysis, all one can ask of a taxonomic system is that the populations classified as lower level taxa be more similar to one another (in some respect) than are the populations classified as higher level taxa. Thus one would logically expect two subspecies to be more similar to one another than two species in the same group; whether this is true or not will depend on the perceptiveness of the taxonomist making the classification and on the information available to him.

There is more unanimity about another philosophical difference between the taxonomy of 40 years ago and the taxonomy of the present. In 1929, it was considered quite acceptable to give names to infraspecific taxa which were based on genetically different members of Mendelian populations, providing that one wished to emphasize the differences between them. The denial of John Ray's 17th-century dictum about the construction of taxa implicit in the taxonomic recognition of such segregating entities went largely undetected until the 1930s, when populations and not individuals were clearly established as the units of biological classification. In general, taxonomists intentionally have not given different formal names to the progeny of a single individual or pair of individuals, no matter how different these might be, and this has been the prevalent tradition for some 300 years. In part, of course, the recognition of such entities as varieties sometimes happens when insufficient information is available; but in the 1920s such a taxon as *Oenothera cheiranthifolia* var. *nitida* could be recognized as distinct, basically because "the aspect of a wholly glabrous plant is quite different from that of a very hairy one . . ." (Munz, Bot. Gaz. 85: 270. 1928), even though such plants were well known to occur as segregating elements in normal populations. Most taxonomists would not at present accord formal recognition to such an entity.

The desire to give formal taxonomic names to distinct populations only and not to the genetically distinctive elements in such populations underlies the modern preoccupation with the geographical race as the only infraspecific entity worthy of recognition, a tendency that was apparent more than a century ago. Many taxonomists of the present day formally recognize only geographic races below the species level, although this may sometimes pose difficulties when the organisms being classified are largely or wholly autogamous.

Subspecies are used herein as the only infraspecific taxon for the following reasons. The Code states explicitly that subspecies are the primary unit into which species are divided, and it is therefore incorrect to use any other infraspecific taxon, such as variety, for the primary division of a species. From a formal standpoint, there is much to recommend Pennell's (Amer. Journ. Bot. 36: 1922. 1949) suggestion to treat subspecies and varieties as synonymous, to use the former word in scientific nomenclature and to relegate the latter to informal usage, where the term "variety" has already gained a multiplicity of meanings quite inconsistent with its employment as a scientific term. Should such a suggestion be adopted, the nomenclatural problem would be simplified and the number of new combinations greatly reduced. A tendency toward the recognition of only one level of taxa below the level of species is already apparent in Europe. For me, the recognition of more than one such level implies a degree of precision in the understanding of relationships which often becomes ludicrous. As H. L. Mason has often emphasized, two of any three taxa will always be more closely related to one another than they are to the third; but is it practical to recognize all such shades of relationship in our formal taxonomy, even if it were possible to ascertain the facts of the case unequivocally? I personally feel that the adoption of the trinomial system in zoology at an early date was a sound solution of this particular problem of nomenclature. I hope that botanists may ultimately adopt such a system and consider it desirable meanwhile for names at both varietal and subspecific levels to be considered for purposes of priority at either one, even though it is not technically necessary to do so.

In the present revision, I have tried to indicate in the synonymy how the concepts of Munz can be integrated with my concept. I have not given references to other taxonomic papers, since this has been done by Munz in his revisions, which have been the only important basis of classification of the groups for some 40 years. I have, however, given full synonymy and citation of types in all cases. Specimens are not cited here for many of the taxa treated in the same sense in which they were understood by Munz; the ranges of such taxa are already sufficiently documented in the literature. For sects. *Chylismia*, *Lignothera*, and *Chylismiella* I have not cited specimens or given distribution maps, since this information has been presented in my earlier revision (Raven, Univ. Calif. Publ. Bot. 34: 1-122. 1962).

Geographical Distribution

Camissonia is primarily a group of the Western United States and adjacent Mexico, although a few autogamous species extend beyond this area. Three species—*Camissonia andina*, *C. breviflora*, and *C. contorta*—are found in the southern part of Western Canada; all of them are autogamous. On the other hand, 79 of the 90 taxa recognized in this revision are found in California, and 21 are endemic to the State (12 other endemics just reach southern Oregon or northwestern Baja California). Three of the four species of *Camissonia* sect. *Eulobus* are endemic to Baja California, as are *C. cardiophylla* subsp. *cedrosensis* (technically also found in Sonora because of its occurrence on Isla Tiburón), *C. claviformis* subsp. *wigginsii*, *C. proavita*, and *C. guadalupensis* subsp. *guadalupensis*, the last two in the California floristic region. No taxon is endemic to Sonora, although eight occur there, and *C. californica* and *C. chamaenerioides* range widely in the State. No species of *Camissonia* is known from Chihuahua, although *C. chamaenerioides*, the only species of the genus that occurs in Texas, may well occur there. Only two species, *C. chamaenerioides* and *C. scapoidea* subsp. *scapoidea*, are definitely known to occur in New Mexico, although *C. refracta* may also occur in that State.

In Arizona, 27 taxa occur, and *C. palmeri* and *C. strigulosa* might also be represented. Of these, *C. claviformis* subsp. *peeblesii*, *C. speculicola* subsp. *hesperia* and subsp. *speculicola*, *C. confertiflora*, *C. scapoidea* subsp. *macrocarpa*, and *C. exilis*, all belonging to sect. *Chylismia*, are endemic. In Colorado, only *C. walkeri* subsp. *walkeri*, *C. eastwoodiae*, and *C. scapoidea* subsp. *scapoidea* of sect. *Chylismia*, *C. parvula* of sect. *Camissonia*, and *C. breviflora* and *C. subacaulis* of sect. *Tetrapteron* are known, and only *C. scapoidea* occurs east of the Rocky Mountains. Utah has 22 taxa, none endemic, and Nevada has 33, with *C. nevadensis* and *C. megalantha* well-marked endemics. In Wyoming, *Camissonia scapoidea* subsp. *scapoidea*, *C. subacaulis*, *C. breviflora*, *C. parvula*, *C. minor*, and *C. andina*, all autogamous, are found, with only *C. subacaulis*, *C. breviflora*, and *C. andina* reaching Montana. Idaho has 13 taxa, Oregon 18, and Washington 10; *Camissonia hilgardii* is virtually endemic to Washington and *C. pygmaea* endemic to the 3-State area.

It is evident, therefore, that *Camissonia* centers in the California floristic area, where the plants chiefly occur in plant associations derived from the Madro-Tertiary Geoflora. Sect. *Holostigma*, with 14 species and 3 additional subspecies, is virtually endemic to this region, as is the close-knit group of 11 taxa comprising species 44–51 of sect. *Camissonia* (this latter group also including the only South American species, the autogamous *C. dentata*). Two other sections (*Chylismia* and *Eremothera*) and the four taxa comprising species 40–43 of sect. *Camissonia* center in the Great Basin and adjacent deserts to the south, as does the monotypic sect. *Chylismiella*. Sect. *Nematocaulis*, comprising two closely related species, is associated with the high, cold deserts north of the Great Basin, and sect. *Tetrapteron*, while probably radiating from floristic regions similar to those represented in cismontane California at the present day, has also radiated in the mountains and deserts of these northern regions. Sect. *Lignothera* has its maximum diversity in the deserts and mountains about the head of the Golfo de California. Finally, sect. *Eulobus*, small but phylogenetically crucial, is primarily associated with the peninsula of Baja

California, well known as one of the most important refugia in the southern part of North America, where it is associated with *Gongylocarpus fruticulosus* (Benth.) T. S. Brandegee, perhaps the most generalized species of the tribe Onagreae surviving at the present day.

Phylogenetic Relationships

In the light of information presented up to this point, what can be said about the relationships of the sections of *Camissonia?* First of all, the nine sections I have recognized are sharply distinct from one another, and there are no transitions between them. Their association into phylogenetic lines or circles of affinity is extremely problematical, and there seems to be absolutely no advantage to be gained by grouping them into subgenera as has been done by Munz (N. Amer. Fl. II. 5: 142–177. 1965); indeed, I would hold that such an association of the sections into artificial groupings is misleading. *Camissonia* is clearly the most heterogeneous of the 11 genera of the tribe Onagreae, and its sections are amply differentiated. Keeping these facts in mind, it is possible to offer a few deductions about the phylogeny of the group and the relationships of its constituent parts.

We have already seen that the genus *Gongylocarpus* comprises the most generalized species in the tribe, and it appears reasonable to use it as a standard for examining phylogenetic relationships in *Camissonia*. The other two genera closely related to *Camissonia*—*Xylonagra* and *Gayophytum*—do not appear to offer much guidance in this respect; although, as we shall see, the restriction of the monotypic *Xylonagra* to central Baja California may well be significant. Within *Gongylocarpus*, the low shrub *G. fruticulosus* is clearly more generalized, in view of its self-incompatibility, woody habit, and large flowers, than the wide-spread autogamous *G. rubricaulis* Schlecht. & Cham. (Carlquist & Raven, Amer. Journ. Bot. 53: 378–390. 1966). *Gongylocarpus fruticulosus* is restricted to two adjacent islands in Bahía Magdalena, southern Baja California, where it is locally abundant.

Geographically, it is clear that *Camissonia* sect. *Eulobus*, the only section of the genus centering in Baja California, where three of its four species are endemic, deserves special attention. One of its species, *Camissonia crassifolia*, has the woodiest habit of any *Camissonia*; also the section shares with *Gongylocarpus* the fleshy disc within the hypanthium which is, among the members of tribe Onagreae, known only in these two genera. Thus the woody habit, the fleshy disc in the hypanthium, and a common habitat in the Baja California littoral all link *Gongylocarpus fruticulosus* with *Camissonia crassifolia*, and I believe the latter to be the most generalized extant species of its genus.

Within *Camissonia*, pinnately lobed or divided leaves are found only in sect. *Eulobus*, sect. *Chylismia*, and sect. *Tetrapteron*, and the members of the latter group are the only species of *Camissonia* which share with sect. *Eulobus* a fleshy disc closing the hypanthium. The relationship between *Eulobus* and *Chylismia* is obviously close; indeed, the basal rosette of *Camissonia californica* (which normally withers by the time the plants flower) is often virtually indistinguishable from that of *C. multijuga*, one of the more generalized species of sect. *Chylismia*. One of the most interesting lines of evidence for a close relationship between these three groups, however, has been developed recently; in some species of each most of each petal is strongly ultraviolet reflective, as usual in the genus, but the basal portion is occupied with a conspicuous, nonultraviolet-reflecting spot which is invisible to the human eye but can be photographed with special techniques (D. P. Gregory and P. H. Raven, MS.). No such nonultraviolet-reflecting areas have been found on the petals of outcrossing species of sect. *Holostigma*, sect. *Camissonia*, or sect. *Eremothera*, and in the first two examples, the place of this nonultraviolet-reflecting spot is obviously taken by the one or two large, bright brownish-red dots at the base of each petal, which doubtless serve the same function as nectar guides. The species of sects. *Chylismia* and *Tetrapteron* that have the nonultraviolet-reflecting spots have petals that appear clear, bright yellow and unspotted to the human eye, whereas those of sect. *Eulobus* have a distinctive, fine red flecking throughout the nonultraviolet-reflective area.

In summary, I hold that sect. *Eulobus* is the most primitive group within the genus *Camissonia*, and that from plants similar to this group were derived the ancestors of sect. *Chylismia*, which radiated into the deserts and later gave rise to the small section *Lignothera*, specialized for pollination by hawk moths. Also from plants similar to sect. *Eulobus*, the species of sect. *Tetrapteron*, which became associated with more mesic habitats, were derived. Presumably among the most primitive species of sect. *Holostigma* is *Camissonia cheiranthifolia*, the only woody or even perennial species found among the last five sections of the genus as I have arranged it here. These sections were probably also derived from plants similar to those of sect. *Eulobus*. All species of these five relatively advanced sections have simple leaves that are never lobed (at the most coarsely serrate); none has a disc in the hypanthium; and none has a nonultraviolet-reflective area on the petal, so far as known.

Evident shifts from the perennial to the annual habit have characterized the first five sections listed here (the last four are strictly annual); these shifts have usually been accompanied by a change from self-incompatibility to self-compatibility. Self-incompatible species are distributed among the nine sections of *Camissonia* as follows:

	Self-incompatible species	*Self-compatible species*	*Total*
I. *Eulobus*	2	2	4
II. *Chylismia*	[a] 7	6	13
III. *Lignothera*	–	2	2
IV. *Tetrapteron*	[b] 2	[c] 4	6
V. *Holostigma*	[d] 2	12	14
VI. *Camissonia*	2	10	12
VII. *Eremothera*	2	[e] 5	7
VIII. *Chylismiella*	–	1	1
IX. *Nematocaulis*	–	2	2
	17	44	61

[a] *C. confertiflora*, *C. eastwoodiae*, and *C. parryi* not tested but listed here provisionally.
[b] *C. tanacetifolia* seems to include self-compatible populations.
[c] Some populations of *C. subacaulis* might be self-incompatible.
[d] *C. cheiranthifolia* subsp. *suffruticosa* in part only; subsp. *cheiranthifolia* wholly self-compatible.
[e] *C. nevadensis* might be self-incompatible, but this seems unlikely.

Of the nine sections recognized in this revision, three small ones contain no self-incompatible species; one (*Chylismia*) consists mainly of self-incompatible species; and the other five contain one or two self-incompatible species each, with a majority of self-compatible ones. It is interesting that of the two groups associated with the most severe desert, *Chylismia* and *Eremothera*, the former is the only section in which as many as half of the species, including nearly all of the common ones, are self-incompatible, and the most widespread species of the latter, *Camissonia boothii*, is likewise self-incompatible. One normally associates exploitation of a desert habitat with self-compatibility or autogamy, but this has evidently not been the case here; perhaps the ability to adjust to the rapidly shifting desert habitats calls for a maximum of recombination, and this is precisely what seems to be favored in both groups, which conform to the definition of homogamic complexes (Raven, Univ. Calif. Publ. Bot. 34: 66–67. 1962).

If pinnately lobed or divided leaves are primitive for the genus *Camissonia*, as the evidence appears to indicate, there have been evolutionary trends toward simple leaves in sect. *Eulobus* (where some populations of *Camissonia crassifolia*, such as those on Isla de Cedros, have lobed leaves, while most others have entire leaves) and sect. *Chylismia* (where lobed or divided leaves predominate, although some species have lost them). Sect. *Lignothera* appears to be a derivative of sect. *Chylismia*, specialized for hawk-moth pollination in its long hypanthia, the longest in the genus. In the two species comprising this group, the pollen is shed in tetrads, a characteristic otherwise unknown in the tribe Onagreae. In sect. *Tetrapteron*, *Camissonia tanacetifolia* and

C. breviflora are characterized by deeply lobed leaves, as are some populations of *C. subacaulis;* whereas the remaining perennial species, *C. ovata*, has entire leaves, as do the two annuals. The superficial similarity between these two annual members of sect. *Tetrapteron* and some species of sect. *Holostigma* provides a clue as to the relationships of the latter group, but probably tells us nothing about the exact route of its derivation.

Within the last five groups listed here, relationships are almost entirely obscure. Sect. *Holostigma* includes the only perennial species and perhaps is morphologically the most generalized of the five sections. There does not, however, appear to be any evidence for close relationship between this group and any other. Sect. *Camissonia* consists entirely of yellow-flowered species, like sect. *Holostigma;* but no species are transitional between the two groups and there is no evidence for close relationship between them. Polyploidy is important in both of these sections, which have diversified largely in the areas derived from the Madro-Tertiary Geoflora and now center in California, with one group of sect. *Camissonia* (species 40–43) centering in the northern Great Basin. Sect. *Eremothera*, consisting of white-flowered species, does not exhibit any evident relationship to any other group, and it seems certain that white-flowered species evolved at least three times in the history of the genus, once here, once in *C. claviformis* (sect. *Chylismia*), and once in *C. pterosperma* (the only species of sect. *Chylismiella*). In the first two instances, the acquisition of white flowers was undoubtedly associated with a shift from bee-pollination to pollination by small moths.

Almost nothing can be said about the relationships of the last two small sections, *Chylismiella* (with one species) and *Nematocaulis* (with two very closely related ones). The white petals of the former, yellow at the base, are found elsewhere in the tribe only in the genus *Gayophytum;* the seeds of *Camissonia pterosperma*, the only species of this section, are unique in the family. Likewise, the flattened capsules of both species of sect. *Nematocaulis* are reminiscent of those of *Gayophytum humile* A. L. de Jussieu, probably the most generalized species of its small genus (Lewis & Szweykowski, Brittonia 16: 343–391. 1964). It appears possible that these two small, distinctive sections of *Camissonia* have been derived from the same evolutionary line that gave rise to *Gayophytum*, but nothing more can be said about their relationships at this time.

Pollination Systems

Most outcrossing species of *Camissonia* are pollinated by bees, and a number of these bees are oligolectic, gathering pollen from no other plants (Linsley, MacSwain, & Raven, Univ. Calif. Publ. Entom.

33: 1–98. 1964). One group of two species, sect. *Lignothera*, has shifted to opening in the evening, when the plants are pollinated by hawk moths; these species have yellow flowers. The outcrossing species of the entirely white-flowered sect. *Eremothera* and the white-flowered and afternoon opening yellow-flowered subspecies of *Camissonia claviformis* (sect. *Chylismia*) are predominantly pollinated by small moths after their opening in the late afternoon or early evening, but in both groups secondary associations with oligolectic bees in the late afternoon have also evolved (Linsley et al., op. cit.). Two species of sect. *Chylismia, Camissonia megalantha* and *C. heterochroma*, are unique in the genus in having purple flowers. In both, the flowers open near sunrise; the former species is pollinated by bees, and the latter is autogamous. Finally, *C. pterosperma* has white petals that are yellow at the base and flowers that open in the morning. This pattern of petal coloration is found elsewhere in the tribe only in *Gayophytum*, where pollination by flower-flies and small bees predominates (MacSwain, Raven, & Thorp, MS.); but *Camissonia pterosperma* is largely if not entirely autogamous.

One of the most interesting aspects of the pollination system in *Camissonia*, and indeed in the Onagraceae as a whole, is the common occurrence of pairs of species—one member large-flowered and outcrossing (and sometimes self-incompatible), the other small-flowered and self-pollinating (and often a polyploid or complex structural heterozygote, depending on the group). In *Camissonia*, many examples of such pairs are evident: *C. multijuga-C. walkeri* subsp. *tortilis* (sect. *Chylismia*); *C. tanacetifolia-C. breviflora* (sect. *Tetrapteron*); *C. bistorta-C. lewisii* (sect. *Holostigma*); *C. kernensis* subsp. *kernensis-C. pubens* (sec. *Camissonia*); *C. refracta-C. chamaenerioides* (sect. *Eremothera*); and *C. hilgardii-C. andina* (sect. *Nematocaulis*). Autogamy doubtless arises with a certain frequency throughout the range of normally outcrossing species, but if it is to spread and become characteristic of entire populations, it must do so because it provides for the duplication of a genotype that is highly successful in some area. This has obviously occurred time after time in the evolution of the genus *Camissonia*.

Chromosome Numbers and Behavior

The earlier reports of chromosome number listed by Lewis, Raven, Venkatesh, and Wedberg (Aliso 4: 73–76. 1958) and those of Gregory and Klein (Aliso 4: 505–521. 1960) are repeated in this paper. On the other hand, the numerous chromosome counts I reported earlier for taxa of sect. *Chylismia, Lignothera*, and *Chylismiella* (Raven, Univ. Calif. Publ. Bot. 34: 1–122. 1962) are not included in this revision, although a few more recent determinations of chromosome numbers for these groups are reported. The only other familiar reports of chromosome number in *Camissonia* are six undocumented counts listed by Johansen (Proc. Nat. Acad. Sci. U.S. 15: 882–885. 1929; Amer. Journ. Bot. 16: 595–597. 1929), without citation of locality or voucher, and the single, probably erroneous count reported by Bell and discussed below. Johansen's counts are mentioned in the accounts of the taxa to which they refer.

Aneuploidy is almost unknown in *Camissonia* and rare in the tribe Onagreae. Only in *Clarkia* (with basic chromosome numbers of $x=5$ 6, 7, 8, and 9) does aneuploidy seem to be a regular feature of the evolutionary pattern which often accompanies speciation. In *Camissonia*, at least two populations of the South American tetraploid *C. dentata* have $n=13$ instead of the usual $n=14$; this appears to be the only documented instance of aneuploidy in the genus. In these populations, aneuploidy does not appear to have had any important bearing on speciation. Bell (Sida 2: 169. 1965) reported $n=6$ in *Camissonia claviformis* subsp. *peeblesii* ("*Oenothera clavaeformis* var. *aurantiaca*") from Maricopa County, Arizona (*Bell* 17558, NCU). In the drawings made from the original preparations, however, which Dr. Bell has kindly allowed me to examine, it appears that $n=7$ is as likely a count as $n=6$. All other individuals of this species that have been examined cytologically (a total of 411) have had $n=7$.

Although detailed information about chromosome number and behavior is given throughout the text of this paper and in the appendix, and summaries are given for each section, it seems worthwhile to summarize the chromosomal information available for *Camissonia* at this point, as follows:

	Individuals	*Populations*	*Species*	*Additional subspecies*	*Polyploid taxa*	
					wholly	*partly*
I. *Eulobus*	108	78	4			1
II. *Chylismia*	683	239	13	14		2
III. *Lignothera*	36	23	2	2		
IV. *Tetrapteron*	49	46	6	1	1	1
V. *Holostigma*	389	335	14	3	5	
VI. *Camissonia*	192	181	12	4	[a] 9	
VII. *Eremothera*	67	57	7	5		1
VIII. *Chylismiella*	1	1	1			
IX. *Nematocaulis*	11	11	2		1	
	1536	971	61	29	16	5

---

[a] Including two Chilean populations of *C. dentata* subsp. *dentata* with $n=13$.

As can be seen from the table, the chromosomal sampling of *Camissonia* has been extensive. Counts are available for at least one population representing each of the nine sections, and for every species and subspecies except the following: *Camissonia confertiflora*, *C. speculicola* subsp. *hesperia*, and *C. scapoidea* subsp. *macrocarpa*, and subsp. *utahensis* of sect. *Chylismia*, and *C. gouldii* of sect. *Ere-*

mothera. Thus 59 of the 61 species recognized here and 85 of the 90 taxa have been examined cytologically. It seems unlikely that the pattern will be modified in any substantial way by further chromosome counts.

The polyploid plants examined in sect. *Eremothera* and sect. *Tetrapteron*, as well as the polyploids of *Camissonia walkeri* (sect. *Chylismia*), are clearly cytologically autopolyploid, with rings of chromosomes forming regularly at meiotic metaphase I. The hexaploid in sect. *Tetrapteron* has almost certainly been derived directly from the tetraploid; these two races are regarded as subspecies of *C. tanacetifolia*. The single diploid plant of this species that has been examined may well have been derived directly from a tetraploid individual as discussed in detail following the taxonomic treatment of the species.

With one possible exception (see appendix) no rings of chromosomes have been observed in the polyploids of sect. *Holostigma* and sect. *Camissonia*, and polyploidy has played the most important role in these two groups in the course of evolution. The same is true of the polyploids of sect. *Nematocaulis*. Morphological and geographical relationships make it virtually certain that the tetraploid populations in *C. californica* (sect. *Eulobus*) and in *C. scapoidea* subsp. *scapoidea* (sect. *Chylismia*) have had an autotetraploid origin, even though they do not form rings of 4 chromosomes at meiotic metaphase I. In all of these groups the chromosomal homology of the diploid entities (see below) makes it clear that the formation of multivalents in polyploids is genetically controlled, and prevented even if the diploid genomes present in a polyploid are largely homologous. In the further interpretation of these data, it is instructive to consider the occurrence of translocation heterozygotes in naturally occurring diploid populations of these sections. It is important to stress the occurrence of such heterozygotes in outcrossing taxa, as rings of chromosomes tend to be eliminated relatively rapidly in the course of autogamous reproduction, except in the special case of balanced structural heterozygosity.

In sect. *Chylismia*, translocation heterozygotes comprised about 20 percent of the individuals examined (Raven, Univ. Calif. Publ. Bot. 34: 40. 1962), and the more limited amount of information available for sect. *Eremothera* suggests that a comparable level of heterozygosity may obtain here also. In one plant of *Camissonia refracta*, a member of this section, a ring of 10 chromosomes was found at diakinesis; this was the largest ring found in the genus. The situation in other well-sampled groups is, however, very different. In sect. *Camissonia*, only about 2 percent of the outcrossing individuals examined had a ring of chromosomes at meiotic metaphase; and in sect. *Holostigma* and sect. *Eulobus*, no multivalents have been observed, even though approximately 500 plants of the two groups have been examined. Even if reciprocal translocations occur frequently in these sections, they must be eliminated rapidly from the populations.

One naturally associates the frequent occurrence of reciprocal translocations within the populations of a species with the role of such translocations in the differentiation of species in the same group. It might therefore be expected that patterns of chromosomal differentiation between species would be different in sect. *Chylismia* from those observed in sects. *Holostigma* and *Camissonia.* This does not, however, appear to be the case; interspecific hybrids in all three groups show chromosomal configurations which indicate that their parents differ by, usually, 2–4 reciprocal translocations. Thus the appearance of reciprocal translocation configurations at a high frequency within the populations of a species may have little to do with the patterns of differentiation between populations of the group. In all three sections, there is a high degree of chromosome association in diploid interspecific hybrids; hence, the control of multivalent formation in polyploids must have a genetic basis and not be related, for example, to the frequent formation of univalents in interspecific hybrids in some of the groups. It may be significant, however, that pair-forming polyploids are frequent and evolutionarily important in those sections in which reciprocal translocations are infrequent or rare in natural populations, and virtually absent in those groups in which reciprocal translocations are abundant in natural populations.

Finally, sect. *Chylismia* is the only group of the genus in which supernumerary chromosomes have been noted. Here, one or more supernumeraries were found in some 3.7 percent of the nearly 700 individuals examined (Raven, Univ. Calif. Publ. Bot. 34: 41. 1962), this observation according well with an earlier hypothesis of a causal relationship between translocation heterozygosity and supernumerary formation (Lewis, Evolution 5: 142–157. 1951; Lewis & Raven, Rec. Adv. Bot. 1466–1469. 1961). Supernumeraries might be expected to occur in sect. *Eremothera* if more extensive sampling was carried out.

Acknowledgments

I am most grateful to Harlan Lewis for suggesting this study initially and supporting it in its early stages, as well as for many useful discussions subsequently; to Lee W. Lenz, Director, Rancho Santa Ana Botanic Garden, for extensive support of the work during the time I was employed at the Garden (1961–62); and to the National Science Foundation for GB–141 (1962–65), which allowed the completion of this project. Philip A. Munz has generously shared his wide experience of the family with me throughout the course of the work.

The Plant Biology Station of the Carnegie Institution of Washington, Stanford, has most kindly allowed the use of their facilities in cultivating selected strains of *Camissonia* during the past five years. Most of the illustrations and all of the maps were prepared by Marilyn Wright, while Joan Burger provided the drawings of sect. *Holostigma*. I am grateful to Mr. Henry R. Mockel, Twentynine Palms, Calif., and to George H. M. Lawrence, Director of the Hunt Botanical Library, Pittsburgh, for permission to reproduce Mr. Mockel's attractive watercolor (frontispiece) of *Camissonia brevipes* subsp. *brevipes*. Figures 57 and 63 are drawn on a base map kindly supplied by the California Insect Survey. Dennis E. Breedlove supplied expert technical assistance in growing the plants, hybridizing them, and determining chromosome numbers, especially during the years 1963–64.

Many individuals have contributed special materials for this study, comprising either herbarium specimens, seeds, or fixed buds for cytological study. Extensive collections were presented by Reid V. Moran and Dennis E. Breedlove, and other material collected especially for this purpose was generously donated by E. R. Blakley, D. P. Gregory, W. Klein, H. Lewis, Mildred E. Mathias, P. A. Munz, R. Ornduff, C. L. Porter, C. F. Smith, H. J. Thompson, E. C. Twisselmann, Frank Vasek, and H. L. Wedberg. Clare Hardham has provided a large number of interesting collections and done much to expedite my field studies in northern San Luis Obispo and southern Monterey Counties, California.

I am also most grateful to the curators of the following herbaria, from which material has been supplied for this study: University of New Mexico, Albuquerque (UNM); Sul Ross State College, Alpine, Texas (SRSC); Iowa State College, Ames (ISC); University of Michigan, Ann Arbor (MICH); University of Texas Herbarium, Austin (TEX); University of California, Berkeley (UC); Jepson Herbarium, Berkeley (JEPS); University of Colorado, Boulder (COLO); Montana State College, Bozeman (MONT);. Gray Herbarium, Harvard University (GH); Field Museum of Natural History, Chicago (F); Pomona College (POM); Rancho Santa Ana Botanic Garden, Claremont, Calif. (RSA); Tracy Herbarium, Texas A & M University, College Station (TAES); Instituto de Biología, Concepcíon, Chile (CONC); Botanical Museum and Herbarium, Copenhagen (C); Oregon State University, Corvallis (OSC); Herbarium of Southern Methodist University, Dallas, Texas (SMU); University of California, Davis (DAV); Royal Botanic Garden, Edinburgh (E); University of Oregon, Eugene (ORE); Colorado State University, Fort Collins (CS); Fresno State College, Fresno, California; Grand Canyon National Park, Arizona; Royal Botanic Gardens, Kew (K); Rocky Mountain Herbarium, University of

Wyoming (RM); Herbarium of the Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad (LE); Intermountain Herbarium, Utah State Agricultural College (UTC); British Museum (Natural History), London (BM); University of California, Los Angeles (LA); Los Angeles County Museum (LAM); University of Wisconsin, Madison (WIS); Tulane University Herbarium, New Orleans (NO); The New York Botanical Garden (NY); University of Notre Dame (ND): National Museum of Canada, Ottawa (CAN); Plant Research Institute, Canada Department of Agriculture, Ottawa (DAO); University of Oxford (OXF); Muséum National d'Histoire Naturelle, Paris (P); Academy of Natural Sciences, Philadelphia (PH); Idaho State College Herbarium, Pocatello (IDS); Brigham Young University, Provo, Utah (BRY); Washington State University, Pullman (WS); University of Nevada, Reno (RENO); Nevada Agricultural Experimental Station, Reno; Missouri Botanical Garden, St. Louis (MO); Peck Herbarium of Willamette University, Salem, Oregon; University of Utah, Salt Lake City (UT); San Diego Museum of Natural History (SD); San Diego State College (here given as SDSC); California Academy of Sciences, San Francisco (CAS); California State Polytechnic College, San Luis Obispo (OBI); Santa Barbara Botanic Garden, Santa Barbara, California (SBSG); Santa Barbara Museum Of Natural History (SBM); University of California, Santa Barbara (UCSB); Museo Nacional de Historia Natural, Santiago, Chile (SGO); University of Washington, Seattle (WTU); Dudley Herbarium, Stanford University, Stanford, California (DS); New Mexico College of Agricultural and Mechanical Arts, State College (NMC); Naturhistoriska Riksmuseum, Stockholm (S); Desert Botanical Garden, Tempe, Arizona (DES); University of British Columbia, Vancouver, British Columbia (UBC); U.S. National Museum, Washington (US); U.S. National Arboretum, Washington (NA). In addition, I have examined the material of *Camissonia* in the private herbarium of Ernest C. Twisselmann, Cholame, California.

Systematic Treatment

Camissonia Link

Camissonia Link, Jahrb. Gewaechsk. 1: 186. 1818.

Sphaerostigma (Seringe) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 49. 1835. Based on *Oenothera* sect. *Sphaerostigma* Seringe, *in* DC., Prod. 3: 46. 1828. Lectotype: *O. dentata* Cav.= *Camissonia dentata* (Cav.) Reiche.

Agassizia Spach, Hist. Veg. Phan. 4: 347. 1835; not Chavannes 1830. Type: *A. cheiranthifolia* (Hornem. ex Spreng.) Spach=*Camissonia cheiranthifolia* (Hornem. ex Spreng.) Raimann.

Holostigma Spach, Nouv. Ann. Mus. Paris III. 4: 332. 1835.

Eulobus Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 514. 1840. Type: *E. californicus* Nutt. ex Torr. & Gray = *Camissonia californica* (Nutt. ex Torr. & Gray) Raven.

Chylismia (Nutt. ex Torr. & Gray) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 217. 1893. Based on *Oenothera* subg. *Chylismia* Nutt. ex Torr. & Gray.[1] Type: *O. scapoidea* Torr. & Gray = *Camissonia scapoidea* (Torr. & Gray) Raven.

Taraxia (Nutt. ex Torr. & Gray) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 216. 1893. Based on *Oenothera* subg. *Taraxia* Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 506. 1840. Lectotype: *O. breviflora* Torr. & Gray = *Camissonia breviflora* (Torr. & Gray) Raven.

Annual or perennial herbs, rarely subshrubs, from a taproot which in some species branches and gives rise to new plants. Leaves basal or cauline and spirally arranged, largest near the base, reduced upward. Flowers opening near sunrise, or in a few taxa near sunset or in the late afternoon, the stigma receptive and anthers shedding pollen simultaneously and immediately and the flowers withering in less than a day, 4-merous or very rarely 3-merous. Petals yellow, rose-purple, or white, reflexed in anthesis in the outcrossing species. Stamens and style yellowish, the stigma greenish yellow. Stamens 8, the episepalous ones longer, or very rarely 4, the epipetalous ones lacking; anthers versatile or basifixed (in sect. *Tetrapteron*), the sporogenous tissue in each locule undivided. Pollen yellow, shed singly or (in sect. *Lignothera*) in tetrads. Stigma capitate or hemispherical. Capsule loculicidal, usually promptly so, straight or contorted, the seeds in 1 or 2 rows in each of the 4 locules, usually adhering to the central partition following dehiscence. Basic chromosome number, $x=7$. Self-incompatibility known in approximately 17 of the 61 species.

TYPE SPECIES: *Camissonia flava* Link = *C. dentata* (Cav.) Reiche.

In the following treatment, an effort has been made to group related species. Within each section, generalized species are listed first, more specialized ones later. The keys have been written for ease of identification and are not intended to display relationships. Sympatric entities have been listed within each section following the taxonomic treatment of each taxon. In the same place a summary of the available chromosomal information and that on self-incompatibility is presented. Only a digest of my earlier treatment of sects. *Chylismia*, *Lignothera*, and *Chylismiella* (Raven, Univ. Calif. Publ. Bot. 34: 1–122. 1962) is presented here, but I have tried to include enough information to make the present revision complete and usable taxonomically without reference to the earlier paper. In the citation of collections, R has consistently been used for *Raven*, except in the case of type collections. Voucher specimens are understood to be

---

[1] As to the status accorded this and comparable groups, see Brizicky, Journ. Arn. Arb. 44: fn. 1963, and Gray, Man. Bot. N. U.S., ed. 2, p. xi., 1856.

deposited in the Dudley Herbarium, Stanford University (DS), with duplicates in the U.S. National Museum (US) and Rancho Santa Ana Botanic Garden, Claremont, California (RSA), in most cases, unless some other indication of their deposition is made.

Key to Sections

Ovary with a long slender sterile projection below the hypanthium, the plants acaulescent or nearly so . . . . Section IV. **Tetrapteron**

Ovary lacking a sterile projection, the plants only occasionally appearing acaulescent, and then when immature.

Seeds with a thick papillate wing surrounding the concave face (fig. 78); petals white, yellow near the base . . . . Section VIII. **Chylismiella**

Seeds not winged; petals yellow, white, or purple.

Capsules on well-defined pedicels, not coiled or contorted; seeds in 2 rows in each locule.

Hypanthium 0.4–8 mm. long; leaves basal or cauline, often pinnately divided or lobed; pollen shed singly . . . . . Section II. **Chylismia**

Hypanthium 4.5–40 mm. long; leaves all cauline, simple, usually cordate-orbicular; pollen shed in tetrads . . . . . . Section III. **Lignothera**

Capsules sessile (see also 40. *C. kernensis*), often coiled or contorted; seeds in 1 row in each locule.

Petals white, the flowers vespertine . . . Section VII. **Eremothera**

Petals yellow, the flowers matinal.

Leaves pinnately lobed, more rarely subentire; petals usually with a pattern of minute maroon flecks near the base; seeds often with purple dots or blotches; capsules often sharply reflexed at maturity (Baja California, Sonora, southern California, Arizona). Section I. **Eulobus**

Leaves subentire; petals unspotted or with 1 or 2 bright red spots near the base; seeds unspotted; capsules not reflexed (widespread).

Plants with naked, capillary stems, each bearing a crowded, leafy inflorescence at its apex; capsule strongly flattened, 0.5–1 cm. long . . . . Section IX. **Nematocaulis**

Plants usually leafy from the base, the inflorescence not crowded; capsule not flattened, usually over 1 cm. long.

Capsules quadrangular, at least when dry; plants usually with flowers at the basal nodes; leaves mostly lanceolate to ovate; seeds dull, flattened, usually over 1 mm. long. Section V. **Holostigma**

Capsules subterete; plants lacking flowers at the basal nodes; leaves mostly linear or very narrowly elliptic; seeds shining, triangular in transection, often under 1 mm. long. Section VI. **Camissonia**

SECTION I. EULOBUS

Stigma cylindrical, 1.4–4.5 mm. long; branches prostrate, radiating from a central axis (central and southern Baja California) . . . . . . **3. C. sceptrostigma**

Stigma globose; branches erect.

Woody perennials, often flowering the first year; stigma held well above the anthers at anthesis; leaves usually entire (west coast of Baja California). **1. C. crassifolia**

Annuals; stigma equaled by at least the longer stamens, their anthers surrounding it at anthesis; leaves usually deeply pinnatifid.
  Capsules usually more or less contorted; hypanthium 3–4.2 mm. long; petals 10–19 mm. long (central Baja California) . . . . . . **2. C. angelorum**
  Capsules straight or nearly so, deflexed at maturity; hypanthium 0.6–1.5 mm. long; petals 6–14 mm. long (widespread) . . . . **4. C. californica**

SECTION II. CHYLISMIA

Stamens 4 (local in Mohave and Coconino Cos., Arizona) . . . . . . **15. C. exilis**
Stamens 8.
  Corollas lavender in anthesis.
    Stigma held above anthers at maturity; hypanthium 4.5–8.5 mm. long; petals 9–13.8 mm. long . . . . **16. C. megalantha**
    Stigma surrounded by anthers at maturity; hypanthium 2–5 mm. long; petals 2–6 mm. long . . . . **17. C. heterochroma**
  Corollas yellow or white at anthesis.
    Capsules distinctly clavate, more than 2 mm. thick (see also 9. *C. walkeri*).
      Stigma surrounded by anthers at maturity, the petals less than 5.5 mm. long.
        Oil cells lining veins on underside of leaves pale yellowish brown, rarely darker; leaves often simple and entire, in compact basal rosette.
          Capsules to 30 mm. long; leaf blades to 5.5 cm. long; base of plants often nearly glabrous (Wyoming, Colorado, eastern Utah, New Mexico) . . . . **13a. C. scapoidea** subsp. **scapoidea**
          Capsules 25–40 mm. long; leaf blades to 3.5 cm. long; base of plants densely strigose (Arizona) . **13b. C. scapoidea** subsp. **macrocarpa**
        Oil cells lining veins on underside of leaves dark brown, conspicuous; leaves remotely dentate and often pinnately compound, in loose basal rosette.
          Leaves with several pairs of lateral leaflets; capsules 16–38 mm. long; petals 4–8 mm. long (western Utah and adjacent Neveda). **13d. C. scapoidea** subsp. **utahensis**
          Leaves with lateral leaflets few or absent; capsules rarely over 20 mm. long; petals 1.8–4 mm. long (Oregon, Idaho, western Utah, and Nevada) . . . . **13c. C. scapoidea** subsp. **brachycarpa**
      Stigma held well above anthers at maturity, the petals usually more than 6 mm. long.
        Mature pedicels and capsules sharply deflexed; corollas bright yellow. **11. C. munzii**
        Mature pedicels and capsules ascending or spreading; corollas yellow or white.
          Branches of the inflorescence numerous and filiform; leaves not strictly basal; capsules less than 10 mm. long, the pedicels slender (southwestern Utah and northwestern Arizona) . . **14. C. parryi**
          Branches of inflorescence not filiform; leaves mostly in a basal rosette; capsules often more than 10 mm. long.
            Stamens differentiated into 2 sets; inflorescence loose; leaves entire or nearly so, rounded, often simple and glabrous (Colorado and Utah) . . . . **12. C. eastwoodiae**
            Stamens subequal; inflorescence dense; leaves generally dentate, often acutely angled, pinnate and pubescent (Oregon and Nevada southward).

Lower parts of the plants with villous, spreading pubescence; sepals with free caudate projections arising below apices.

Petals fading reddish (Arizona, Sonora, Baja California).

Petals 3–5 mm. long; style 7–12 mm. long (Arizona, and Sonora) . . . . . **10k. C. claviformis** subsp. **rubescens**

Petals 1.5–2 mm. long; style 5–7 mm. long (Baja California) **10j. C. claviformis** subsp. **wigginsii**

Petals not fading reddish (San Diego and Imperial Cos., California, and adjacent Baja California) **10h. C. claviformis** subsp. **peirsonii**

Lower parts of plants short-appressed pubescent or glabrous but not villous with spreading trichomes; sepals entire or with caudate projections.

Petals white, the hypanthium orange brown.

Plants variously pubescent on stems and in inflorescence; lateral leaflets often reduced.

Lateral leaflets reduced in number, the leaves often nearly simple; basal rosette compact (Nevada, southern Oregon, local in Mono and Inyo Cos., California). **10c. C. claviformis** subsp. **integrior**

Lateral leaflets generally well developed and numerous, the basal rosette not compact.

Sepals often with projections arising below the apices; terminal leaflets often large and nearly cordate; buds and inflorescences often silky-strigose (Death Valley region, California). **10d. C. claviformis** subsp. **funerea**

Sepals usually entire; terminal leaflets usually inconspicuous; buds and leaflets not silvery.

Pubescence on leaves, stems, and often inflorescences glandular (Arizona). **10g. C. claviformis** subsp. **peeblesii**

Pubescence on leaves and stems rarely glandular, that of inflorescences never so (southern Nevada, California, rare in Arizona). **10f. C. claviformis** subsp. **aurantiaca**

Buds and inflorescences usually glabrous or nearly so; lateral leaflets usually well developed (western deserts of California) . . **10e. C. claviformis** subsp. **claviformis**

Petals yellow, the hypanthium yellow or orange brown.

Plants with strigose pubescence above and in the inflorescence, the sepals sometimes with free projections (southern California, Arizona, and northern Mexico). **10i. C. claviformis** subsp. **yumae**

Plants usually glabrous above, the sepals entire; northern part of species range.

Leaves lanceolate, narrow, and evenly dentate, often nearly entire by loss of lateral leaflets; hypanthium dark (Inyo and Mono Cos., California). **10b. C. claviformis** subsp. **lancifolia**

Leaves pinnate, the terminal leaflets ovate, often blunt, the lateral leaflets often well developed (Washoe Co., Nevada, northward). **10a. C. claviformis** subsp. **cruciformis**

Capsules elongate, often linear, usually less than 2 mm. thick; pedicels often inconspicuous.
  Stigma surrounded by anthers at maturity; petals less than 6 mm. long; style less than 6 mm. long; inflorescence erect in bud.
    Clumped perennials with somewhat woody base; leaves glabrous or sparsely pubescent; anthers glabrous (Colorado R. in and below Grand Canyon, Arizona).
      Leaves and style glabrous . . . **8a. C. speculicola** subsp. **speculicola**
      Leaves and style pubescent . . . **8b. C. speculicola** subsp. **hesperia**
    Annuals or short-lived perennials, the base usually not at all woody; leaves pubescent, usually densely so; anthers pubescent or glabrous (widespread) . . . . **9. C. walkeri**
  Stigma elevated above anthers at maturity; petals usually more than 6 mm. long; style more than 6 mm. long.
    Inflorescence erect or drooping, elongating before flowers open, the mature buds mostly individually pendulous; plants virgate; hypanthium less than 3 mm. long (Utah, southern Nevada, and northwestern Arizona). **7. C. multijuga**
    Inflorescence drooping, mostly elongating after flowers open; stems stout, not virgate; hypanthium more than 3 mm. long.
      Sepals with free caudate tips arising just below apices, glandular-pubescent; inflorescence often branched; stamens differentiated into 2 sets (Toroweap area, Mohave Co., Arizona). **5. C. confertiflora**
      Sepals lacking free caudate tips, or if they are present, the sepals variously pubescent, but not glandular; inflorescence branched or unbranched; stamens subequal (widespread) . **6. C. brevipes**

SECTION III. LIGNOTHERA

Hypanthium 18–40 mm. long; style 30–58 mm. long . . . . **19. C. arenaria**
Hypanthium 4.5–14 mm. long; style 8–23 mm. long.
  Leaves ovate-acuminate, longer than broad; petals less than 4.5 mm. long; pubescence predominantly glandular. **18. C. cardiophylla** subsp. **cedrosensis**
  Leaves cordate to cordate-orbicular, about as long as broad; petals mostly more than 4.5 mm. long.
    Plants coarse; pubescence mostly glandular (Inyo Co., California). **18b. C. cardiophylla** subsp. **robusta**
    Plants more slender; pubescence mostly villous (San Bernardino Co., California, southward and eastward). **18a. C. cardiophylla** subsp. **cardiophylla**

SECTION IV. TETRAPTERON

Plants perennial, strictly acaulescent; capsule not winged.
  Leaves pinnatifid, the plants more or less densely pilose or appressed pubescent.
    Style 9.5–20 (–25) mm. long, the stigma held above the anthers at anthesis; petals (8–) 10–23 mm. long.
      Less than 5 percent of pollen 4-pored; pubescence variable (widespread). **22a. C. tanacetifolia** subsp. **tanacetifolia**
      More than 10 percent of pollen 4-pored; plants densely gray-pubescent (Sierra Valley area in Plumas and immediately adjacent Lassen and Sierra Cos., California) . **22b. C. tanacetifolia** subsp. **quadriperforata**
    Style 3–6.5 mm. long, the stigma surrounded by anthers of longer stamens at anthesis; petals 5.5–7 (–8) mm. long . . . . **23. C. breviflora**

Leaves not pinnatifid or, if so, plants subglabrous.

Leaves more or less densely white-ciliate; capsule subterete, the thin walls much distended by the seeds . . . . **20. C. ovata**

Leaves subglabrous, rarely minutely and sparsely strigulose; capsule more or less 4-angled, the nearly flat walls not distended by the seeds. **21. C. subacaulis**

Plants annual, sometimes branching; capsule broadly winged in upper half.

Petals 5–18 mm. long; style 3–5.5 mm. long; pubescence pilose. **24. C. graciliflora**

Petals 2–3.5 mm. long; style 1–2.2 mm. long; pubescence strigose . **25. C. palmeri**

SECTION V. HOLOSTIGMA

Plants perennial, often somewhat woody near the base.

Petals (10–)12–20 mm. long; styles 13–23 mm. long (near Goleta, Santa Barbara Co., California, south to near San Quintín, Baja California; San Nicolas and San Martin Isls.) . . . **26a. C. cheiranthifolia** subsp. **suffruticosa**

Petals 6–11 mm. long; styles 6–9 mm. long (Point Conception, Santa Barbara Co., California, north to Coos Bay, Curry Co., Oregon; several islands). **26b. C. cheiranthifolia** subsp. **cheiranthifolia**

Plants annual (except for a few populations of *C. bistorta*, q.v.).

Stigma evidently held above the anthers at anthesis, the flowers large (southern California, north to Ventura Co., and adjacent Baja California). **27. C. bistorta**

Stigma surrounded by at least the anthers of the longer set of stamens at anthesis, the flowers small to large (widespread).

Capsule very heavy, 2.8–3.5 mm. thick near the base, straight or nearly so, deeply grooved along the lines of dehiscence (Guadalupe and San Clemente Isls.).

Pubescence strigose; petals not spotted (Guadalupe Isl.). **28a. C. guadalupensis** subsp. **guadalupensis**

Pubescence spreading; petals with a prominent red dot near the base (San Clemente Isl.) . . . **28b. C. guadalupensis** subsp. **clementina**

Capsule 0.75–2.2 mm. thick near the base, straight or curved into 1 or more spirals, not deeply grooved (widespread).

Pollen 25–100 percent 4- or 5-pored; hexaploid species.

Inflorescence lacking glandular trichomes; 4-pored pollen comprising 25–60 percent of the total (Santa Lucia Mts., Monterey Co., and inner Coast Ranges south to Santa Barbara Co., California). **38. C. luciae**

Inflorescence with an understory of short glandular trichomes; 4- and 5-pored pollen comprising 70–100 percent of the total (not in area of *C. luciae*).

Capsule 1.3–1.6 mm. thick, subterete in transection (southernmost Monterey to central San Luis Obispo Co., California). **37. C. hardhamiae**

Capsule 1.5–2 mm. thick, more or less quadrangular in transection (San Diego Co., California, and adjacent Baja California; offshore islands) . . . . **39. C. robusta**

Pollen up to 5 percent 4-pored (rarely more in *C. intermedia*); diploid or tetraploid species.

Capsule markedly quadrangular in transection, 1.8–2.2 mm. thick (Los Angeles Co., California, south throughout the northwestern quarter of Baja California) . . . . **29. C. lewisii**

Capsule not markedly quadrangular in transection, at least in living material, 0.75–1.2 (–1.8) mm. thick (widespread).

Plants subglabrous, usually with 50 or more flowers in the basal rosette, subcaespitose or with very thick prostrate branches from the base (coastal Baja California) . . . . . . **30. C. proavita**

Plants subglabrous to densely villous, with few flowers in basal rosette (widespread).

Upper leaves evidently petiolate, attenuate at the base; capsule usually more contorted; plants subglabrous to strigulose, often reddish (Yolo Co., California, to 30° N. lat. in Baja California; Madera Co., California; Santa Cruz Isl.) . . . **33. C. ignota**

Upper leaves usually not evidently petiolate, rounded or truncate at the base; capsule straight to coiled once or twice; plants strigulose to villous, always evidently so (widespread).

Conspicuously gray-strigose plants of the deserts, the branches usually decumbent (deserts of southern California to Arizona and northern Baja California).

Petals 6.5–13 mm. long; style 6.5–10.5 mm. long (western Riverside and San Bernardino Cos., California).
34a. C. pallida subsp. **hallii**

Petals (2–) 3.5–6 (–8) mm. long; style (2.1–) 3–6.5 mm. long (widespread on deserts) . . **34b. C. pallida** subsp. **pallida**

Plants not conspicuously gray-strigose, barely reaching the margins of the deserts (except for *C. confusa* in central Arizona).

Capsule 0.75–0.9 mm. thick; upper leaves narrowly ovate or ovate; plants erect; $n=7$ . . . . **32. C. hirtella**

Capsule 0.9–1.2 (–1.8) mm. thick; upper leaves narrowly lanceolate to narrowly ovate; plants erect or decumbent; $n=7$ or 14.

Plants with decumbent branches from the basal rosette; upper leaves usually narrowly lanceolate; short glandular trichomes usually absent in inflorescence; $n=7$ (Coast Ranges of California, Sonoma Co. to San Diego Co.) . . . . **31. C. micrantha**

Plants erect; upper leaves lanceolate or narrowly ovate; short glandular trichomes almost always present in inflorescence; $n=14$ (widespread).

Plants gray-villous; petals (2.5–) 5–10.5 mm. long; style (2.5–) 4.5–7.5 mm. long (San Luis Obispo Co. to San Diego Co., California; central Arizona).
36. C. confusa

Plants usually not gray-villous; petals 1.5–3.5 (–4.5) mm. long; style 2–3.5 mm. long (Lake and Yolo Cos., California, to 30° N. lat. in Baja California; Santa Cruz and Santa Catalina Isls.) . . **35. C. intermedia**

SECTION VI. CAMISSONIA

Plants of North America.

Sepals reflexed singly; plants often with conspicuous spreading pubescence (Great Basin and neighboring areas).

Stigma elevated well above the anthers at anthesis; petals 8–15 (–18) mm. long.

Plants compact, the leaves clustered at the base; pubescence dense, spreading; fruiting pedicel 3–15 mm. long (northeastern Kern Co., California) . . . . **40a. C. kernensis** subsp. **kernensis**

Plants not compact, the leaves not clustered at the base; pubescence variable; fruiting pedicel 0–5 (–15) mm. long (Kern, Inyo, Mono, and San Bernardino Cos., California, and adjacent Neveda). **40b. C. kernensis** subsp. **gilmanii**

Stigma surrounded by the anthers at anthesis; petals 1.8–4 mm. long.

Basal rosette well developed, the plants usually with long, spreading trichomes.

Leaves 0.4–1.8 mm. wide; hypanthium 0.8–1.6 mm. long; style 1.6–3.2 mm. long; $n=7$ . . . . **41. C. pusilla**

Leaves 2–5 (–6.2) mm. wide; hypanthium 1.3–3 mm. long; style 3.2–4.1 mm. long; $n=14$ . . . . **42. C. pubens**

Basal rosette not well developed, the stems bare near the base; plants usually with appressed pubescence or subglabrous . . **43. C. parvula**

Sepals usually reflexed in pairs, remaining attached (widespread).

Stigma held above the anthers at anthesis; petals (3.5–) 4–15.5 mm. long.

Leaves lanceolate or narrowly ovate, entire or nearly so (Sierra Nevada, California, in Madera and Mariposa Cos.) **45a. C. sierrae** subsp. **sierrae**

Leaves linear to narrowly elliptic or narrowly oblanceolate, serrulate to coarsely serrate (widespread in California).

Leaves linear to narrowly elliptic or narrowly oblanceolate, serrulate or serrate; stems usually erect (widespread in central and southern California). . . . . **44a. C. campestris** subsp. **campestris**

Leaves narrowly elliptic, coarsely serrate; plants usually decumbent (southern Monterey to northern Santa Barbara Co., California). **44b. C. campestris** subsp. **obispoensis**

Stigma surrounded by the anthers at anthesis.

Leaves entire, very rarely with 1 or 2 small teeth; pubescence dense, strigulose (upper Kern R. drainage, California) . . **50. C. integrifolia**

Leaves serrulate or serrate; pubescence variable (widespread).

Leaves narrowly elliptic, rounded or obtuse at the base; $n=7$ (central Sierra Nevada, California).

Petals 4–7 mm. long; style 4.5–7 mm. (Madera and Mariposa Cos., California) . . . . **45a. C. sierrae** subsp. **sierrae**

Petals 2.2–4 mm. long; style 2.8–5 mm. long (Fresno Co., California). **45b. C. sierrae** subsp. **alticola**

Leaves linear or very narrowly elliptic, narrowly cuneate or attenuate at the base; $n=14$, 21 (widespread).

Often more than 30 percent of the pollen grains 4-pored; plants usually with spreading pubescence on the stems; $n=21$ (widespread in California south to Kern Co.) . . . . . . **51. C. contorta**

Very rarely with more than 10 percent of the pollen grains 4-pored; pubescence variable; $n=14$ (California from Lake Co. southward, and adjacent Baja California).

Petals (4–)4.5–7 mm. long; style 4–7 mm. long; pubescence of stems long, spreading (Lake Co. and Sierra Nevada foothills from Eldorado Co. to Fresno Co., California). . . **46. C. lacustris**

Petals 2.1–4.2(–4.5) mm. long; style 2.3–4.8 mm. long; pubescence variable (Coast Ranges from Sonoma Co., California, south to northern Baja California, and Sierra Nevada of Kern Co., California).

Plants villous, the inflorescence glandular (serpentine soils, San Benito Co., California) . . . . **47. C. benitensis**

Plants strigulose or with villous trichomes on the lower stem, rarely villous and glandular only (widespread in range given above). **48. C. strigulosa**

Plants of South America.

Leaves linear or very narrowly lanceolate; plants erect, decumbent, or prostrate; capsules 0.6–0.9 mm. thick (widespread) . . **49a. C. dentata** subsp. **dentata**

Leaves broadly elliptical, thick; plants prostrate; capsules 1.1–1.3 mm. thick, heavy (coastal sands in Prov. Concepción, Aruco, and Cautín, Chile). **49b. C. dentata** subsp. **littoralis**

SECTION VII. EREMOTHERA

Capsules not thickened near the base; plants lacking flowers at the lower nodes.

Petals 3.5–7 mm. long; stigma held well above the anthers at anthesis. **52. C. refracta**

Petals 1.8–3 mm. long; stigma surrounded by the anthers at anthesis. **53. C. chamaenerioides**

Capsules thickened near the base; plants with or without flowers at the lower nodes.

Inflorescence erect to the tip at anthesis; plants flowering from the base.

Petals 3–5 mm. long; style 6–7 mm. long, glabrous (west-central Nevada). **57. C. nevadensis**

Petals 0.8–1.3 mm. long; style 1.2–3.2 mm. long, pubescent near the base (widespread) . . . . **58. C. minor**

Inflorescence nodding at anthesis; plants flowering from near the base or not.

Petals (3–) 4–7.5 mm. long; stigma held well above the anthers at anthesis.

Cluster of large basal leaves prominent at the time of flowering, the inflorescence relatively leafless; plants blooming in the spring, never with prominent spreading pubescence.

Capsules 2–3.8 mm. thick near the base, woody, the inflorescence very condensed (Sonoran and eastern Mojave Desert; San Juan Co., Utah) . . . . **54c. C. boothii** subsp. **condensata**

Capsules 1–2.3 mm. thick near the base, not woody, the inflorescence not highly condensed.

Capsules 1.7–2.3 mm. thick near the base, curved outward (cismontane central and southern California, south to Los Angeles Co.). **54a. C. boothii** subsp. **decorticans**

Capsules 1–1.6 mm. thick near the base, often curved downward (western Mojave Desert of California; upper Kern R. drainage). **54b. C. boothii** subsp. **desertorum**

Cluster of basal leaves rarely prominent at time of flowering, the inflorescence leafy; plants blooming in summer or late spring, often with prominent spreading pubescence.

Plants villous and glandular pubescent, blooming in the summer.

Plants usually 1.5–4 dm. tall, robust; cauline leaves coarsely serrulate, lanceolate or narrowly ovate (Mono Co., California, north to eastern Washington and southwestern Idaho; Mohave Co., Arizona) . . . . **54f. C. boothii** subsp. **boothii**

Plants usually 0.5–2 dm. tall; cauline leaves serrulate, narrowly lanceolate or lanceolate (southern Lander and eastern Churchill Cos., Nevada, south to northeastern Inyo Co., California, and southern Nye Co., Nevada; Kingston Range, San Bernardino Co., California) . . . . **54e. C. boothii** subsp. **intermedia**

Plants strigose, sometimes densely so, rarely villous or with an admixture of glandular trichomes; plants blooming in late spring and early summer (eastern Oregon and southern Idaho south to Lassen Co., California, through eastern Nevada to northern Clark Co., and in western Utah) . . . . **54d. C. boothii** subsp. **alyssoides**

Petals 1.5–2.5 mm. long; stigma surrounded by the anthers at anthesis.

Pubescence villous and glandular; seeds dimorphic, the basal ones coarsely papillose (eastern Washington, eastern Oregon, southern Idaho). **55. C. pygmaea**

Pubescence glandular; seeds monomorphic, all smooth or nearly so (southwestern Utah and Coconino Co., Arizona) . . . . . . **56. C. gouldii**

SECTION VIII. CHYLISMIELLA

One species . . . . **59. C. pterosperma**

SECTION IX. NEMATOCAULIS

Petals 2.5–5 mm. long; style 4.5–6 mm. long (eastern Washington and along the Columbia R.) . . . . **60. C. hilgardii**

Petals 0.8–2.3 mm. long; style 1.7–3 mm. long (widespread) . . . **61. C. andina**

Section I. *Eulobus*

Camissonia sect. *Eulobus* (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 283. 1964.

Eulobus Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 514. 1840.

Oenothera sect. *Eulobus* (Nutt. ex Torr. & Gray) Baill., Hist. Pl. 6: 461. 1877.

Oenothera subg. *Eulobus* (Nutt. ex Torr. & Gray) Munz, Amer. Journ. Bot. 16: 254. 1929.

Woody subshrubs or annuals, the plants caulescent, flowering from near the base or not. Inflorescence erect. Flowers opening near sunrise. Ovary lacking a sterile projection. Hypanthium lined with a lobed, red brown, fleshy disc within or with a smaller, circular disc at the base of the style. Sepals reflexed separately or united. Petals yellow, usually finely flecked with red near the base, this area of the petals not ultraviolet reflective, the remainder of the petals strongly so; petals fading orange red after pollination. Stamens 8, subequal or with the epipetalous ones shorter; anthers versatile, villous or glabrous. Pollen shed singly. Capsule sessile, regularly and promptly loculicidal, the midrib of each valve yellowish brown, prominent, straight or contorted, somewhat torulose, subterete in living material, the seeds in 1 row in each locule. Seeds monomorphic, narrowly obovoid, more or less triangular in transection, pointing up or down in capsule, finely papillose.

Type species: *Camissonia californica* (Nutt. ex Torr. & Gray) Raven.

Distribution: Sandy slopes and flats, from southern San Benito, central Kern, and eastern San Bernardino Counties, California, and western and southern Arizona (from the vicinity of Kingman south),

south-central Sonora at about 28°20′ N. lat., and in Baja California to the vicinity of Bahía de la Magdalena at about 24°30′ N.; Santa Cruz and Santa Catalina Islands, California; Isla de Cedros, Baja California; and Isla San Lorenzo, Golfo de California.

Camissonia sect. *Eulobus* is here taken in exactly the same sense in which it was constituted by Munz in 1929 (Amer. Journ. Bot. 16: 253–257). At the time he prepared this revision, Dr. Munz remarked that herbarium material of three of the four species of this group was meager. In spite of this, the examination of the abundant material that has been collected in the succeeding 40 years has not given me any reason to disagree with the delimitation of species presented in 1929. I have, however, cited specimens to document the ranges of the three species endemic to Baja California, as this has not been possible until recently.

The woody *Camissonia crassifolia* appears to be the most generalized species within the group. It is one of the two self-incompatible species in the section and the only one known to be regularly associated with a group of oligolectic bees, one of which is *Andrena* (*Onagrandrena*) *eulobi* Linsley & MacSwain. *Camissonia angelorum* is closely related to and doubtless best thought of as an annual, self-pollinated derivative of *C. crassifolia.* More distantly related, but evidently derivable from the same ancestral stock, are the self-incompatible *C. sceptrostigma,* with its unique cylindrical stigma, of a form unknown elsewhere in Onagreae and the regularly self-pollinating *C. californica,* the most widespread species of the section and the only one to contain tetraploid populations. *Camissonia californica,* probably the most specialized species in the section, is rarely visited by insects.

In sect. *Eulobus,* 108 individuals have been examined chromosomally, representing 78 populations. Not one of these has had a multivalent association of chromosomes in meiosis, all being strictly pair-forming. In this respect, sect. *Eulobus* resembles sect. *Holostigma:* reciprocal translocations appear to play no adaptive role in natural populations, and multivalents have not been observed either in diploid or in polyploid populations, even though it is highly probable that some of the polyploids combine relatively homologous diploid genomes (see Appendix A, p. 381).

1. **Camissonia crassifolia** (Greene) Raven, Brittonia 16: 283. 1964.
Oenothera crassifolia Greene, Bull. Calif. Acad. 1: 188. 1885.

Erect well-branched shrub up to 1.4 m. tall, or sometimes prostrate; plants flowering the first year, and then as little as 1.5 cm. tall, with no distinct basal rosette, sometimes flowering at the basal nodes; plants subglabrous or with a few strigulose trichomes in the inflorescence, especially around the hypanthium and on the upper portions of the ovary. Leaves somewhat fleshy and glaucescent, narrowly elliptic to narrowly lanceolate, rarely very narrowly elliptic, 1–6 cm. long, 2.5–12 mm. wide, entire to rather coarsely serrate or crenate, the apex obtuse, the base cuneate; leaves subsessile or with a petiole 1–2 mm. long. Inflorescence long and virgate. Hypanthium 1.5–2.5 mm. long, 2–3 mm. across at the summit, densely villous within. Sepals 5–9 mm. long, 1.2–2 mm. wide, reflexed in pairs or groups of 3 or 4. Petals (5.5–) 7.5–15 mm. long, (4–) 6.5–13 mm. wide, finely flecked with red in the basal third. Filaments of the episepalous stamens 3–7 mm. long, those of the epipetalous ones 2–5 mm. long; anthers 2.5–4 mm. long, sparsely long-ciliate or glabrous. Style (7–) 8.5–12 mm. long, densely villous in basal half; stigma globose, 0.8–1.1 mm. thick, held well above the stamens at anthesis. Capsules irregularly contorted, ca. 1.5–3.5 cm. long, 1.2–2 mm. thick. Seeds 1.7–2 mm. long, 0.7–0.8 mm. thick, brownish with small purple dots, often distorted or curved by the tough capsule walls. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Cabo San Quintín, Baja California, 10 May 1885, *E. L. Greene* (ND; isotypes, BM, CAS, DS, F, GH, K, NY, US).

DISTRIBUTION (Figure 4): Sandy soil, especially on beaches, or rocky headlands, along the west coast of Baja California from just north of San Isidro, at about 31°20′ N. lat., to the region of Bahía de la Magdalena, at about 24°40′ N. lat.; ranging away from the immediate coast only in the region of the Desierto Vizcaíño at about 27° N. lat. Also on Isla de Cedros and Isla Santa Magdalena. From near sea level to a few hundred feet in elevation.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

BAJA CALIFORNIA: 3 mi. N. of San Quintín, *Breedlove* 4173 (progeny); 20.6 mi. S. of road to San Quintín, R12391 (K, LA, UC); Pabellon Beach, ca. 10 mi. S. of San Quintín, *Klein et al.* 13 (RSA, UC); Punta Baja, *Klein & Gregory* 1236; Isla Cedros, *Moran* 10763.

REPRESENTATIVE SPECIMENS EXAMINED:

BAJA CALIFORNIA: About 5 mi. N. of San Isidro, *Tillett* 799 (RSA); San Antonio del Mar (Johnson Ranch), *Chambers* 704 (DS, UC); Santo Domingo (Hamilton Ranch), *Nelson & Goldman* 7174 (US); W. of Bahía de San Quintín, *Wiggins* 11890 (DAO, DS, OSC, SD, UC); 14 mi. S. of San Quintín, *Raven* 17024 (RM, RSA, UC); Punta Baja, *Harbison* in 1950 (SD); Santa Catarina Landing, *Wiggins* 4438 (DS, GH, POM, US); ca. 14 mi. S. of Puerto San José, *Wiggins & Thomas* 207 (DS): Playa María, *Street* in 1875 (GH); 28 mi. SW. of Punta Prieta, *Haines & Stewart* in 1935 (ARIZ, DS, GH, K, LA, NY); Lagoon Head, 1889, *Palmer* 769 (GH, K, US); Viscaíño Depression S. and W. of Laguna Scammon, *Gentry* 7353 (ARIZ, DS, RSA, UC); Picachos de Santa Clara, *Gentry* 7740 (ARIZ, DS, UC); stabilized dunes 13 mi. W. of Rancho San Angel, *Wiggins* 16267 (DS); 1.6 km. E. of Laguna de San Ignacio, 59 km. SW. of San Ignacio, *Carter et al.* 2515 (DS); Punta Santo Domingo, *Nelson & Goldman* 7174 (POM); San Juanico, *Street* in 1876 (GH). CEDROS ISLAND: Slope above low beach cliffs, southwest coast, NNW. of Cerro Redondo, *Moran* 10772 (DS, SD); behind beach NNW. of Cerro Redondo, *Moran* 10763 (DS, SD); W. coast 0.5–1 mi. NE. of Red Rock, *Haines & Hale* in 1939 (ARIZ, CAS, COLO, DS, POM, SD, UC). ISLA SANTA MAGDALENA: *Barclay* 3126 (BM, RSA), *Orcutt* 28 (GH, US). Mangrove I., Bahía de la Magdalena, *Greene* in 1938 (SD).

Colonies of *Camissonia crassifolia* may be variable in the degree of lobing of the leaves; thus *Gregory* 352 (RSA), from Pabellon Beach, has coarsely serrate leaves and *Gregory* 350 (RSA), which grew with it, has entire leaves. Collections with deeply lobed leaves are rather common, those of Palmer and Street cited above being extreme in this respect. Plants growing on the beach at certain localities are prostrate and distinctive in appearance. *Camissonia crassifolia* grows sympatrically with tetraploid populations of *C. californica*.

Plants from Isla de Cedros, where the species is local, flower regularly the first year. The flowers are borne in the rather compact rosette of deeply lobed leaves, and the plants only occasionally persist to flower a second year. A progeny of *Moran* 10763, from Isla de Cedros, and one from *Breedlove* 4173, from near San Quintín, on the mainland, were grown at Stanford, and both were found to consist entirely of self-incompatible plants. Reciprocal hybrids were made between these two strains and grown to maturity. In the F_1 individuals, the stems elongated rapidly and no flowers were formed at the basal nodes; in both of these respects they resembled the mainland parent. The F_1 individuals were self-incompatible like their parents and had 86 percent stainable pollen (based on a sample of 200 grains in cotton blue in lactophenol), compared with about 90 percent in most nonhybrid individuals. In meiosis, they formed 7 pairs of chromosomes, including 6 ring bivalents, indicating nearly complete homology between the chromosomes of the parental plants.

2. Camissonia angelorum (S. Wats.) Raven, Brittonia 16: 283. 1964.

FIGURES 1, 2

Oenothera angelorum S. Wats., Proc. Amer. Acad. 24: 49. 31 January 1889.

Oenothera crassiuscula Greene, Pittonia 1: 290. 16 April 1889. Type: Low plains around the southern shore of Bahía de San Bertólome, Baja California, March 1889, *Lieutenant Pond* (location of specimen not known).

Sphaerostigma angelorum (S. Wats.) A. Nels., Bot. Gaz. 40: 63. 1905.

Erect, sparingly branched, virgate annual 8–90 cm. tall, with no distinct basal rosette, not flowering at the basal nodes, glabrous or sparsely strigulose, the inflorescence strigulose. Leaves deeply pinnatifid, very narrowly elliptic, 1–7.5 cm. long, 1–15 mm. wide, the apex acuminate, the base attenuate; leaves subsessile or with a petiole up to 3 mm. long. Inflorescence long and virgate. Hypanthium 3–4.2 mm. long, 3–4.5 mm. across at the summit, sparsely pubescent or subglabrous in lower half within. Sepals 6.5–11 mm. long, 1.2–2.2 mm. wide, reflexed in pairs or groups of 3 or 4. Petals 10–19 mm. long, 8–21 mm. wide, finely flecked with red in basal third. Filaments of the

FIGURES 1–3.—Species of *Camissonia* sect. *Eulobus*, × ¾: 1–2, *C. angelorum*: 1, Portion of a fruiting branch (*Wiggins* 18189, DS); 2, a flowering plant (*Wiggins & Thomas* 299, DS). 3, Flowering branch of *C. sceptrostigma* (*Wiggins* 16824, DS).

episepalous stamens 3–5 mm. long, those of the epipetalous ones 2–3.5 mm. long; anthers 2–3.2 mm. long, long-ciliate. Style 5–9 mm. long, subglabrous or with scattered erect trichomes near its base; stigma globose, 1.3–2 mm. thick, held at the level of the anthers of the longer stamens at anthesis, or perhaps a little above them in certain plants. Capsules contorted, but often not as much so as in *C. crassifolia*, 1.5–3.5 cm. long, 1–1.4 mm. thick. Seeds as in *C. crassifolia*. Gametic chromosome number, $n=7$. Self-compatible and capable of self-pollination, but probably often outcrossed in nature.

Type: Bahía de los Angeles, Baja California, 22 November to 20 December 1887, *E. Palmer* 519 (GH; isotypes, BM, C, K, NY, UC, US).

Distribution (Figure 4): Sandy flats and washes in Baja California, ranging across the peninsula, from the vicinity of Punta Final on the gulf coast at about 29°45′ N. lat. south to the northern edges of the Desierto Vizcaíño at about 27°40′ N. lat.; also on Isla San Lorenzo in the Golfo de California. From sea level to about 1,500 ft. alt.

Vouchers for chromosome number (9 individuals, 9 populations), $n=7$ (all with 7 pairs):

BAJA CALIFORNIA: 2 mi. inland from Ensenada de San Francisquito, *Moran* 12391 (DS, SD); 17 mi. S. of Laguna Seca Chapala, *Thorne & Hendrickson* 32640 (DS, RSA); Salorio, *Moran* 12314 (DS, SD); ca. 10 mi. E. of Bahía de los Angeles, ca. 1,500 ft., *Wiggins* 14808 (DS, progeny); Bahía de los Angeles, *Moran* 12298 (DS, SD); just N. of San Borja, *Moran* 12461 (DS, SD); Bahía de San Francisquito, *Moran* 12618 (DS, SD); Arroyo Salinito, *Moran* 12860 (DS, SD); El Datillar, 8 mi. N. of Rancho Miramar, *Moran* 12847 (DS, SD).

Representative specimens examined:

BAJA CALIFORNIA: 25 mi. N. of Rancho Laguna Chapala on road to San Felipe, 1,130 ft., *Wiggins & Ernst* 662 (DS, UC); just W. of Bahía de San Luis Gonzaga, *I. L. & D. B. Wiggins* 15906 (DS); 25 mi. N. of Punta Prieta, *Wiggins* 5361 (CAS, DS, GH, NY, POM, RM, UC, US, WTU); 20 mi. E. of Punta Prieta, *Wiggins* 7662 (DS, GH, UC, US); Bahía de Los Angeles, *Wiggins* 7692 (DS, GH, LA, UC, US); near San Andreas, *Wiggins & Thomas* 215 (DS); 18 mi. S. of Punta Prieta, *I. L. & D. B. Wiggins* 18189 (CAS, DS); 12 mi. NE. of Rancho Rosarito on road to San Borja, *Porter* 559 (CAS, DS, GH, RSA); Bahía de San Francisquito, *Johnston* 3572 (CAS, GH, K, US); Rancho Barril, *Wiggins* 7822 (DS, F, GH, US); Laguna de Guerrero Negro, *Thomas* 8508 (DS); 21 mi. E. of Laguna de Guerrero Negro on road to El Arco, *Wiggins* 16828 (DS); 40 mi. inland from Lagoon Head, 1889, *Palmer* 771 (GH, K, POM, US); 8 mi. W. of Calmallí, *Haines & Stewart* in 1935 (ARIZ, DS, GH, K, LA, NY, POM, RM, RSA, UC, WTU); El Cañon Rancho near Calmallí, *Haines & Stewart* in 1935 (ARIZ, DS, F, GH, K, LA, POM, RM, RSA, UC); 7 mi. SE. of Rancho La Cantina, *Wiggins* 16209C (DS); Bahía de San Bertólome, *Rose* 16208 (GH, US); 5.5 mi. N. of El Huizache, Vizcaíño Desert, *Porter* 541 (CAS, DS, RSA). South San Lorenzo Island: *Moran* 4130 (DS, UC).

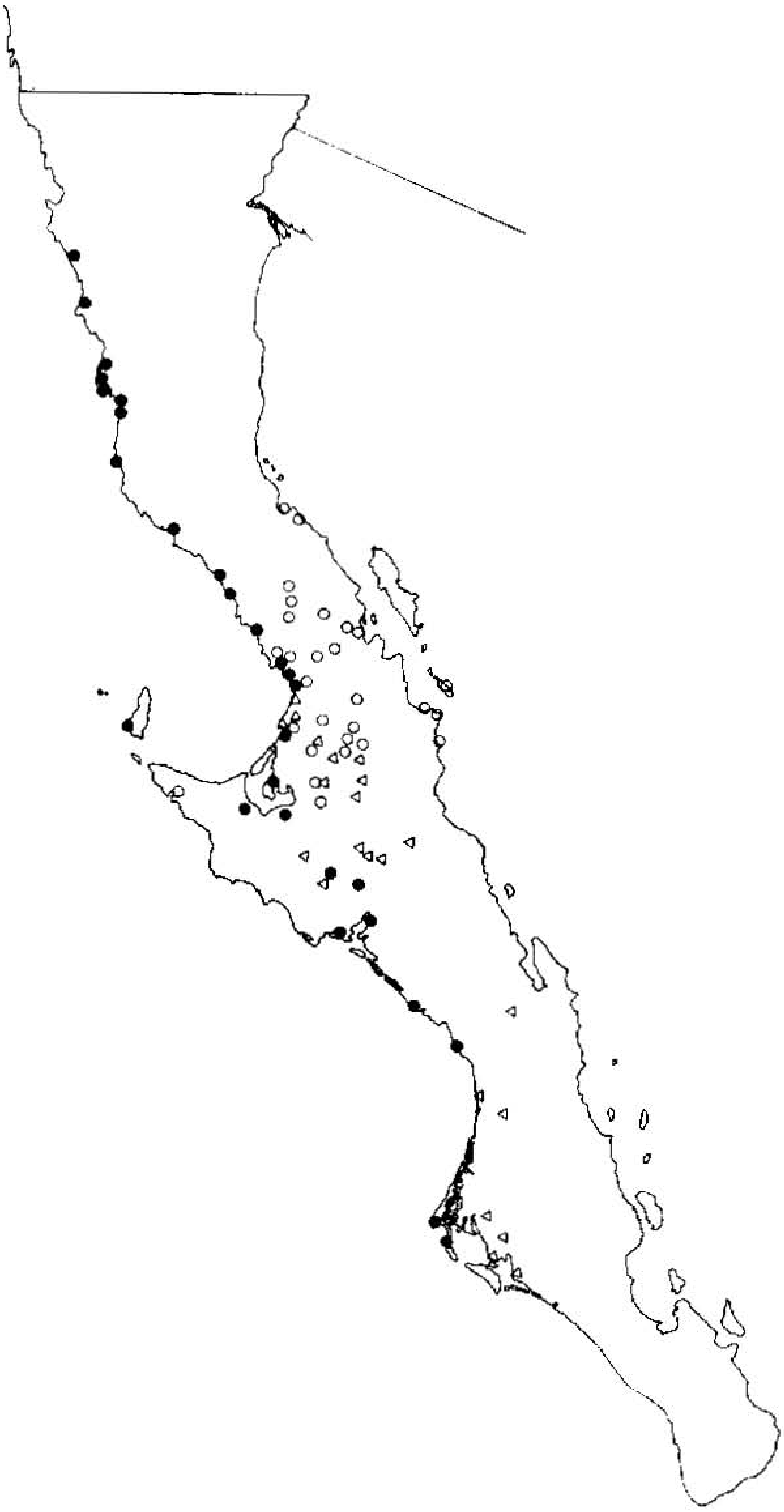


FIGURE 4.—Baja California, showing ranges of *Camissonia* sect. *Eulobus:* ●=*C. crassifolia;* ○=*C. angelorum;* △=*C. sceptrostigma.*

The collection cited from Bahía de San Bertólome has deeply cut leaves and very probably is similar to the unlocated type of *Oenothera crassiuscula*, from the same region. *Camissonia angelorum* is rather obviously an annual derivative of *C. crassifolia* and certain populations, notably some to those from the Desierto Vizcaíño region at the southern limits of *C. angelorum*, can be assigned to one species or the other only with the greatest difficulty. The two species might be regarded as geographical subspecies, but the shift in breeding system and ensemble of morphological features distinctive of each are sufficient to make their continued recognition as species desirable, in my opinion. Progeny of *Wiggins* 14808, grown at Stanford, set seed abundantly in the absence of insects and when isolated from one another; nevertheless, the showy flowers of *Camissonia angelorum* suggest strongly that this species must at least occasionally be cross-pollinated by insects in nature. *Camissonia angelorum* has been observed growing sympatrically with tetraploid populations of *C. californica*.

3. Camissonia sceptrostigma (T. S. Brandeg.) Raven, Brittonia 16: 283. 1964.
FIGURE 3

Oenothera sceptrostigma T. S. Brandeg., Proc. Calif. Acad. II. 2: 156. 1889.

Rosette-flowering annual, with prostrate branches tardily elongating from the base, these to at least 35 cm. long, with the leaves, flowers, and capsules standing erect from them; entire plant finely strigulose, often grayish-pubescent. Leaves thin, deeply and irregularly pinnatifid with narrow lobes, narrowly elliptic, 1.5–16 cm. long, 4–27 mm. thick, the apex acuminate, the base attenuate. Hypanthium 3.2–6 mm. long, 2.5–5 mm. across at the summit, glabrous within. Sepals 3–8.5 mm. long, 1–2.4 mm. wide, spreading (not reflexed), separate from one another. Petals 6.5–17.5 mm. long, 8–19 mm. wide, with diffuse red flecking near the base. Filaments of the episepalous stamens 1.7–4.5 mm. long, those of the epipetalous ones 0.8–1.8 mm. long; anthers 1.2–2.5 mm. long, glabrous or finely pubescent, held erect. Style 3.5–8.3 mm. long, glabrous; stigma cylindrical, 1.4–4.5 mm. long, 0.4–1.2 mm. thick, held ± above the anthers at anthesis. Capsules in the rosette straight or nearly so, those of the branches somewhat flexuous, 1.7–4 cm. long, 1.5–1.8 mm. thick. Seeds 0.8–1.2 mm. long, 0.4–0.6 mm. thick, pale brownish, not spotted. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: San Gregorio, Baja California, 1 February 1889, *T. S. Brandegee* (CAS; isotypes, DS, PH, US).

DISTRIBUTION (Figure 4): Sandy fields and washes in central and southern Baja California, from 11 miles south of Millers Landing, at about 28°20′ N. lat., to the south end of Bahía de la Magdalena, at about 24°30′ N. From near sea level to ca. 1,200 ft. alt.

Voucher for chromosome count (2 individuals, 2 populations; $n=7$):

BAJA CALIFORNIA: 3¼ mi. W. of Rancho Miramar, 28°08′ N. lat., 113°40′ W. long., ca. 150 m, *Moran* 12857 (DS, SD); *Verity* in 1967 (R68-302; DS).

ADDITIONAL SPECIMENS EXAMINED:

BAJA CALIFORNIA: 11 mi. S. of Millers Landing, *Wiggins* 15099 (DS); 3 mi. W. of main road and ca. 4–5 mi. N. of Rancho Mesquital, *Wiggins* 16768 (DS); 24 mi. E. of Laguna de Guerrero Negro, *Wiggins* 16824 (DS); Lagoon Head, 1889, *Palmer* 772 (C, CAS, GH, K, NY, UC, US); 23.2 mi. NW. of El Arco, *Porter* 207 (DS, GH); 11 mi. W. of El Arco, *Wiggins* 1683A (DS); El Arco, *Epling & Robinson* in 1935 (DS); 10 mi. E. of El Soltero, *Wiggins* 15148 (DS); 15 mi. S. of El Arco, *Wiggins* 15156 (DS, UC); 22 mi. S. of Pozo Alemán, *Wiggins* 7849 (DS, F, GH, UC, US); Arroyo de Tecolote, Desierto Vizcaíno, *Gentry* 7835 (ARIZ, DS, UC); Picachos de Santa Clara, Desierto Vizcaíno, *Gentry* 7759 (ARIZ, DS, UC); 5–7 mi. E. of Los Picachos de Santa Clara, *Gentry* 7593 (RSA, UC); 15 mi. E. of El Soliyo, *Wiggins* 15148 (UC); 7 mi. S. of Los Angeles, San Ignacio to El Arco road, *Wiggins & Ernst* 626 (DS, UC); E. edge of Desierto Vizcaíño, 56 km. S. of El Arco, *Carter et al.* 1940 (SD); 40 mi. W. of San Ignacio, *Hake* in 1921 (DS); 50 km. NW. of San Ignacio, *Carter et al.* 1960 (DS, F, GH, K SD, US); 25 mi. N. of San Ignacio, *Wiggins & Ernst* 615 (DS, UC); 14 mi. N. of San Ignacio, *Reed* 6203 (POM); 24 mi. N. of La Purísima, *Wiggins & Ernst* 589 (DS, UC); Punta San Juanico, *Moran* 3524 (DS); Santo Domingo, *Orcutt* (UC); San Jorge, *Gentry* 4176 (DS); 51 mi. NW. of El Crucero, *Porter* 488 (CAS, DS, GH); 10 km. N. of Medano Amarillo, Bahía de la Magdalena, *Johansen* 644 (CAS, DS); S. of El Refugio, *Wiggins* 5526 (DS); 14 mi. S. of El Refugio, *Shreve* 7179 (ARIZ, DS, F); Estero Salinas, *Porter* 462 (CAS, DS, GH, UC), *Wiggins* 11477 (DS, GH UC, US); Bahía de la Magdalena, *Lung* in 1894 (UC).

Camissonia sceptrostigma is uniform morphologically and, while an undoubted member of sect. *Eulobus*, is entirely distinct within the group. It has not been observed growing sympatrically with any of the other three species of the section, but occurs in the same vicinity as each one of them in the region of the northern Desierto Vizcaíño. Four plants of the Verity collection cited above were grown in the experimental garden and found to be self-incompatible.

4. **Camissonia californica** (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 283. 1964.

Eulobus californicus Nutt. ex Torr. & Gray, Fl. N. Amer. 1:515. 1840. Not *Oenothera californica* S. Wats. 1876.

Oenothera leptocarpa Greene, Pittonia 1: 302. 1889.

Oenothera eulobus H. Lév., Monogr. Onoth. 231. 1905.

Oenothera crassifolia var. *leptocarpa* (Greene) H. Lév., Monogr. Onoth. 209 1905.

Virgate annual 2–180 cm. tall, with a well-defined basal rosette which is usually withered by the time of flowering; no flowers formed in the lower nodes; stems thick, fleshy, hollow, bluish green, sometimes glaucescent, or bright green. Plants subglabrous, the leaves occasionally finely strigulose or with a few glandular trichomes on the margins and midvein. Leaves irregularly and sharply pinnatifid-lobed, very much reduced upward and in the inflorescence, mostly in the basal rosette, narrowly elliptic, up to 30 cm. long and 6.5 cm. wide, the apex acute, the base narrowly cuneate. Inflorescence with a few glandular trichomes, very rarely strigulose. Hypanthium 0.6–1.5 mm. long, 1–1.8 mm. across at the summit, glabrous within, closed by a conspicuous rounded fleshy disc. Sepals 3.9–8 mm. long, 0.7–1.5 mm. wide. Petals 6–14 mm. long, 3.5–8.5 mm. wide, with or without fine red flecking at the base. Filaments of the episepalous stamens 3–9 mm. long, those of the epipetalous ones 2–5 mm. long; anthers of longer stamens 1–2.5 mm. long, those of the shorter ones greatly reduced 0.5–1.2 mm. long. Style 4–10 mm. long, glabrous; stigma 0.8–2 mm. thick, held at the same level as the anthers of the longer stamens, which more or less surround it at anthesis. Capsules straight or slightly curved, (4.5–) 6–11 cm. long, 1–1.2 mm. in diameter, subterete when fresh, becoming quadrangular in transection when dry, sharply reflexed at maturity. Seeds 1.3–1.6 mm. long, 0.5–0.7 mm. thick, olive, often flecked with purple dots. Gametic chromosome numbers, $n=7$, 14. Mostly self-pollinating, and apparently always self-compatible; rarely visited by insects.

TYPE: Near San Diego, San Diego County, California, March–May 1836, *T. Nuttall* (NY; isotypes, BM, GH, K, PH).

DISTRIBUTION (Figure 5): Open or brushy hillsides and washes, or desert flats, often in loose soil: upper Austin Creek, Sonoma County, California (*Kruckeberg* 5933, DS); from the southern half of San Benito County and westernmost Fresno County, California, south through the Coast Ranges and mountains of southern California; the low foothills for about 20 miles east of Bakersfield, Kern County, California; and across the deserts (common along their western margins; absent in the Colorado Desert east of the Salton Sink; rare in the Providence and Old Woman Mountains of the eastern Mojave Desert) to western and southern Arizona (vicinity of Kingman, Mohave County; southernmost Yavapai, Gila, and Graham Counties southward); whence south to central Sonora (to ca. 7 miles west of Mina San José on road to Misa, *Wiggins* 6317, DS, POM, US; north of Bocoachic, 3,730 ft., *Wiggins* 11704, DS) at about 28°20′ N. lat. and throughout Baja California south to the Sierra Vizcaíño at about 27°15′ N. lat. (e.g., *Gentry* 7416, DS, POM; *Gentry* 7515, DS); also on Santa Cruz and Santa Catalina Islands, California. From sea level to 4,000 ft. alt.

Vouchers for chromosome number (39 individuals, 24 populations), $n=7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Santa Monica Mts.: Decker Canyon, *Mathias* 3159 (COLO, LA, RSA, UC); Latigo Canyon, *Venkatesh* 6 (3 plants; LA), 7 (2 plants; ARIZ, LA, RSA, UC); South Sepulveda Way, *Lewis* 1629 (LA); Mulholland Drive, 6.3 mi. from intersection with Beverly Glen Blvd., *Venkatesh* 4 (LA), 2.5 mi. from intersection, *Venkatesh* 2 (11 plants; LA). ORANGE CO.: 2.3 mi. above gate on Silverado Canyon Truck Trail, R17749. RIVERSIDE CO.: 3.5 mi. W.

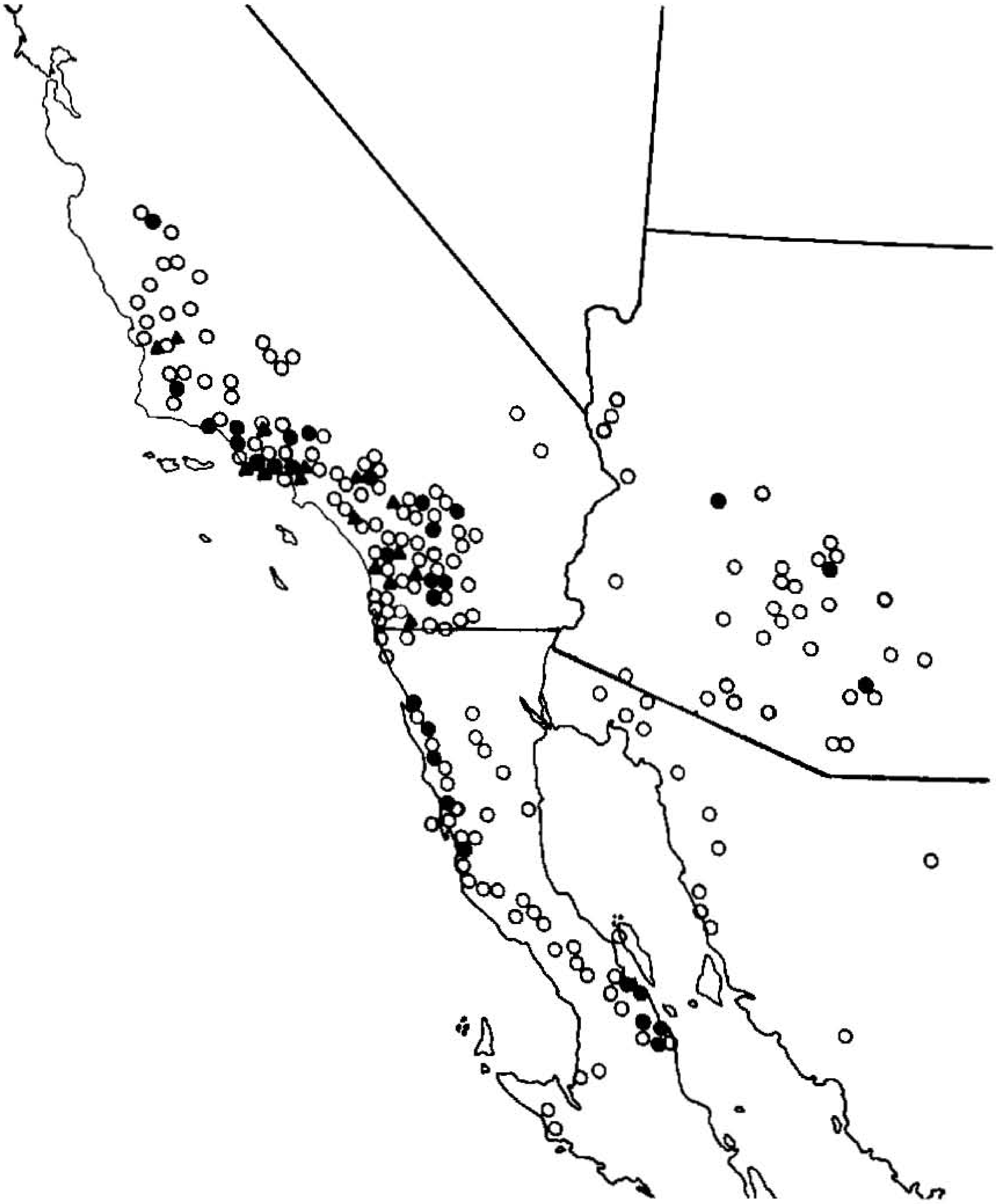


FIGURE 5.—Portion of southwestern United States and adjacent Mexico, showing range of *Camissonia californica* (O): ▲=diploid chromosome counts ($n=7$) and ●=tetraploid ($n=14$).

of Cabazon, *Lewis* 1679 (LA); 2 mi. N. of Aguanga, *Klein* 1299 (RSA). SAN BERNARDINO CO.: N. of Muscovy, *Gregory* 362 (RSA). SAN DIEGO CO.: 2.3 mi. S. of Rincon Springs, R17399; Lake Wohlford, R20170; 2 mi. E. of Escondido, 700 ft., R17405; 2 mi. E. of San Pasqual, R17410; Rincon Springs, R20172; 1.8 mi. from Ballena on road to Ramona, R9581 (LA); 0.7 mi. W. of Banner, 3,000 ft., R17421; 0.9 mi. W. of Barrett Lake Road on State Hwy. 94, *Breedlove* 1832. SAN LUIS OBISPO CO.: Parkhill Road, Calf Canyon, La Panza Campground, ca. 2,000 ft., R18325; La Panza Campground, 2,100 ft., R18324; 4.5 mi. NE. of Santa Margarita, R20157. VENTURA CO.: 11.4 mi. N. of Fillmore on Cow Springs Road, Topatopa Mts., 2,500 ft., *Breedlove* 2653; 9 mi. S. of Oxnard, State Hwy. 101A, *Copp in 1962*.

BAJA CALIFORNIA: Ensenada, *Bates* 2340.

Vouchers for chromosome number (53 individuals, 38 populations), $n=14$:

U.S.: ARIZONA: MARICOPA CO.: 12 mi. SW. of Roosevelt, *Gregory* 61 (RSA). PIMA CO.: Santa Catalina Mts.: 2.8 mi. below Molina Basin Picnic Area, *Lewis* 1075 (LA); Molina Basin Picnic Area, *Lewis* 1077 (LA, RSA). YAVAPAI CO.: 2 mi. E. of Congress Junction, *Munz et al.* 22972 (RSA). CALIFORNIA: LOS ANGELES CO.: Soledad Canyon, *Lewis & Thompson* 1615 (LA); Mint Canyon at road to Acton, R13906. SANTA MONICA MTS.: Latigo Canyon, R20162; 2.5 mi. W. of Seminole Hot Springs, R20163; 4.1 mi. NW. of Tapia Park, R14046; Topanga Canyon, *Venkatesh* 5 (8 plants; LA); Mulholland Drive 1.3 mi. W. of Laurel Canyon Blvd., R14081 (COLO, LA, RSA); Mulholland Drive 6.3 mi. from junction with Beverly Glen Blvd., *Venkatesh* 3 (6 plants; LA). RIVERSIDE CO.: Aqueduct Road 5.9 mi. S. of Garnet, *Lewis* 1620 (LA); Pinyon Crest Road 2.5 mi. from Palms-to-Pines Hwy., *Theobald* 61; Pushawalla Canyon, *H. & M. Lewis* 1610 (LA). SAN BENITO CO.: Call Mts., E. of a point 18 mi. N. of New Idria, R10875 (LA, RSA). SAN BERNARDINO CO.: 1.5 mi. W. of Mill Creek Ranger Station, R17468; Morongo Valley, *Kyhos* 65–125. SAN DIEGO CO.: 0.4 mi. from U.S. Hwy. 395 on road to Fallbrook, *Wedberg* 205 (herb. San Diego State College); Earthquake Valley, R11537; Borrego Valley, *H. & M. Lewis* 1544 (LA); 0.7 mi. W. of summit of Yaqui Pass, R11520. SANTA BARBARA CO.: Head of Buckhorn Canyon, summit of San Rafael Mts., on Tepusquet Canyon Road, *Breedlove* 2780; Santa Barbara, *Breedlove* 2227; 1 mi. S. of Prisoners Harbor, Santa Cruz I., *Breedlove* 2816. VENTURA CO.: 0.5 mi. N. of turn to Matilija Hot Springs, 1,400 ft., R17495; 0.3 mi. SW. of Camp Comfort, S. of Ojai, 600 ft., R17494; Little Sycamore Canyon, Santa Monica Mts., *Lewis* 1646 (LA).

BAJA CALIFORNIA: 7.5 mi. N. of Santa Tomás, R17049; 5.5 mi. S. of San Vicente, R17023; 5 km. N. of Colonia Guerrero, R12152 (LA, UC); 2 km. N. of Colonia Guerrero, R12142 (LA, UC); 14 mi. S. of San Quintín, R17031; 7.5 mi. S. of Socorro, *Klein* 1222 (RSA); 2 mi. inland from Ensenada de San Francisquito, *Moran* 12392; Bahía de los Angeles, *Moran* 12308; Las Trincheras, *Moran* 12608; Cuesta la Ley, Barril road, *Moran* 12642.

Camissonia californica, with its virgate habit, nearly leafless branches, and long, sharply reflexed capsules, superficially resembles some species of Cruciferae more than members of the family Onagraceae. Its capsules have been said to be imperfectly 4-celled, or 2-celled as in the related genus *Gayophytum* (Munz, Amer. Journ. Bot. 16: 253–254. 1929; N. Amer Fl. II. 5: 80. 1965), but I have been unable to confirm this in the wide range of material examined. This species, while very distinct, is obviously closely related to the other three grouped with it by Munz (loc. cit.) and recognized in the present revision as comprising *Camissonia* sect. *Eulobus*. It has been observed growing sympatrically with *C. crassifolia* and *C. angelorum*, but no hybrids have been found.

The only tetraploids in sect. *Eulobus* are found in the present species. I have found no character or combination of characters by which they can be separated from the diploids, and their pollen appears to be identical in size and number of pores. As pointed out by Munz (N. Amer. Fl. II. 5: 146. 1965), coastal populations of this species tend to consist of relatively robust, large-flowered plants; yet it is by no means true that all such populations are diploid. On the basis of the 92 individuals and 62 populations reported here (including earlier reports by Lewis et al., Aliso 4: 73–86. 1958), the diploids are much more narrowly distributed than the tetraploids (fig. 5). Diploids are known from coastal San Luis Obispo County, and occur sporadically near the coast in Ventura and Los Angeles Counties. From the Los Angeles basin to San Diego County, they range much farther inland, occurring to the margin of the desert near San Gorgonio Pass and near Aguanga; but they are intermixed with tetraploid populations in some pattern not yet properly understood, occurring as far west as the vicinity of Fallbrook in northwestern San Diego County. Unfortunately, no counts are available for extreme western Riverside County or for Orange County. In San Diego County, aside from the Fallbrook record just mentioned, most of the populations appear to be diploid, the tetraploid being confined to the margins of the desert. In Baja California, on the other hand, only a single diploid count is known, that from Ensenada, and all of the interior populations and those near the coast farther south (which consist of robust, large-flowered individuals similar to the coastal ones found farther north) are tetraploid. There does not appear to be any point in attempting to separate the diploid and tetraploid populations of this species taxonomically, and indeed there does not seem to be any practical possibility of doing it even if it were thought to be highly desirable.

No multivalent configurations have been observed in the tetraploid, but the lack of chromosome associations larger than bivalents is undoubtedly genetically controlled, as it is in sect. *Holostigma* and sect. *Camissonia*, and certainly does not indicate a complete lack of homology between the two sets of chromosomes present in these tetraploid populations. Indeed, an autotetraploid origin appears most likely for these tetraploids and would be consistent with their morphological relationships. If this is true, however, it is somewhat difficult to explain the occurrence of the tetraploids over a much wider range than the diploids, unless one could postulate that they recombine the genetic material present in diploid populations in some novel way (or ways) highly adaptive in more interior sites. This favorable genetic combination could be maintained by the tetraploidy of the interior plants, which are probably also more highly self-pollinating than those found nearer the coast, judging from their smaller flowers. Two diploid populations (R20157, cited above, from San Luis Obispo County, California, 7 plants; and R20166, San Pasqual Grade, San Diego County, California, 8 plants) and three tetraploid populations (Morongo Valley, San Bernardino County, California, *Kyhos* 65–125, 2 plants; Santa Monica Mountains, Los Angeles County, California, R20162, 5 plants; R20163, 6 plants the last two cited above) were tested by pollen-tube growth and found to be self-compatible. *Kruckeberg* 5933, cited above, was grown in a greenhouse at the University of Washington and found also to be self-compatible (A. R. Kruckeberg, pers. comm.). This collection was undoubtedly also tetraploid. In the smaller flowered interior populations, the anthers deposit pollen directly on the stigma and there is no doubt that autogamy predominates.

The disjunct occurrence of this species on serpentine near Austin Creek in western Sonoma County, California, is of considerable interest. I have no record of its occurrence on serpentine elsewhere, but it is characteristic for species occurring in highly marginal situations to occur in edaphic conditions that are unusual or unknown in their main area of distribution (Raven, Evolution 18: 336–338, 1964).

Section II. *Chylismia*

Camissonia sect. *Chylismia* (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 281 1964.

Oenothera subg. *Chylismia* Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 506. 1840.

Chylismia (Nutt. ex Torr. & Gray) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 217. 1893.

Oenothera sect. *Euchylismia* (Nutt. ex Torr. & Gray) Munz, Amer. Journ. Bot. 15: 224. 1928.

Oenothera sect. *Chylismia* Raven, Univ. Calif. Publ. Bot. 34: 80. 1962.

Oenothera sect. *Tetranthera* Raven, Univ. Calif. Publ. Bot. 34: 114. 1962. Type species: *Oenothera exilis* Raven = *Camissonia exilis* (Raven) Raven.

Camissonia sect. *Tetranthera* (Raven) Raven, Brittonia 16: 282. 1964.

Perennial or annual herbs, the plants caulescent, not flowering at the basal nodes, with or without a well-developed basal rosette. Leaves pinnately divided or entire. Inflorescence erect or drooping in bud. Flowers opening near sunrise or in the late afternoon (in *C. claviformis* only). Ovary lacking a sterile projection. Hypanthium lacking a fleshy disc within. Sepals reflexed separately. Petals yellow, white, or lavender, if yellow strongly ultraviolet reflective, with or without one or more red dots near the base, and some yellow-flowered species[2] with the basal area of the petals with a large, nonultraviolet reflective area; petals, if white or yellow, often fading orange red after pollination. Stamens 8 or 4; anthers versatile, long-ciliate or glabrous. Pollen shed singly. Capsule long-pedicellate, regularly and promptly loculicidal, each valve with a brown, prominent midrib, terete, the seeds in 2 rows in each locule. Seeds monomorphic, lenticular, with a more or less pronounced membranous margin when immature, lance-ovoid when mature, finely lacunose.

TYPE SPECIES: *Camissonia scapoidea* (Torr. & Gray) Raven.

---

[2] *Camissonia brevipes, C. confertiflora, C. eastwoodiae,* and *C. multijuga*. Other species did not show a contrasting pattern of this sort.

Distribution: Sandy desert slopes, flats, and washes, often with *Artemisia tridentata* in the northern part of its area, or on rock slides or cliffs, from southeastern Oregon, east-central and southern Idaho, and central and western Wyoming, south throughout the Great Basin in eastern California, Nevada, and western Colorado, to northwesternmost New Mexico, throughout Arizona, and widespread in the Mojave and Colorado Deserts, south to northwesternmost Sonora above the head of the Golfo de California, and in eastern Baja California south to the vicinity of Bahía de los Angeles at about 29° N. lat. Also, *Camissonia scapoidea* has been collected twice on the upper drainage of the Arkansas River in eastern Colorado and is the only species of its section and one of the two in the genus—the other is *C. chamaenerioides*—to occur east of the crest of the southern Rocky Mountains. Plants of *Camissonia* sect. *Chylismia* do not occur west of the Cascade-Sierra Nevada axis and constitute the only major group of the genus strictly confined to the deserts; however, the distribution of sect. *Eremothera* is generally similar.

The phylogeny and relationships of this group were discussed by me in detail in 1962 (Univ. Calif. Publ. Bot. 34: 1–122), and the section is included here only to bring it into line with my treatment of the rest of the genus and to bring my account of it up to date. The only specimens cited in the present treatment are types and recently collected vouchers for chromosome number determinations and range extensions. Distribution maps were presented in my 1962 revision and are not reprinted here.

Only one major change is made in the present treatment. Impressed with its loss of the epipetalous stamens, I set up a new monotypic section, sec. *Tetranthera,* for *Camissonia exilis* in my 1962 revision. Subsequently, however, I have found that some individuals of *C. andina* (sect. *Nematocaulis*) likewise have lost the epipetalous stamens, and some individuals of *C. minor* (sect. *Eremothera*) approach this condition. In all of these cases, the loss of this whorl of stamens appears to be associated with autogamy. In the light of this information, and considering the close overall resemblance between *C. exilis* and *C. walkeri, C. scapoidea,* and *C. parryi,* I now feel that my earlier segregation of *C. exilis* as a monotypic section reflected an unwarranted overemphasis of a single characteristic. The relationships of this species appear to be reflected more accurately when it is included in sect. *Chylismia* with its close relatives.

5. Camissonia confertiflora (Raven) Raven, Brittonia 16: 281. 1964.
Oenothera confertiflora Raven, Univ. Calif. Publ. Bot. 34: 80. 1962.

Stout annual herb 15–50 cm. tall, branched at the base and above, with a well-developed basal rosette; stems densely villous at the base, mixed with shorter strigose pubescence, and villous above with short glandular pubescence. Basal leaves oblanceolate, 7–20 cm. long, pinnate, the lateral leaflets to 2 cm. long, alternating with shorter pinnules, or reduced; terminal leaflet narrowly ovate, to 5 cm. long and 2.5 cm. wide, sparsely villous. Inflorescence dense and corymbiform in bud, later elongating, glandular-puberulent. Hypanthium 3-5 mm. long, 3–5 mm. across at the summit, short-villous within below. Sepals 9–12 mm. long, 2.5–4 mm. wide, glandular-pubescent, or with a few scattered long trichomes; free caudate portions conspicuous, arising just below the apices, these with a median row of light brown oil cells. Petals 12–18 mm. long, 12–17 mm. wide, bright yellow, of same color as stamens, style, and inside of hypanthium, red dotted at the base, fading purplish. Filaments of the episepalous stamens 6–8 mm. long, those of the epipetalous ones 4–5 mm. long; anthers 4–6 mm. long, ciliate. Style 11–18 mm. long; stigma ca. 1.5 mm. thick, held well above the anthers at anthesis. Immature capsule to 35 mm. long, on a pedicel 5–15 mm. long, glandular-pubescent. Seeds not known. Presumably self-incompatible.

TYPE: In cinder soil, on east side, base of Vulcan's Throne, Toroweap Valley, ca. 4,200 ft., Grand Canyon National Monument, Mohave County, Arizona, 30 April 1952, *E. McClintock* 52–294 (CAS 373481; isotypes, ARIZ, NY, WS).

DISTRIBUTION: Known only from the type locality.

Camissonia confertiflora is most closely related to *C. brevipes* and to *C. multijuga*. It is easily distinguished from the latter by its larger flowers, drooping inflorescence, and large buds; and from the former by its glandular sepals, unequal stamens, and uniformly branched habit. In addition, the single locality for *C. confertiflora* is outside the range of *C. brevipes*. *Camissonia multijuga* grows within less than a mile of this locality, but in this area is very distinct; some collections, however, such as one from Searchlight Ferry, Mohave County, Arizona (*Shreve* 7870), are more similar to *C. confertiflora* in their crowded inflorescences and larger flowers. No more is known about this species at present than when I described it in 1962.

6. Camissonia brevipes (A. Gray) Raven, Brittonia 16: 281. 1964.

Annual, 3–75 cm. tall, the stems often densely clothed below with spreading white trichomes. Leaves mostly in a basal rosette, spatulate, the terminal leaflet to 6.5 cm. long and 5 cm. wide, sometimes cordate at the base, the lateral leaflets reduced or absent. Inflorescence nodding, elongating in flower and fruit. Hypanthium 3–8 mm. long, densely short-villous in lower portions within, 1.5–7 mm. across at the summit. Sepals 5–9 mm. long, the apices covered with brown oil cells, the caudate appendages present or absent. Petals 3–18 mm. long, 4–25 mm. wide, bright yellow, rarely red dotted, the same color as the stamens and style. Stamens subequal; filaments 3–6 mm. long;

anthers 2.5-6 mm. long, ciliate. Style 10–18 mm. long; stigma 1–2 mm. thick held above the anthers at anthesis. Capsule 18–92 mm. long, glabrous or sparsely villous, ascending or spreading, straight or curved; pedicel 2–20 mm. long. Seeds 1–1.5 mm. long, 0.6–1 mm. wide. Gametic chromosome number, $n=7$. Self-incompatible.

DISTRIBUTION: Alluvial slopes, flats, and canyon sides, Washington County, Utah, Lincoln and Esmeralda Counties, Nevada, and Inyo County, California, south to Yuma County, Arizona, and Imperial County, California. From ca. 230 ft. below sea level to 6,000 ft. alt.

6a. Camissonia brevipes subsp. **brevipes** FRONTISPIECE

Oenothera brevipes A. Gray, Pac. R. R. Rept. 4: 87. 1857.

Oenothera divaricata Greene, Bull. Torrey Cl. 10: 125. 1883. Type: CAS 866, labeled: "The specimen found among the 'Cruciferae' of State Geo. Survey"; isotype, GH. As indicated in a note penciled by Katherine Brandegee, probably the same as a specimen from gravelly banks, Fort Mojave, Mojave County, Arizona, 15 February 1861, *J. G. Cooper* (GH), bearing the characteristic printed label, "Geological Survey of California 1860–61."

Chylisma brevipes (A. Gray) Small, Bull. Torrey Cl. 23: 194. 1896.

Oenothera brevipes var. *typica* Munz, Amer. Journ. Bot. 15: 228. 1928.

Oenothera brevipes subsp. *brevipes;* Raven, Univ. Calif. Publ. Bot. 34: 81. 1962.

Stout, generally unbranched above, the stems villous. Terminal leaflet ovate. Inflorescence dense, nodding. Hypanthium 4–8 mm. long, villous without, yellow within. Sepals usually villous, with a caudate protection arising below the apex. Petals 6–18 mm. long, 7–25 mm. wide. Anthers 4–6 mm. long. Capsule 20–92 mm. long; pedicel 5–20 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: On gravelly hills, Colorado River, California or Arizona, February 1854, *J. M. Bigelow* (GH; isotypes, NY, PH, US).

DISTRIBUTION: Hillsides and alluvial fans, sometimes in great abundance on sandy slopes, southern Esmeralda County, Nevada, and southwestern Washington County, Utah, south to northern Yuma County, Arizona, and northern Imperial County, California. From ca. 230 ft. below sea level to 6,000 ft. alt.

Camissonia brevipes subsp. *brevipes* grows in more mesic habitats than those occupied by subsp. *arizonica* or subsp. *pallidula.* In the mountains east of Death Valley, for example, *C. claviformis* subsp. *aurantiaca* and *C. brevipes* subsp. *pallidula* are found growing on dry flats, *C. munzii* above in more mesic sites, and *C. brevipes* subsp. *brevipes* in the best watered situations near the tops of the passes. It grows sympatrically with *C. claviformis* subsp. *aurantiaca, C. claviformis* subsp. *claviformis, C. claviformis* subsp. *funerea, C. claviformis* subsp. *integrior, C. claviformis* subsp. *peeblesii, C. multijuga, C. munzii,* and *C. walkeri* subsp. *tortilis,* and forms hybrids with *C. claviformis, C. multijuga,* and *C. munzii.* It intergrades with subsp. *pal-*

lidula over a wide area in Utah, Nevada, California, and Arizona, but not with subsp. *arizonica*, with which it does not come in contact. The most densely villous and succulent individuals within subsp. *brevipes* are found in Mohave County, Arizona, and Clark County, Nevada, in the region about Hoover Dam. Progeny of *Everett & Balls* 23034, grown at Claremont, California, were self-incompatible, as were 12 plants from Frenchman Flat, Nye County, Nevada, R18853; 3 from State Hwy. 95, 33.4 miles north of junction with U.S. Hwy. 60–70, San Bernardino County, California, *Kyhos* 65–237; and 3 from 2.9 miles south of Twentynine Palms, San Bernardino County, California, *Kyhos* 64–31. Individuals from the last three populations were tested by pollen-tube growth in selfed and outcrossed individuals. It is surprising that insect visitors to this self-incompatible species appear to be relatively uncommon; nevertheless, full seed set appears to be the rule, except in isolated individuals. Probably a wide spectrum of visitors, active throughout the hours of daylight, is effective in cross-pollinating the plants.

6b. Camissonia brevipes subsp. **pallidula** (Munz) Raven, Brittonia **16**: 281. 1964.
Oenothera brevipes var. *pallidula* Munz, Amer. Journ. Bot. 15: 229. 1928.
Oenothera pallidula (Munz) Munz, Leafl. West. Bot. 2: 88. 1938.
Oenothera brevipes subsp. *pallidula* (Munz) Raven, Univ. Calif. Publ. Bot. 34: 83. 1962.

Slender, usually branched above, the stems generally strigose. Terminal leaflet narrowly ovate to ovate. Inflorescence dense, nodding. Hypanthium 4–5 mm. long, yellow within. Sepals strigose, lacking projections, or these poorly developed. Petals 7–12 mm. long, 8–14 mm. wide, often red-dotted near the base. Anthers 4–6 mm. long. Capsule 2–4.2 cm. long; pedicel 2–10 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Las Vegas, Clark County, Nevada, 25 April 1905, *M. E. Jones* (POM 38034).

DISTRIBUTION: Dry flats, often on desert pavement, often with *Larrea* and *Ambrosia dumosa*, from Washington County, Utah, to southeastern Inyo County, California, and south to Riverside County, California, and Mohave County, Arizona, but only along the Colorado River south of Clark County, Nevada. From 250–3,500 ft. alt.

Fourteen plants of this entity from Frenchman Flat, Clark County, Nevada (R18905), were tested for self-compatibility by pollen-tube growth; all were found to be self-incompatible. *Camissonia brevipes* subsp. *pallidula* intergrades with *C. brevipes* subsp. *brevipes* over a wide area, and no evidence for reduction of fertility or for cytological abnormality has been found in the intermediate plants, in spite of the very different phenotypes of these two subspecies (Raven, Univ. Calif. Publ. Bot. 34: 84. 1962). *Camissonia brevipes* subsp. *pallidula* grows sympatrically with *C. claviformis* subsp. *aurantiaca, C. claviformis* subsp. *peeblesii, C. munzii, C. walkeri* subsp. *tortilis,* and *C. multijuga,* forming natural hybrids with the first two.

6c. **Camissonia brevipes** subsp. **arizonica** (Raven) Raven, Brittonia 16: 281. 1964.

Oenothera brevipes subsp. *arizonica* Raven, Univ. Calif. Publ. Bot. 34: 84. 1962.

Slender, often branched above, the stems villous. Terminal leaflet narrowly ovate. Inflorescence nodding, the buds individually deflexed before opening. Hypanthium 3–5 mm. long, orange brown within. Sepals villous to strigose, with free caudate portions nearly terminal or lacking. Petals 3–8 mm. long, 4–7 mm. wide, often red-dotted at base, and often fading reddish. Anthers 2.5–5 mm. long. Capsule 1.8–6 cm. long; pedicel 2.5–5 mm. long. Gametic chromosome number, $n=7$.

TYPE: Mohawk Mountains, Yuma County, Arizona, 29 March 1935, *A. & R. A. Nelson* 1343 (RM 172249; isotypes, GH, MO, NY, UC, US).

DISTRIBUTION: Rocky slopes and flats, Yuma County, Arizona, and eastern Imperial County, California. From 250–900 ft. alt.

Plants of *Camissonia brevipes* subsp. *arizonica* from western Arizona are similar to *C. claviformis* subsp. *rubescens,* and the two taxa occur sympatrically in that area. Hybrids between them, however, seem to be rare. The present taxon also grows with *C. claviformis* subsp. *peeblesii* and with *C. claviformis* subsp. *yumae,* forming occasional natural hybrids with each of them.

7. **Camissonia multijuga** (S. Wats.) Raven, Brittonia 16: 281. 1964.

Oenothera multijuga S. Wats., Amer. Nat. 7: 300. 1873.

Oenothera brevipes var. *parviflora* S. Wats., Amer. Nat. 9: 271. 1875. Type: Valley of the Virgin R., near St. George, Washington Co., Utah, 1874, *C. C. Parry* 74 (GH; isotypes, MO, F); not *Oenothera parviflora* L. 1758.

Chylisma multijuga (S. Wats.) Small, Bull. Torrey Cl. 23: 193. 1896.

Chylisma venosa A. Nels. & Kennedy, Muhlenbergia 3: 140. 1908.

Chylisma hirta A. Nels., Bot. Gaz. 47: 428. 1909. Type: in stony washes, Tuly's Ranch, 13 mi. from Las Vegas, Clark Co., Nevada, 1 May 1905, *L. N. Goodding* 2348 (RM 65187; isotypes, UC, GH, MO).

Chylisma parviflora (S. Wats.) Rydberg, Fl. Rocky Mts. 1064. 1917.

Oenothera brevipes var. *multijuga* (S. Wats.) Jeps., Man. Fl. Pl. Calif. 687. 1925.

Oenothera multijuga var. *typica* Munz, Amer. Journ. Bot. 15: 230. 1928.

Oenothera multijuga var. *parviflora* (S. Wats.) Munz, Amer. Journ. Bot. 15: 231. 1928.

Oenothera watsoni Tidestr., Proc. Biol. Soc. Wash. 48: 41. 1935.

Oenothera phlebophylla Tidestr. Proc. Biol. Soc. Wash. 48: 41. 1935.

Virgate annual or biennial 20–150 cm. tall, with a well-developed basal rosette, nearly leafless above, with numerous divergent branches;

stems villous, at least below, glabrous or even glaucous above, rarely glandular-pubescent. Basal leaves oblanceolate, villous to nearly glabrous, sometimes purple-dotted, 6–30 cm. long, pinnate or bipinnate, with well-developed narrowly ovate, irregularly serrate lateral leaflets to 2.5 cm. long and 2 cm. wide, alternating with smaller pinnules, the leaflets often divided further; terminal leaflet irregularly serrate, to 6 cm. long and 4 cm. wide, the veins below prominently lined with dark brown oil cells. Inflorescence erect to drooping, sparse, elongating in bud, the buds individually pendulous when mature. Hypanthium 1–3 mm. long, 1–1.5 mm. wide at the summit, glandular-puberulent, villous, or glabrous without, glabrous or villous in lower portions within. Sepals 3–8 mm. long, 1.5–2 mm. wide, glandular-puberulent, strigose, villous, or glabrous, short-caudate at or slightly below the apices. Petals spreading in anthesis, 4–9 mm. long, 4–8 mm. wide, bright yellow, rarely cream, sometimes fading purplish, and of the same color as the stamens, style, and usually the inside of the hypanthium, which may rarely be greenish. Filaments of the episepalous stamens 2.5–4 mm. long, those of the epipetalous ones 1.3–3 mm. long. Anthers 2–4 mm. long, ciliate. Style 7–11 mm. long; stigma 0.7–1 mm. thick, held well above the anthers at maturity. Capsule 1–5.2 cm. long, 1.3–2 mm. thick, slender, straight to slightly curved, glabrous or sparsely villous; pedicel 7–20 mm. long, spreading or rarely slightly deflexed. Seeds 1–1.3 mm. long, 0.8–1 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Near Kanab, Washington County, Utah, 1872, *Mrs. Ellen P. Thompson* (GH).

DISTRIBUTION: Forming colonies on rocky slopes and banks of eroded sedimentaries, sometimes on gypsum or limestone, often on conglomerates, often with *Pinus edulis* and *Juniperus* or with *Larrea* and *Encelia farinosa*, Washington County, Utah, and southern Lincoln County, Nevada, to northern Mohave County, Arizona. From 1,000–3,500 ft. alt.

Although occupying a relatively limited range, *Camissonia multijuga* is one of the most variable species in its section. Nevertheless, it has not been possible to identify well-marked infraspecific taxa. Plants of *Gullion* 259, 8 miles southwest of Davis Dam, Clark County, Nevada, grown in the experimental garden, were self-incompatible, as were 12 individuals from a population in Eldorado Canyon, Clark County, Nevada, R18970, judging from the comparative growth of pollen tubes in selfed and outcrossed individuals. The autogamous *C. walkeri* subsp. *tortilis* was very probably derived from this entity, and grows sympatrically with it at several localities in southern Nevada, with no direct evidence for hybridization. *Camissonia multi-*

juga also grows sympatrically with *C. brevipes* subsp. *brevipes, C. brevipes* subsp. *pallidula, C. claviformis* subsp. *aurantiaca,* and *C. parryi,* rarely forming hybrids with both subspecies of *C. brevipes.*

8. Camissonia speculicola (Raven) Raven, Brittonia 16: 282. 1964.

Tufted perennial 10–50 cm. tall, with numerous divergent branches from the base; stems and leaves glabrous or sparsely villous below. Leaves broadly elliptical, 3–20 cm. long, pinnate or often bipinnate, mostly in a basal rosette; lateral leaflets well developed, to 15 mm. long and 7 mm. wide, often further divided and alternating with smaller pinnules; oil cells beneath prominent, dark brown. Inflorescence erect, elongating in flower and fruit, the mature buds individually drooping. Hypanthium 1.5–2 mm. long, 1 mm. across at the summit, glandular-pubescent without, glabrous within. Sepals 2–5 mm. long, 0.5–0.8 mm. wide, glandular-pubescent, caudate with short appendages at the apices, these free in bud. Petals 2–6 mm. long, 1.5–4 mm. wide, bright yellow, fading light purplish, red-dotted near the base, of the same color as inside of hypanthium, stamens, and style; filaments of the episepalous stamens 1.5–3 mm. long, those of the epipetalous ones 1–2 mm. long; anthers 1.2–2 mm. long, glabrous. Style 4–7 mm. long; stigma ca. 0.8 mm. thick, at about the same level as the anthers at anthesis. Capsule straight to slightly curved, spreading to ascending; 0.8–2 cm. long, 1–1.5 mm. thick; glandular-pubescent or glabrous; pedicel 6–10 mm. long; seeds 0.6–1 mm. long, to 0.6 mm. thick. Gametic chromosome number, $n=7$.

DISTRIBUTION: Washes and debris slides, along the Colorado River in Coconino and Mohave Counties, Arizona, in several disjunct localities. From 2,300–5,600 ft. alt.

8a. Camissonia speculicola subsp. **speculicola**

Oenothera speculicola subsp. *speculicola* Raven, Univ. Calif. Publ. Bot. 34: 87. 1962.

Densely tufted and somewhat woody at base, occasionally with secondary flowering axes arising above from the decumbent stems. Leaves glabrous, glutinous, shining. Style 4–5 mm. long, glabrous. Gametic chromosome number, $n=7$.

TYPE: Debris slides and crevices in Redwall limestone, Kaibab Trail at 5,400 ft. alt., south rim of Grand Canyon, Coconino County, Arizona, 8 June 1958, *P. H. Raven* 13119 (RSA).

DISTRIBUTION: Crevices of broken limestone, south rim of the Grand Canyon, Coconino County, Arizona. From 4,500–5,600 ft. alt.

At its type locality, *Camissonia speculicola* subsp. *speculicola* occurs in narrow crevices in the solid limestone, *C. walkeri* subsp. *walkeri* nearby on loose rockslides; no evidence of hybridization between these two entities was noted.

8b. **Camissonia speculicola** subsp. **hesperia** (Raven) Raven, Brittonia 16: 281. 1964.

Oenothera speculicola subsp. *hesperia* Raven, Univ. Calif. Publ. Bot. 16: 84. 1962.

Less densely tufted and not woody. Leaves sparsely pubescent. Style 5–7 mm. long, pubescent at base.

TYPE: Near Mooney Falls, Havasu Canyon, Coconino County, Arizona, 23 May 1950, *J. T. Howell* 26486 (CAS 359774; isotype, ARIZ).

DISTRIBUTION: Washes and dry stream beds, often on limestone, in two disjunct areas along the Colorado River, Arizona: Havasu and Hualapi Canyons, Coconino County; from Separation Canyon to Spencer Canyon, Mohave County. From 2,300–3,500 ft. alt.

Camissonia speculicola subsp. *hesperia* resembles the allopatric subsp. *speculicola* in its glabrous anthers and distinctive habit. Both of these taxa appear to be outcrossers, but they are probably not self-incompatible, judging from their relatively small flowers (compared with those of the self-incompatible *C. multijuga*). *Camissonia speculicola* subsp. *hesperia* grows sympatrically with *C. walkeri* subsp. *walkeri*.

9. **Camissonia walkeri** (A. Nels.) Raven, Brittonia 16: 281. 1964.

Slender herb 10–60 cm. tall, villous below and with a basal rosette, the cauline leaves well developed or absent. Basal leaves oblong, with brown oil cells prominently lining veins below, often purple-dotted, doubly serrate, 3–22 cm. long, villous, often densely so below; terminal leaflet 1–5 cm. long, 0.5–3 cm. wide. Inflorescence branching, erect, elongating in flower and fruit, the buds individually drooping. Hypanthium 0.5–1.5 mm. long, glandular-pubescent or hispid without, glabrous to sparsely villous within. Sepals 1.2–4 mm. long, 0.5–1 mm. wide, often purple-dotted, short-caudate at the apices. Petals 1.2–6 mm. long, 0.6–6 mm. wide, bright yellow and of same color as stamens, style, and inside of hypanthium. Filaments of the episepalous stamens 1–3 mm. long, those of the epipetalous ones 0.3–2 mm. long; anthers 0.6–2 mm. long, glabrous or ciliate. Style 1.5–6 mm. long, glabrous or villous at base; stigma ca. 0.6 mm. thick, surrounded by the anthers at maturity. Capsule 1.2–4.5 cm. long, 1.2–1.8 mm. thick, spreading or ascending, the valves often twisted at maturity, straight or slightly curved. Seeds 0.6–1.2 mm. long, 0.4–0.6 mm. thick. Gametic chromosome numbers, $n=7$, 14. Autogamous.

DISTRIBUTION: Washes and alluvial slopes, from Mesa County, Colorado, to southern Elko and Mineral Counties, Nevada, and south to Inyo and northeastern San Bernardino Counties, California; Clark County, Nevada; and Coconino County, Arizona. From ca. 2,000–6,000 ft. alt.

9a. Camissonia walkeri subsp. **tortilis** (Jeps.) Raven, Brittonia 16: 281. 1964.

Oenothera scapoidea var. *tortilis* Jeps., Man. Fl. Pl. Calif. 687. 1925.

Oenothera multijuga var. *parviflora* sensu Munz, Amer. Journ. Bot. 15: 231. 1928, for the most part, excluding the type.

Oenothera walkeri subsp. *tortilis* (Jeps.) Raven, Univ. Calif. Publ. Bot. 34: 90. 1962.

Annual or short-lived perennial, nearly leafless above and with well-developed basal rosette. Leaves pinnate or more rarely bipinnate, the lateral leaflets usually well developed, to 3 cm. long and 1.5 cm. wide, often alternating with smaller pinnules. Hypanthium 1–1.5 mm. long. Sepals 1.5–4 mm. long, often purple-dotted. Petals 2.8–6 mm. long, 2–6 mm. wide. Anthers 1–2 mm. long, glabrous to sparsely ciliate. Style 4–6 mm. long. Capsule on a pedicel 5–30 mm. long. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Wild Rose Canyon, Panamint Mountains, Inyo County, California, 24 May 1917, *W. L. Jepson* 7131 (JEPS 2669).

DISTRIBUTION: Colonial in rocky debris near cliffs and along ephemeral streams, often on limestone, Logan (?) and Millard Counties Utah, southern Elko and Mineral Counties, Nevada, and Inyo and northeastern San Bernardino Counties, California, to Clark County, Nevada, and Washington County, Utah. Common only in Inyo County, California. From ca. 2,000–6,000 ft. alt.

Camissonia walkeri subsp. *tortilis* grows sympatrically with *C. brevipes* subsp. *brevipes*, *C. brevipes* subsp. *pallidula*, *C. heterochroma*, and *C. multijuga* without any evidence of hybridization. Although modally very distinct from *C. walkeri* subsp. *walkeri*, subsp. *tortilis* replaces it geographically and their variation patterns overlap to such an extent that I consider it desirable to retain both within the same species.

9b. Camissonia walkeri subsp. **walkeri**

Chylisma walkeri A. Nels., Bot. Gaz. 56: 66. 1913.

Oenothera multijuga var. *orientalis* Munz, Amer. Journ. Bot. 15: 232. 1928. Type: Moab, Grand Co., Utah, 7 June 1913, *M. E. Jones* (POM 38608).

Oenothera walkeri (A. Nels.) Raven, Univ. Calif. Publ. Bot. 34: 88. 1962.

Annual, usually leafy above, the leaves cordate to ovate and simple by reduction of the lateral leaflets, or more rarely these developed; basal rosette not conspicuous. Hypanthium 0.5–1.3 mm. long. Sepals 1.5–2 mm. long. Petals 1.2–3 mm. long, 0.6–1.8 mm. wide. Anthers 0.6–0.8 mm. long, glabrous. Style 1.5–4 mm. long. Capsule on a pedicel 5–15 mm. long. Gametic chromosome numbers, $n=7$, 14. Autogamous.

TYPE: Dry gypsum hills, Paradox Valley, Montrose County, Colorado, 1 July 1912, *E. P. Walker* 200 (RM 75864; isotypes, DS, GH, POM, US).

DISTRUBUTION: Loose slides of limestone and other sedimentaries, or in sandy washes, Mesa County, Colorado, and Emery County, Utah, south to Montezuma County, Colorado, and central Coconino County, Arizona. From 3,200–5,500 ft. alt.

Under conditions of cultivation, plants of this subspecies develop a rather full rosette of leaves similar to that characteristic of subsp. *tortilis*; in the field, the cauline leaves are very often the only ones present at the time of flowering. Plants of this taxon probably occasionally hybridize with *C. scapoidea* subsp. *scapoidea*; one remarkable intermediate population is represented by *Eastwood* 5077 (CAS) from Grand Junction, Mesa County, Colorado, with the pubescence and cauline leaves of *C. walkeri* subsp. *walkeri* but the habit of *C. scapoidea* subsp. *scapoidea*. *Camissonia walkeri* subsp. *walkeri* grows sympatrically with both subspecies of *C. speculicola* but in less stable soil and without any evidence of hybridization. *Camissonia scapoidea* subsp. *scapoidea*, on the other hand, is mostly restricted to alkaline clay flats and is thus usually ecologically separated from *C. walkeri* subsp. *walkeri*.

An apparent autotetraploid population of *C. walkeri* subsp. *walkeri* has been found growing on the walls of the Marble Gorge, Coconino County, Arizona. These plants had up to 4 rings of 4 chromosomes at meiotic metaphase I (Raven, Univ. Calif. Publ. Bot. 34: 40. 1962). Seven other individuals from four other populations were diploid.

10. Camissonia claviformis (Torr. & Frém.) Raven, Brittonia 16: 282. 1964.

Annual 3–70 cm. tall, branching mostly from the base. Leaves in a prominent basal rosette, reduced upward, pinnately divided or entire by reduction, 1.5–20 cm. long, broadly oblanceolate, the terminal segment 0.8–9 cm. long, 0.2–4 cm. broad, lanceolate to cordate, the lateral segments lacking or to 2.5 cm. long; veins beneath prominently lined with brown oil cells. Inflorescence nodding, not elongating much in flower. Flowers opening in late afternoon in all except subsp. *cruciformis*. Hypanthium 1.5–6.5 mm. long, 1–5 mm. across at the summit, short-villous in lower portions within. Sepals 2–8 mm. long, 1–2.5 mm. wide, with brown oil cells on midribs above and on free tips, if present. Petals 1.5–8 mm. long, 1.5–10 mm. wide, yellow or white, reflexed in anthesis, and of same color as stamens and style. Stamens subequal, the filaments 1.5–5.5 mm. long, dilated at base; anthers 1.5–6 mm. long, long-ciliate. Style 5–16 mm. long, held well above the stamens at anthesis; stigma greenish, 0.6–1.3 mm. thick. Capsule 0.9–3.8 cm. long, 1.5–2.3 mm. thick, straight or curved, clavate, on a spreading or ascending pedicel 4–40 mm. long. Seeds pale brown, narrowly obovoid, lenticular, 0.6–1.5 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

DISTRIBUTION: Sandy slopes and flats, often in washes, from southeastern Oregon and adjacent Idaho south to eastern California, Nevada, and Arizona, northwestern Sonora, and to near latitude 29° N. in eastern Baja California. From ca. 250 ft. below sea level to 6,500 ft. alt.

Camissonia claviformis is the most complex and one of the most widely distributed species of the genus. The central part of its range is occupied by five closely related white-flowered subspecies, *claviformis, aurantiaca, funerea, integrior,* and *peeblesii,* so similar morphologically that they could be regarded as a single taxon. South of this area are found four additional subspecies, all yellow-flowered, namely, *peirsonii, rubescens, wigginsii,* and *yumae.* These entities have sepals and flower color similar to those of *C. brevipes,* and it is likely that they were derived following hybridization between that species and white-flowered populations of *C. claviformis.* North of the range of the white-flowered subspecies are found two additional yellow-flowered subspecies, *cruciformis* and *lancifolia,* the latter apparently derived following hybridization between the former and some of the white-flowered subspecies. Most populations of subsp. *cruciformis* consist of plants in which the flowers open in the early morning; all other subspecies consist of plants that have flowers opening in the late afternoon. In this and other morphological respects, *C. claviformis* subsp. *cruciformis* (including subsp. *citrina*) resembles *C. eastwoodiae* and *C. munzii* and is undoubtedly close to the ancestral stock from which *C. claviformis* was derived.

10a. Camissonia claviformis subsp. **cruciformis** (Kell.) Raven, Brittonia 16: 282. 1964.

Oenothera cruciformis Kell., Proc. Calif. Acad. Sci. 2: 227, *fig. 71.* 1873.

Chylisma clavaeformis var. *cruciformis* (Kell.) Small, Bull. Torrey Cl. 23: 193. 1896.

Chylisma cruciformis (Kell.) Howell, Fl. N. W. Amer. 233. 1898.

Oenothera clavaeformis var. *cruciformis* (Kell.) Munz, Amer. Journ. Bot. 15: 235. 1928.

Oenothera clavaeformis var. *purpurascens* sensu Munz, Leafl. West. Bot. 3: 53. 1941; not S. Wats. 1873:

Oenothera clavaeformis subsp. *cruciformis* (Kell.) Raven, Univ. Calif. Publ. Bot. 34: 108. 1962.

Oenothera clavaeformis subsp. *citrina* Raven, Univ. Calif. Publ. Bot. 34: 108. 1962. Type: Roadbanks of decomposed conglomerate, in clay soil, 1.4 mi. NE. of Oregon State line on U.S. Hwy. 95, Jump Creek Canyon, Owyhee Co., Idaho, 23 June 1958, *P. H. Raven & O. T. Solbrig* 13385A (RSA).

Plants 3–55 cm. tall, strigose or glandular below and often glandular above, or glabrous. Lateral leaflets few to numerous; terminal leaflet to 8 cm. long and to 4 cm. wide, narrowly ovate to nearly cordate, serrate with scattered teeth. Flowers usually opening near sunrise. Hypanthium 2–6.5 mm. long, sparsely strigose or glandular without, yellow or orange brown within. Sepals sparsely strigose or glandular-pubescent. Petals 2.5–8 mm. long, 2.5–10 mm. wide, bright yellow, often red-dotted at the base and often fading purple. Filaments 2–5 mm. long; anthers 2–6 mm. long. Style 7–16 mm. long. Capsule 0.8–2.8 cm. long, glandular-pubescent to glabrous, pedicel 4–30 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

NEOTYPE: Steamboat Springs, Washoe County, Nevada, 28 May 1959, *P. H. Raven* 14269 (RSA). The type specimen, if one was prepared, has not been preserved; the proposed neotype is from the type locality and a close match for Proc. Calif. Acad. Sci. 2, *fig. 71* (p. 228). See Raven, Univ. Calif. Publ. Bot. 34: 108. 1962.

DISTRIBUTION: Sandy or clayey flats and slopes, with *Artemisia tridentata, Purshia tridentata, Grayia spinosa,* or *Chrysothamnus,* Lake, Harney, and Malheur Counties, Oregon, western Canyon and Owyhee Counties, Idaho, central and southern Washoe County, Nevada, and Lassen County, California. From 2,000–4,600 ft. alt.

Camissonia claviformis subsp. *cruciformis* is unusually variable, probably owing to hybridization between its southern populations (which occupy a disjunct area) and subsp. *integrior,* which they contact locally. The populations of this taxon found in the vicinity of Sparks, Washoe County, Nevada, consist of plants that have flowers opening in the evening; all other populations of the subspecies appear to have flowers opening in the morning, near sunrise. This taxon intergrades with *C. claviformis* subsp. *integrior* and occurs sympatrically with *C. scapoidea* subsp. *brachycarpa.*

Four populations of this subspecies were tested for pollen-tube growth following self- and cross-pollination and found to be self-incompatible: 4.5 miles north of Sparks, Washoe County, Nevada (8 plants); Steamboat Springs, Washoe County, Nevada (15 plants); 4.2 miles west of Rome, Malheur County, Oregon (3 plants, *Kyhos* 65–255); Jump Creek Canyon, Owyhee County, Idaho (13 plants).

10b. Camissonia claviformis subsp. **lancifolia** (Heller) Raven, Brittonia 16: 282. 1964.

Chylismia lancifolia Heller, Muhlenbergia 2: 226. 1906.

Oenothera clavaeformis var. *cruciformis* sensu Munz, Amer. Journ. Bot. 15: 235. 1928.

Oenothera clavaeformis subsp. *lancifolia* (Heller) Raven, Univ. Calif. Publ. Bot. 34: 109. 1962.

Plants 5–60 cm. tall, strigose below, glabrous and often glaucous above; rosette not strictly basal, the leaves erect. Lateral leaflets few or wanting; terminal leaflet to 5 cm. long and 2.8 cm. wide, lanceolate, the apex acuminate, unevenly serrate, the serrations tipped with light brown clusters of oil cells. Hypanthium 3.5–6 mm. long, glabrous without and orange brown within. Sepals glabrous or sparsely strigose near the apices. Petals 3.5–7 mm. long, 4–9 mm. wide, bright yellow, usually red-dotted near the base. Filaments 3–5 mm. long; anthers

3.5–5 mm. long. Style 9–16 mm. long. Capsule 1.1–2.8 cm. long, glabrous or nearly so; pedicel 8–18 mm. long, Gametic chromosome number, $n=7$.

TYPE: Base of the White Mountains east of Laws, Inyo County, California, 11 May 1906, *A. A. Heller* 8231 (US 611229; isotypes, CAS, COLO, DS, MO, UC).

DISTRIBUTION: Sandy slopes and flats, often with *Artemisia tridentata* or *Chrysothamnus*, east of the Sierra Nevada in southern Mono and Inyo Counties, California. From 4,000–5,500 ft. alt.

The southernmost station for *C. claviformis* subsp. *lancifolia*, in the Owens Valley, Inyo County, California, 3 miles north of Big Pine, is approximately 24 miles north of the northernmost for subsp. *claviformis*, 7.7 miles north of Independence. The yellow-flowered subspecies reaches its peak of bloom several weeks later than the white-flowered one. *Camissonia claviformis* subsp. *lancifolia* grows sympatrically with *C. heterochroma.*

10c. Camissonia claviformis subsp. **integrior** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea var. *purpurascens* S. Wats., Proc. Amer. Acad. 8: 595. 1873. Lectotype: Not abundant, islands in Mono L., Mono Co., California, 10–11 July 1863, *W. H. Brewer* 1845 (GH; isotypes, UC, US).

Oenothera clavaeformis var. *typica* sensu Munz, Amer. Journ. Bot. 15: 236. 1928.

Oenothera clavaeformis subsp. *integrior* Raven, Univ. Calif. Publ. Bot. 34: 106. 1962.

Plants 6–70 cm. tall, strigose below and usually glandular-pubescent above, the leaves sometimes purple-dotted. Lateral leaflets few or absent; terminal leaflet to 7 cm. long and 3 cm. wide, narrowly ovate to ovate, often subcordate at the base, serrate, the serrations often tipped with clusters of oil cells. Hypanthium 3–6 mm. long, strigose, glandular, or nearly glabrous without, orange brown within. Sepals rarely purple-dotted, strigose, glandular, or nearly glabrous, rarely with short free caudate portions. Petals 4.5–8 mm. long, 4–10 mm. wide, occasionally purple-dotted at base, fading purple. Filaments 3–5.5 mm. long. Anthers 3–5.5 mm. long. Style 10–16 mm. long. Capsule 13–25 mm. long, glabrous, strigose, or glandular; pedicel 15–40 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Palisade, Eureka County, Nevada, 14 June 1882, *M. E. Jones* 3869 (POM 38505; isotypes, CAS, DS, MO, NY, UC, US, UTC).

DISTRIBUTION: Dry flats in Great Basin desert, with *Artemisia tridentata*, *Chrysothamnus*, or *Juniperus*, often forming large colonies on banks and flats, from southern Harney County, Oregon, southward nearly throughout Nevada to Lincoln and Esmeralda Counties and to

Mono and northeastern Inyo Counties, California. From 4,000–6,500 ft. alt.

This is the most widely distributed subspecies of *C. claviformis*, and is markedly variable in kind and amount of pubescence. It intergrades with subsp. *aurantiaca* and with subsp. *cruciformis* and grows sympatrically with *C. brevipes* subsp. *brevipes* (forming occasional hybrids), *C. heterochroma* and *C. scapoidea* subsp. *brachycarpa*. Three populations from Nevada were sampled for self-compatibility, and 15 plants from 20 miles northeast of Lovelock, Pershing County (R18542), 9 from Palisade, Eureka County, and 20 from 28.9 miles southwest of Lovelock, Churchill County (*Kyhos* 65–254) were found to be self-incompatible by pollen-tube growth.

10d. Camissonia claviformis subsp. **funerea** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera clavaeformis var. *aurantiaca* sensu Munz, Amer. Journ. Bot. 15: 237. 1928; pro parte.

Oenothera clavaeformis subsp. *funerea* Raven, Univ. Calif. Publ. Bot. 34: 106. 1962.

Plants 6–60 cm. tall, strigose below, often densely so. Lateral leaflets well developed or more often wanting; terminal leaflet to 8 cm. long and to 4.5 cm. wide, ovate, often cordate at the base, very prominent, dentate. Hypanthium 3–5.5 mm. long, strigose without, usually densely so, orange brown within. Sepals usually densely strigose, with conspicuous free caudate segments arising on midribs just below apices. Petals 3.5–7.5 mm. long, 3.5–7.5 mm. wide, often fading purple. Filaments 3–5.5 mm. long; anthers 3–4.5 mm. long. Style 8–12 mm. long, Capsule 1.2–3.2 cm. long, strigose; pedicel 8–22 mm. long. Gametic chromosome number, $n=7$.

TYPE: Dry wash, 2 miles east of Stovepipe Wells, Death Valley, Inyo County, California, 7 April 1928, *P. A. Munz & C. L. Hitchcock* 11030 (POM 159488; isotypes, GH, UC, US).

DISTRIBUTION: Dry slopes and flats, with *Larrea* and *Ambrosia dumosa*, Eureka Valley, Saline Valley, and the region of Death Valley, Inyo County, and northernmost San Bernardino County, California. From ca. 250 ft. below sea level to 3,000 ft. alt.

This taxon is geographically coherent and distinct in its more extreme forms, but intergrades with subsp. *aurantiaca* and subsp. *claviformis* over a broad front, producing an array of intermediate forms. It occurs sympatrically with *C. munzii* and with *C. brevipes* subsp. *brevipes*, forming occasional hybrids with each of these species.

10e. Camissonia claviformis subsp. **claviformis**

Oenothera clavaeformis Torr. & Frém., Rep. Expl. Exped. Rocky Mts. 314. 1845.

Oenothera scapoidea var. *clavaeformis* (Torr. & Frém.) S. Wats., Bot. King Expl. 109. 1871.

Chylisma scapoidea var. *clavaeformis* (Torr. & Frém.) Small, Bull. Torrey Cl. 23: 194. 1896.

Chylisma clavaeformis (Torr. & Frém.) Heller, Muhlenbergia 2: 105. 1906.

Oenothera clavaeformis var. *typica* Munz, Amer. Journ. Bot. 15: 236. 1928.

Chylismia clavaeformis var. *typica* (Munz) Johansen, Amer. Journ. Bot. 16: 597. 1929.

Oenothera clavaeformis subsp. *clavaeformis* Raven, Univ. Calif. Publ. Bot. 34: 99. 1962.

Plants 6–55 cm. tall, glabrous or strigose below and occasionally glandular, the leaves sometimes purple-dotted. Lateral leaflets usually well developed; terminal leaflet to 6 cm. long and 3.5 cm. wide, narrowly ovate, irregularly sinuate-dentate. Hypanthium 3–5.5 mm. long, glabrous, sparsely strigose, or rarely glandular without, orange brown within. Sepals glabrous, sparsely strigose, or rarely glandular, with short-caudate terminal portions. Petals 3.5–8 mm. long, 4–8 mm. wide, white, very rarely pale yellow, sometimes purple-dotted at base, often fading purple. Filaments 3–5 mm. long; anthers 3–4 mm. long. Style 8–12 mm. long. Capsule 1.2–3 cm. long, glabrous or sparsely pubescent; pedicel 10–25 mm. long. Gametic chromosome number, $n = 7$. Self-incompatible.

TYPE: Frémont's 2d Expedition (NY). Collected in 1844 by J. C. Frémont. The herbarium specimen selected as the lectotype by Munz (Amer. Journ. Bot. 15: 236. 1928) and cited by him as "Fremont's Pac. R. R. Exp., 1843–'44, 'probably collected in California,' " has not been located, but this may be an erroneous citation of a specimen from the Torrey Herbarium (NY) labeled "Fremont's Pacific R. Road Expedition, 1853–54 (Probably collected in California)." This collection might be an isotype, but if so it is incorrectly labeled.

DISTRIBUTION: Alluvial slopes and flats, with *Larrea* and *Ambrosia dumosa*, western Inyo County, eastern Kern County, northern Los Angeles County, western San Bernardino County, and northern Riverside County, California, almost entirely on the Mojave Desert. From 2,800–5,500 ft. alt.

This subspecies intergrades gradually and throughout a broad area with subsp. *aurantiaca* and with subsp. *funerea*. It occurs sympatrically with *C. brevipes* subsp. *brevipes*, forming occasional hybrids with this entity. Isolated plants of this subspecies fail to set fruit, and more direct evidence of its self-incompatibility was provided by a study of pollen-tube growth following self- and cross-pollination in three plants from each of the following localities in California: near Pearblossom, Los Angeles County, *Kyhos* 64–14; Joshua Tree, San Bernardino County, *Kyhos* 64–33.

10f. Camissonia claviformis subsp. **aurantiaca** (S. Wats.) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea var. *aurantiaca* S. Wats., Proc. Amer. Acad. 8: 595. 1873.

Chylismia scapoidea var. *aurantiaca* (S. Wats.) A. Davids. & Moxley, Fl. S. Calif. 254. 1923.

Oenothera clavaeformis var. *aurantiaca* (S. Wats.) Munz, Amer. Journ. Bot. 15: 237. 1928.

Chylismia aurantiaca (S. Wats.) Johansen, Desert 3: 78. 1931.

Oenothera clavaeformis subsp. *aurantiaca* (S. Wats.) Raven, Univ. Calif. Publ. Bot. 34: 100. 1962.

Plants 5–50 cm. tall, strigose, especially below, and rarely glandular-pubescent above, the leaves sometimes purple-dotted. Lateral leaflets up to 25 on each side of rachis, irregular, and well developed; terminal leaflet to 3 cm. long and 1.5 cm. wide, narrowly ovate, irregularly sinuate-dentate. Hypanthium 3–5 mm. long, strigose without, orange brown within. Sepals strigose, rarely with short free caudate tips in bud. Petals 2.5–8 mm. long, 3.5–8 mm. wide, white, rarely purple-dotted at base, often fading purple, rarely orange. Filaments 2–5 mm. long; anthers 2.5–4.5 mm. long. Style 7.5–14 mm. long. Capsule 1.3–3 cm. long, sparsely strigose or glabrous; pedicel 8–25 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

LECTOTYPE: Fort Mohave, Mohave County, Arizona, 1861, *J. G. Cooper* (GH; isotypes, UC, US); Munz, Amer. Journ. Bot. 15: 237. 1928.

DISTRIBUTION: Common on sandy flats and washes, with *Larrea, Ambrosia dumosa*, and *Fouquieria splendens*, from Lincoln County, Nevada, south to northeasternmost Baja California, and in Arizona only in westernmost Mohave and Yuma Counties. From 230 ft. below sea level to 3,000 ft. alt.

Camissonia claviformis subsp. *aurantiaca* is variable in leaf outline and color and in amount of pubescence. It intergrades completely with the other four white-flowered subspecies, *claviformis, funerea, integrior*, and *pebblesii*. It likewise intergrades with subsp. *yumae* and subsp. *peirsonii* where it comes in contact with them. Occasional plants have large amounts of glandular pubescence in the inflorescence and elsewhere, as subsp. *peeblesii*, but nowhere west of the Colorado River do such individuals exceed 50 percent of any population known to me. *Camissonia claviformis* subsp. *aurantiaca* grows sympatrically with *C. brevipes* subsp. *brevipes, C. brevipes* subsp. *pallidula, C. multijuga*, and *C. munzii*, forming occasional hybrids with the first two and last entities. Three individuals each from two populations of this subspecies from California were shown to be self-incompatible by pollen-tube growth in selfed and outcrossed flowers: 0.7 mile from U.S. Hwy. 99 on road to Snow Creek, Riverside County, *Kyhos* 64–3; 4.3 miles south of Mortmar, Imperial County, *Kyhos* 64–13.

10g. Camissonia claviformis subsp. **peeblesii** (Munz) Raven, Brittonia 16: 282. 1964.

Oenothera clavaeformis var. *aurantiaca* sensu Munz, Amer. Journ. Bot. 15: 237. 1928.

Oenothera clavaeformis var. *peeblesii* Munz, Leafl. West. Bot. 2: 158. 1939.

Camissonia clavaeformis subsp. *peeblesii* (Munz) Raven, Univ. Calif. Publ. Bot. 34: 101. 1962.

Plants 5–60 cm. tall, glandular-pubescent, especially above, and often also strigose below. Leaves glandular-pubescent, the lateral leaflets numerous, irregular, and well developed, the terminal leaflet narrowly ovate, irregularly sinuate-dentate, to 7 cm. long and 3 cm. wide. Hypanthium 3–5.5 mm. long, glandular-pubescent or strigose without, orange brown within. Sepals glandular-pubescent, strigose, or both, usually lacking caudate appendage. Petals 3–7.5 mm. long, 3–5 mm. wide, often fading purple. Filaments 2–3 mm. long; anthers 2.5–4 mm. long. Style 7.5–14 mm. long. Capsule 1.5–3 cm. long, glandular-pubescent or strigose; pedicel 4–32 mm. long. Gametic chromosome number, $n=7$.

TYPE: Casa Grande, Pinal County, Arizona, 25 February 1927, *Peebles & Harrison* 3537 (US 1367424; isotype, ARIZ).

DISTRIBUTION: Flat sandy plains and washes, with *Prosopis*, *Carnegiea gigantea*, *Larrea* and *Ambrosia dumosa*, throughout almost all the southwestern half of Arizona and locally in northwesternmost Sonora. From 400–2,000 ft. alt.

I have included in *Camissonia claviformis* subsp. *peeblesii* all populations in which a majority of the plants have some glandular pubescence, and the resulting taxon has a coherent geographical range. It intergrades completely with subsp. *aurantiaca* and with subsp. *rubescens*, growing in part in the same area as the latter. It also occurs sympatrically with all three subspecies of *C. brevipes*, forming occasional hybrids with them.

10h. Camissonia claviformis subsp. **peirsonii** (Munz) Raven, Brittonia 16: 282. 1964.

Oenothera clavaeformis var. *peirsonii* Munz, Amer. Journ. Bot. 15: 238. 1928.
Chylismia peirsonii (Munz) Johansen (as "piersonii"), Desert 3: 78. 1931.
Oenothera clavaeformis subsp. *peirsonii* (Munz) Raven, Univ. Calif. Publ. Bot. 34: 105. 1962.

Plants 5–60 cm. tall, spreading-villous below and often above, more rarely strigose or with glandular pubescence. Lateral leaflets usually well developed; terminal leaflets to 9 cm. long and to 3.5 cm. wide, narrowly ovate, irregularly sinuate-dentate. Hypanthium 2.5–4.5 mm. long, villous or strigose without, orange brown within. Sepals villous or strigose, with conspicuous free caudate segments arising just below apices of midribs. Petals 4.5–7 mm. long, 4–9 mm. wide, yellow, more rarely white, not changing color in fading. Filaments 3.5–5 mm. long; anthers 3.5–5 mm. long. Style 9–14 mm. long. Capsule 1.2–3.8 cm. long, spreading pubescent (rarely glabrous); pedicel 10–20 mm. long. Gametic chromosome number, $n=7$.

TYPE: Twenty-eight miles south of Coachella, Imperial County, California, 12 April 1922, *F. W. Peirson* 4512 (POM 138409; isotype, RSA).

DISTRIBUTION: Sandy fields and washes, with *Larrea*, *Ambrosia dumosa*, and *Fouquieria splendens*, east of the Salton Sea and Imperial Valley in San Diego and Imperial Counties, California, and in northeastern Baja California to the Gulf of California. From 240 ft. below sea level to 1,000 ft. alt.

This subspecies intergrades with subsp. *aurantiaca* in northeastern San Diego County, California, where it is extremely variable in pubescence, leaf color, and flower color. Since publishing my revision of the group, I have seen a specimen of *C. claviformis* subsp. *peirsonii* from 41 miles south of San Felipe, Baja California, *Wiggins* 18162 (DS), this record establishing a new southern limit for the subspecies. One additional determination of chromosome number has been made in this entity, $n=7$, in *Klein* 1175 (RSA), from 2 miles south of San Felipe, Baja California.

10i. Camissonia claviformis subsp. **yumae** (Raven) Raven, Brittonia 16: 282. 1964.
Oenothera clavaeformis subsp. *yumae* Raven, Univ. Calif. Publ. Bot. 34: 104. 1962.

Plants 5–40 cm. tall, strigose pubescent below, often densely, and sometimes glandular-pubescent above. Lateral leaflets well developed or reduced; terminal leaflet to 6.5 cm. long and to 2 cm. wide, lanceolate, irregularly sinuate-dentate. Hypanthium 2.5–4 mm. long, strigose without, orange brown within. Sepals strigose with short free caudate portions arising just below the apices, or these absent. Petals 3–5 mm. long, 4–5.5 mm. wide, pale yellow, fading reddish or not changing color after pollination. Filaments 2–4 mm. long, anthers 2–4 mm. long. Style 7.5–10 mm. long. Capsule 1.2–3.2 cm. long, strigose; pedicel 5–30 mm. long. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Covering dunes, Yuma Desert 4.8 miles west of summit of Telegraph Pass, Yuma County, Arizona, 28 February 1958, *P. H. Raven* 11724 (RSA).

DISTRIBUTION: Very dry dunes and sandy flats with *Larrea* and *Ambrosia dumosa*, southeastern Imperial County, California, Yuma Desert, Arizona, and from El Gran Desierto to Puerto Peñasco in northwestern Sonora, and in northeastern Baja California (8 miles northwest of La Ventana, *Moran* 12354, DS, SD). From sea level to 300 ft. alt.

This subspecies, which is unusually variable, was almost certainly derived following hybridization between the yellow-flowered subsp. *peirsonii* and the white-flowered subsp. *aurantiaca*. It intergrades with subsp. *aurantiaca* in California and Baja California and with subsp. *peeblesii* in Arizona and Sonora. It grows sympatrically with *C. brevipes* subsp. *arizonica*, but no hybrids have been found. Three individuals from a population along U.S. Hwy. 80, 0.4 mile west of the junction with U.S. Hwy. 98, Imperial County, California, *Kyhos* 64–11, were found to be self-incompatible, judging from pollen-tube growth in self-pollinated flowers.

10j. Camissonia claviformis subsp. **wigginsii** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera clavaeformis subsp. *wigginsii* Raven, Univ. Calif. Publ. Bot. 34: 103. 1962.

Plants 5–20 cm. tall, covered with spreading white trichomes below and glandular pubescence above. Lateral leaflets reduced or absent; terminal leaflet to 3 cm. long and to 1.5 cm. wide, narrowly ovate, irregularly sinuate-dentate. Hypanthium 1.5–2 mm. long, villous and often purple-dotted without, orange brown within. Sepals villous, often purple-dotted, with short free caudate portions arising on midribs below the apices. Petals 1.5–2 mm. long, 1.5–2 mm. wide, yellow, fading brick red after pollination. Filaments 1.5–2 mm long; anthers 1.5–2 mm. long. Style 5–7 mm. long. Capsule (1.5–) 2.5–3.5 cm. long, often purple-dotted, villous; pedicel 8–20 mm. long. Gametic chromosome number, $n=7$.

TYPE: Wash 3 miles from Los Angeles Bay, Baja California, Mexico, 20 February 1935, *I. L. Wiggins* 7684 (DS 265606; isotypes F, GH, UC, US).

DISTRIBUTION: Central Baja California, in washes. From ca. 500–ca. 2,000 ft. alt.

This is apparently a rare and rather restricted subspecies most similar to subsp. *peirsonii* and subsp. *rubescens*, from which it differs principally in flower size. It is, however, separated from the former subspecies, the nearest geographically within the species, by a gap of about 75 miles. In spite of its relatively small flowers, the stigma is held well above the anthers and this subspecies is presumably self-incompatible like the rest of the species. The chromosome number was determined in a collection from the Arroyo San Francisquito 5 miles northwest of Las Arrastras, 29°37′ N. lat., 114°27′ W. long., *Moran* 12402 (DS, SD).

10k. Camissonia claviformis subsp. **rubescens** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera clavaeformis subsp. *rubescens* Raven, Univ. Calif. Publ. Bot. 34: 103. 1962.

Plants 5–40 cm. tall, covered, especially below, with spreading white trichomes, and also with short glandular trichomes. Lateral leaflets few or absent; terminal leaflet to 4 cm. long and 2 cm. wide, lanceolate, irregularly dentate. Hypanthium 3.5–5 mm. long, glandular-pubescent or villous or both, orange brown within. Sepals villous or glandular-pubescent, with conspicuous free caudate segments arising from midribs below the apices. Petals 3–5 mm. long, 3–5 mm. wide, yellow, fading brick red after pollination. Filaments 2.5–5 mm. long; anthers 2.5–4 mm. long. Style 7–12 mm. long. Gametic chromosome number, $n=7$.

TYPE: On sandy flats, 24 miles south of Sonoyta on road to Rocky Point (Punta Peñasco), Distrito de Altar, Sonora, 14 March 1936, *D. D. Keck* 4178 (DS 287997; isotypes, GH, POM, UC, US).

DISTRIBUTION: Sandy flats, with *Larrea*, *Ambrosia dumosa*, and *Carnegiea gigantea*, western Maricopa, eastern Pima, and southeastern Yuma Counties, Arizona, and northwestern Sonora. From 200–1,000 ft. alt.

This entity grows sympatrically with *C. brevipes* subsp. *arizonica* and occasionally forms natural hybrids with it. It intergrades with *C. claviformis* subsp. *peeblesii*.

11. **Camissonia munzii** (Raven) Raven, Brittonia 16: 281. 1964.
Oenothera munzii Raven, Univ. Calif. Publ. Bot. 34: 91. 1962.

Annual herb 8–50 cm. tall, with numerous branches at the base and above, the leaves mostly in a subbasal rosette. Stems and leaves strigose, often densely so above and in the inflorescence. Leaves to 20 cm. long, pinnate, with well-developed lateral leaflets; terminal leaflet ovate, to 6 cm. long and 3 cm. wide, the veins lined below with brownish oil cells. Inflorescence nodding, not congested, elongating in mature bud. Hypanthium 2–3 mm. long, 2–3 mm. across at the summit, strigose without, villous and orange brown within. Sepals 4–7 mm. long, 1.5–2 mm. wide, strigose. Petals 3–10 mm. long, 3–10 mm. wide, bright yellow, red-dotted near the base. Stamens subequal, the filaments 4–8 mm. long; anthers 3–6 mm. long, ciliate. Style 8–18 mm. long; stigma 0.6–0.8 mm. thick, held well above the anthers at anthesis. Capsule 0.8–2.4 cm. long, 1.5–2 mm. thick, clavate; pedicel 8–28 mm. long, widely divergent and becoming sharply deflexed at maturity. Seeds pale brown, 0.8–1.6 mm. long, 0.5–0.8 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Sandy desert wash, Salsberry Pass, south end of Death Valley, Inyo County, California, 9 April 1940, *P. A. Munz* 16474 (POM 255191; isotypes, CAS, GH, NA, POM, RSA, UC, US, WS, WTU).

DISTRIBUTION: Relatively mesic slopes and washes at middle elevations in the mountains at the north end, eastward, and south of Death Valley, from Saline Valley and the Grapevine Mountains, Inyo County, California, and Yucca Flat, Nye County, Nevada, southward to the Kingston Range, San Bernardino County, California. From 2,000–5,000 ft. alt.

Camissonia munzii grows sympatrically with *C. brevipes* subsp. *brevipes*, *C. brevipes* subsp. *pallidula*, *C. claviformis* subsp. *funerea*, *C. claviformis* subsp. *aurantiaca*, and *C. heterochroma*, forming occasional hybrids with the first and fourth mentioned taxa. It is readily distinguished by its long, deflexed pedicels and clavate capsules. A population from 7.2 miles south of Mercury, Nye County, Nevada, R18865, was tested for self-compatibility, and 14 individuals were found to be self-incompatible by pollen-tube growth.

12. Camissonia eastwoodiae (Munz) Raven, Brittonia 16: 282. 1964.
Oenothera scapoidea var. *eastwoodae* Munz, Amer. Journ. Bot. 15: 234. 1928.
Oenothera eastwoodiae (Munz) Raven, Univ. Calif. Publ. Bot. 34: 92. 1962.

Succulent annual 3–30 cm. tall, the stems glabrous, glandular-pubescent, or villous below. Leaves mostly basal, entire or sparsely denticulate, simple, the blades oblanceolate to cordate, darker green above, 0.8–7.5 cm. long, 0.4–3 cm. wide; veins below lined with pale brown oil cells; petioles 0.5–8 cm. long. Inflorescence drooping, elongating in flower and fruit. Hypanthium 2–4.5 mm. long, 1.5–3.4 mm. across at the summit, glandular-pubescent or strigose without, villous in lower portions within. Sepals 3–8 mm. long, 1–2.5 mm. wide, glandular-pubescent, strigose, or glabrous, without caudate appendage. Petals 5.5–9 mm. long, 4–10 mm. wide, bright yellow and of same color as stamens, style, and inside of hypanthium, red-dotted near the base. Filaments of the episepalous stamens 3–8 mm. long, those of the epipetalous ones 2.8–5.5 mm. long; anthers 2–4 mm. long, ciliate. Style 10–17 mm. long; stigma 0.6–0.8 mm. thick, held well above the stamens at anthesis, villous near the base. Capsule 1.8–4 cm. long, curved, erect, on a spreading or slightly deflexed pedicel 4–28 mm. long. Seeds tan, 1.2–1.7 mm. long. Gametic chromosome number, $n=7$.

TYPE: Grand Junction, Mesa County, Colorado, May 1892, *A. Eastwood* (GH; isotypes, UC, US).

DISTRIBUTION: Clay flats, on gray alkaline marine-deposited gumbo, and in sandy draws, Mesa County, Colorado, and Emery County, Utah, south to San Juan County, Utah. From 4,000–5,500 ft. alt.

Camissonia eastwoodiae, the only outcrossing species in the eastern part of the range of sect. *Chylismia*, is undoubtedly self-incompatible. It grows sympatrically with the autogamous *C. scapoidea* subsp. *scapoidea* and in the same vicinity as the ecologically distinct *C. walkeri* subsp. *walkeri*.

13. Camissonia scapoidea (Torr. & Gray) Raven, Brittonia 16: 95. 1964.

Annual 3–45 cm. tall; stems strigose, villous, or glandular-pubescent below. Leaves mostly in a basal rosette, greatly reduced upward, spatulate, 1–18 cm. long, the lateral leaflets well developed or absent. Inflorescence drooping, glandular-pubescent, strigose, or nearly glabrous. Hypanthium 1–4 mm. long, 1–3.5 mm. across at the summit, glandular-pubescent, strigose, or glabrous without, sparsely villous to glabrous within. Sepals 1.2–5 mm. long, 1–2 mm. wide, strigose, glandular-pubescent, or glabrous, entire or short-caudate at the apices. Petals 1.5–5.5 mm. long, 1–4 mm. wide, bright yellow, of same color as stamens, style, and inside of hypanthium. Filaments of the episepalous stamens 1.2–6 mm. long, those of the epipetalous ones 0.5–4 mm.; anthers 1–2.5 mm. long, ciliate or glabrous. Style glabrous or short-villous at the base, 3–11 mm. long; stigma 0.3–0.6 mm. thick, surrounded by anthers, at least the longer ones, at anthesis. Capsule ascending, curved to nearly straight, 0.8–4 cm. long, 1.8–2.6 mm. thick, sparsely pubescent to glabrous, the valves sometimes twisted at maturity, on an ascending or spreading pedicel 4–20 mm. long. Seeds pale brown, 1–2 mm. long. Gametic chromosome numbers, $n=7$, 14. Autogamous.

DISTRIBUTION: Sandy or clayey slopes and flats, from southeastern Oregon, southwestern and central Idaho, and western and central Wyoming, western Colorado, northeastern Arizona, and adjacent New Mexico, throughout Utah, and in northeastern Nevada. From 2,500–6,000 ft. alt.

13a. Camissonia scapoidea subsp. **scapoidea**

Oenothera scapoidea Torr. & Gray, Fl. N. Amer. 1: 506. 1840.

Chylisma scapoidea (Torr. & Gray) Small, Bull. Torrey Cl. 23: 193. 1896.

Oenothera brevipes var. *scapoidea* (Torr. & Gray) H. Lév., Monogr. Onoth. 146. 1905.

Chylismia scapoidea var. *seorsa* A. Nels., Bot. Gaz. 54: 140. 1912. Lectotype: Evanston, Uinta Co., Wyoming, 27 July 1897, *A. Nelson* 4125 (RM 10458).

Oenothera scapoidea var. *typica* Munz, Amer. Journ. Bot. 15: 233. 1928.

Oenothera scapoidea var. *seorsa* (A. Nels.) Munz, Amer. Journ. Bot. 15: 233. 1928.

Oenothera scapoidea subsp. *scapoidea* Raven, Univ. Calif. Publ. Bot. 34: 94. 1962.

Leaves usually simple, more rarely with a few reduced lateral leaflets, the blades narrowly ovate to ovate, often cordate at the base, to 5.5 cm. long and 3 cm. wide, subglabrous, very rarely villous on both surfaces, the oil cells below pale yellowish brown, rarely darker. Petals acute, 1.7–5 mm. long, 1.5–3.5 mm. wide, often red-dotted near the base. Filaments of the episepalous stamens 1–4 mm. long, those of the epipetalous ones 0.5–2.5 mm. long; anthers 0.5–1.9 mm. long, glabrous or ciliate. Style 2.5–9 mm. long. Capsule (1–)1.5–3 cm. long; pedicel 5–18 mm. long. Gametic chromosome numbers $n=7$, 14. Autogamous.

TYPE: Clay hills, probably near the rendezvous of 1834, on Ham's Fork of the Green River, Sweetwater County, Wyoming, 22 June to 2 July 1834, *T. Nuttall* (NY; isotypes BM, GH). See Raven, Univ. Calif. Publ. Bot. 34: 93. 1962.

DISTRIBUTION: Sandy or clay flats, throughout western Wyoming, west to Lake County, Oregon, and Elko and White Pine Counties, Nevada, south to Beaver County, Utah, northern Coconino, Navajo, and Apache Counties, Arizona, San Juan County, New Mexico, and western Colorado; also on the headwaters of the Arkansas River in eastern Colorado. The only member of sect. *Chylismia* that occurs east of the Continental Divide. From 4,000–8,000 ft. alt.

Camissonia scapoidea subsp. *scapoidea* grows sympatrically with *C. eastwoodiae* and in the same vicinity as the ecologically distinct *C. walkeri* subsp. *walkeri*. It is highly variable, as would be expected in such widely ranging, principally autogamous entity. Both diploid and tetraploid populations occur in this taxon. The first series of tetraploids I studied (Univ. Calif. Publ. Bot. 34: 38–39. 1962), from Emery County, Utah, was growing with *C. eastwoodiae* and diploid plants of *C. scapoidea* subsp. *scapoidea*. At the time, it seemed possible that these tetraploids might have had an allopolyploid origin between the two diploids. It seemed even more likely, however, that they were autotetraploids derived from diploid *C. scapoidea* subsp. *scapoidea*, from which they were morphologically almost indistinguishable. This possibility is now considerably strengthened by the discovery of a tetraploid individual in Sweetwater County, Wyoming, along Interstate Hwy. 80, 4.8 miles southwest of junction with U.S. Hwy. 30N, R19544. This locality is some 150 miles north of the nearest station for *Camissonia eastwoodiae*. The plant examined formed 14 pairs of chromosomes, like the individuals from Utah studied earlier. A diploid individual was likewise found in southwestern Wyoming, 1.7 miles west of Fort Bridger, Uinta County, *Mosquin & Mulligan* 5128. These two chromosome counts constitute the first from the northern portion of the range of the subspecies and suggest the necessity for further chromosome counts of this taxon before its cytological pattern of variation can properly be assessed.

13b. Camissonia scapoidea subsp. **macrocarpa** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea subsp. *macrocarpa* Raven, Univ. Calif. Publ. Bot. 34: 95. 1962.

Basal rosette compact, the leaves simple, rarely with reduced lateral leaflets. Leaf blades ovate, often cordate at the base, to 3.5 cm. long and 1.5 cm. wide, nearly glabrous, the oil cells below pale yellowish brown. Petals 1.5–2 mm. long, ca. 1.5 mm. wide. Filaments of the episepalous stamens ca. 2 mm. long, those of the epipetalous ones ca. 1 mm. long; anthers ca. 1 mm. long, ciliate. Style ca. 3 mm. long. Capsule 2.5–4 cm. long, stout, very large for size of plant, ascending; pedicel 4–6 mm. long. Autogamous.

TYPE: 9 miles northeast of Black Point, 5,700 ft., Apache County, Arizona, 11 June 1937, *R. H. Peebles & E. G. Smith* 13529 (US 1739264; isotypes, ARIZ, US).

DISTRIBUTION: On detrital clay knobs and gravelly flats, northern Apache and Navajo Counties and northeastern Coconino County, Arizona. From 5,000–6,500 ft. alt.

13c. Camissonia scapoidea subsp. **brachycarpa** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea subsp. *brachycarpa* Raven, Univ. Calif. Publ. Bot. 34: 95. 1962.

Slender, the leaves simple or often pinnate with well-developed lateral leaflets. Terminal leaflets narrowly ovate, often cordate at the base, to 10 cm. long and 5 cm. wide, glabrous or weakly pubescent, the oil cells below dark brown, prominent. Petals 1.8–4 mm. long, acute, 1–4 mm. wide, often red-dotted near the base. Filaments of the episepalous stamens 1.2–3.2 mm. long, those of the epipetalous ones 0.5–1.5 mm. long; anthers 0.9–1.8 mm. long, ciliate. Style 4–7.5 mm. long. Capsule 0.8–2 (–2.8) cm. long; pedicel 10–16 mm. long. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Loose dry open slopes with sagebrush and shrubs, 7 miles north of Brogan, T. 14 S., R. 42 E., sec. 27, 3,000 ft., Malheur County, Oregon, 10 June 1955, *A. Cronquist* 7808 (NY; isotypes, DS, GH, ID, MO, RM, RSA, UC, US, UTC, WS, WTU).

DISTRIBUTION: Sandy slopes and flats, with *Grayia*, *Artemisia*, or *Juniperus*, southeastern Oregon, southwestern Idaho, northwestern Utah, and northeastern Nevada. From 2,500–6,000 ft. alt.

Camissonia scapoidea subsp. *brachycarpa* grows sympatrically with *C. claviformis* subsp. *cruciformis* and subsp. *integrior*, and overlaps morphologically with *C. scapoidea* subsp. *scapoidea*, from which it is separated geographically. The possible derivation of this species from populations similar to *C. claviformis* subsp. *cruciformis* and *C. eastwoodiae* has been discussed earlier (Raven, Univ. Calif. Publ. Bot. 34: 71. 1962).

13d. C. scapoidea subsp. **utahensis** (Raven) Raven, Brittonia 16: 282. 1964.

Oenothera scapoidea subsp. *utahensis* Raven, Univ. Calif. Publ. Bot. 34: 96. 1962.

Leaves pinnate, sparsely pubescent, the lateral leaflets well developed, up to 1 cm. long; terminal segment ovate, cordate at the base, up to 4.5 cm. long and 3 cm. wide, the oil cells below dark brown. Petals 4–5.5 (–8) mm. long, 3–4 mm. wide, blunt, often red-dotted near the base. Filaments of the episepalous stamens 5–6 mm. long, those of the epipetalous ones 3.5–4 mm. long; anthers 2–2.5 mm. long, ciliate. Style 8–11 mm. long. Capsule 1.6–3.8 cm. long; pedicel 8–20 mm. long. Autogamous.

TYPE: Black Rock, 4,300 ft., Salt Lake County, Utah, June 1869, *S. Watson* (US 70527; isotype, GH).

DISTRIBUTION: On dry rocky slopes and flats, with *Atriplex* and *Chrysothamnus*, western Utah and extreme northeastern Nevada (Elko County). From 4,100–5,500 ft. alt.

No new information is available about this enigmatic subspecies, which stands in an intermediate position, both morphologically and geographically, between *C. scapoidea* and *C. walkeri* subsp. *tortilis*.

14. **Camissonia parryi** (S. Wats.) Raven, Brittonia 16: 282. 1964.
    Oenothera parryi S. Wats., Amer. Nat. 9: 270. 1875.
    Oenothera scapoidea var. *parryi* (S. Wats.) M. E. Jones, Proc. Calif. Acad. II. 5: 682. 1895.
    Oenothera tenuissima M. E. Jones, Proc. Calif. Acad. II. 5: 683. 1895. Type: In clay washes, Rockville, 4,000 ft., Washington Co., Utah, 26 September 1894, *M. E. Jones* 6083 (POM 38644; isotypes, MO, NY, UC, US).
    Chylisma parryi (S. Wats.) Small, Bull. Torrey Cl. 23: 193. 1896.
    Oenothera brevipes race *parryi* (S. Wats.) H. Lév., Monogr. Onoth. 146. 1905.
    Chylismia tenuissima (M. E. Jones) Rydb., Bull. Torrey Cl. 40: 66. 1913.
    Oenothera parryi f. *tenuissima* (M. E. Jones) Raven, Univ. Calif. Publ. Bot. 34: 111. 1962.

Erect and often intricately branched annual herb 5–80 cm. tall, with poorly defined basal rosette, densely covered below with white trichomes ca. 2 mm. long, forming a villous pubescence on the stems and leaves. Leaves simple or very rarely with a few small lateral leaflets, ovate, often cordate at the base, sparsely dentate, reduced upward, the veins below lined with pale or dark brown oil cells. Inflorescences nodding, mostly glabrous, with intricate, filiform branches, corymbiform. Hypanthium 0.5–2 mm. long, 0.3–0.5 mm. across at the summit, glabrous or villous without and within. Sepals 1.5–4 mm. long, 0.5–1.3 mm. wide, villous to glabrous, with clusters of light-brown oil cells at tip, the caudate appendages absent. Petals 2–7 mm. long, 2–6 mm. wide, bright yellow, of same color as stamens, style, and inside of hypanthium, often red-dotted near the base, sometimes fading rose. Filaments of the episepalous stamens 1.7–3.5 mm. long, those of the epipetalous ones 1.2–2.5 mm. long; anthers 0.9–1.2 mm. long, glabrous. Style 4–9 mm. long, glabrous; stigma 0.3–0.6 mm. thick, held well above the anthers at anthesis. Capsule 0.4–1 cm. long, 1.2–1.5 mm. thick, glabrous or glandular-pubescent, on a filiform pedicel 4–20 mm. long, the pedicel widely spreading or reflexed but the capsule erect. Seeds light brown, finely pitted, lenticular, with narrow cellular rim, few and crowded in 4-septate capsule so as to appear 1-rowed, 0.7–1.2 mm. long, 0.5–0.6 mm. thick. Gametic chromosome number, $n=7$. Outcrossing.

Type: Abundant on bare gypseous clay hills near St. George, Washington County, Utah, 1874, *C. C. Parry* 72 (GH; isotypes, DS, F, GH, MO, ND, NY).

Distribution: Red clay and sand slopes weathered from red (fresh-water-deposited) sandstone cliffs, with *Larrea* or *Juniperus*, southwestern Utah and northwestern Arizona. From 2,700–4,000 ft. alt.

FIGURE 6.—*Camissonia arenaria*, × ⅜ (*Raven* 11743, DS).

Camissonia parryi is highly restricted geographically and edaphically and distinctive morphologically. It no longer appears desirable to accord formal taxonomic recognition to the late season plants Jones described as *Oenthera tenuissima*. *Camissonia parryi* is very likely self-incompatible. It grows sympatrically with *C. multijuga*, but the latter is confined to firm rock walls, whereas *C. parryi* grows on red-clay flats, which it often carpets.

15. Camissonia exilis (Raven) Raven, Brittonia 16: 383. 1964. FIGURE 7
Oenothera exilis Raven, Univ. Calif. Publ. Bot. 34: 114. 1962.

Slender and copiously branched, with purplish-brown stems, covered with glandular puberulence, and with occasional scattered white-villous pubescence. Leaves to 3.5 cm. long, reduced upward, with narrowly ovate blades to 2 cm. long and 0.7 cm. wide, the margins feebly denticulate, the veins below lined with brownish oil cells. Inflorescence erect, sparse, elongating in fruit, each flower subtended by a bract to 3.5 mm. long, with a petiole to 1 mm. long. Hypanthium 0.4–0.5 mm. long, 0.4 mm. across at the summit, glabrous within. Sepals 1–1.2 mm. long, ca. 0.5 mm. wide, with small clusters of oil cells at apices. Petals 1–1.5 mm. long, ca. 1 mm. wide, yellow fading purplish, the same color as stamens, style, and inside of hypanthium. Stamens 4, episepalous; filaments ca. 0.5 mm. long; anthers ca. 0.5 mm. long, glabrous. Style ca. 1.5 mm. long, glabrous; stigma ca. 0.2 mm. thick, surrounded by the anthers at anthesis. Capsule 0.45–0.7 cm. long, ca. 1.5 mm. thick, clavate; pedicel 4–9 mm. long; pedicels spreading, the capsules spreading or ascending. Seeds light brown, ca. 0.8 mm. long, ca. 0.5 mm. wide. Gametic chromosome number, $n=7$. Autogamous.

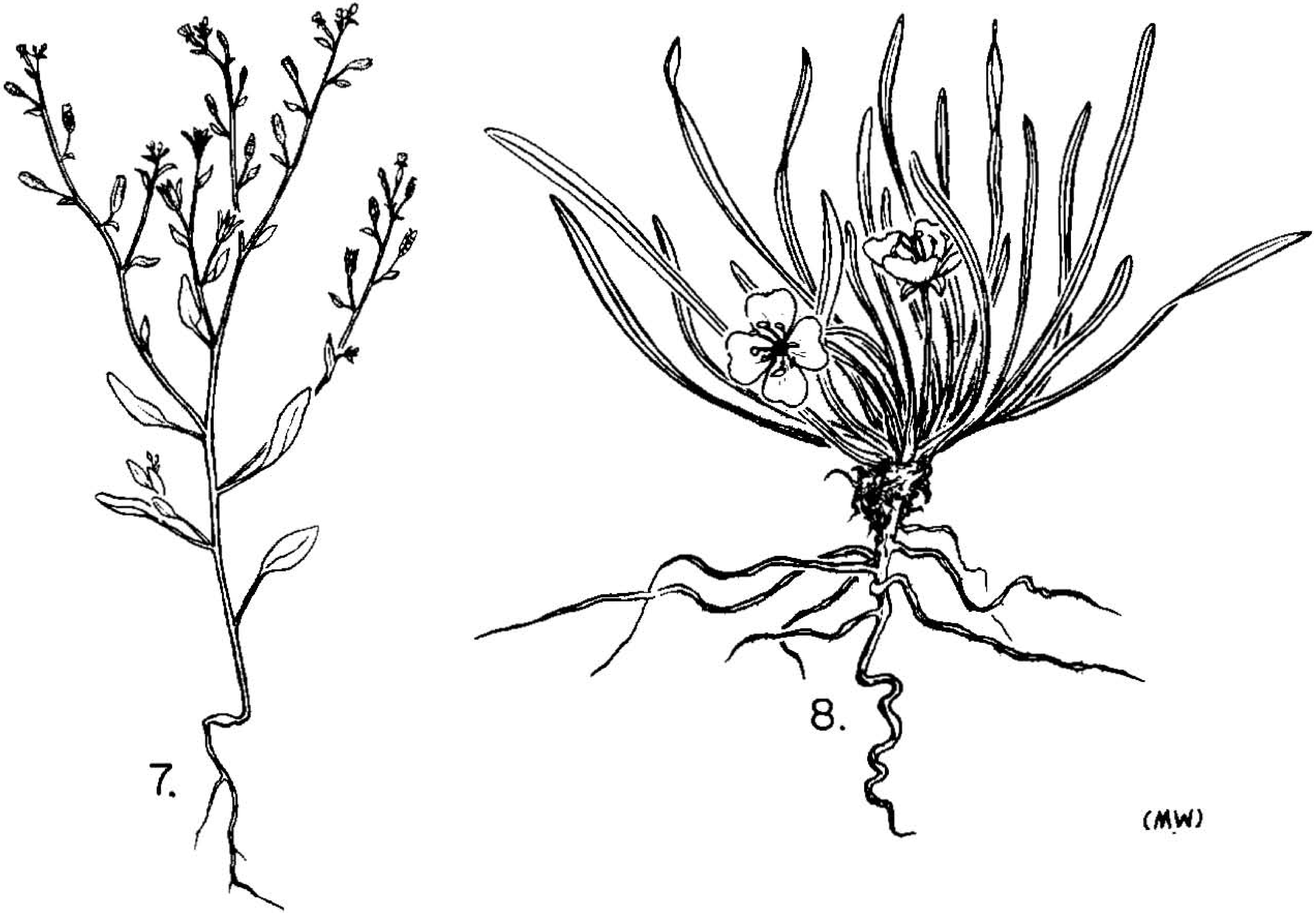
TYPE: "Gypsum-covered flat," near Cottonwood Spring, east base of Virgin Mountains, 3,500 ft., Mohave County, Arizona, 6 June 1941, *P. A. Munz* 16779 (POM 264197; isotype, DS).

DISTRIBUTION: Travertine-covered flats, east base of Virgin Mountains, ca. 3,500 ft., Mohave County, Arizona; Buckskin Mountains, between Willow Springs and Lees Ferry, ca. 5,000 ft., Coconino County, Arizona.

This exceedingly rare and local species is the only member of the genus characterized by the absence of the epipetalous stamens. On the other hand, certain plants of *C. andina* have also lost this whorl of stamens, and the epipetalous stamens are sometimes greatly reduced in *C. minor*. In all other respects, *C. exilis* is closely similar to *C. parryi* and to other species of sect. *Chylismia*, and I no longer recognize it as constituting a distinct, monotypic section, which procedure would confer undue emphasis to a single distinctive characteristic.

16. Camissonia megalantha (Munz) Raven, Brittonia 16: 282. 1964.
Oenothera heterochroma var. *megalantha* Munz, Leafl. West. Bot. 3: 52. 1941.
Oenothera megalantha (Munz) Raven, Univ. Calif. Publ. Bot. 34: 111. 1962.

Robust annual with glandular pubescence, 0.1–2 m. tall, with an ill-defined basal rosette, the cauline leaves larger below; secondary branches numerous. Leaves simple, broadly ovate, cordate at the



FIGURES 7-8.—Species of *Camissonia*, × ¾: 7, *C. exilis* (*Munz* 16779, isotype, DS); 8, *C. graciliflora* (*Bacigalupi* 1096, DS).

base, sinuate-dentate, the veins below prominently lined with yellowish oil cells, the blades up to 8 cm. long and 7 cm. wide, the petioles to 5.5 cm. long. Hypanthium 4.5–8.5 mm. long, 1.5–3 mm. across at the summit, glandular-pubescent without, cream (greenish yellow near summit) with matted villous pubescence within, except for the glabrous lower 2 mm. Sepals 4.5–9 mm. long, 1.5–2.4 mm. wide, with clusters of oil cells at the apices, often reflexed in pairs; caudate appendages absent. Petals 9–13.8 mm. long, 6–15.5 mm. wide, pale to dark lavender, diffusely flecked with purplish near the base, and white at the very base. Filaments pale greenish yellow, those of the episepalous stamens 6–12 mm. long, those of the epipetalous ones 3.5–8 mm. long; anthers ca. 2 mm. long, glabrous. Style 14–22.5 mm. long, white, densely villous above the lowest 3–4 mm., up to a point above the summit of the hypanthium (ca. 5–5.5 mm. below the stigma); stigma depressed-globose, ca. 1 mm. across, ca. 0.5 mm. high, held well above the anthers at anthesis. Capsule 0.8–1.4 cm. long, 1.3–2 mm. thick, clavate; pedicel 2–3.5 mm. long. Seeds brown, 1–1.3 mm. long. Gametic chromosome number, $n=7$. Outcrossing but self-compatible.

TYPE: Volcanic alkali soil, Cane Springs, Skull Mountains, Nye County, Nevada, 24 August 1938, *P. Train* 2358 (POM 253923; isotypes, ARIZ, CAS, DS).

DISTRIBUTION: Known only from rubble derived from volcanic tuff, partly on moist soil about springs, at the type locality, at ca. 4,100 ft. alt., in southern Nye County, Nevada. Flowering mostly from June to October; germinating in the late spring.

Camissonia megalantha is outcrossed and visited by such large, polylectic bees as *Anthophora urbana* Cress. and *Centris rhodopus* Ckll. soon after its flowers open near sunrise (Raven, MS.). It is, however, self-compatible, as shown by comparative studies of pollen-tube growth in 46 selfed and outcrossed individuals from the type locality. This species and its obvious derivative, the autogamous *C. heterochroma*, are the only lavender-flowered species in the genus *Camissonia*, and two of the very few that regularly bloom in the autumn. They are highly specialized vegetatively within this group. In the tribe Onagreae, species with lavender or purplish petals are found in the following genera: *Gongylocarpus*, *Clarkia*, *Heterogaura*, and *Oenothera*. In species of most genera, however, the petals may fade purplish after fertilization, indicating that the capability of producing such pigments exists throughout the tribe. *Camissonia megalantha* occurs sympatrically with *C. claviformis* subsp. *claviformis*.

17. Camissonia heterochroma (S. Wats.) Raven, Brittonia 16: 282. 1964.
Oenothera heterochroma S. Wats., Proc. Am. Acad. 17: 373. 1882.
Chylisma heterochroma (S. Wats.) Small, Bull. Torrey Cl. 23: 193. 1896.
Oenothera heterochroma var. *typica* Munz, Aliso 2: 83. 1949.

Oenothera heterochroma var. *monoensis* Munz, Aliso 2: 84. 1949. Type: Sherwin Grade, 5,500 ft., Mono Co., California, 16 August 1947, *J. T. Howell* 24172 (CAS 342092; isotypes, DS, RSA).

Oenothera heterochroma subsp. *heterochroma* Raven, Univ. Calif. Publ. Bot. 34: 112. 1962.

Oenothera heterochroma subsp. *monoensis* (Munz) Raven, Univ. Calif. Publ. Bot. 34: 113. 1962.

Annual herb 0.1–1 m. tall, with an ill-defined basal rosette; secondary branches numerous; entire plant covered with glandular pubescence, or nearly glabrous and glaucous above. Leaves simple, ovate, often cordate at the base, sinuate-dentate, glandular-pubescent, to 7 cm. long and 5 cm. wide, the veins below prominently lined with brown oil cells, the petioles to 6 cm. long. Inflorescences erect, elongating in flower, mostly axillary. Hypanthium 2–5 mm. long, 0.5–1.7 mm. wide at the summit, glandular-pubescent without, villous within. Sepals 1.5–3.5 mm. long, 0.6–1.5 mm. wide, with clusters of oil cells at tips; caudate appendages absent. Petals 2–6 mm. long, 1–4 mm. wide, lavender, paler below, often yellow at very base and often with lavender flecks below. Filaments creamy, those of the episepalous ones 1.8–3 mm. long, those of the epipetalous ones 1–2.5 mm. long; anthers 0.6–1 mm. long, glabrous or sparsely ciliate. Style creamy, villous near the base, 4–7 mm. long, stigma ca. 0.8–1 mm. thick, surrounded by the anthers at anthesis. Capsule 0.7–1.3 cm. long, 1.3–2 mm. thick, erect, clavate, straight, glandular-pubescent; pedicel 2–5 mm. long. Seeds brown, 1–1.2 mm. long. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Candelaria, Mineral County, Nevada, 1881, *W. H. Shockley* 19 (GH).

DISTRIBUTION: Alluvial slopes and rocky slides, often on rocky soil, Churchill and Lander Counties, Nevada, south to Lincoln and southern Nye Counties, Nevada, Mono Lake, Mono County, and central Inyo County, California. From 2,200–7,000 ft. alt.

Camissonia heterochroma is highly colonial, rare, and autogamous. Although it grows adjacent to *C. brevipes* subsp. *brevipes*, *C. claviformis* subsp. *funerea*, *C. claviformis* subsp. *integrior*, *C. claviformis* subsp. *lancifolia*, and *C. munzii*, its time of flowering only rarely coincides with that of any of these entities. I can no longer see any justification for separating the relatively glabrous and glaucous populations within this species (=subsp. *monoensis*) as a separate entity, particularly in view of their poorly separated geographical ranges; plants from Lincoln County, Nevada, are more or less intermediate in pubescence characters.

The following two collections, seen since I completed my revision of the group in 1962, extend the then known range: Cerro Gordo, 3.8 miles east of Keeler, Inyo Mountains, Inyo County, ca. 5,300 ft., California, *Thompson* 3383 (DS); east side road south of Rainier Mesa, 5.4 miles north of junction of Tippipah Road, East Forty-Mile Drainage, 5,000 ft., Nye County, Nevada, *Beatley* 391 (DS).

Section III. *Lignothera*

Oenothera subg. *Chylismia* sensu Munz, Amer. Journ. Bot. 16: 224. 1929; N. Amer. Fl. II. 5: 163. 1965; pro parte.

Oenothera sect. *Euchylismia* sensu Munz, Amer. Journ. Bot. 16: 224. 1929; pro parte.

Oenothera sect. *Lignothera* Raven, Univ. Calif. Publ. Bot. 34: 76. 1962.

Camissonia sect. *Lignothera* (Raven) Raven, Brittonia 16: 281. 1964.

Suffrutescent perennials, flowering the first year, the plants caulescent, not flowering at the basal nodes. Inflorescence nodding. Flowers opening in the late afternoon. Ovary lacking a sterile projection. Hypanthium lacking a fleshy disc within. Sepals reflexed separately. Petals dull yellow or rarely cream, unmarked, fading brick red or yellowish, with no contrasting ultraviolet-reflective pattern. Stamens and style yellow, the stigma depressed globose, greenish yellow. Stamens 8, subequal; anthers versatile, ciliate. Pollen shed in tetrads. Capsule subsessile or with a prominent, stout pedicel, straight or slightly curved, subterete, the seeds in 2 rows in each locule. Seeds monomorphic, narrowly obovoid, finely lacunose.

TYPE SPECIES: *Camissonia cardiophylla* (Torr.) Raven.

DISTRIBUTION: Alluvial slopes and washes from Inyo County, California, south through San Diego County, California, and Pinal County, Arizona, to northwestern Sonora and about 27°50′ N. lat. in Baja California; Isla de Cedros and islands in the Golfo de California.

In 1962, I regarded this group as an early evolutionary offshoot within *Camissonia* (Univ. Calif. Publ. Bot. 34: 67). In my present view, however, it is more logical to regard the late afternoon opening of the flowers, pollen shed in tetrads, and perhaps woody habit as specializations within the tribe Onagreae, and consequently to regard sect. *Lignothera* as a specialized offshoot of some species similar to the relatively generalized ones in sect. *Chylismia*. The hypanthium in plants of sect. *Lignothera* is not approached in length by any other species of *Camissonia*, and it now appears likely that the two closely related species comprising this group are best regarded as primarily moth-pollinated derivatives in a mainly bee-pollinated (and morning-opening) group. Hawk-moth pollination is probably important here, particularly with respect to *C. arenaria*, in which the hypanthium may be up to 4 cm. long. The relationship of sect. *Lignothera* to the remainder of *Camissonia* might therefore be analogous to the relationship between the hawk-moth-pollinated *Gaura mutabilis* Cav. and the rest of the genus *Gaura*. There seems to be no reason to regard the shedding of pollen in tetrads as primitive in the tribe Onagreae or in the family, and relatively generalized species of sect. *Eulobus* and sect. *Chylismia* are somewhat woody.

Of the 36 plants of sect. *Lignothera* for which chromosome number determinations have been made, pairing has been observed in 30. Two of these had a ring of 4, and one had 2 rings of 4. Thus 10 percent of the plants examined were chromosomally heterozygous, which is a relatively high proportion but much lower than that found in sect. *Chylismia*.

18. Camissonia cardiophylla (Torr.) Raven, Brittonia 16: 281. 1964.

Plants to 1 m. tall, covered with villous or glandular pubescence. Leaves reduced upward, ovate to cordate-orbicular, blades to 5.5 cm. long and 5.5 cm. wide, pubescent, erose-dentate, the teeth tipped with clusters of brown oil cells, the petioles to 7.5 cm. long. Hypanthium 4.5–14 mm. long, 3–7 mm. across at the summit, villous within, pubescent without; sepals 3–9 mm. long, 2–3.5 mm. wide. Petals 3–12 mm. long, 2–13 mm. wide, yellow or cream. Filaments 1–3 mm. long; anthers 2–4 mm. long. Style 8–23 mm. long, stigma 2–3.5 mm. thick surrounded by or held just above the anthers at anthesis. Capsule 2–5.5 cm. long, 2.5–3.5 mm. thick, straight or slightly curved, ascending; pedicel 1–18 mm. long. Seeds 0.5–0.7 mm. long. Gametic chromosome number, $n=7$. Self-compatible but often outcrossing.

DISTRIBUTION: Alluvial slopes and washes from Inyo County, California, south through San Diego County, California, and Pinal County, Arizona, to 27°50′ N. lat. in Baja California. Also on Isla de Cedros and on several islands in the Golfo de California, both in Baja California and in Sonora. From sea level to 4,500 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1.* 1962.

18a. Camissonia cardiophylla subsp. **cardiophylla**

Oenothera cardiophylla Torr., Pac. R. R. Rep. 5: 360. 1858.

Oenothera cardiophylla var. *petiolaris* M. E. Jones, Proc. Calif. Acad. II, 5: 682. 1895. Lectotype: Rosario Mission, Baja California, 30 April 1886, *C. R. Orcutt* 1333 (US 47096; isotypes, F, GH, MO, NY, PH).

Chylismia cardiophylla (Torr.) Small, Bull. Torrey Cl. 23: 193. 1896.

Oenothera cardiophylla var. *typica* Munz, Amer. Journ. Bot. 15: 226. 1928.

Oenothera cardiophylla subsp. *cardiophylla*; Raven, Univ. Calif. Publ. Bot. 34: 78. 1962.

Pubescence villous, sometimes glandular, often mixed. Leaves cordate. Hypanthium 4.5–12 mm. long, villous or more rarely glandular-pubescent without. Petals 3–12 mm. long, 2–12 mm. wide. Style 8–23 mm. long, often held above the anthers at anthesis. Gametic chromosome number, $n=7$. Self-compatible but often outcrossing.

TYPE: Fort Yuma, Yuma County, Arizona, *Major G. H. Thomas* (NY).

DISTRIBUTION: Rocky walls and sandy alluvial flats with *Hyptis emoryi*, *Larrea* and *Ambrosia dumosa*, southern San Bernardino County, California, south to eastern San Diego County, California, and Yuma County (and possibly western Pinal County), Arizona, and south in northeastern and central Baja California, Mexico, to approximately 27°50′ N. lat.; also on Isla Angel de la Guarda, Isla San Marcos, Isla San Luis, Isla San Pedro Mártir, and Isla San Esteban in the Golfo de California. Isla San Esteban is the only locality for this subspecies in Sonora. From sea level to 2,000 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1*. 1962.

Progeny of *Balls & Everett* 22918, grown at Claremont, California, were self-compatible, as were two individuals from Yaqui Pass, San Diego County, California, *Kyhos* 64–6, judging by pollen-tube growth in selfed individuals, and two from Box Canyon, Riverside County, California, *Kyhos* 65–109 (DS). Gametic chromosome counts of $n=7$ have recently been made in two collections from Mexico: Isla San Esteban, Golfo de California, Sonora, *Moran* 13047; Las Trincheras, 28°29′ N. lat., 113°07′ W. long., ca. 430 m., Baja California, *Moran* 12600. *Wiggins* 18159 (DS), from 41 miles south of San Felipe, Baja California, represents a previously unreported station for this taxon. *Camissonia cardiophylla* subsp. *cardiophylla* has been found growing sympatrically with *C. arenaria*, with no evidence of hybridization.

18b. Camissonia cardiophylla subsp. **robusta** (Raven) Raven, Brittonia 16: 281. 1964.

Oenothera cardiophylla subsp. *robusta* Raven, Univ. Calif. Publ. Bot. 34: 79. 1962.

Entire plant glandular-pubescent and with scattered long, white, eglandular trichomes. Leaves broadly ovate, often cordate at the base, the petioles stout. Hypanthium 9–14 mm. long, glandular-pubescent without. Petals 7–11 mm. long, 9–13 mm. wide. Style 14–20 mm. long, the stigma usually held above the anthers at anthesis. Gametic chromosome number, $n=7$. Self-compatible but often outcrossed.

TYPE: Rocky canyon slopes, Jail Canyon, west slope of Panamint Range, 2,500 ft., Inyo County, California, 14 April 1937, *P. Train* (US 1737210; isotypes, ARIZ, COLO, DS, NA, OSC, UC).

DISTRIBUTION: Rocky borders of washes and hillsides, with *Larrea* and *Ambrosia dumosa*, western and southern margins of Death Valley, Inyo County, California. From 2,000–4,500 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1*. 1962.

Camissonia cardiophylla subsp. *robusta* is presumably self-compatible, as isolated individuals have on two occasions been observed setting fruit.

18c. Camissonia cardiophylla subsp. **cedrosensis** (Greene) Raven, Brittonia 16: 281. 1964.

Oenothera cedrosensis Greene, Bull. Calif. Acad. 1: 187. 1885.

Oenothera cardiophylla subsp. *cedrosensis* (Greene) Raven, Univ. Calif. Publ. Bot. 34: 79. 1962.

Mostly annual, the plants entirely glandular-pubescent, with scattered long, eglandular trichomes. Leaves ovate, acuminate at the apex, much longer than broad, broadly cuneate or very rarely slightly cordate at the base. Hypanthium 8–12 mm. long, glandular-pubescent without. Petals cream or even (?) white, 3–4.5 mm. long, 3–4 mm. wide. Style 10–15 mm. long; stigma surrounded by the anthers at anthesis. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Isla de Cedros, Baja California, 1859, *J. A. Veatch* (CAS 862).

DISTRIBUTION: Arroyos and borders of washes, with *Pachycormus*, *Larrea*, *Pachycereus*, and *Bursera*, Isla de Cedros west to Bahía de los Angeles and El Desierto Vizcaíño, Baja California; Isla Tiburón, Sonora. From near sea level to perhaps 1,000 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1*. 1962.

Camissonia cardiophylla subsp. *cedrosensis* is local and apparently not common. This entity is undoubtedly more highly self-pollinating than the other races of this self-compatible species, judging from its smaller flowers. A plant from Bahía de los Angeles, Baja California, *Moran* 12419, had 7 pairs of chromosomes at meiotic metaphase I.

19. Camissonia arenaria (A. Nels.) Raven, Brittonia 16: 281. 1964. FIGURE 6

Chylisma arenaria A. Nels., Amer. Journ. Bot. 21: 575. 1934.

Oenothera cardiophylla var. *splendens* Munz & Johnst., Bull. Torrey Cl. 49: 354. 1923. Type: UC 196590, with same data as type of *Oenothera cardiophylla* var. *longituba* Jeps.; not located.

Oenothera cardiophylla var. *longituba* Jeps., Man. Fl. Pl. Calif. 686. 1925. Type: High among rocks at the foot of the Needles, Colorado R., Mohave Co., Arizona, 7 March 1910, *J. Grinnell* (JEPS 2668); see above.

Oenothera arenaria (A. Nels.) Raven, Univ. Calif. Publ. Bot. 34: 76. 1962.

Plants to 1.8 m. tall, villous, occasionally with scattered glandular trichomes in the inflorescence. Leaves reduced upward, the petioles to 6 cm. long, the blades to 6 cm. long and 6 cm. wide, villous above and densely so below, ovate, cordate at the base, the apex sometimes acuminate, coarsely dentate or doubly dentate. Inflorescence less compact than that of *C. cardiophylla*. Hypanthium 18–40 mm. long, 5–8 mm. across at the summit, villous without, finely pubescent within. Sepals 8–15 mm. long, 3–5.5 mm. wide. Petals 8–20 mm. long, 7–28 mm. wide. Filaments 5–9 mm. long; anthers 5–8 mm. long. Style 30–58 mm. long; stigma 2.5–3 mm. thick, held above the anthers at anthesis. Capsule 3–4.4 cm. long, 2.5–3.5 mm. thick; pedicel 2–5 mm. long. Seeds 0.5–0.7 mm. long. Gametic chromosome number, $n=7$. Outcrossed.

TYPE: Sandy washes in the Fortuna Range (western Gila Mountains), ca. 20 miles east of Yuma, Yuma County, Arizona, 26 February 1930, *A. Nelson* 10140 (RM 138602).

DISTRIBUTION: Sandy washes, rocky conglomerate cuts, and granitic slopes and draws, with *Larrea, Prosopis, Carnegiea,* and *Ambrosia dumosa,* foot of the Needles, Mohave County, Arizona; from the north end of the Salton Sea, Riverside County, California, southeastward to the Tinajas Atlas Range, Arizona and Sonora. From below sea level to 1,400 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 1.* 1962.

This species has twice been found growing sympatrically with *C. cardiophylla* subsp. *cardiophylla,* but no intermediates have been observed.

Section IV. *Tetrapteron*

Oenothera subg. *Heterostemon* Nutt., Journ. Acad. Sci. Philad. 7: 22. 1834. Type: *Oenothera heterantha* Nutt. = *Camissonia subacaulis* (Pursh) Raven.

Oenothera subg. *Primulopsis* Torr. & Gray, Fl. N. Amer. 1: 507. 1840; nom. subs.

Oenothera subg. *Taraxia* Nutt. ex. Torr. & Gray, Fl. N. Amer. 1: 506. 1840. Lectotype: *Oenothera breviflora* Torr. & Grya = *Camissonia breviflora* (Torr. & Gray) Raven.

Taraxia (Nutt. ex. Torr. & Gray) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 216. 1893.

Oenothera sect. *Tetrapteron* Munz, Amer. Journ. Bot. 16: 247. 1929.

Oenothera sect. *Eutaraxia* Munz, Amer. Journ. Bot. 16: 247. 1929.

Oenothera sect. *Heterostemon* (Nutt.) Munz, N. Amer. Fl. II. 5: 143. 1965.

Perennials or annuals, the plants acaulescent or subacaulescent with a crown of leaves and flowers at summit of the taproot. Flowers opening near sunrise. Ovary with a long, slender, sterile projection below the hypanthium on which the flower is placed. Hypanthium closed by an evident fleshy disc. Sepals reflexed separately or in pairs. Petals yellow, unspotted, strongly ultraviolet reflective, with a large nonreflective area near the base in *C. ovata.* Stamens, style, and inside of the hypanthium yellow, the stigma greenish yellow. Anthers attached near the base, erect in anthesis. Pollen shed singly. Capsule subsessile, irregularly loculicidal, the seeds in two rows in each locule, these rows often much crowded. Seeds monomorphic, with a linear raphe on one side, variable.

LECTOTYPE SPECIES: *Camissonia graciliflora* (Hook. & Arn.) Raven (cf Raven, Brittonia 16: 283. 1964).

DISTRIBUTION: South-central British Columbia and Alberta at about 51° N. lat. and southwestern Saskatchewan, and from the region of the Continental Divide westward south to southern Utah, central Nevada, and throughout California to northwestern Baja California.

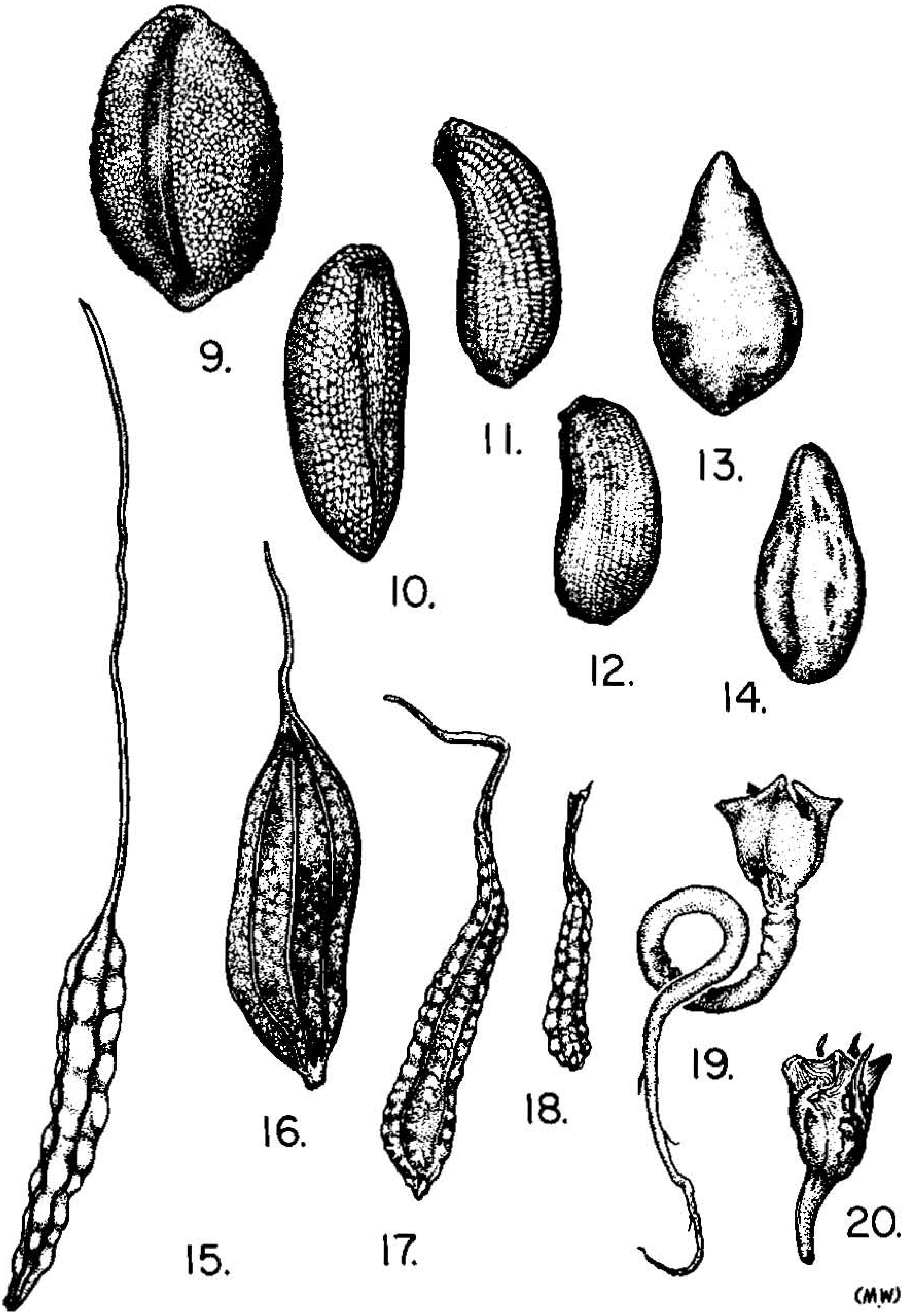
This section of six species consists of four groups very distinct from one another: *C. ovata, C. subacaulis, C. tanacetifolia-C. breviflora,* and *C. graciliflora-C. palmeri.* The last two species are annual, the others perennial. In view of their habit and clearly specialized capsules, it is believed that *C. graciliflora* and *C. palmeri* were derived from a perennial stock; but they are not especially similar to any of the extant perennials. *Camissonia ovata* and *C. tanacetifolia* consist largely or entirely of self-incompatible individuals, whereas *C. subacaulis* and *C. graciliflora* are facultatively outcrossed although self-compatible. *Camissonia breviflora* and *C. palmeri* are rather obviously specialized autogamous derivatives of species similar to *C. tanacetifolia* and *C. graciliflora*, respectively. Five of the six species in this section are diploid ($n=7$) but *C. tanacetifolia* is primarily tetraploid ($n=14$), with a local hexaploid ($n=21$) race and at least one diploid ($n=7$) population. A further discussion of chromosomal evolution in this species is included following its taxonomic description (p. 247).

Chromosomal heterozygosity is unknown in natural populations of this section, for which 173 diploid counts are available. Multivalent associations in the 25 tetraploid and 4 hexaploid plants of *C. tanacetifolia* examined clearly reflect autopolyploid pairing, not structural rearrangement.

20. Camissonia ovata (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 283. 1964.
FIGURES 9, 15

Oenothera ovata Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 507. 1840. Munz, Amer. Journ. Bot. 16: 251. 1929; N. Amer. Fl. II. 5: 144. 1965.
Taraxia ovata (Nutt. ex Torr. & Gray) Small, Bull. Torrey Cl. 23: 185. 1896.
Oenothera primuloidea H. Lév., Monogr. Onoth. 65. 1902.

Subsucculent acaulescent perennial from a thick taproot which often branches at the crown in age. Leaves ovate to very narrowly elliptic, 3–15 cm. long, 1.6–5 cm. wide, more or less densely white-ciliate with erect trichomes ca. 0.5 mm. long, subentire to shallowly sinuate or crisped, rarely deeply sinuate, the apex acute to acuminate, the base attenuate to a narrowly winged petiole 8–150 mm. long, slightly dilated at the base. Buds erect just before anthesis. Sterile prolongation of ovary 2.5–18 cm. long. Hypanthium 2–3 mm. long, 3.5–5 mm. across at the summit, sparsely pubescent outside, with short matted trichomes inside near the base. Sepals 11–19 mm. long, 1.2–4 mm. wide, sparsely pubescent, reflexed separately. Petals often apiculate, 8–23 mm. long, 5–19 mm. wide. Filaments of the episepalous stamens 3.5–8 mm. long, those of the epipetalous ones 2–6 mm. long; anthers 3–4.8 mm. long. Style 4.5–11 mm. long, short-pubescent near the base; stigma 0.8–2 mm. in diameter, held slightly above the anthers at anthesis. Capsule 11–30 mm. long, 3–5 mm. thick, subterete, the walls thin, much distended by the seeds, rarely with a pedicel up to 0.4 mm. long. Seeds elongate-ovoid, uniform brown, densely and coarsely papillose, 1.8–2.2 mm. long, 1.2–1.4 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.



Figures 9–20.—Seeds and capsules of *Camissonia* sect. *Tetrapteron:* 9–14, Seeds, × 20: 9, *C. ovata* (*K. Brandegee* 127, DS); 10, *C. subaculis* (*Raven* 19601, DS); 11, *C. tanacetifolia* subsp. *tanacetifolia* (*Thompson* 11962, DS); 12, *C. breviflora* (*Cottam et al.* 15285, DS); *13*, *C. graciliflora* (*Dudley* in 1899, DS); 14, *C. palmeri* (*Parish* 4861, DS). 15–20, Capsules, from same collections as seeds unless otherwise noted, × 2: 15, *C. ovata;* 16, *C. subaculis;* 17, *C. tanacetifolia* subsp. *tanacetifolia* (*Applegate* 7635, DS); 18, *C. breviflora* (*Raven* 19551, DS); 19, *C. graciliflora*, entire fruiting plant (*Sharsmith* 3395, DS); 20, *C. palmeri*.

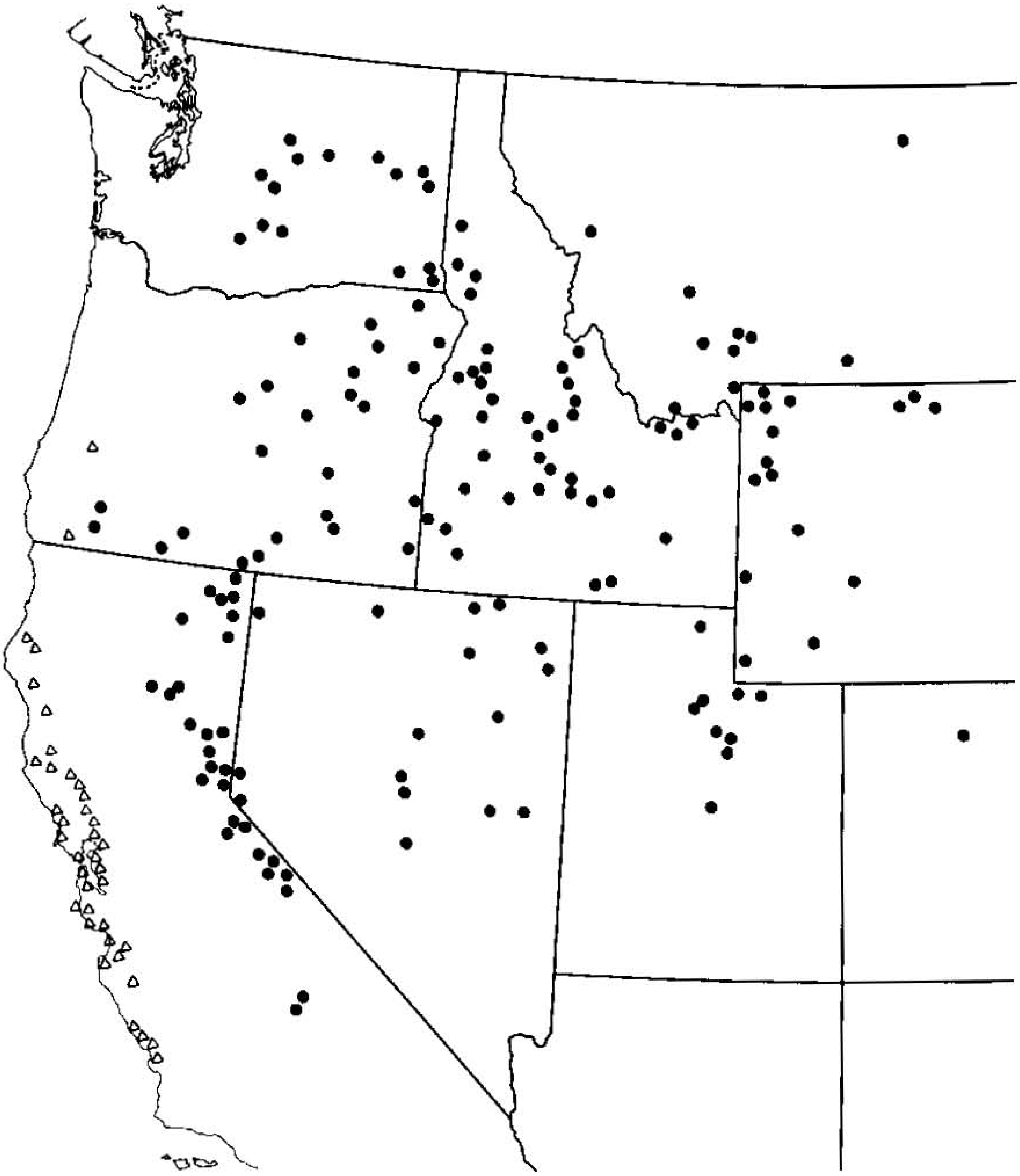
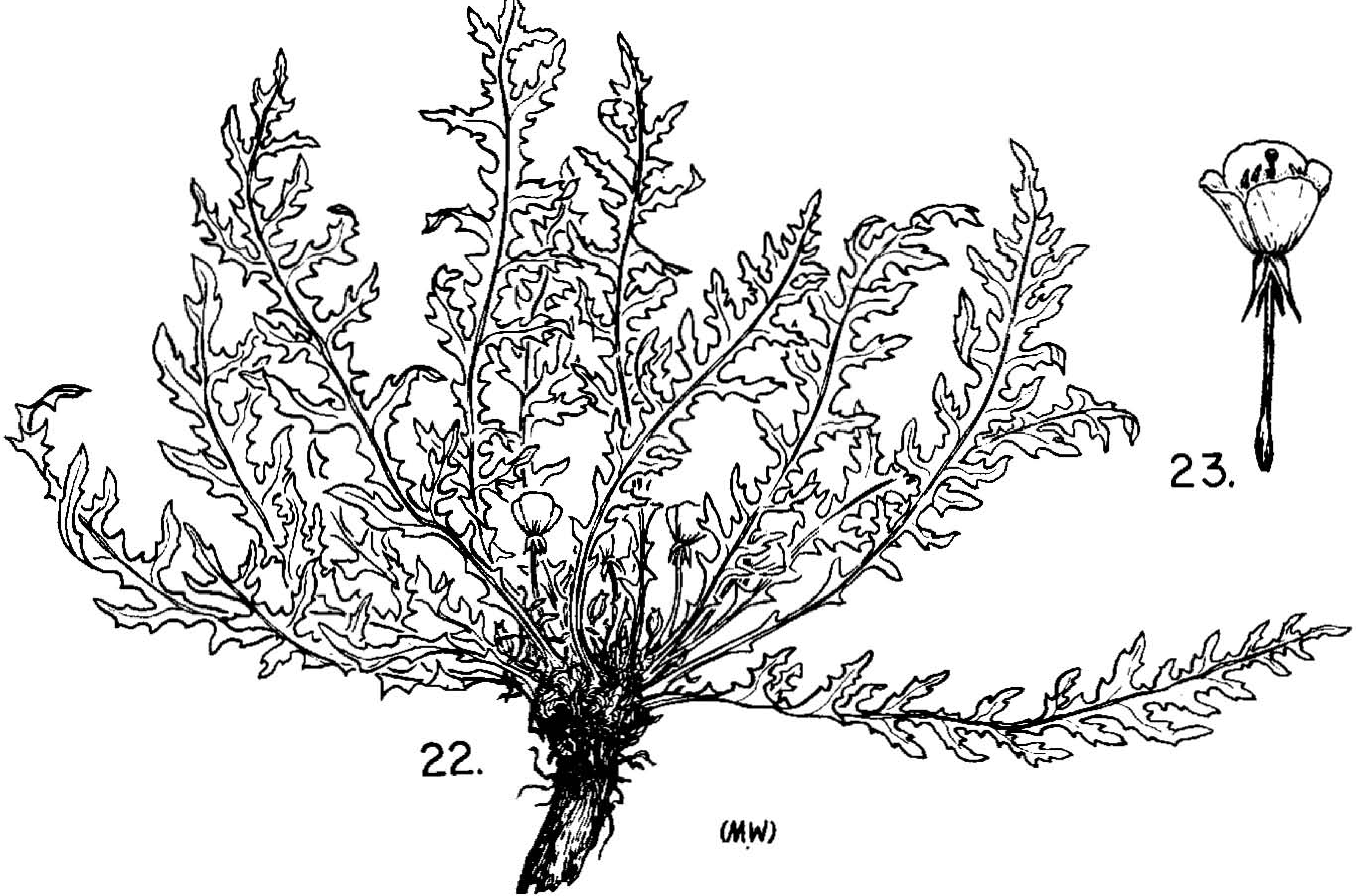


FIGURE 21.—Western United States, showing ranges of *Camissonia* sect. *Tetrapteron*: △=*C. ovata*; ●=*C. subacaulis*.

TYPE: Moist plains in the immediate vicinity of Monterey, Monterey County, Calif., March 1836, *T. Nuttall* (NY; isotypes, BM, GH).

DISTRIBUTION (Figure 21): Grassy fields, often in clay soil, not far from the coast; Umpqua Valley, Douglas County and Josephine County, Oregon; Humboldt, Mendocino, and Lake Counties south to the vicinity of Monterey Bay, Monterey County and again south of the Santa Lucia Mountains in northern San Luis Obispo County, from about 2 miles north of the mouth of Arroyo de la Cruz south to Los Osos Valley near Morro Bay, California. From sea level to about 1,500 ft. alt.



Figures 22–23.—Species of *Camissonia* sect. *Tetrapteron*, × ¾: 22, Plant of *C. breviflora* (*Cottam et al.* 15825, DS); 23, flower of *C. tanacetifolia* subsp. *tanacetifolia* (*Thompson* 11953, DS).

Vouchers for chromosome number, $n=7$ (no structural heterozygosity observed; 10 individuals, 7 populations):

U.S.: CALIFORNIA: LAKE CO.: 0.8 mi. W. of Lakeport, *Breedlove* 4567. MONTEREY CO.: Carmel Valley, R18148; 7 mi. SW. of San Juan Bautista on Old San Juan Grade, R18194. SAN BENITO CO.: 1 mi. W. of San Juan Bautista, R18193. SAN LUIS OBISPO CO.: 1 mi. N. of Cambria, R18140; 1 mi. S. of Cambria, R18747 (4 plants). SAN MATEO CO.: Pigeon Point, *Ornduff* 4746.

Individuals of *Camissonia ovata* are self-incompatible (contrary to the assertion of Katherine Brandegee, Univ. Calif. Publ. Bot. 6: 46. 1914), as judged by the lack of pollen-tube growth in 71 selfed individuals from a population near the intersection of Sand Hill Road and Whiskey Hill Road, near Woodside, San Mateo County, California; 7 individuals from the Lake County, California, population cited above, and 12 plants from the population from south of Cambria, San Luis Obispo County, California, cited above. I am grateful to Gretchen M. Mills for these observations on the San Mateo County population. *Camissonia ovata* has been found growing sympatrically with *C. graciliflora*. The oligolectic bee *Andrena* (*Diandrena*) *chalybea* (Cress.) is consistently associated with it throughout its range and usually effects pollination in the early morning (MacSwain, Raven & Thorp, MS.). Other species of bees gather pollen from *Camissonia ovata* and visit it locally, sometimes in competition with *Andrena chalybea*.

This species might possibly occur or have occurred in the Sierra Nevada foothills of central California, judging from a specimen labeled "Roseville, May 1884, M.K.C." (DS); it is uncertain whether the record refers to the community of this name in Sacramento County, California. At any rate, the occurrence of this species east of the Sacramento Valley has not been confirmed by modern collections.

The chromosome number of this species was earlier reported by Johansen (Amer. Journ. Bot. 16: 597. 1929; Ann. Bot. 45: 111–124, *pl. 6*. 1931), but without any definite indication of locality or voucher specimen.

Camissonia ovata is a distinctive species without any close relatives. It might be confused superficially with *C. subacaulis*, but the structure of the capsules and seeds in these two species is very different (figs. 9, 10, 15, 16), as is the marking of the petals when viewed in ultraviolet light. White-flowered plants are found in a very low frequency.

21. Camissonia subacaulis (Pursh) Raven, Brittonia 16: 283. 1964.

FIGURES 10, 16

Jussiaea subacaulis Pursh, Fl. Amer. Sept. 1: 304. 1814.

Oenothera heterantha Nutt., Journ. Acad. Philad. 7: 22. 1834. Type: Near Camas Creek, in or near Jefferson Co., Idaho, 23 June 1833, *N. J. Wyeth* (PH; isotypes, BM, NY).

Oenothera heterantha var. *taraxacifolia* S. Wats., Proc. Amer. Acad. 8: 589. 1873. Type: Near Austin, Lander Co., Nevada, July 1868, *S. Watson* (GH).

Taraxia heterantha (Nutt.) Small, Bull. Torrey Cl. 23: 186. 1896.

Taraxia heterantha var. *taraxacifolia* (S. Wats.) Small, Bull. Torrey Cl. 23: 186. 1896.

Taraxia taraxacifolia (S. Wats.) Heller, Muhlenbergia 1: 1. 1900.

Taraxia subacaulis (Pursh) Rydb., Mem. N.Y. Bot. Gard. 1: 281. 1900.

Oenothera primuloidea H. Lév., Monogr. Onoth. 65. 1902, pro parte; nom. subs.

Oenothera subacaulis (Pursh) Garrett, Spr. Fl. Wasatch 64. 1911.

Oenothera subacaulis var. *taraxacifolia* (S. Wats.) Jeps., Man. Fl. Pl. Calif. 683. 1925.

Subsucculent acaulescent perennial from a deep, thick taproot which may branch in age to produce more than a single rosette. Leaves lanceolate to narrowly elliptic, 2–22 cm. long, 0.7–4.2 cm. wide, rarely minutely and sparsely strigulose along veins and margins, subentire to sinuate or less commonly deeply and irregularly pinnatifid, the apex acuminate, the base attenuate to a narrowly winged petiole 1–12 cm. long. Buds erect just before anthesis. Sterile prolongation of ovary 1.5–8 cm. long. Hypanthium 1.5–3 mm. long, 3–4 mm. across at summit, subglabrous outside, with short matted trichomes inside near the base. Sepals 4.1–13 mm. long, 0.8–3 mm. wide, sometimes very minutely strigulose, reflexed separately. Petals often apiculate, 5–16 mm. long, 5–16 mm. wide. Filaments of the episepalous stamens 1.8–6.5 mm. long, those of the epipetalous ones 0.5–2.5 mm. long; anthers 0.9–2 mm. long. Style 4–8.5 (–11) mm. long, glabrous or sparsely pubescent near the base; stigma 1–2 mm. in diameter, usually surrounded by the longer anthers at anthesis, but very rarely held above them. Capsule 11–28 mm. long, 5–8 mm. in diameter, 4-angled with flat walls, these thick and smooth and scarcely distended by the seeds, rarely with a pedicel up to 1 cm. long, becoming blackened and persistent on the plants for one or more years after shedding seeds. Seeds oblong, uniform tan to light brown, 1.3–1.9 mm. long, 0.6–1 mm. thick, coarsely pitted, the pits in ca. 25 parallel rows. Gametic chromosome number, $n=7$. Self-compatible but often outcrossed.

TYPE: Moist ground, Quamash Flats (Squamash Flats), on Weippe (Oyipe) Prairie, Shoshone County, Idaho, 14 June 1806, *M. Lewis* (PH). See Coues, Proc. Acad. Nat. Sci. Philad. 1898: 302. 1898. Locality incorrectly given by Pursh as "the banks of the Missouri," to which he credited many of the species from the Lewis and Clark Expedition even when the labels indicated other, more specific data (letter from F. W. Pennell to P. A. Munz, Feb. 17, 1928, filed at POM). See also Torrey & Gray, Fl. N. Amer. 1: 507. 1840; Raven, Brittonia 16: 283. 1964, as to the application of this name to this species.

Distribution (Figure 21): Wet, often clayey meadows, sometimes growing in deep grass, from Yakima, Kittitas, Chelan, Lincoln, and Spokane Counties, Washington, and Phillips County, Montana (Lake Bowdoin, *Blankinship* in 1903, MONT), south through Sheridan and Fremont Counties, Wyoming, to Routt County, Colorado; Summit Duchesne, and Sanpete Counties, Utah; White Pine, northern Nye, and Douglas Counties, Nevada; and in California east of the Cascade axis to the vicinity of Bodie, Mono County, and again on the Kern Plateau, Tulare County; 1,500–8,600 ft. alt.

Vouchers for chromosome number, $n=7$ (no structural heterozygosity observed; 4 individuals, 4 populations):

U.S.: California: mono co.: 4.4 mi. NW. of Bridgeport, R18548. Idaho: adams co.: 3 mi. W. of Big Payette Lake, R18508. valley co.: 2 mi. S. of McCall, R18510. Oregon: lake co.: Hart Mountain Antelope Refuge Headquarters, R18430.

Individuals of the two populations of *Camissonia subacaulis* tested by pollen-tube growth have been found to be self-compatible and facultatively self-pollinating. In the first Idaho population mentioned above 16 individuals were tested, and 17 were tested in the California population. Pollinators were extremely rare at both localities, and the flowers were more or less hidden from view at the base of the rosette. In a few populations (such as *Hitchcock & Muhlick* 14048, DS, POM, Valley County, Idaho) the stigmas seem to be held above the anthers at anthesis, and some of the populations of this species might prove to consist of self-incompatible individuals. *Camissonia subacaulis* has been found growing sympatrically with *C. tanacetifolia* subsp. *tanacetifolia* and very probably occurs sympatrically with *C. breviflora* as well. This species appears to have no near relatives. An earlier approximate report of the chromosome number of this species was made by Johansen (Amer. Journ. Bot. 16: 597: 1929), but without any citation of voucher or locality.

22. **Camissonia tanacetifolia** (Torr. & Gray) Raven, Brittonia 16: 283. 1964.

Acaulescent perennial from a woody, deep taproot from which numerous slender branches arise in age to produce additional rosettes. Leaves very narrowly elliptic, 6.5–32 cm. long, 0.7–3.3 cm. wide, more or less densely short-pilose, or the trichomes appressed; deeply and irregularly pinnatifid, the apex acute to long acuminate, the base attenuate to narrowly cuneate to a petiole 1–8 cm. long. Buds erect just before anthesis. Sterile prolongation of ovary 1.4–5.5 cm. long. Hypanthium 4–6.5(–8.5) mm. long, 5–7(–11) mm. across at summit, short-pilose outside, soft-pilose in lower half within. Sepals 5.5–13 mm. long, 1.8–4.2 mm. wide, short-pilose, reflexed separately. Petals

(8–)10–23 mm. long, 7–15(–18) mm. wide. Filaments of the episepalous stamens 5.5–12 mm. long, those of the epipetalous ones 2.5–8 mm. long; anthers (2.3–) 2.8–3.5 mm. long. Style 9.5–20(–25) mm. long, pilose near the base; stigma depressed-globose, more or less 4-notched, 1.3–3.5 mm. in diameter, held well above the anthers at anthesis. Capsule 7–25 mm. long, 3–5 mm. thick, gradually attenuate to the sterile prolongation, subterete, the walls thick but evidently distended by the seeds, sessile, disintegrating irregularly the season after their formation. Seeds oblong, uniform tan to brown, 1.5–2 mm. long, 0.6–0.8 mm. thick, pitted in rows, with ca. 20 rows of pits. Gametic chromosome numbers, $n=7$, 14, 21. Self-incompatible, probably with some self-compatible populations.

DISTRIBUTION (Figure 24): Open clayey fields and moist slopes, sometimes by streams or lakes, Klickitat, Douglas, and Spokane Counties, Washington, and Owyhee, Ada, Elmore, Camas, and Blaine Counties, Idaho, south on the east side of the Sierra-Cascade axis to Elko, northernmost Nye, and Douglas Counties, Nevada, and the vicinity of Bodie and Conway Summit, Mono County, California. From about 1,300 ft. alt. in the north to 8,200 ft. in the south. Gregarious and often coloring large fields yellow when in bloom.

22a. Camissonia tanacetifolia subsp. **tanacetifolia.** FIGURES 11, 17, 23

Oenothera nuttallii Torr. & Gray, Fl. N. Amer. 1: 506. 1840; not Sweet 1830. Type: Said to be from "Plains in the Rocky Mountains, near Blackfoot River," which would put it in or near Caribou County, Idaho, 10–11 July 1834, *T. Nuttall* (isotype PH), at the type locality for the following species and far from any known locality for the present one; therefore, the locality as given is probably in error.

Oenothera tanacetifolia Torr. & Gray, Pac. R. R. Rept. 2: 121, *pl. 4*. 1854.

Taraxia longiflora Nutt. ex Howell, Fl. N.W. Amer. 231. 1891–1896.

Taraxia tanacetifolia (Torr. & Gray) Piper, Contr. U.S. Nat. Herb. 11: 405. 1906.

Taraxia tikurana A. Nels., Bot. Gaz. 54: 140. 1912. Lectotype: Tikura, Blaine Co., Idaho, 4,500 ft. elev., 22 July 1911, *A. Nelson & J. F. Macbride* 1302 (RM; isolectotypes, DS, GM, NMC, POM, US.)

Plants more or less densely pilose or the trichomes appressed; rarely more than 5 percent of the pollen with 4 pores. Gametic chromosome numbers, $n=7$, 14. Self-incompatible, probably with self-compatible populations.

TYPE: Vicinity of Pah-Rum Peak, Lake Range, Washoe County, Nevada, 18 June 1854, *E. G. Beckwith* 43 (GH, the specimen from which the illustration was prepared; isotype, NY). Type locality given as "On the higher parts of the Sierra Nevada" but the actual locality was reconstructed from Beckwith's account of the expedition (Pac. R.R. Rept. 2(1b): 1–70. 1854).

DISTRIBUTION (Figure 24): That of the species, but not found in and near Sierra Valley in Plumas and immediately adjacent portions of Lassen and Sierra Counties, California.

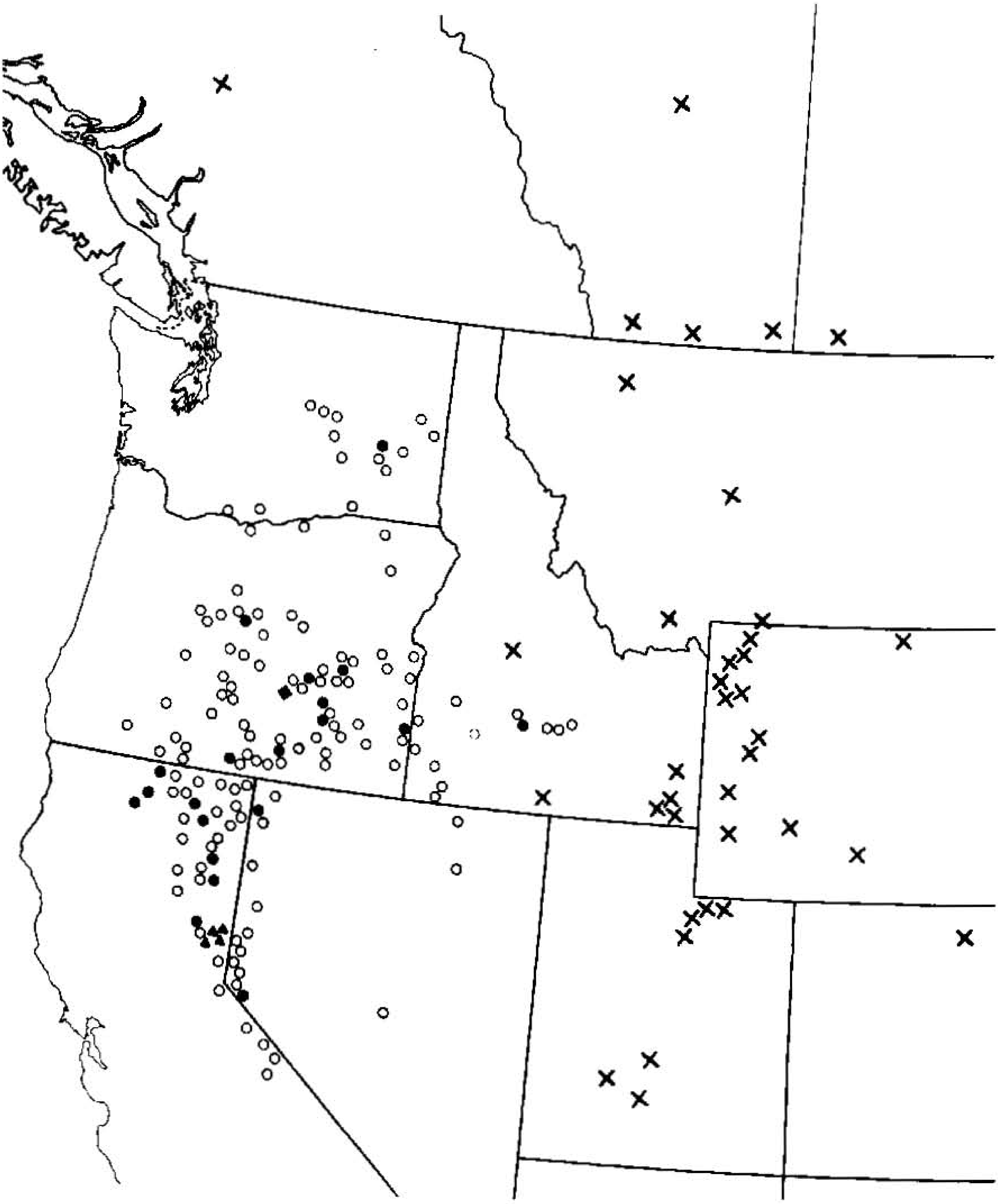


FIGURE 24.—Western United States and a portion of adjacent Canada, showing ranges of species of *Camissonia* sect. *Tetrapteron:* ○ = *C. tanacetifolia* subsp. *tanacetifolia*, with ● = tetraploid chromosome counts ($n=14$) and ◆ = the single diploid count ($n=7$); ▲ = *C. tanacetifolia* subsp. *quadriperforata* (all hexaploid, $n=21$); × = *C. breviflora.*

Voucher for chromosome number, $n=7$ (1 structurally homozygous individual):

U.S.: OREGON: HARNEY CO.: 0.6 mi. N. of Wagontire, R18432.

Vouchers for chromosome number, $n=14$ (with variable numbers of rings of 4 chromosomes in meiotic metaphase I, the maximum number of such rings observed in each case indicated in parentheses following the collection number; other chromosomes present as bivalents; 25 individuals, 25 populations):

U.S.: CALIFORNIA: LASSEN CO.: U.S. Hwy. 395, 11.1 mi. N. of Litchfield, R18423 (3); 0.9 mi. N. of Ravendale, R18426; 11.6 mi. N. of Litchfield, R17875 (3); 0.5 mi. N. of Ravendale, R17876 (5). MODOC CO.: 13 mi. NW. of Canby, R17893; State Hwy. 139 at S. road to Lava Beds National Monument, R17896 (4). PLUMAS CO.: Middle Fork of Feather R. just N. of Mohawk, *Mosquin & Gillett* 5302 (3). SISKIYOU CO.: Grass Lake, *Bates* 2436; 14 mi. S. of Macdoel, R17900; 4.4 mi. S. of Dorris, R17898. IDAHO: CAMAS CO.: Near Camas Creek and State Hwy. 46, R18526 (5). ELMORE CO.: 2.7 mi. N. of Mountain Home, R18523. OWYHEE CO.: U.S. Hwy. 395, 9.3 mi. NE. of the Oregon line R19576. NEVADA: DOUGLAS CO.: U.S. Hwy. 395, 2.9 mi. N. of junction with State Hwy. 3, R18546; S. end of Double Spring Flat, R14267. WASHOE CO.: 20 mi. E. of Cedarville (Calif.) on State Hwy. 8A, R17885 (3). OREGON: CROOK CO.: N. road from Prineville to Big Summit Prairie, *Chambers & Lewis* 1934. HARNEY CO.: U.S. Hwy. 20, 7.4 mi. E. of junction with U.S. Hwy. 395, R18457; 8.4 mi. N. of Narrows, R18456; 23.2 mi. S. of Narrows, R18454 (4); U.S. Hwy. 20, 2.1 mi. W. of junction to Ft. Harney, *T. & L. Mosquin* 4345 (DAO). LAKE CO.: 0.9 mi. E. of Hart Mountain Antelope Refuge Headquarters, R18341 (5); 4.1 mi. E. of Drew's Reservoir, W. of Lakeview, R18428. MALHEUR CO.: 6 mi. N. of Jordan Valley, R19583. WASHINGTON: ADAMS CO.: 4 mi. NE. of Ritzville, R18496.

Twelve individuals from the Washington population just cited appeared to be self-compatible, judging from pollen-tube growth in selfed, caged individuals. On the other hand, 25 plants of the first-mentioned Lake County, Oregon, population proved to be self incompatible, as did 17 individuals from the Douglas County, Nevada, population. *Andrena* (*Onagrandrena*) *raveni* Linsley & MacSwain is oligolectic on plants of the tribe Onagreae, and females of this species have been observed abundantly gathering pollen on *Camissonia tanacetifolia* subsp. *tanacetifolia* in a number of populations. Outcrossing is certainly the mode in *Camissonia tanacetifolia*, and the existence and distribution of self-compatible plants needs to be studied in greater detail.

From a chromosomal point of view, 25 of the 26 populations of this subspecies examined have been effectively autotetraploid, usually with 3 rings of 4 chromosomes in each diakinesis or metaphase I cell, but occasionally with up to 5 rings of 4. It is not known whether the diploid set of chromosomes duplicated twice in these plants is structurally homologous with that in the related diploid *C. breviflora*, but that species is autogamous and small-flowered, and cannot be identical with the ancestor of the self-incompatible, large-flowered, polyploid *C. tanacetifolia*. No other related diploid is known.

The single diploid strain of *C. tanacetifolia* subsp. *tancetifolia* was found during the course of an extensive survey of chromosome numbers throughout the range of this taxon (fig. 24). It is morphologically identical to the tetraploid plants that occur in the same area, and it could therefore be their diploid ancestor. In my opinion, however, it is at least equally probable that this single diploid population (perhaps no more than a single plant) is a polyhaploid derivative of the predominant tetraploid. The chromosomes of the tetraploid are like those of other tetraploids that have given rise occasionally to fertile polyhaploid (=diploid) derivatives (Raven & Thompson, Amer. Nat. 98: 251–252. 1964). Meiotic accidents that could lead to the formation of such a diploid derivative are known to occur sporadically in plants of this sort. I can think of no way to distinguish these two competing hypotheses concerning the origin of this diploid plant or population at present.

Camissonia tanacetifolia subsp. *tanacetifolia* has been found growing sympatrically with *C. subacaulis*. It is closely related to the autogamous, diploid *C. breviflora* but sharply distinct in flower size.

22b. Camissonia tanacetifolia subsp. **quadriperforata** Raven, subsp. nov.

A subsp. *tanacetifolia* differt: foliis villose incanis; plus quam 10 percentum pollinis grana plerumque quadripora; chromosomatum numero gametico, $n=21$.

TYPE: Common on flats with *Artemisia*, 6.2 miles north of Sierraville on road to Loyalton, Sierra County, California, 28 May 1963, *P. H. Raven* 18416 (DS 502795; isotypes RSA, US).

DISTRIBUTION (Figure 24): Common on more or less open clay flats, often with *Artemisia*, in Sierra Valley, Plumas County, and immediately adjacent portions of Lassen and Sierra Counties, California; 4,300–5,100 ft. alt.

Vouchers for chromosome number, $n=21$ (with many rings of 6 at diakinesis and meiotic metaphase I; 4 individuals, 4 populations):

U.S.: CALIFORNIA: PLUMAS CO.: The type collection, cited above; 3.1 mi. W. of Vinton, R18419; 6.9 mi. S. of Vinton, R18417: ca. 2.5 mi. SE. of Beckwourth, ca. 5,000 ft., *Ornduff* 4347 (LA). SIERRA CO.: State Hwy. 49, 2.4 mi. WNW. of Sierraville, R18415.

ADDITIONAL SPECIMENS EXAMINED:

U.S.: CALIFORNIA: LASSEN CO.: Long Valley, sec. 34, T. 45 N., R. 17 E., 4,300 ft., *Sawyer* 219 (RSA, UC): Chat, 5,000 ft., *Hillman* in 1897 (POM), *Jones* in 1897 (POM): 3 mi. N. of Omira, *Howell* 11857 (CAS). PLUMAS CO.: Sierra Valley, *Bolander & Keller* in 1872 (NY), *Lemmon* 87 (GH), in 1873 (GH), *Hillman* in 1898 (POM); Portola, *Eastwood* 7051 (CAS); 1.7 mi. NE. Vinton, 5,000 ft., *Cantelow* in 1941 (CAS, RSA); 8 mi. N. of Chilcoot, 5,000 ft., *Munz* 11823 (COLO, NY, RSA, RM, SD, UT, WTU); Chilcoot, 4,995 ft., *Rose* 34411 (CAS, RM); 4¾ mi. SE. of Sugarloaf, 4,900 ft., *Sawyer* 90 (POM, RSA); along road to Beckwourth, from Calpine, Sierra Valley, ca. 4,800 ft., *Bacigalupi* 4282 (JEPS, RSA): Beckwith Pass, 4,800 ft., *Jepson* 7767 (DS, JEPS): near Beckwourth, 4,900 ft., *Howell* 30753 (CAS), 37769 (CAS). SIERRA CO.: Loyalton, *Clemens* in 1920 (CAS). WITHOUT DEFINITE LOCALITY: *Lemmon* in 1875 (POM), 104 (NY).

Camissonia tanacetifolia subsp. *quadriperforata* is narrowly distributed and can be recognized most easily by a characteristic directly related to its hexaploid chromosome number: namely, the relatively high proportion of 4-pored pollen grains. Plants of this taxon are essentially identical in all other respects to those of subsp. *tanacetifolia* found in neighboring areas, although they do differ morphologically from a majority of the populations of subsp. *tanacetifolia* found in other areas. There is no known diploid population that could have combined with the tetraploid subsp. *tanacetifolia* to give rise to this hexaploid. In view of this and the local distribution of subsp. *quadriperforata*, its lack of morphological distinctness from adjacent tetraploid populations of the species, and the behavior of its chromosomes in meiosis, it seems likely that this hexaploid arose directly from the adjacent tetraploid populations by the functioning of an unreduced gamete. Probably the hexaploid originated recently and only once and has since spread to occupy its present area, which is less than 25 miles across at its broadest point. The habitat occupied is uniform and continuous. In order to understand how this postulated series of events could have occurred, however, it is necessary to assume that the hexaploid is physiologically superior to the tetraploid in its area, for it has apparently replaced the tetraploid where it does occur.

The nearest stations of hexaploid and tetraploid plants appear to be approximately 9 miles apart at present, with subsp. *tanacetifolia* at Graeagle (*Mason* 1037, DS, POM, UC) and subsp. *quadriperforata* to the east at Portola. Both of these stations are on the Middle Fork of the Feather River in Plumas County, California.

23. **Camissonia breviflora** (Torr. & Gray) Raven, Brittonia 16: 283. 1964.
FIGURES 12, 18, 22

Oenothera breviflora Torr. & Gray, Fl. N. Amer. 1: 506. 1840.
Taraxia breviflora (Torr. & Gray) Nutt. ex Small, Bull. Torrey Cl. 23: 185. 1896.

Similar to *C. tanacetifolia*. Plants densely clothed with appressed long trichomes. Leaves 1.7–10 cm. long, 0.35–3.3 cm. wide, the petiole 1.5–3 cm. long. Sterile prolongation of ovary 0.4–1.5 cm. long. Hypanthium 1.8–2 (–2.5) mm. long, 2.3–4 mm. across at the summit. Sepals 3.8–5 (–7.5) mm. long, 0.9–2.2 mm. wide. Petals 5.5–7 (–8) mm. long. 2.8–5 (–6) mm. wide. Filaments of the episepalous stamens 2.8–4 (–5) mm. long, those of the epipetalous ones 1.5–1.8 (–2) mm. long; anthers 0.9–1.3 mm. long. Style 3–6.5 mm. long; stigma globose, 1.1–1.6 mm. in diameter, surrounded by and receiving pollen directly from the anthers of the longer stamens at anthesis. Capsule 8–17 mm. long, 2–5 mm. thick. Seeds 1.5–1.8 mm. long, 0.7–0.9 mm. thick. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Near the Blackfoot River, in or near Caribou County, Idaho, 10–11 July 1834, *T. Nuttall* (GH; isotypes, BM, K, NY, PH).

DISTRIBUTION (Figure 24): Moist, often muddy or sandy flats, sometimes on lakeshores or in the dried beds of ponds in the vicinity of Chilko Lake (Nemiah Trail, 4,500 ft., *Copley* 440, DAO), at ca. 51° N., 124° W. in central British Columbia; from the region of Drumheller, Alberta (Handhills Lake, 51°30′ N., 112°07′ W., *Macoun* 144, BM, GH, NY), and Loomis, southwestern Saskatchewan (*Hudson* 1966, DAO), south to Montana (Glacier, Cascade-Meagher, Park, and Madison Counties), Wyoming (Yellowstone National Park, Teton, Sublette, Sheridan, Sweetwater, and Lincoln Counties), Colorado (Larimer County: North Park, *Osterhout* 1036, RM), Idaho (Caribou, Bear Lake, Franklin, Custer, and Cassia Counties), and Utah (Summit, Wasatch, Sevier, Piute, and Garfield Counties, reaching its southern limit on the Aquarius Plateau); from 3,500 ft. (at its northern limits) to 10,000 ft. elevation, apparently always above 6,500 ft. in the United States, In south-central Idaho, populations of *C. breviflora* are found within 65 miles of populations of the related *C. tanacetifolia*, but the former is found in mountain meadows at approximately 8,000 ft. elevation, the latter on more or less alkaline flats from 3,000–4,500 ft. elevation. Records of *C. breviflora* from south and west of Cassia County, Idaho, are based on misidentifications of sometimes stunted specimens of *C. tanacetifolia*. One such erroneous record is that of Munz (Calif. Fl. 952. 1959), based on *Wheeler* 3744 (POM, NY, US) from the Warner Mountains of Modoc County, California; *Camissonia breviflora* is not known from any locality in or near California.

Voucher for chromosome number, $n=7$ (1 structurally homozygous individual):

U.S.: WYOMING: SWEETWATER CO.: Eden Valley Reservoir, ca. 6,600 ft., R19551.

Plants of the collection just cited were grown at Stanford for several years and found to be autogamous, shedding pollen directly on the stigma and setting full capsules even when protected from insects. It is presumed that *Camissonia breviflora*, which is relatively uniform morphologically, is an autogamous derivative of the diploid ancestor of *C. tanacetifolia*. These two species have been confused in the past, but are sharply distinct both morphologically and ecogeographically. *Camissonia breviflora* almost certainly occurs sympatrically with *C. subacaulis*.

24. Camissonia graciliflora (Hook. & Arn.) Raven, Brittonia 16: 283. 1964.

Oenothera graciliflora Hook. & Arn., Bot. Beechey Voy. 341. 1838.

Taraxia graciliflora (Hook. & Arn.) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 216. 1893.

Annual, acaulescent or less commonly with short ascending lateral branches up to 2.5 cm. long. Leaves linear to very narrowly lanceolate, 1–9.8 cm. long, 0.1–0.9 cm. wide, more or less densely pilose, entire or very sparsely serrulate, sessile, dilated at the base, the margins of the basal portion membranous. Buds nodding before anthesis but flowers erect. Sterile prolongation of ovary 0.6–4.5 cm. long. Hypanthium 1.6–3.2 mm. long, 1.8–5 mm. across at the summit, pilose outside, more sparsely so inside, especially near the base. Sepals 4.5–8 mm. long, 1.2–2.9 mm. wide, pilose, reflexed in pairs. Petals 5–18 mm. long, 4.8–13 mm. wide. Filaments of the episepalous stamens 1.8–3.2 mm. long, those of the epipetalous ones 0.8–1.6 mm. long. Style 3–5.5 mm. long, short-pubescent near the base; stigma 1–1.6 mm. in diameter, surrounded by the anthers of the longer stamens at anthesis. Capsule 4–8 mm. long, 2.6–4.8 mm thick, sharply 4-angled and with a pointed wing near the center top of each valve, thick-walled (almost woody) and very tardily dehiscent, splitting for only about a third of its height. Seeds obovoid, tan mottled with brown, finely papillose, 1.2–2 mm. long, 1–1.2 mm. thick. Gametic chromosome number, $n=7$.

TYPE: California, 1833, *D. Douglas* (K; isotypes, BM, GH, NY).

DISTRIBUTION (Figure 25): Colonial on open or brushy slopes, often in clayey soil, from near sea level to about 2,500 ft. elevation; from Josephine County, Oregon, south in the Coast Ranges and foothills of the Sierra Nevada to Ventura and Los Angeles Counties, California; San Ysabel, San Diego County, *Henshaw* in 1893 (NY); red clay soil in once-cultivated field, Rancho Aguajito, 300 m., 29°59′N., 115°15′W., Baja California, *Raven et al.* 12675 (UC; the only known occurrence of the section in Mexico). Usually away from the coast, but collected both in Marin County (Mt. Tamalpais (*Wood* in 1915, CAS) and in San Francisco (*Cannon* in 1896, CAS), California. Once collected as an introduced plant in a dry, weedy field, St. George, Rockland County, New York, 20 July 1933, *Moldenke* 8008 (NY).

Voucher for chromosome number, $n=7$ (1 structurally homozygous individual):

U.S.: CALIFORNIA: MONTEREY CO.: Jolon, *Breedlove* 4279.

Camissonia graciliflora has been collected growing sympatrically with the very closely related *C. palmeri* (1 mile west of Pearblossom, Los Angeles County, California, *Mosquin* 3264, DAO; 3260, *C. palmeri*) and with *C. ovata*. It is self-compatible and facultatively self-pollinated, as shown by pollen-tube growth in three plants of R18153, Monterey County, California, that were caged in the field, and eight plants of R18177, San Luis Obispo County, California, that were grown in the experimental garden at Stanford. This species is probably not regularly outcrossed, judging from observations made at Jolon, Monterey County, California, on 31 March 1963 (Raven, MS.). With *C. palmeri* it forms a very distinctive group in the section, marked by annual habit, distinctive capsule morphology, obovoid seeds, nodding buds, and sepals reflexing in pairs; nonetheless, these two species so closely resemble the perennial members of the section in details of floral morphology (such as the sterile projection on the ovary, and the

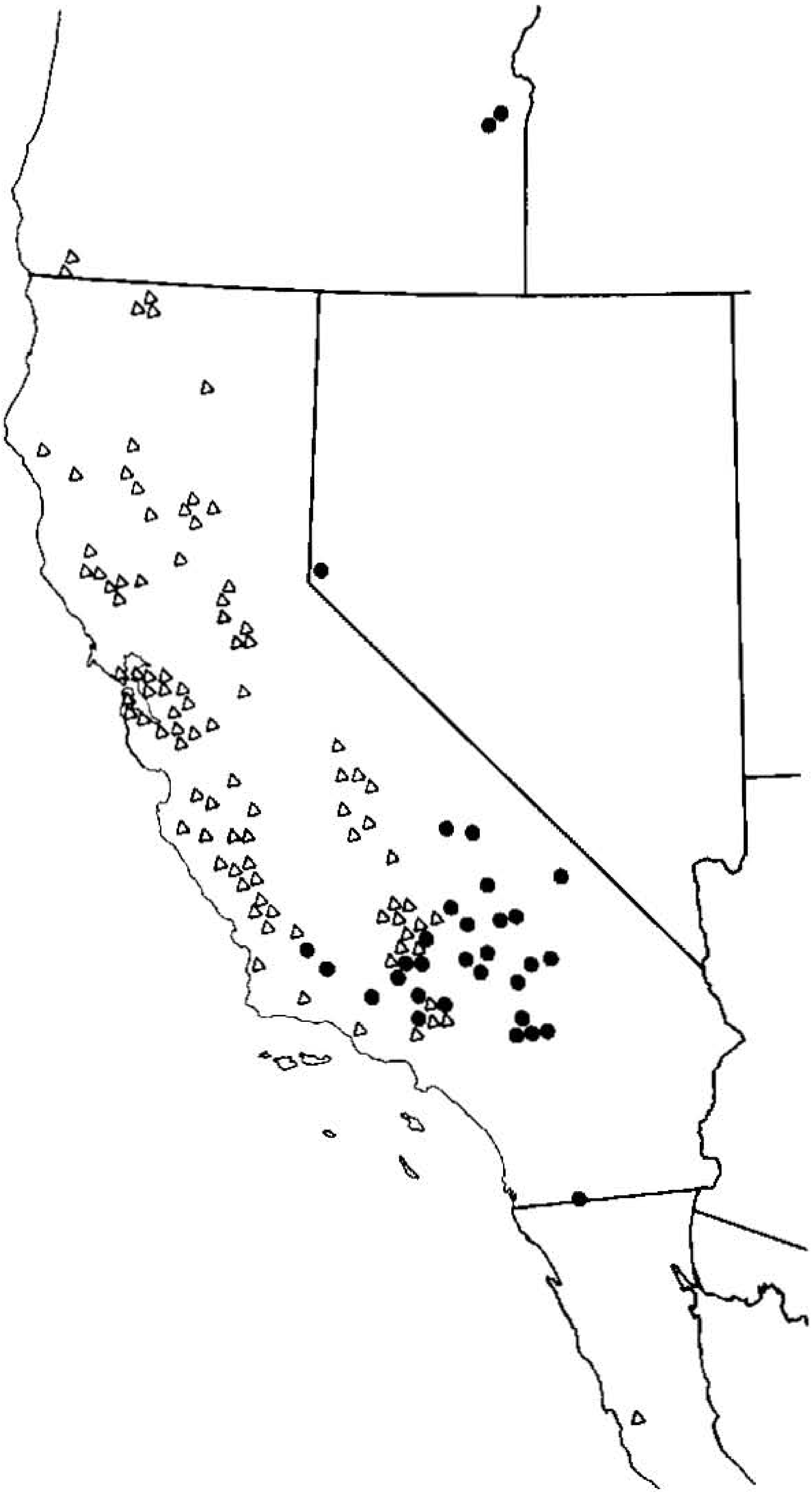


FIGURE 25.—Portion of the western United States and adjacent Mexico, showing the ranges of species of *Camissonia* sect. *Tetrapteron:* △=*C. graciliflora;* ●=*C. palmeri.*

fleshy ring closing the bottom of the hypanthium), that I believe they are best kept together in a single section.

25. Camissonia palmeri (S. Wats.) Raven, Brittonia 16: 283. 1964. FIGURES 14, 20
Oenothera palmeri S. Wats., Proc. Amer. Acad. 12: 251. 1877.
Taraxia palmeri (S. Wats.) Small, Bull. Torrey Cl. 23: 184. 1896.

Similar to *C. graciliflora.* Branches swollen, to 5 mm. thick, with conspicuously exfoliating white rhytidome. Leaves narrowly oblanceolate, 1.5–5.5 cm. long, 0.18–0.6 cm. wide, strigose, rarely with a few spreading trichomes near the base, sparsely but evenly serrulate.

Sterile projection of ovary 0.55–1.2 cm. long. Hypanthium 0.8–1.3 mm. long, 0.8–1.2 mm. across at the summit, strigose outside, glabrous within. Sepals 1.6–2.3 mm. long, ca. 1 mm. wide, strigose. Petals 2–3.5 mm. long, 1.8–4 mm. wide. Filaments of the episepalous stamens 0.8–1 mm. long, those of the epipetalous ones ca. 0.2 mm. long. Style 1–2.2 mm. long, glabrous; stigma 0.3–0.6 mm. in diameter, surrounded by the anthers of the long and short stamens, both of which shed pollen directly onto it at anthesis. Capsule 5–7 mm. long, 4.5–7 mm. thick, with much more prominent points than in *C. graciliflora*. Seeds narrowly obovoid. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Arizona, 1876, *E. Palmer* 597 (GH), perhaps from the Colorado River valley. The only known collection from this State, where the occurrence of the species needs to be confirmed; cf. McVaugh & Kearney, Amer. Midl. Nat. 29: 775–778. 1943.

DISTRIBUTION (Figure 25): Deserty flats, often under sagebrush, 2,000–4,650 ft. elevation, along the Malheur River near Vale, Malheur County, Oregon; 20 miles north of Winnemucca, Humboldt County. (*Ripley & Barneby* 4568, NY) and Empire City, Ormsby County. (*M. E. Jones* in 1882, GH, POM, UC), Nevada; in California fairly common from southern Inyo County, to the southwestern borders of the Mojave Desert, west to the vicinity of Tejon Pass and southeastern San Luis Obispo County in the inner South Coast Ranges, and also east of Jacumba on road to Mountain Springs, San Diego County (*Eastwood* 9553, CAS). May also occur in Arizona (cf. the type collection).

Voucher for chromosome count, $n=7$ (1 structurally homozygous individual):

U.S.: CALIFORNIA: SAN LUIS OBISPO CO.: Temblor Grade, Elkhorn Valley Road, south of Crocker Grade, *Lewis & Thompson* 1635 (LA, RSA).

As noted under that species, *Camissonia palmeri* has been collected growing sympatrically with *C. graciliflora*. Its floral structure provides unequivocal evidence of its autogamy. Indeed, some plants of both *C. palmeri* and *C. graciliflora* become cleistogamous under certain circumstances, these conditions being poorly understood. Such cleistogamous individuals, or other plants lacking flowers, can be determined only with difficulty. Plants of both species remain rooted in the ground long after they have died, the capsules shedding the seeds slowly after the first autumn rains.

Section V. *Holostigma*

Agassizia Spach, Hist. Vég. Phan. 4: 347. 1835; not Chavannes 1830.
Holostigma Spach, Nouv. Ann. Mus. Paris III. 4: 332. 1835.
Oenothera subg. *Sphaerostigma* sensu Munz, Bot. Gaz. 85: 234. 1928; pro parte.
Oenothera sect. *Holostigma* (Spach) Munz, N. Amer. Fl. II. 5: 159. 1965.

Perennials or annuals, the plants caulescent but with a well-developed basal rosette, flowering from the base. Inflorescence nodding at anthesis, becoming erect in fruit. Flowers opening near sunrise. Ovary lacking a sterile projection. Sepals reflexed separately or in pairs. Petals yellow, often with one to several red dots near the base, fading reddish, with no contrasting pattern visible in ultraviolet light. Stamens, style, and inside of hypanthium yellow, the stigma yellow or greenish yellow. Capsule regularly loculicidal, often contorted, not torulose, with a prominent brown rib down the center of each valve, the seeds in one row in each locule. Seeds with a scar at the micropylar end and a poorly developed pellucid chalazal crest, dull, brownish black, minutely lacunose in rows, narrowly obovoid.

TYPE SPECIES: *Camissonia cheiranthifolia* (Hornem. ex Spreng.) Raimann.

DISTRIBUTION: Brushy or open slopes and flats throughout cismontane California and the northern half of Baja California, with two species ranging across the deserts from southern Inyo County, California, and Esmeralda County, Nevada, across southern Arizona to the vicinity of Tucson, and one species ranging north along the coast to Coos Bay, Curry County, Oregon. Not known from, but possibly to be expected in, Sonora.

In all species of sect. *Holostigma*, the leaves of the basal rosette and the first formed capsules are more densely pubescent than those formed later. The leaves of the basal rosette tend to be broadest near the middle, and those of the stems and inflorescence tend to be broadest near the base and often subsessile or with shorter petioles. The first formed flowers are small, the largest ones are formed later and decrease markedly in size as the flowering season comes to an end. For all of these reasons it is especially necessary to deal with comparable stages when evaluating material of some of the critical species in this section.

The group of species comprising sect. *Holostigma* has always been a particularly difficult one taxonomically, both for the reasons just mentioned and because of their reticulate, polyploid pattern of evolution (see Appendix). In the treatment presented here, I have recognized 14 species, 3 of which are divided into 2 subspecies each. Of these 14 species, 9, including all of the polytypic ones, are diploid; 2 are tetraploid; and 3 are hexaploid.

All 9 diploids are relatively distinct from one another, although there is some intergradation between them. Both self-incompatible entities in the section are diploid: the ditypic, perennial *C. cheiranthifolia*, a species of the coastal strand from Coos Bay, Oregon, south to northern Baja California (partly consisting of self-compatible individuals), and the mostly annual *C. bistorta* that intergrades broadly with *C. cheiranthifolia* along the coast of southern California. Of the remaining seven diploids, *C. guadalupensis* of San Clemente and Guadalupe Islands, *C. ignota* of southern California and scattered localities northward, and *C. proavita* of coastal northern Baja California are extremely distinct and do not appear to have contributed to the origin of any of the polyploid species.

The difficulty lies with the remaining four diploid species and their polyploid derivatives. *Camissonia lewisii,* found along the coast of southern California and the northern half of Baja California, may have been derived more or less directly from coastal populations of *C. bistorta.* In northern and central California and also extending into the main area of the group in southern California, *C. micrantha* is largely a species of sandy beaches, washes, and flats at relatively low elevations, whereas *C. hirtella* is a species of cleared brushy slopes and chaparral margins away from the coast. Although these two diploids are modally extremely distinct, they have apparently combined to produce a tetraploid, *C. intermedia,* which bridges the morphological and ecological gap between them and contributes materially to the taxonomic difficulties of the group. *Camissonia pallida,* a diploid with a very wide range in the deserts of southern California and adjacent Nevada, western and southern Arizona, and northeastern Baja California, is very closely related to *C. hirtella* and at times difficult to distinguish from it, although the species come into contact only at the margins of their ranges. Given this pattern of variation, it is not at all surprising that *C. confusa,* the probable allotetraploid between *Camissonia hirtella* and *C. pallida,* should compound the taxonomic problems of separating its two diploid ancestors and be difficult to recognize when compared with certain populations of the diploids.

Although *Camissonia confusa,* the rarer of the two tetraploids, does not appear to have contributed to the origin of any hexaploid species, *C. intermedia* has rather obviously done so. In Monterey and San Luis Obispo Counties, California, north of the main area of the section, *C. intermedia* appears to have combined with each of its parents, *C. hirtella* and *C. micrantha,* to have given rise to the local hexaploids *C. luciae* and *C. hardhamiae,* respectively. In Baja California, *C. intermedia* has evidently combined with *C. lewisii* to give rise to the hexaploid *C. robusta.*

With a reticulate pattern of variation of this sort, it is no wonder that taxonomic treatments accorded the group have varied widely, particularly in the absence of knowledge about chromosome number. Although there has been some variation in the number of species and varieties recognized, the perennial *C. cheiranthifolia* and the annual, self-incompatible *C. bistorta* generally have been recognized as distinct from the remainder of the group by virtue of their large flowers and long styles. The same is largely true of *C. guadalupensis*, described in 1876 but excessively rare in collections until the past five years. Most of the difficulty then has concerned the remaining species of the section, usually treated collectively as *Oenothera micrantha*.

How have different authors treated the *Oenothera micrantha* complex? E. L. Greene in 1891 subdivided this group into the more or less prostrate or trailing coastal *Oenothera micrantha*, which he allied to *Oenothera bistorta* of southern California, and the erect plant of the interior with broader leaves that he called *Oenothera hirtella*. Greene was the first author who had seen many populations in nature to deal with this group. In 1905, LeRoy Abrams realized the distinctiveness of the densely strigose desert populations, which he described as *Oenothera pallida*. Later the same year Aven Nelson, working largely with herbarium material, treated some material of both species that had been described as varieties of his *Sphaerostigma micranthum*, but also recognized *Sphaerostigma hirtellum* and described another species based on material of the same diploid taxon as *S. arenicola*. Nelson was evidently puzzled by the striking changes in plants of this group that occur with increasing maturity and had no acquaintance with them in the field; his work cannot be regarded as a forward step.

In 1907 appeared what were clearly the most perceptive remarks on the plants of this section written without knowledge of chromosome numbers. This paper was entitled "Notes on *Sphaerostigma*," by Anstruther Davidson, an enthusiastic amateur botanist of southern California. From his excellent vantage point Davidson was able to present a remarkably accurate picture of the entities represented in the group. He recognized as species *S. pallidum*, *S. hirtellum* ("a good and quite distinct species, and not a merely hirsute variety of *micranthum* as some have supposed"), and *S. micranthum*, and also described *S. hallii*, here regarded as a subspecies of *Camissonia pallida*. Davidson's remarks about the pattern of variation in his *S. micranthum* are remarkable and deserve to be quoted at some length (Muhlenbergia 3: 107. 1907):

> The typical plant of this species is, I presume, the ordinary moderately hirsute, semi-prostrate form found from San Francisco southward. In the coast region round Los Angeles there are two well marked forms. One, the congesta form, has very congested foliage, with the leaves larger and more hirsute, and with very small flowers; the other, the macrocarpa form, with the same foliage, has the short stout capsule of *bistorta*. The latter is the rarer form, examples of which are found from Los Angeles, San Diego, and Lower California. A typical interior form is found in Parish's collections from San Bernardino county, and is frequently met with in other interior valleys. It is to the eye quite smooth in all its parts.

In retrospect, it is obvious that Davidson was quite correct about the typical form of the species, which is here recognized as *Camissonia* *micrantha*; this also includes his "congesta" form. Davidson's "macrocarpa" form is obviously the species described 60 years later in the present revision as *C. lewisii*; and his "typical interior form" is the plant described by Jepson in 1925 as a variety of *Oenothera micrantha* and here regarded as a distinct species *Camissonia ignota*. In other words, Davidson recognized and quite accurately described all seven diploids with which he was familiar; it is probable that he saw no material of *C. proavita* or *C. gudalupensis*. The relatively few polyploid populations that he encountered were presumbly referred to one of the diploids, depending on their morphological relationships.

No subsequent author gained quite as clear a picture of the major patterns of variation in the group, possibly because of an increasing awareness of the way in which the polyploids recombined the characteristics of what otherwise would have been distinctive diploid races.

In 1928, P. A. Munz published his comprehensive review of the section. His concept of this complex was based on a comprehensive species, *Oenothera hirta* (=*Camissonia micrantha*), with four varieties corresponding broadly to the diploids *Camissonia micrantha*, *C. hirtella*, *C. ignota*, and *C. pallida*. Dr. Munz did not realize the distinctiveness of *C. lewisii* and *C. proavita* and had very little material of the latter upon which to base any judgment. Again the polyploids were redistributed among the diploid taxa they most closely resembled.

In 1964, I outlined the limits of sect. *Holostigma* accepted here and made new combinations at the specific level for the available names in the group (Brittonia 16: 276–288). This led Dr. Munz to accept his earlier varieties as species (Fl. N. Amer. II. 5: 159–163. 1965). He was unable to list *C. lewisii*, *C. proavita*, and the five polyploid species, as no earlier names were available for these entities.

The present study of *Camissonia* sect. *Holostigma* is clearly not a definitive one, and much work remains to be done. On the other hand, it represents 10 years of intensive fieldwork, cultivation of the plants in the experimental garden, and the determination of the chromosome numbers of 389 individuals from 335 populations (see Appendix). I believe that the taxonomy presented here leads to a clearer picture of the pattern of variation in the section than anything published previously, and I have had much more material to draw on than any earlier worker concerned with the group. Lines within and between the nine diploid species appear clearly drawn, but the nature and derivation of both tetraploids need to be investigated in much greater detail, preferably by the techniques of experimental hybridization. The delimitation of the three hexaploids seems clearer, but the same sort of work could profitably be done here also. At any rate, it is hoped that the present taxonomic synopsis offers a sound basis for such studies. As pointed out in the Appendix, the group appears to have several cytogenetic peculiarities which should make a further investigation of the evolutionary patterns in it of more than usual interest.

26. Camissonia cheiranthifolia (Hornem. ex Spreng.) Raimann, *in* Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 217. 1893.

Oenothera spiralis f. *arcuata* H. Lév., Monogr. Onoth. 222. 1905. Léveillé says simply "Fruit simplement arque—falque" and this cannot be placed with either of the two subspecies in the absence of authentic material.

Oenothera spiralis f. *clypeata* H. Lév., Monogr. Onoth. 222. 1905. Léveillé says "Feuilles *scutiformes*, sessiles, comme mucronees au sommet"; to assign this name to either subspecies in the absence of authentic material would be a guess.

Sphaerostigma spirale var. *clypeatum* (H. Lév.) A. Nels., Bot. Gaz. 40: 60. 1905.

Short-lived perennial, usually flowering the first year, with a circle of prostrate, decumbent, or more or less ascending stems radiating from a central rosette which withers in age, the stems to 0.6 (–1.3) m. long, ultimately somewhat woody and developing a conspicuously exfoliating reddish brown (less commonly whitish) rhytidome. Plants more or less densely strigose pubescent on all parts, rarely glabrous. Leaves narrowly ovate, 0.5–5 cm. long, 0.25–2.2 cm. wide, sparsely and weakly serrulate, the apex acute, the base cuneate to cordate or (in the basal rosette) attenuate; petioles to 2.5 cm. long in the basal rosette, 0–10 mm. long on the branches. Inflorescence with two types of trichomes, short-erect and long-villous. Hypanthium 2.1–8.5 mm. long, 1.5–5 mm. across at the summit, glabrous within. Sepals 4–11.5 mm. long, 1.3–3.4 mm. wide, reflexed in pairs. Petals 6–20 mm. long, 5–22 mm. wide, often red-dotted near the base. Filaments of the episepalous stamens 2.8–8 mm. long, those of the epipetalous ones 1.5–6 mm. long; anthers 1.3–3 mm. long. Style 6–23 mm. long, glabrous; stigma 0.4–1.5 mm. in diameter, surrounded by or held above the anthers at anthesis. Capsule 1–2.5 cm. long, ca. 2–2.5 mm. thick, quadrangular in transection, often curled in one or two spirals. Seeds 1.2–1.3 mm. long, 0.5–0.7 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible, self-compatible but outcrossing, and autogamous races known.

DISTRIBUTION (Figure 30): Sandy slopes and flats along the immediate coast and on islands from Coos Bay, Curry County, Oregon, to the vicinity of San Quintín, Baja California; also known from the east shore of San Francisco Bay and locally on sand dunes along the lower Sacramento River, California. Near sea level to several hundred feet elevation.

Although some 35 miles separate the southern limit of subsp. *cheiranthifolia*, at Point Conception, from the northern limit of subsp. *suffruticosa*, just above Goleta, both of the subspecies occur on San Nicolas Island. Here, as on the other Channel Islands where the species occurs, subsp. *cheiranthifolia* is common and has been collected a number of times. On 24 April 1966, I found a small colony of about 40 plants of subsp. *suffruticosa* on the open dunes ca. 1 mile east-southeast of Seal Beach, at the northwest end of San Nicolas Island (my no. 20761, collected with H. J. Thompson). The colony was surrounded by about 15 intermediates and located near a road in a much larger population of subsp. *cheiranthifolia*. It is possible that subsp. *suffruticosa* was introduced on the island, but it was collected as early as 1901 (*Trask* 45, GH, NY), so it more likely reached the island by natural means. The population I studied presumably consists of self-compatible plants, although the stigma was held well above the anthers as usual in this subspecies.

Experimental hybrids were made between plants of subsp. *suffruticosa* from Point Dume, Los Angeles County, California, and subsp. *cheiranthifolia* from Jalama Beach, Santa Barbara County, California. Both parental strains had 7 pairs of chromosomes at meiotic metaphase I, and both consisted of self-compatible plants. The F_1 hybrids (Raven 17746, 17747, 17934) were intermediate between the parents morphologically, self-compatible, and fully fertile, although the stigma was held above the anthers as in the subsp. *suffruticosa* parent. Reciprocal hybrids were indistinguishable, and one hybrid made in each direction was examined cytologically and found to form 7 pairs at meiosis, indicating a lack of structural differences. In terms of pollen stainability, three plants with subsp. *suffruticosa* as the pistillate parent had, respectively, 93, 80, and 88 percent stainable pollen (based on samples of 100 grains in cotton blue in lactophenol), and five with subsp. *cheiranthifolia* as the pistillate parent had, respectively, 66, 72, 58, 53, and 77 percent stainable pollen. Both parents had consistently more than 95 percent stainable pollen, thus indicating a definite, but limited, reduction in fertility in the F_1 hybrids apparently not associated with chromosomal differentiation between the parental strains.

26a. Camissonia cheiranthifolia subsp. **suffruticosa** (S. Wats.) Raven, Brittonia 16: 284. 1964. FIGURES 26, 27

Oenothera viridescens Hook., Fl. Bor. Amer. 1: 214. 1833. Type: From Santa Barbara, Santa Barbara Co., Calif., or San Diego, San Diego Co., Calif., November or December 1793, *A. Menzies* (K).

Sphaerostigma viridescens (Hook.) Walp., Rep. 2: 77. 1843.

Oenothera cheiranthifolia var. *sufflruticosa* S. Wats., Proc. Amer. Acad. 8: 592 1873.

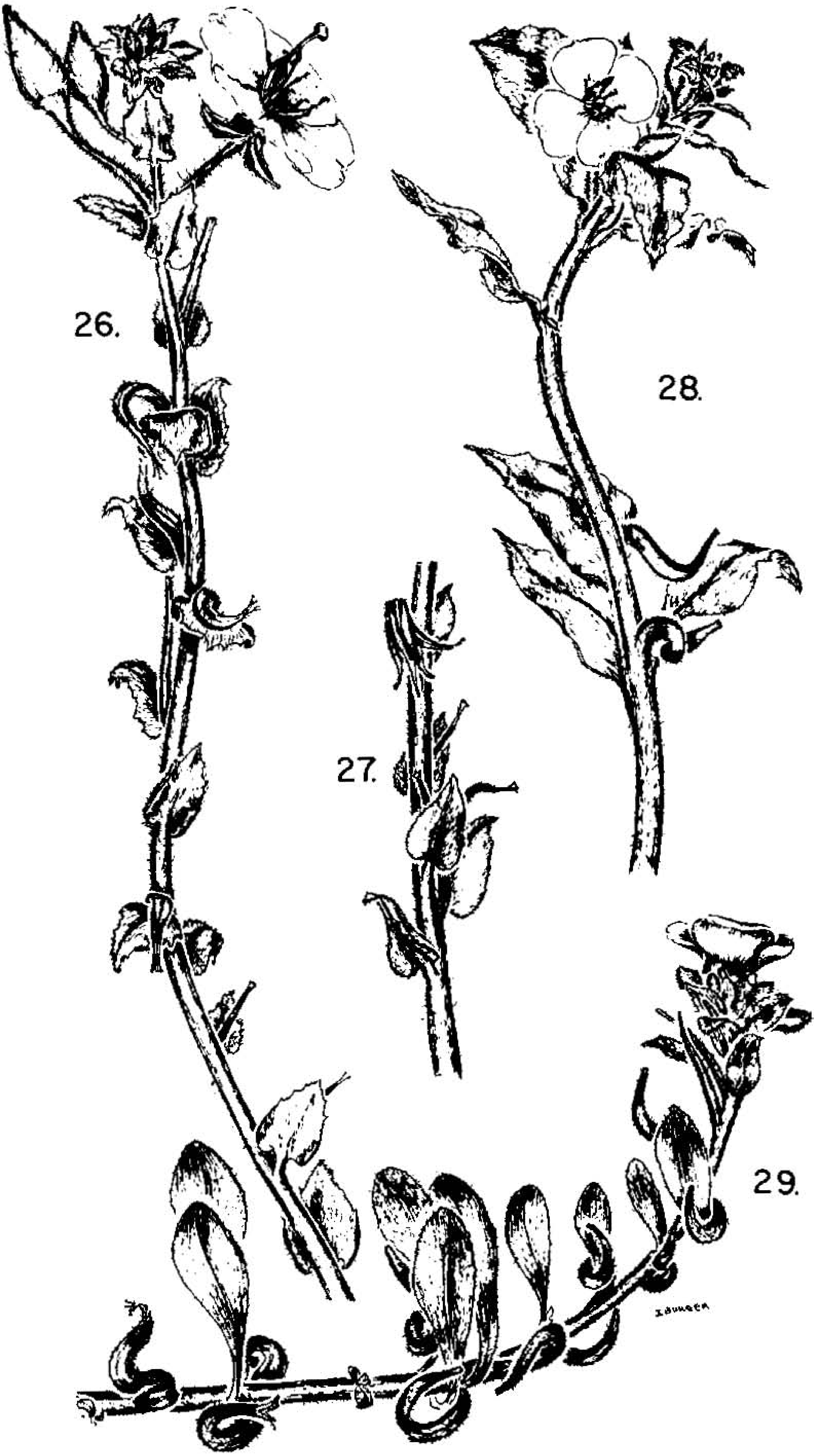
"*Oenothera virescens* Hook.," Greene, Fl. Francisc. 214. 1891.

Sphaerostigma spirale var. *viridescens* (Hook.) A. Nels., Bot. Gaz. 40: 60. 1905.

Oenothera spiralis f. *viridescens* (Hook.) H. Lév., Monogr. Onoth. 222. 1905.

Oenothera spiralis var. *linearis* Jeps., Man. Fl. Pl. Calif. 684. 1925. Type: Sunnyside, San Diego Co., Calif., April 1903, *H. M. Ha* 3908 (UC).

Oenothera spiralis var. *viridescens* (Hook.) Jeps., Man. Fl. Pl. Calif. 684. 1925.



FIGURES 26–29.—*Camissonia cheiranthifolia*, × 1: 26–27, *C. cheiranthifolia* subsp. *suffruticosa* (*Gregory* 468, DS): 26, Flowering branch; 27, portion of fruiting branch. 28–29, *C. cheiranthifolia* subsp. *cheiranthifolia*, flowering branches: 28, *Raven* 20825, DS; 29, *Randall* 220, DS.

Often bushy, the branches ascending and the plants quite woody; pubescence often dense and silvery, particularly in the summer and fall. Hypanthium 5–8.5 mm. long, 3–5 mm. across at the summit. Sepals 6–11.5 mm. long, 2.4–3.4 mm. wide. Petals (10–) 12–20 mm. long, 14–22 mm. wide, usually with one or two red dots at the base. Filaments of the episepalous stamens 5–8 mm. long, those of the epipetalous ones 3–6 mm. long. Anthers 2.2–3 mm. long. Style 13–23 mm. long; stigma held well above the anthers at anthesis. Gametic chromosome number, $n=7$. Outcrossing, with self-incompatible and self-compatible populations known.

LECTOTYPE: Santa Barbara, Santa Barbara County, California, *Brewer* 307 (GH). This appears to be the only specimen in the Gray Herbarium annotated with this name by Watson. Considering this, and the fact that it is from a definite locality, it appears to be a better choice of lectotype than the first-listed specimen assumed by Munz (Bot. Gaz. 85: 269. 1928) to be the type.

DISTRIBUTION (Figure 30): Sand dunes and beaches along the immediate coast, from Deveraux Dunes just west of Goleta, Santa Barbara County, California, to 6 miles south of San Quintín, Baja California (*Ballou & Canby* in 1925, C, F, POM, UC); San Nicolas Island, Ventura County, California (see below); San Martín Island, Baja California. From near sea level to several hundred feet elevation.

The chromosome number has been determined from 8 individuals from 7 different populations scattered throughout the range of this entity (see Appendix). Populations from 5.5 miles southeast of Point Mugu, Ventura County, California (R20161—6 plants tested for growth of pollen tubes), Point Dume (see below), and Playa del Rey (Kyhos 65–47, 1 plant grown at Stanford), Los Angeles County, California, consisted of self-compatible plants, which were however outcrossing, with the stigma elevated well above the stamens at anthesis and not contacting them even when the flowers closed. On the other hand, populations from farther south, in San Diego County, California, consisted of self-incompatible individuals: Del Mar Beach, R20167 (11 plants tested for pollen-tube growth); DeAnza Cove, Mission Bay, *Wedberg* (15 plants grown at Stanford as R66–224). *Andrena (Onagrandrena) oenotherae* Timb. was an abundant visitor to the flowers of this subspecies at all localities investigated, extending from the northern limit to south of Ensenada, Baja California; this large, black, oligolectic bee doubtless is a very important agent promoting outcrossing in this subpecies. *Andrena (Diandrena) parachalybea* Viereck, a somewhat smaller oligolectic bee, is locally frequent as an early morning visitor to the present subspecies also.

It appears likely that populations very similar to the self-incompatible ones presently referred to *Camissonia cheiranthifolia* subsp.

FIGURE 30.—Portion of the western United States and adjacent Mexico, showing the ranges of species of *Camissonia* sect. *Holostigma:* ●=*C. cheiranthifolia* subsp. *suffruticosa;* ○=*C. cheiranthifolia* subsp. *cheiranthifolia;* △=*C. bistorta.*

suffruticosa gave rise on the one hand to the self-incompatible, annual *C. bistorta* and on the other to the autogamous, perennial *C. cheiranthifolia* subsp. *cheiranthifolia.* An account of the anatomy of subsp. *suffruticosa* has been given by Purer, Ecol. Monogr. 6: 1–88. 1936.

At the present time, it occurs sympatrically with both of its presumed derivatives, and its relationship with subsp. *cheiranthifolia* has been considered above. It also occurs sympatrically with *C. lewisii* at many localities.

Often *Camissonia bistorta* and *C. cheiranthifolia* subsp. *suffruticosa* occupy adjacent but sharply distinct habitats. At Point Dume, Los Angeles County, California, the former occurs on the upper reaches of the sandy beach and the latter forms colonies in the sandy grassland on the tops of the bluffs. Here the two do not grow immediately adjacent to one another, and intermediates have not been observed. On the other hand, where the habitats of the two species do intergrade more subtly, hybrids occur rather commonly. Populations of perennial plants otherwise resembling *C. bistorta* are characteristic of some areas and occur frequently along the entire coast of San Diego County, California, and in northern Baja California. Extensive series of intermediate populations occupy the sandy riverbeds in the vicinity of San Diego, a habitat that is clearly intermediate between the coastal dunes and flats inhabited by *C. cheiranthifolia* and the firmer sandy soil farther inland where *C. bistorta* occurs. Where intermediate plants do occur, they generally appear as relatively uniform local populations. The fertility of such plants is usually not reduced; for the collections indicated with an asterisk in the following list, pollen stainability was at least 96 percent for the average of two samples each of 200 pollen grains in cotton blue in lactophenol. In the Jones collection from Pacific Beach, pollen stainability was reduced to 79 percent; this collection might represent an F_1, or might be sterile for some other reason.

Specimens of apparent hybrids between *Camissonia cheiranthifolia* subsp. *suffruticosa* and *C. bistorta* examined:

U.S.: CALIFORNIA: SAN DIEGO CO.: Encinitas, *Lewis* 1202* (LA), *Epling & Robison* in 1932 (LA); Cardiff, *Benson* 10352* (POM); Oneonta, *Chandler* 5094 p.p. (NY); U.S. Hwy. 101 N. of La Jolla, *Benson* 4286 (POM); Valley Center, *Woodcock* in 1928 (SD); Crown Point near Pacific Beach, *Purer* in 1935 (POM)r Sunnyside, *Hall* 3908 (F); Foster, 400 ft., *Smith* 5257 (F); San Diego River nea; the Mission, *Abrams* 3412 (CAS, GH, LE, NMC, NY, PH, POM, UC); Mission Valley, *Purer* 6124 (DS, POM, SD), *Gander* 4929 (SD); Cuyamaca Road 0.5 mi. N. of Mission Gorge Road, San Diego R., Santee, *Wedberg* 533* (DS) El; Monte Park Grove, *Alderson* in 1934 (SD); San Luis Rey, *Gander* 3309 (;SD) foot of San Miguel Mt., *Youngberg* 44 (POM), *Gander* 154.5 (SD); S. San Diego, *Chandler* 5097 (DS, NY); wash between National City and Chula Vista, *Wolf* 2086 (DS, RSA, UC), *Gander* 4920 (SD); Otay Creek, 2 mi. below dam, *Peirson* 3410 (RSA); Otay, *Higgins* in 1954 (UC); Nestor, near Tia Juana, *Wiggins* 3229 (DS LA, UC).

BAJA CALIFORNIA: Dry Tijuana R. bed, 80 ft., *Smith* 5206 (F, PH); 2 mi. N. of Rosarito Beach, *Wiggins & Gillespie* 3882 (CAS, DS, F, GH, NY, POM, RSA); Descanso Dunes, R17059* (DS) *Higgins* in 1949 (RSA), in 1950 (RSA, SD), *Creighton* 525 (COLO), *Purer* in 1932 (SD); sea bluffs 32 mi. N. of Ensenada, *Munz* 22702 (RSA); Pinita, *Harbison* in 1950 (SD); Hot Springs, *Jones* in 1882 (POM, RM, UC); Cariso Creek, *T. S. Brandegee* in 1893 (UC).

These two entities have been hybridized experimentally, using a strain of *C. bistorta* from 6.5 miles east of San Juan Capistrano, Orange County, California (R18782), and one of *C. cheiranthifolia* subsp. *suffruticosa* from De Anza Cove, Mission Bay, San Diego County, California, collected by H. L. Wedberg. Both parental strains were self-incompatible, and both regularly formed 7 pairs of chromosomes at meiotic metaphase I. Seeds were readily obtained in both directions, but only those derived from the cross using *C. cheiranthifolia* as the female parent germinated. Four individuals from a large F_1 progeny were examined cytologically. The maximum association of chromosomes observed was a ring of 8 and 3 ring bivalents, with the large ring most often present as a chain and one of the bivalents being a rod (i.e., forming only one chiasma) in most cells. Samples of 200 pollen grains from each of three individuals, stained in cotton blue in lactophenol, gave the following percentages of apparently viable pollen: 24.5, 24.5, and 34.7%. Although the hybrids were self-incompatible like both of their parents, cross-pollination gave essentially full seed-set, and doubtless these plants would easily backcross with either parent, thus producing individuals similar to many of the putative hybrids observed in the field.

Two of the apparent hybrids (possibly backcrosses with *C. cheiranthifolia*) found in the field were examined cytologically and showed no evidence of structural heterozygosity:

BAJA CALIFORNIA: Meadows E. of Rosarito, *Bates* 2331; ca. 29 mi. S. of Tijuana, *Klein & Gregory* 1274* (RSA).

One of the early binomials applied to plants of this section was *Holostigma bottae* Spach, Nouv. Ann. Mus. Paris 4: 336. 1835. Its description is such that Munz (N. Amer. Fl. II. 5: 163. 1965) appropriately stated, "Possibly an earlier name for *Oenothera bistorta*" [= *Camissonia bistorta*]. Thus it is of considerable interest and importance to establish the identity of Spach's plant, with its type locality "In Californiâ australi." Through the kindness of Dr. Alicia Lourteig, I have been able to ascertain that there is apparently no specimen in the Paris herbarium annotated "*Holostigma bottae*." There is, however, a specimen collected by Paolo Emilio Botta at San Diego, California, in 1827, labeled (probably in Spach's hand) "*Sphaerostigma*." Spach used the names *Sphaerostigma* and *Holostigma* essentially interchangeably, and this appears to be the only specimen of the group present at Paris that was collected by Botta. Furthermore, it agrees perfectly and in detail with Spach's rather extensive description of *Holostigma bottae*. Consequently, I designate it the lectotype of this species.

Unquestionably, the specimen is one of the series of populations intermediate between *Camissonia bistorta* and *C. cheiranthifolia* subsp.

suffruticosa so common in the vicinity of San Diego and perfectly matched by many individuals growing today along the sandy bed of the San Diego River (e.g., *Wedberg* 533 or *Abrams* 3412, cited above). Its percentage of stainable pollen based on a sample of 200 grains, is 93%. In view of this, the name *Holostigma bottae* cannot be regarded as belonging to either of its parental species, and there seems no need to transfer it to *Camissonia* to serve as a binomial designation for the series of interspecific hybrids from which its type collection was derived more than 140 years ago.

26b. Camissonia cheiranthifolia subsp. **cheiranthifolia** FIGURES 28, 29

Oenothera cheiranthifolia Hornem. ex Spreng., Syst. 2: 228. 1825.

Oenothera spiralis Hook., Fl. Bor. Amer. 1: 213. 1833. Type: Coastal California (either at Trinidad Head, San Francisco, Santa Cruz, or Monterey), 1792–1794, *A. Menzies* (K).

Holostigma cheiranthifolium (Hornem. ex Spreng.) Spach, Nouv. Ann. Mus. Paris III. 4: 335. 1835.

Sphaerostigma cheiranthifolium (Hornem. ex Spreng.) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 50. 1835.

Sphaerostigma spirale (Hook.) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 50. 1835.

Agassizia cheiranthifolia (Hornem.) Spach, Hist. Nat. Vég. 4: 348. 1835.

Holostigma spirale (Hook.) Spach, Nouv. Ann. Mus. Paris III. 4: 336. 1835.

Oenothera nitida Greene, Pittonia 1: 70. 1887. Type: San Miguel I., Santa Barbara Co., Calif., September 1886, *E. L. Greene* (ND; isotypes, NY, PH, UC, US).

Sphaerostigma nitidum (Greene) Small, Bull. Torrey Cl. 23: 190. 1896.

Oenothera spiralis var. *nitida* (Greene) Jeps., Man. Fl. Pl. Calif. 684. 1925.

Oenothera cheiranthifolia var. *typica* Munz, Bot. Gaz. 85: 268. 1928.

Oenothera cheiranthifolia var. *nitida* (Greene) Munz, Bot. Gaz. 85: 269. 1928.

Branches usually prostrate or decumbent and largely herbaceous; pubescence rarely dense and silvery. Hypanthium 2.1–4.2 (–4.8) mm. long, 1.5–3 mm. across at the summit. Sepals 4–5.6 (–6.7) mm. long, 1.3–1.9 (–2.1) mm. wide. Petals 6–11 mm. long, 5–12 mm. wide, rarely with one or two red dots near the base. Filaments of the episepalous stamens 2.8–4.5 mm. long, those of the epipetalous ones 1.5–3 mm. long. Anthers 1–1.5 mm. long. Style 6–9 mm. long; stigma surrounded by both sets of anthers which shed pollen directly onto it at anthesis, or very rarely held above the anthers. Gametic chromosome number, $n=7$. Facultatively autogamous, but sometimes outcrossing; self-compatible.

LECTOTYPE: "Ex hort. semina e California mis. Wormskiold" (C), doubtless from seed collected in the vicinity of Fort Ross, Sonoma County, or San Francisco, California. During most of the 19th century, the species was erroneously attributed to Chile, based on Sprengel's statement in the protologue; no evidence for this has ever been found, and it is assumed that Sprengel made a simple mistake (cf. Munz, Bot. Gaz. 85: 268. 1928).

DISTRIBUTION (Figure 30): Sandy slopes and flats along the coast, from Coos Bay, Curry County, Oregon, south to Point Conception, Santa Barbara County, California; also on the east shore of San Francisco Bay in Alameda and Contra Costa Counties, California; sand dunes and flats along the lower Sacramento River, California, often with *Lupinus arboreus*, another beach species (4 miles west of Antioch, Contra Costa County, *Heller* in 1942, WTU; between Antioch and Rio Vista bridges, Sacramento County, *Eastwood & Howell* 8636, CAS; Brannan Island State Park, Sacramento County, R20178, DS); San Miguel, Santa Rosa, Santa Cruz, San Nicolas, and San Clemente Islands.

The gametic chromosome number of this subspecies has been determined as $n=7$, with no evidence of structural heterozygosity, in single individuals from eight populations throughout its range (see Appendix). Although self-pollination generally occurs in this taxon upon the closing of the flowers, some populations, especially in the San Francisco Bay area, are much visited by oligolectic bees of the genus *Andrena* (*Onagrandrena*) and are doubtless outcrossed to a large extent. Other populations, such as those around Monterey Bay and farther south, appear not to be visited often by insects of any kind and are probably predominantly self-pollinated. The flowers of subsp. *cheiranthifolia* generally open more tardily than those of subsp. *suffruticosa*, which also occupies areas where the mornings are not often foggy.

This subspecies is quite variable in pubescence, and there appears to be a cline extending from the San Francisco area, where the plants are usually decumbent and greenish, to the region of Morro Bay, San Luis Obispo County, where many of the plants are more erect and silvery pubescent, resembling indiviuals of subsp. *suffruticosa*. Such plants may also have larger flowers than usual for subsp. *cheiranthifolia* but in general are not exceptional in flower size.

Other variants in pubescence may occur as individual plants, mixed in populations of more usual individuals. For example, at the mouth of Hazard Canyon, San Luis Obispo County, California, Robert Hoover collected an interesting local race with large bright green but still pubescent leaves, up to 4.5 cm. long and 2 cm. wide, growing with the usual more heavily pubescent and smaller leaved plants. Occasional completely glabrous or subglabrous plants occur in populations; these individuals have been named *Oenothera nitida* Greene. Such plants agree with the rest of the species in chromosome number. They obviously comprise only one of the more conspicuous segregating elements in their interbreeding populations, and do not merit formal taxonomic recognition. Such glabrous plants have been collected around Monterey Bay, Monterey County, California, where they are well known; in Santa Barbara County, California, at Surf (*Pierson* 8308, POM, RSA) and at Jalama Beach (*Smith* 2848, RSA); and on Santa Rosa (East Point, *Munz & Hoffmann* 11744, POM) and San Miguel Islands.

On San Martín Island, off the coast of Baja California, individuals of subsp. *suffruticosa* occur which are more prostrate than usual for that subspecies and thus resemble subsp. *cheiranthifolia: Moran* 10571 (ARIZ, COLO, BS, RSA, SD, UC). As these plants agree with other Baja California populations of subsp. *suffruticosa* in flower size and pubescence, I have regarded them as representing a maritime ecotype of that taxon. The possibility that they may in fact belong with subsp. *cheiranthifolia* and represent a relictual station for that more northern subspecies cannot, however, be completely ruled out at present. It does seem more likely that they have converged with it in habit on the basis of their similar ecology.

Camissonia cheiranthifolia subsp. *cheiranthifolia* occurs sympatrically with *C. micrantha*, and with *C. guadalupensis* subsp. *clementina* and locally intergrades with *C. cheiranthifolia* subsp. *suffruticosa* as discussed above.

27. Camissonia bistorta (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 284. 1964. FIGURE 31

Oenothera heterophylla Nutt. ex Hook. & Arn., Bot. Beechey Voy. 341. 1938; non Spach 1835. Type: San Diego, San Diego Co., California, April-May 1836, *T. Nuttall* (BM).

Oenothera bistorta Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 508. 1840.

Sphaerostigma bistortum (Nutt.) Walp., Rep. 2: 77. 1843.

Oenothera bistorta var. *veitchiana* Hook., Bot. Mag. 84: *pl. 5078.* 1858. Lectotype: Plains about San Gabriel Mission, Los Angeles Co., California *W. Lobb* 416, grown at *Hort. Veitch* in 1857 (K).

Sphaerostigma veitchianum (Hook.) Small, Bull. Torrey Cl. 23: 191. 1896.

Sphaerostigma bistortum var. *veitchianum* (Hook.) A. Nels., Bot. Gaz. 40: 59. 1905.

Oenothera cheiranthifolia f. *delicatula* H. Lév., Monogr. Onoth. 216, fig. on p. 214. 1905.

Oenothera bistorta var. *typica* Munz, Bot. Gaz. 85: 266. 1928.

Annual, or rarely a short-lived perennial, with one to several ascending or several spreading, decumbent stems radiating from a central rosette, these to 0.8 mm. long, with a conspicuously exfoliating pale rhytidome. Plants strigose or more commonly villous. Leaves very narrowly elliptic in the basal rosette to narrowly lanceolate or lanceolate on the stems and in the inflorescence, rarely all linear, 1.2–12 cm. long, 0.15–1.5 cm. wide, denticulate, but often only sparsely and inconspicuously so, the apex acute, the base narrowly cuneate (in the basal rosette) to cuneate or subcordate; petioles to 4 cm. long in the basal rosette, the upper leaves usually subsessile. Inflorescence with two types of trichomes, short-erect and long-villous. Hypanthium

FIGURES 31–32.—Species of *Camissonia* sect. *Holostigma*, × 1: 31, *C. bistorta* (*Raven* 16935 DS); 32, *C. lewisii* (*Raven* 17021, DS).

2–5 (–7.5) mm. long, 1.5–4 mm. across at the summit, glabrous to pubescent in lower portions within, often with prominent red dots near the summit within. Sepals (2.3–) 5–8 (–11) mm. long, (0.8–) 1–2 mm. wide, reflexed in pairs. Petals (4.2–) 7–15 mm. long, (2.5–) 6.5–12 (–16) mm. wide, each petal almost always with a bright red spot (rarely two) near the base. Filaments of the episepalous stamens (1–) 1.5–3.5 mm. long, those of the epipetalous ones (0.5–) 1–2.5 mm. long; anthers (0.5–) 1.3–2 (–2.5) mm. long. Style (5.5–) 7–12 mm. long, usually glabrous but occasionally pubescent near the base; stigma (0.7–) 1–1.8 mm. in diameter, held well above the anthers at anthesis. Capsule 1.2–4 cm. long, 1.5–2.5 mm. thick, more or less quadrangular in transection, straight or somewhat contorted. Seeds 0.9–1 mm. long, 0.3–0.55 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: San Diego, San Diego County, California, April-May 1836, *T. Nuttall* (NY; isotypes, BM, K, GH, PH).

DISTRIBUTION (Figure 30): Sandy fields near the coast or clayey grassland, often in openings of coastal sage, from Piru Creek and the Ojai Valley in Ventura County south and east through southern Los Angeles, southwestern San Bernardino, Orange, western Riverside, and the western two-thirds of San Diego Counties, California, and south in cismontane Baja California to Ojos Negros and San Vicente, never far from the coast; reaching the margins of the desert in San Bernardino (near Hesperia) and San Diego Counties. Usually at low elevations, sea level to 2,000 ft., but exceptionally as high as 8,000 ft. alt. in the mountains, where it occurs about the borders of meadows. Collected as a waif beyond its main area in the Goleta salt marsh, Santa Barbara County, California, "Introduced apparently with Stream gravel . . . ," 20 June 1959, *Pollard* (CAS) and on ballast heaps at Nanaimo, Vancouver Island, British Columbia, 13 July 1893, *Macoun* (NMC). *Camissonia bistorta* has occasionally been cultivated in Europe, at least in the 19th century.

The chromosome number has been determined from 29 individuals derived from 22 populations scattered throughout the range of the species (see Appendix). Populations from 6.5 miles northeast of San Juan Capistrano, Orange County, California, R18782 (8 individuals); lower edge of Cleveland National Forest, just above San Juan Campground, Santa Ana Mountains, Orange County, California, R18783 (6 individuals); Point Dume, Los Angeles County (2 individuals); and Claremont, Los Angeles County, California (10 individuals), were grown in the experimental garden and found to be self-incompatible. In addition, the Claremont strain was grown by Hagen (Indiana Univ. Publ. Sci. Ser. 16: 309. 1950) who also found it to be self-incompatible. Several species of large bees of the genus *Andrena* subgenera *Diandrena* and *Onagrandrena* are frequent oligolectic visitors to the flowers of *Camissonia bistorta* soon after they open in the early morning and doubtless are the most important agents in effecting cross-pollination in this species.

Camissonia bistorta may well be an annual derivative of populations similar to the self-incompatible ones referred to *C. cheiranthifolia* subsp. *cheiranthifolia*, although the reverse hypothesis cannot be excluded at present. Depauperate individuals of this species, found in dry years or unfavorable sites, often have relatively small flowers, as do plants at the end of their flowering period. The stigma is, however, consistently held above the anthers, and such plants can thereby easily be separated from the numerous related autogamous species in sect. *Holostigma*. This species occurs sympatrically with *C. lewisii*, and a single obvious F_1 hybrid between the two species has been collected at Playa del Rey, Los Angeles County, California, *Wedberg* 272 (herb. San Diego State College). This plant had about 23 percent stainable pollen and apparently full seed-set; at meiosis it formed variable configurations of chromosomes, the maximum observed in 14 cells being 1 pair, 1 ring of 4, 1 chain of 3, and 5 univalents (H. L. Wedberg, pers. comm.). *Camissonia bistorta* also occurs adjacent to and hybridizes extensively with *C. cheiranthifolia* subsp. *suffruticosa*,

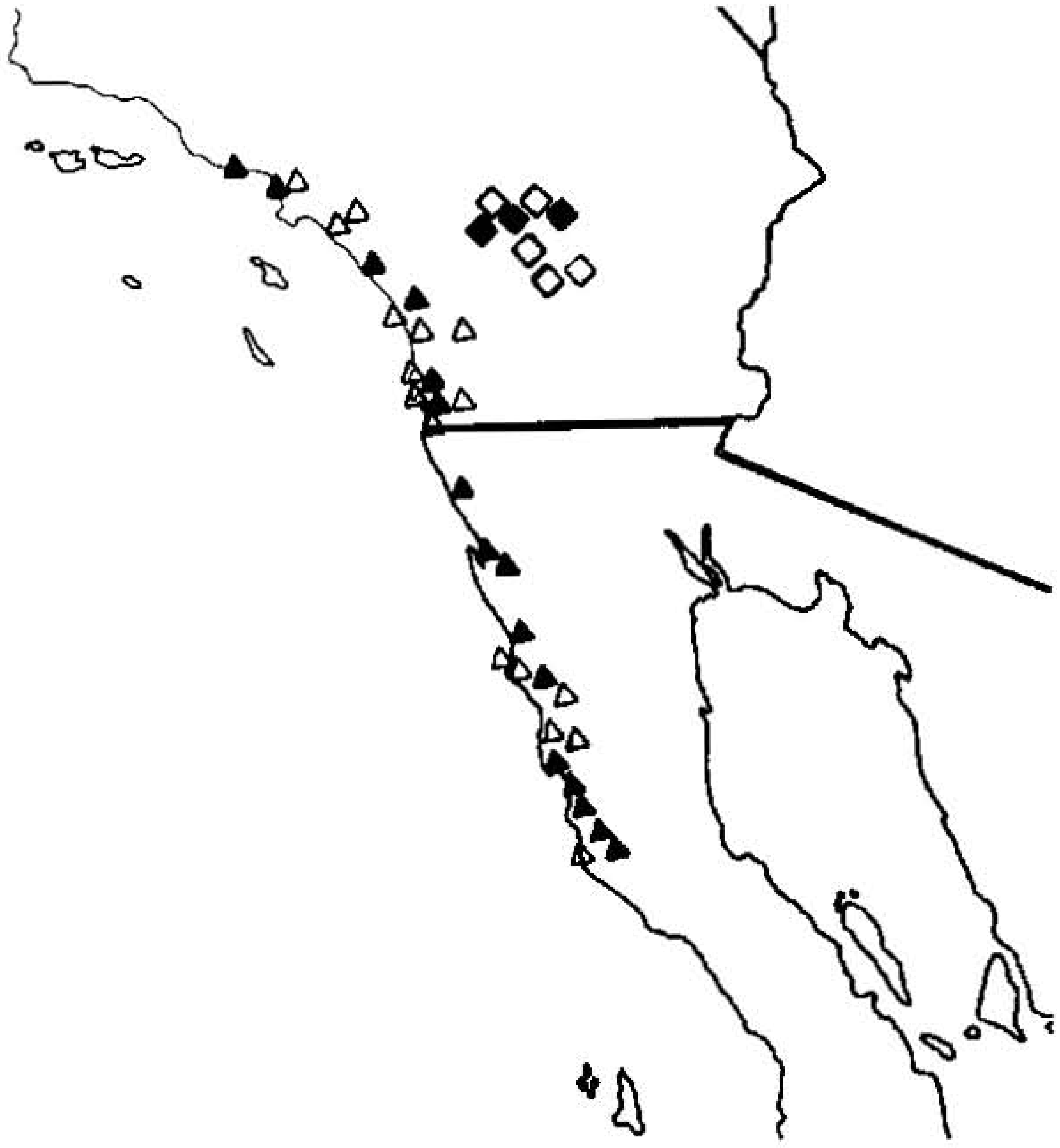


FIGURE 33.—California and Baja California, showing ranges of species of *Camissonia* sect. *Holostigma:* △=*C. lewisii*, with ▲=diploid chromosome counts ($n=7$); ◇=*C. pallida* subsp. *hallii* with ◆=diploid counts ($n=7$).

as explained in the section dealing with that taxon. It has likewise been observed growing sympatrically with *C. micrantha*, *C. hirtella*, *C. ignota*, *C. intermedia*, *C. confusa*, and *C. robusta*, but hybrids between these predominantly autogamous species and *C. bistorta* have not been found. *Camissonia bistorta* is probably relatively similar to the populations ancestral to at least some of the autogamous taxa in this section, the most obvious relationship being that with *C. lewisii*.

In his original treatment of this species (Bot. Gaz. 85: 266–267. 1928), Munz included two varieties in addition to the typical one. The first of these, *Oenothera bistorta* var. *veitchiana* Hook., was applied to inland populations with relatively slender, long, and straight capsules which differed in these respects from the series of coastal populations, including the type of the species, which have thicker, shorter, usually coiled capsules. These two entities intergrade so broadly that it does not appear useful to segregate them taxonomically. The other variety recognized by Munz, *O. bistorta* var. *hallii* (Davids.) Jeps., intergrades completely with the entity designated by Munz *O. hirta* var. *exfoliata* (A. Nels.) Munz and is here treated, together with that taxon, as the species *Camissonia pallida* (Abrams) Raven. *Camissonia pallida* and *C. bistorta* do not occur together, as far as I know, and, although both entities are diploid ($n=7$), there appears to be no evidence for morphological intergradation or even of overlapping patterns of variation.

The report of *Camissonia bistorta* from Santa Catalina Island, California (Millspaugh & Nuttall, Field Mus. Publ. Bot. 5: 183. 1923; as *Sphaerostigma bistortum*) is based on misidentified specimens of *C. robusta* and *C. californica*, which I have seen.

28. Camissonia guadalupensis (S. Wats.) Raven, Brittonia 16: 284. 1964.

Erect annual with short branches usually arising above the base; plants thick-stemmed, heavy-set, with conspicuously exfoliating epidermis, subsucculent, villous or strigose all over, 2–18 (–35) cm. tall. Leaves narrowly elliptic in the basal rosette to narrowly ovate on the stems and in the inflorescence, 1.2–3.8 (–9.5) cm. long, 0.5–1.2 (–1.8) cm. wide, sparsely and weakly denticulate, the apex acute (lower leaves) to obtuse (upper leaves), the base attenuate (lower leaves) to rounded or truncate (upper leaves); leaves subsessile. Inflorescence with short glandular trichomes in addition to the predominant sort found on other parts of the plant. Hypanthium 1.6–2.4 mm. long, 1.2–1.6 mm. across at the summit, sparsely pubescent with short erect trichomes in lower portions within. Sepals 1.9–3.2 mm. long, 0.8–1.6 mm. wide. Petals 2.8–4.2 mm. long, 2–3.6 mm. wide, sometimes with a prominent red dot near the base of each one. Filaments of the episepalous stamens 1.3–2.3 mm. long, those of the epipetalous ones 0.4–1.6 mm. long; anthers 0.4–0.8 mm. long. Style

3.2–4.5 mm. long, short-pubescent near the base; stigma 0.5–0.8 mm. in diameter, surrounded by the anthers at anthesis. Capsule 10–18 mm. long, 2.8–3.5 mm. thick near the base, very heavy in appearance, quadrangular in transection and deeply grooved along the lines of dehiscence, straight or slightly curved outward. Seeds 0.75–0.9 mm. long, 0.4–0.55 mm. thick. Gametic chromosome number, $n=7$. Autogamous.

DISTRIBUTION (Figure 36): Sandy flats, dunes, and arroyo bottoms, San Clemente Island, Los Angeles County, California (subsp. *clementina*), and Isla Guadalupe, Baja California (subsp. *guadalupensis*). Sea level to perhaps 1,200 ft. alt.

Reciprocal F_1 hybrids were made between progenies of R17628 (subsp. *clementina*) and *Moran & Ernst* 6737 (subsp. *guadalupensis*). These plants had a mixture of all three sorts of pubescence found in the two subspecies, the strigose pubescence of subsp. *guadalupensis*, however, being relatively sparse. The hybrids had a red dot near the base of each petal, as in subsp. *clementina*, but this was reduced in size. They appeared to have full seed-set, comparable to that of the parents. Two of the F_1 individuals in which subsp. *guadalupensis* was the pistillate parent (=R18771) and one in which subsp. *clementina* was the pistillate parent had 7 bivalents at meiotic metaphase I and diakinesis, and thus no evidence of chromosomal structural heterozygosity. The pollen stainability in cotton blue in lactophenol, calculated from a sample of 200 grains in each case, was measured in three plants in which subsp. *guadalupensis* was the pistillate parent and found to be 41.5, 49.5, and 41.5 percent; in two F_1 plants in which subsp. *clementina* was the pistillate parent, the percentages of stainable pollen were, respectively, 58 and 38 percent. As compared with the 98–100 percent stainable pollen found in samples taken from both parents grown under the same conditions, these figures indicate a substantial reduction in fertility in the hybrids, although seed-set does not appear to be impaired. Nonetheless, the very close morphological relationship between these two entities and their evident distinctiveness when compared with other species can seemingly best be indicated by retaining them within a single taxonomic species.

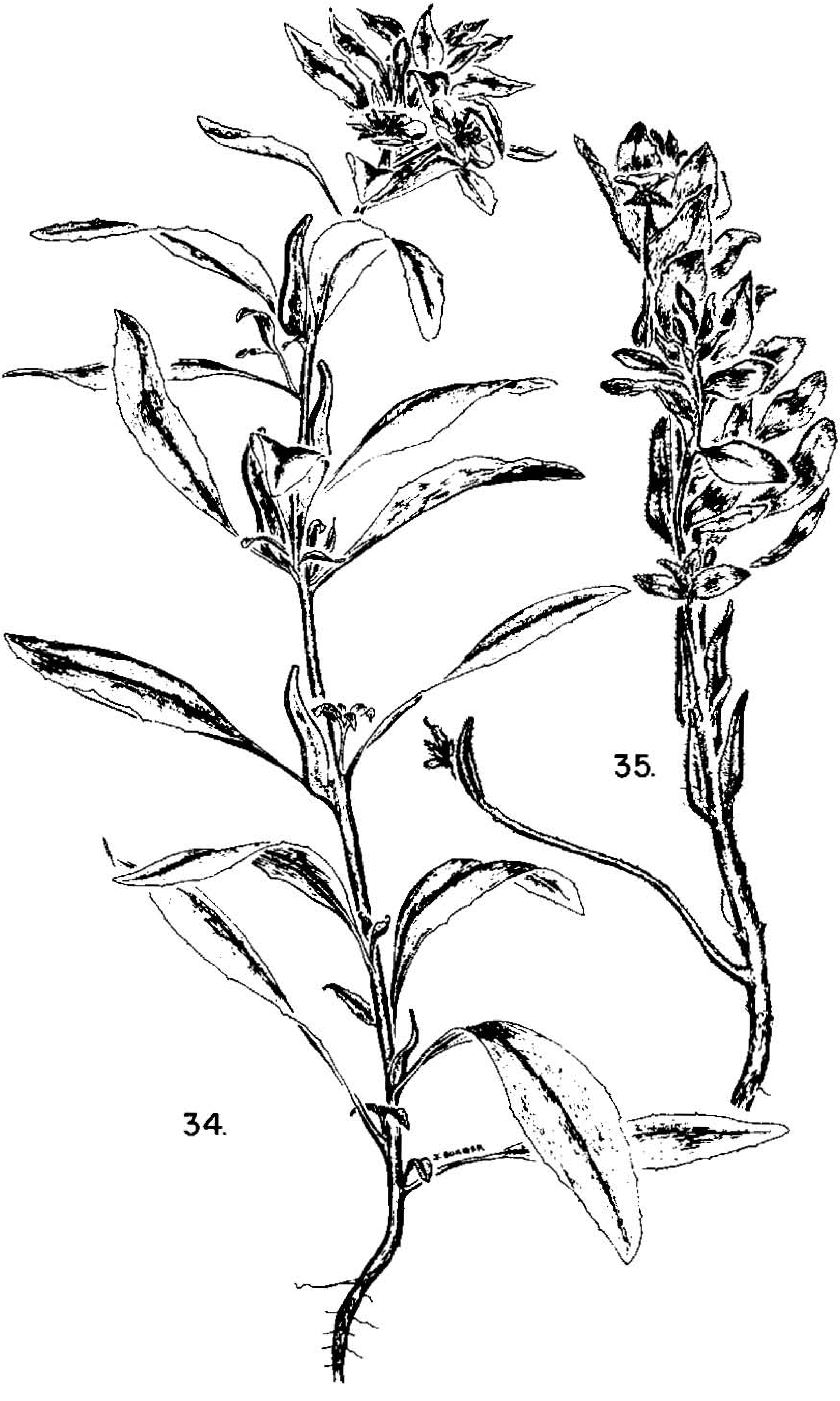
28a. Camissonia guadalupensis subsp. **guadalupensis** FIGURE 34

Oenothera guadalupensis S. Wats., Proc. Amer. Acad. 11: 115. 1876.

Oenothera guadalupensis subsp. *guadalupensis* Munz, N. Amer. Fl. II. 5: 160. 1965.

Pubescence strigose with some longer trichomes in inflorescence, but no glandular ones. Petals without red dot at base. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Isla Guadalupe, Baja California, February–May 1875, *E. Palmer* (GH).



FIGURES 34–35.—*Camissonia guadalupensis*, × 1: 34, *C. guadalupensis* subsp. *guadalupensis* (*Raven* 18175, DS); 35, *C. guadalupensis* subsp. *clementina* (*Raven* 17284, DS).

DISTRIBUTION (Figure 36): Isla Guadalupe, Baja California, known with certainty only from the sandy bed of Arroyo Melpomone, 900–1,300 ft. alt.

ADDITIONAL SPECIMENS EXAMINED:

BAJA CALIFORNIA: ISLA GUADALUPE: Bed of Arroyo Melpomone, *Moran* 12070 (SD), *Moran & Ernst* 6737 (SD); progeny of *Moran & Ernst* 6737, R17530 (DS), 18175 (DS).

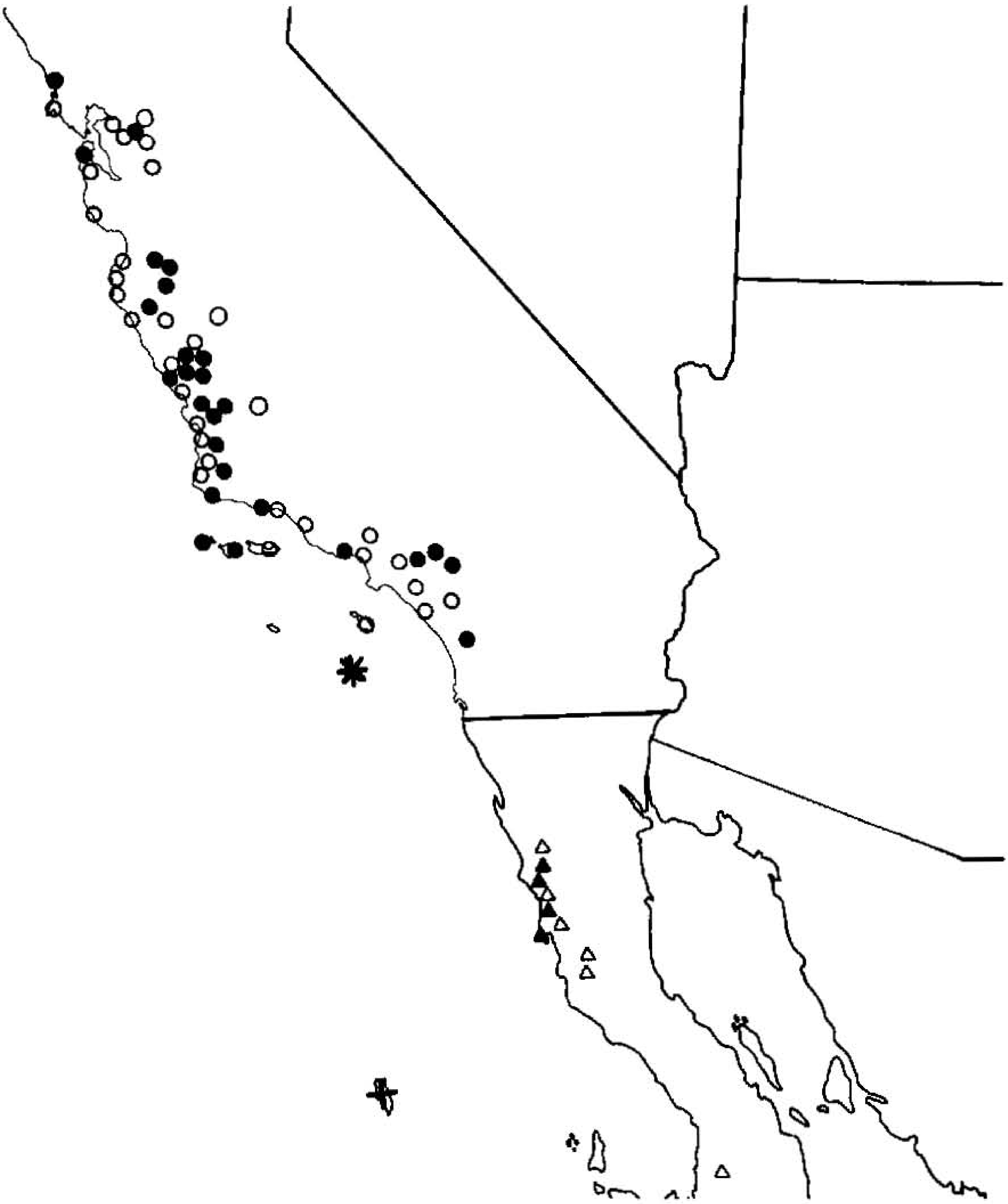


FIGURE 36.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia* sect. *Holostigma;* + = *C. guadalupensis* subsp. *guadalupensis;* ✳ = *C. guadalupensis* subsp. *clementina;* △ = *C. proavita*, with ▲ = diploid chromosome counts ($n=7$); ○ = *C. micrantha*, with ● = diploid counts ($n=7$).

The chromosome number has been determined from two plants of this population, grown in the experimental garden (see Appendix). Plants of this subspecies were more highly autogamous than those of subsp. *clementina* when the two were grown in the experimental garden.

28B. Camissonia guadalupensis subsp. **clementina** (Raven) Raven, Brittonia 16: 284. 1964. FIGURE 35

Oenothera guadalupensis subsp. *clementina* Raven, Aliso 5: 332. 1963.

Pubescence dense, villous, with short glandular trichomes also present in the inflorescence. Petals each with a red dot near the base. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Common on pebbly dune above ocean south of Eel Point, San Clemente Island, elevation 40 ft., Los Angeles County, California, 9 April 1962, *P. H. Raven* 17125 (RSA).

DISTRIBUTION (Figure 36): Restricted to San Clemente Island, Los Angeles County, California, where it is common on dunes around the north end and down the west shore, perhaps to the south end; up to 100 ft. elevation.

ADDITIONAL SPECIMENS EXAMINED:

U.S.: CALIFORNIA: SAN CLEMENTE I., LOS ANGELES CO.: *Trask* 1684 (E, POM, US), *Murbarger* 154 (UC), *Piehl* 631101 (SBBG), *Blakley* 5224, 5254 (both SBBG), R17260, 17284, 17301, 17628, 17954, 18023 (all DS).

The chromosome number has been determined from single individuals of three populations, including the type collection (see Appendix). Plants of the subspecies were facultatively autogamous when grown in the experimental garden at Stanford, the flowers not selfing as early in the day on which they open as in subsp. *guadalupensis*. In the latter, the anthers scarcely left contact with the stigma at any time after opening. *Camissonia guadalupensis* subsp. *clementina* has been observed growing sympatrically with *C. cheiranthifolia* subsp. *cheiranthifolia*.

29. Camissonia lewisii Raven, sp. nov. FIGURE 32

Oenothera hirta var. *typica* Munz, Bot. Gaz. 85: 262. 1928; pro parte.

Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 106. 1965; pro parte.

Herba annua villosa, ad *C. micrantha* similis, ramis plurimis decumbentibus e rosula centrali radiantibus, rariore caule singulari erecto; rami ad 0.6 m. longi. Folia 1–8 cm. longa. 0.2–1.1 cm. lata, denticulata. Inflorescentia pilis brevibus gladulosis longioribusque erectis patentibus pilosa. Hypanthium 1.5–4 mm. longum, ostio 1–2.5 mm. diameter. Sepala 1.7–3.5 mm. longa, 1–1.5 mm. lata. Petala (2.5 –) 3–5.5 mm. longa, (2–)2.5–5 mm. lata, plerumque prope basin puncto rubro uno vel duo. Filamenta staminum episepalorum 2–2.8 mm. longa, illa epipetalorum 1–1.7 mm. longa; antherae 0.7–1.2 mm. longae. Sylus 2.8–4.5(–5.5) mm. longus; stigma 0.7–1.8 mm. diametro, sub antheris circumnexum. Capsula 13–20 mm. longa, 1.8–2.2 mm. crassa, transectione valde quadrangularis in spiram laxam contorta. Semina 0.7–0.8 mm. longa, 0.5–0.6 mm. crasa, obovoidea. Chromosomatum numerus gameticus, $n=7$. Autogama.

TYPE: Common in open clayey grassland, with *Eschscholzia*, *Abronia*, and grasses, 1.1 mile north of Colonia Guerrero, elevation 200 ft., Baja California, 30 March 1962, *P. H. Raven* 17035 (DS; isotypes, RSA, US).

DISTRIBUTION (Figure 33): Open sandy and clayey grassland, coastal dunes and beaches, never far from the coast, from sea level to 1,000 ft. alt., Point Dume and the Los Angeles Basin, Los Angeles County, California, south to Cardón Grande at the northern edge of Territorio de la Baja California Sur.

SELECTED SPECIMENS EXAMINED:

U.S.: CALIFORNIA: LOS ANGELES CO.: Hollywood, *Davidson* 1437 (LAM); Inglewood, *Abrams* 3232 (DS, GH, LA, NMC, NY, PH, POM, UC, US); Roscoe, *Eastwood* 242 (CAS); Point Dume, *Mars* (LA); Ballona Harbor, *Abrams* 1192 (DS, POM); San Pedro, *Eastwood* 166 (CAS). ORANGE CO.: Santa Ana, *King* in 1908 (JEPS); Bee Canyon, Rancho Santa Ana, *Howell* in 1928 (RSA). SAN DIEGO CO.: Fallbrook, *Jones* in 1882 (DS, GH, NY, POM, RM, UC); Agua Hedionda, *Peirson* 3409 (DS, RM, RSA); 4.6 mi. E. of San Pasqual, R17406 (DS); El Segundo, *Purer* in 1931 (SD); San Luis Rey, *Gander* in 1937 (SD); Crown Point, *Gander* 143.8 (SD); Oneonta, *Chandler* 5094 p.p. (NY); Bird Rock, *F. E. & E. S. Clements* 184 (COLO, F, GH, NY, PH, UC, UCSB), 185 (COLO, F, GH, NY, PH, UC, UCSB); Point Loma, *Eastwood* in 1913 (CAS, GH, NY, US); Ocean Beach, *Brandegee* 1645 (CAS, F, GH, LE, NMC, NY, POM, RM, UC, US); 1.5 mi. from Jamul toward Otay Dam, *Wiggins* 1923 (DS).

BAJA CALIFORNIA: Tijuana valley, *Orcutt* 82 (F, GH, US); ranch 29 mi. SW. of Tijuana, *Jones* in 1925 (POM); Descanso Dunes, R17060 (DS); S. end of Ensenada Bay, R17006 (DS); 9.3 mi. S. of San Vicente, R17044 (DS); 2.5 mi. W. of San Vicente, *Kadish* in 1956 (LA); 7.4 mi. N. of Ejido México, R17041 (DS); 4 km. S. of Ejido México, R12230 (DS); 4 mi. W. of Colonia Guerrero, *Blakley* 6302 (DS, SBBG); Santo Domingo (Hamilton's Ranch and vicinity), *Wiggins* 4494 (CAS, DS, GH, LA, NY, POM, UC, US); near Red Rock above Hamilton's Ranch, *Thomas* 130 (DS, OSC); San Quintín, *Epling & Robison* in 1935 (DS, UC, NY), San Quintín Bay, 1889, *Palmer* 617 (CAS, F, GH, NY, PH, UC, US); Socorro, *Cronemiller* 3076 (DS, POM); 20.6 km. S. of road to San Quintín, R12396 (DS); 20 mi. N. of El Rosario, *Harbison* in 1935 (SD); 3.7 mi. E. of Punta Baja toward El Rosario, *Gregory* 356 (RSA); 16 km. SE. of El Rosario, R12466 (DS); El Cañón Rancho, near Calmallí, *Haines & Stewart* in 1935 (DS); El Poso Allemán, *Brandegee* in 1889 (UC); Cardón Grande, *Brandegee* in 1889 (UC).

Camissonia lewisii, an autogamous diploid species, can easily be recognized by its short, usually once-coiled capsules that are square in transection in living material. It is quite similar to some coastal populations of *C. bistorta*, such as those found in San Diego County, California, and may have been derived from populations of this sort. The chromosome number has been determined from 23 individuals representing 19 populations, scattered throughout the range of the species, including the type collection (see Appendix). An apparent hybrid with *C. bistorta* was once collected, as discussed under that species, and *C. lewisii* likewise occurs sympatrically with *C. cheiranthifolia* subsp. *suffruticosa*, *C. proavita*, *C. micrantha* (at Point Dume and Playa del Rey, Los Angeles County, California), *C. ignota*, *C. intermedia*, and *C. robusta*. No hybrids with these species have been observed.

Camissonia lewisii is named in honor of Harlan Lewis, who introduced me to the study of Onagraceae when I was a graduate student at the University of California, Los Angeles. Judging from its morphology and distribution, this species is certainly one of the parents of the hexaploid *C. robusta*, which can, however, easily be distinguished by its more robust, erect habit, less sharply angled capsules, and high proportion of 4- and 5-pored pollen grains. *Camissonia lewisii* is probably not directly involved in the ancestry of any other polyploid species.

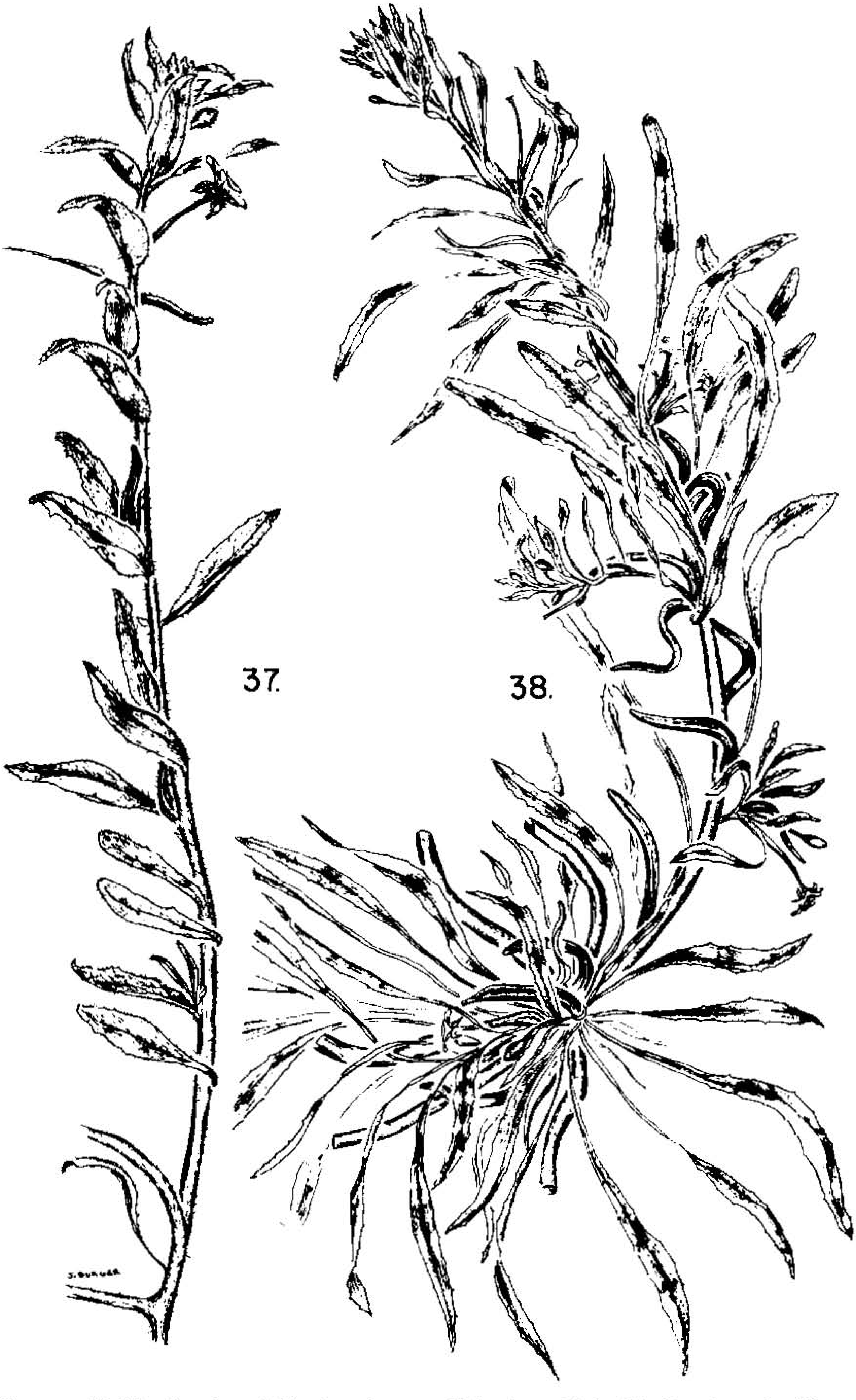
30. Camissonia proavita Raven, sp. nov. FIGURE 38

Oenothera hirta var. *typica* sensu Munz, Bot. Gaz. 85: 262. 1928; pro parte.
Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 160. 1965; pro parte.

Herba annua sparsissime strigulosa, omnino eglandulosa, ad *C. micrantha* similis, rosula densissime florens, ramis prostratis crassiusculis ad 45 cm. longis tarde e rosula crescentibus. Folia conferta lineares vel angustissime elliptica, 2–9 cm. longa, 0.2–0.55 cm. lata, ad petiolum gradatissime attenuate, sparsissime denticulata; petiolus ad 2 cm. longus. Inflorescentia densiore strigulosa, conferta, interdum pilis paucis longioribus patentibus praedita. Hypanthium 1.2–1.8 mm. longum, ostio 1–1.2 mm. diametro. Sepala 1.8–2.8 mm. longa, 0.8–1.2 mm. lata. Petala 2.6–3.5 mm. longa, 1.8–2.2 mm. lata, immaculata. Filamenta staminum episepalorum 1.2–1.6 mm. longa, illa epipetalorum 0.5–1.3 mm. longa; antherae 0.6–0.8 mm. longae. Stylus 2–3.2 mm. longus; stigma 0.8–1 mm. diametro, sub anthesi antheris circumnexum. Capsula 15–20 mm. longa, 1.3–1.5 mm. crassa, transectione in sicco quadrangularis sed in vivo subquadrangularis, angulis subrotundatis; capsulae rosulae rectae, illae ramorum in spiram unam vel in spiras duas contortae. Semina 0.8–0.9 mm. longa, 0.5–0.6 mm. crassa. Chromosomatum numerus gameticus, $n=7$. Autogama.

TYPE: Disturbed soil by roadside, with *Orthocarpus purpurascens*, *Eschscholzia*, *Brassica*, near kilometer 201, 5.5 miles south of San Vicente, 950 ft., Baja California, 29 March 1962, *P. H. Raven* 17020 (DS; isotypes, RSA, US).

DISTRIBUTION (Figure 36): Sandy flats and dunes along the beaches or in the valleys up to 2,200 ft. alt., northern Baja California from the vicinity of San Vicente to near Misión San Borjas.



FIGURES 37–38.—Species of *Camissonia* sect. *Holostigma* × 1: 37, *C. micrantha* (*Raven* 18245, topotype, DS); *C. proavila* (*Raven* 17020, holotype, DS), showing only a portion of the dense central tuft and one of the branches.

ADDITIONAL SPECIMENS EXAMINED:

BAJA CALIFORNIA: 21 mi. S. of Santo Tomás, *Wiggins* 4273 (DS, NY, POM, US); San Telmo Plains, 7 mi. E. of San Telmo on road to Rancho San José (Meling's Ranch), *Wiggins* 9735A (DS); San Telmo, *Brandegee* in 1893 (UC); Los Alisos, ca. 5 mi. S. of Meling's Ranch, ca. 750 m, *Moran* 11341 (SD); San Quintín Bay, 1889, *Palmer* 656 (C, F, GH, NY, PH, US); 20.6 km. S. of road to San Quintín, R12397 (DS); near Rosario, *Orcutt* in 1886 (UC); 16 km. SE. of El Rosario, R12493; sandy wash at junction of El Mármol and San Fernando roads, 25 mi. W. of El Mármol, *Wiggins* 4343 (DS); Rancho Ramona, 29°53′N. lat., 115°06′W. long., *Huey* in 1958 (SD); San Borjas, *Brandegee* in 1889 (UC).

Camissonia proavita is an autogamous species obviously closely related to *C. micrantha* but easily distinguished by its very crowded habit and subglabrous vestiture. Most collected plants have no side branches and present a very dense cluster of 50 or more capsules in the basal rosette when mature. The branches are thicker than in any other member of the section, and the plant presents a very distinctive aspect at all stages of its life cycle. More than 200 miles separate the northernmost station of this species from the southernmost mainland locality of its close relative, *C. micrantha*.

The name "*proavita*" (=ancestor) was assigned to this species because of the hypothesis that it was one of the diploid ancestors of tetraploid populations of Baja California assigned in the present revision to *C. intermedia*, the other being *C. ignota*. At present, it appears more likely that all populations of *C. intermedia* have had a common allotetraploid origin involving *C. micrantha* and *C. hirtella*, but concrete evidence is not available to disprove the earlier hypothesis completely.

Camissonia proavita occurs sympatrically with *C. cheiranthifolia* subsp. *suffruticosa*, *C. lewisii*, *C. hirtella*, *C. ignota*, *C. intermedia*, and *C. robusta*, but no natural hybrids have been observed. The chromosome number of these species has been determined from 4 individuals, each from a different population, including the type collection (see Appendix).

31. Camissonia micrantha (Hornem. ex Spreng.) Raven, Brittonia 16: 284. 1964. FIGURE 37

Oenothera hirta Link, Enum. Hort. Berol. 1: 378. 1821; non *Oenothera hirta* L. 1760. Type: Seeds from California, grown in the Berlin Botanical Garden (authentic material, NY).

Oenothera micrantha Hornem. ex Spreng., Syst. 2: 228. 1825.

Holostigma micranthum (Hornem. ex Spreng.) Spach, Nouv. Ann. Mus. Paris 4: 335. 1835.

Sphaerostigma hirtum (Link) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 22. 1835.

Sphaerostigma micranthum (Hornem. ex Spreng.) Walp., Rep. 2: 77. 1843.

Oenothera hirta var. *typica* Munz, Bot. Gaz. 85: 261. 1928.

Annual with sprawling branches up to 0.6 m. long from a basal rosette, or more rarely with a single erect stem. Plants more or less densely villous all over. Leaves very narrowly elliptic in the basal rosette, the upper ones proportionately broader near the base but rarely broad enough to be called lanceolate, 1–12 cm. long, 0.2–1.7 mm. wide, denticulate, the apex acute, the base narrowly cuneate (in the basal rosette) to rounded; petioles of lower leaves to 2 cm. long, the upper leaves subsessile. Inflorescence more densely villous than the rest of the plant, usually grayish, rarely with an understory of short, glandular trichomes. Hypanthium 1.2–2 mm. long, 0.8–1.5 mm. across at the summit, a few trichomes within near the base. Sepals 1–2.2 (–2.5) mm. long, 0.4–1 mm. wide. Petals 1.5–3.5 (–4.5) mm. long, 0.8–2.2 (–2.5) mm. wide, occasionally with 1 or 2 red dots near the base. Filaments of the episepalous stamens 0.8–1.5 mm. long, those of the epipetalous ones 0.5–0.8 (–1) mm. long; anthers 0.4–0.6 mm. long. Style 2–3.5 mm. long, with a few trichomes near the base; stigma 0.5–0.6 mm. in diameter, surrounded by the anthers at anthesis. Capsule 1.3–2 (–2.5) cm. long, 1.1–1.2 (–1.8) mm. thick, subterete in living material but drying more or less quadrangular in transection, straight or curved in up to slightly more than one complete spiral. Seeds 0.7–1.1 mm. long, 0.3–0.6 mm. thick. Gametic chromosome number, $n=7$. Autogamous.

LECTOTYPE: Grown in the Copenhagen Botanical Garden, probably in 1821, from seeds doubtless collected in the vicinity of Fort Ross, Sonoma County, California (probably at Bodega Bay) (C).

DISTRIBUTION (Figure 36): Endemic to California, where it grows on coastal dunes and beaches or away from the ocean in sandy fields and in washes, from the vicinity of Bodega Bay, Sonoma County, and near Rio Vista, Sacramento County, south in the Coast Ranges to the Los Angeles Basin and the northern edge of San Diego County; also on San Miguel, Santa Rosa, Santa Cruz, and Santa Catalina Islands. From sea level to about 1,000 ft. alt. very rarely up to about 2,500 ft. Also collected once, probably on ballast heaps, in the vicinity of Nanaimo, Vancouver Island, British Columbia, 13 July 1893, *Macoun* (BM). Rather widely grown in European botanical gardens from the 1820s to the present, as a curiosity.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: CONTRA COSTA CO.: San Leandro, *Edwards* in 1877 (NY); Strawberry Canyon, Berkeley Hills, ca. 1,300 ft., R8982 (CAS); sand hills E. of Antioch, *Heller* 8892 (DS, F, GH, NY, PH, US, WTU); near Byron, *Heller* 14496 (DS). FRESNO CO.: Los Gatos Canyon 4 mi. N. of Coalinga, *Howell* 5804 (CAS). KERN CO.: Alec Cook Rocks, Cedar Canyon, 2,200 ft., *Twisselmann* 1194 (CAS). LOS ANGELES CO.: Big Tujunga wash, *Abrams* 1390 (DS, POM); Pomona, *Munz et al.* 2300 (DS, POM); Playa del Rey, *Ewan* 7536 (DS, LA, RM, UC); mouth of Hamilton Canyon, Santa Catalina I., *Fosberg* S4315 (F, LAM, NY, PH, POM, SBM, UC, US); Avalon, Santa Catalina I., *Trask* in 1898 (US). MARIN CO.: Near Radio Station, Pt. Reyes Peninsula, *Howell* 20956 (CAS, RSA). MON-

TEREY CO.: Near Del Monte, *Heller* 6659 (DS, F, GH, LE, NY, PH, POM, UC, US); San Ardo, *Hardham* 10004 (DS); Pajaro Hills, *Chandler* 386 (UC); 20 mi. from Carmel up Carmel R., road to Tassajara Springs, *Wolf* 3773 (UC); Pacific Valley, Santa Lucia Mts., *Plaskett* in 1898 (CAS); Vineyard Canyon Road 12 mi. W. of Parkfield, *Wiggins* 8020 (DS, GH, UC); Los Laurelos Road, 8 mi. N. of Carmel Valley, ca. 600 ft., *Rose* 57052 (COLO, RSA, US); Sycamore Canyon, 1 mi. S. of Big Sur State Park, *Bristol* 27 (Fresno State College herb.). ORANGE CO.: Bryant Ranch, *Wolf* 3778 (DS, RSA). RIVERSIDE CO.: Elsinore, *McC.* in 1892 (DS); 1.4 mi. W. of junction of Hwy. 60 with Van Buren Ave., *Wedberg* 227 (San Diego State College herb.). SACRAMENTO CO.: Brannan I. State Park, near Rio Vista, R20177 (DS). SAN BENITO CO.: About 4 mi. N. of Pinnacles Lodge, *Baker* 9282 (RSA). SAN BERNARDINO CO.: Red Hill near Upland, *Johnston* 1196 (DS, POM, UC, US). SAN DIEGO CO.: U.S. Hwy. 395, 2 mi. S. of turn to Lilac, R16950, R17457 (both DS). SAN FRANCISCO CO.: Fleishacker Pool, *Abrams* 12192 (DS; basis for *fig. 3434* in Abrams, Ill. Fl. Pac. States 3: 203. 1951). SAN JOAQUIN CO.: Corral Hollow, *Hoover* 3034 (UC). SAN LUIS OBISPO CO.: Baywood Park, Morro Bay, *Hardham* 9072 (DS, RSA); 3 mi. E. of Santa Margarita, *Linsley & MacSwain* 59–84 (RSA, UC); 10 mi. E. of Creston on La Panza Road, *Hoover* 7099 (RSA); Arroyo Grande, *Brewer* 446 (GH, UC, US). SAN MATEO CO.: San Pedro, *Elmer* 4813 (ARIZ, CAS, DS, NY, OSC, POM, UC, US); Ano Nuevo Point, *Thomas* 10178 (DS). SANTA BARBARA CO.: 5 mi. S. of Surf, *Ferris* 7543 (DS, POM, UC); 5 mi. from Lompoc, *Munz* 9269 (C, POM); Fox Canyon, Santa Barbara, *Smith* 1698 (RSA, WTU); 3 mi. S. of Carpinteria, *Lewis* 1298 (LA); San Miguel I., *Blakley* 5083 (DS, SBBG); Santa Rosa I., Water Canyon, *Munz & Crow* 11694 (GH, LA, OSC, POM, RSA); Santa Cruz I., vicinity of Pelican Bay, *Abrams & Wiggins* 41 (CAS, DS, GH, UC). SANTA CRUZ CO.: Ben Lomond sand hills, *Rose* 33241 (WTU); ca. 3.5 mi. W. of Watsonville, *Thomas* 3104 (DS, RSA). SONOMA CO.: Bodega Point, *Eastwood* 4831 (CAS, GH, PH). VENTURA CO.: Beach near mouth of Ventura R., *Pollard* in 1947 (COLO, RSA).

Camissonia micrantha is a diploid, autogamous species which has in the past been interpreted much more broadly (Munz, Bot. Gaz. 85: 260–265. 1928), including all species of this section except *C. cheiranthifolia*, *C. bistorta*, and *C. guadalupensis*. As interpreted here, it includes most of the material referred by Munz (loc. cit.) to *Oenothera hirta* var. *hirta*, excluding mostly collections of the tetraploid *C. intermedia*, which in part blurs the morphological distinctions between its two diploid ancestors, *C. micrantha* and *C. hirtella*. The chromosome number of *C. micrantha* has been determined in 47 individuals representing 39 populations from throughout the range of the species (see Appendix).

Camissonia micrantha is most closely related to the allopatric *C. proavita*, as discussed under that species. It is one of the diploid ancestors not only of the tetraploid *C. intermedia*, as just mentioned, but has probably combined with this tetraploid to give rise to the hexaploid *C. hardhamiae*. *Camissonia micrantha* occurs sympatrically with *C. cheiranthifolia* subsp. *cheiranthifolia*, *C. bistorta*, *C. lewisii*, *C. hirtella*, *C. intermedia*, *C. confusa*, *C. hardhamiae*, *C. luciae*, and *C. robusta*, but no hybrids with any of these species have been observed.

The populations of *C. micrantha* growing on the coastal dunes and beaches of northern Marin and southern Sonoma Counties consist of plants that are more robust and larger flowered than those found farther south. Such plants match the type material very closely and also are identical with plants grown from seed sent from the Copenhagen Botanical Garden and grown at Stanford (R18242). These seeds may have been derived from direct descendants of the original introductions, the species apparently having been in cultivation in Europe continuously since the 1820s.

32. Camissonia hirtella (Greene) Raven, Brittonia 16: 284. 1964.
FIGURES 39, 40

Oenothera hirtella Greene, Fl. Francisc. 215. 1891.

Sphaerostigma hirtellum (Greene) Small, Bull. Torrey Cl. 23: 190. 1896.

Sphaerostigma arenicola A. Nels. ("arenicolum"), Bot. Gaz. 40: 58. 1905. Type: Tassajara Hot Springs, Santa Lucia Mts., Monterey Co., Calif., June 1901, *A. D. E. Elmer* 3192 (DS: isotype, US).

Oenothera hirta var. *jonesii* H. Lév., Monogr. Onoth. 213. 1905. Lectotype: Drytown, Amador Co., Calif., 500 ft., *G. Hansen* 543 (DS; isotypes, NY, POM, UC. Cf. A. Nelson, Bot. Gaz. 40: 59. 1905).

Sphaerostigma micranthum var. *jonesii* (H. Lév.) A. Nels., Bot. Gaz. 40: 59. 1905.

Sphaerostigma bistortum var. *reedii* Parish, Muhlenbergia 3: 60. 1907. Lectotype: Waterman Road, 3,000 or 3,500 ft., San Bernardino Mts., San Bernardino Co., Calif., *S. B. Parish* 5794 (isotypes, GH, NY, UC).

Sphaerostigma hirtellum var. *montanum* Davidson, Muhlenbergia 3: 108. 1907.

Oenothera micrantha var. *hirtella* (Greene) Jeps., Man. Fl. Pl. Calif. 684. 1925.

Oenothera micrantha var. *reedii* (Parish) Jeps., Man. Fl. Pl. Calif. 684. 1925.

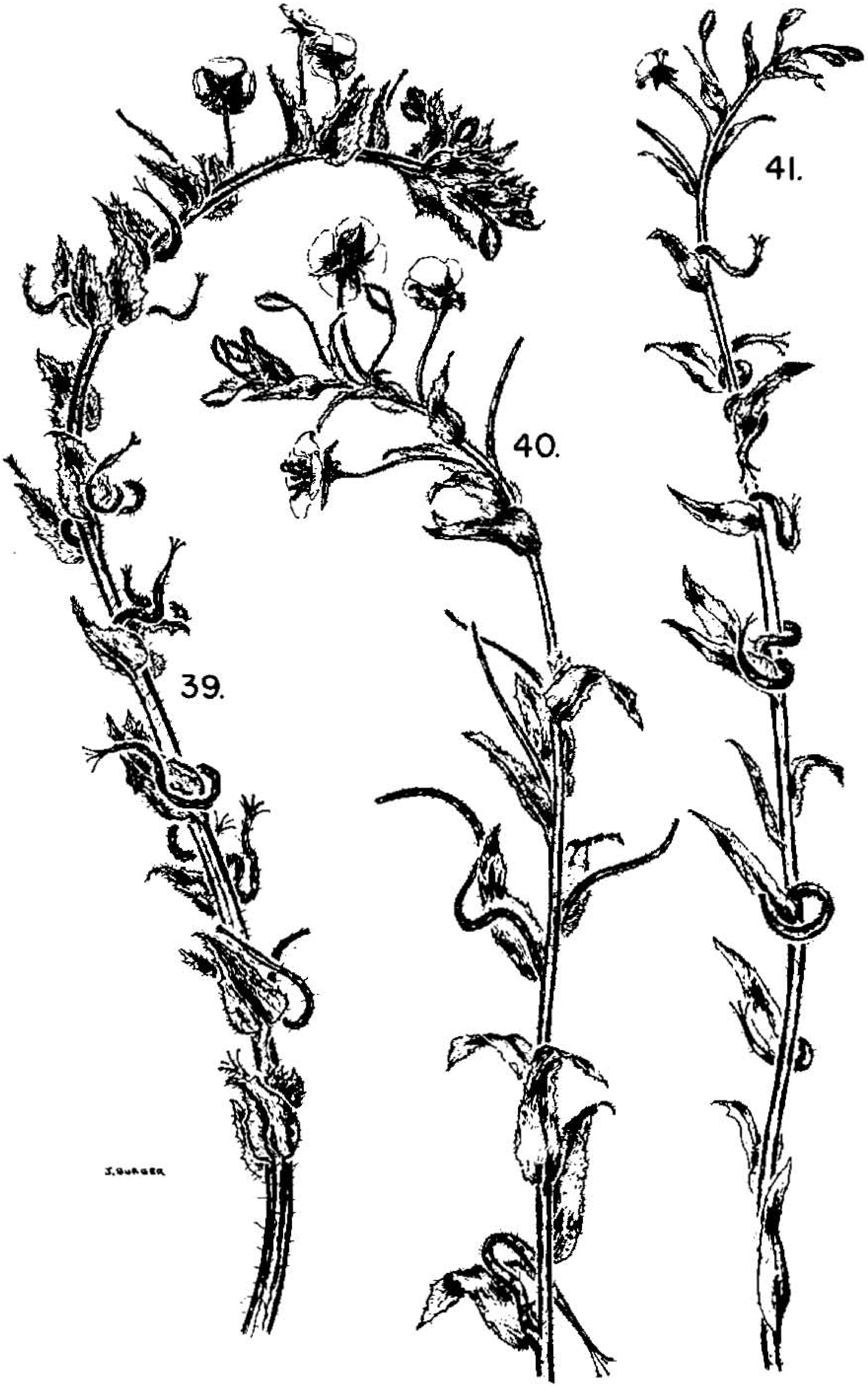
Oenothera hirta var. *jonesii* f. *reedii* (Parish) Munz, Bot. Gaz. 85: 263. 1928.

Oenothera micrantha var. *jonesii* (H. Lév.) Munz, Amer. Journ. Bot. 19: 778. 1932.

Erect annual, generally similar to *C. micrantha*, with one or more ascending branches from the basal rosette. Upper leaves narrowly ovate or ovate (rarely lanceolate), the apex acute, the base cordate to truncate. Inflorescence almost always with an understory of short glandular trichomes. Hypanthium 1–3 mm. long, 1–3 mm. across at the summit. Sepals 2.5–6 mm. long, 0.6–2 mm. wide. Petals 2–9 mm. long, 1.3–7 mm. wide, sometimes red-dotted near the base, occasionally with a salient tooth arising from the emarginate apex. Filaments of the episepalous stamens 1.2–6 mm. long, those of the epipetalous ones 0.5–3 mm. long; anthers 0.4–1 mm. long. Style 2–8 mm. long; stigma 0.5–1 mm. in diameter, surrounded by the anthers at anthesis. Capsule 0.75–0.9 mm. thick, terete, once or twice contorted. Gametic chromosome number, $n=7$. Autogamous, rarely cleistogamous.

LECTOTYPE: Mt. Hamilton, Santa Clara County, California, July 1891, *E. L. Greene* (ND).

DISTRIBUTION (Figure 42): On brushy hills and slopes, often locally abundant on burns, from Trinity and Amador Counties southward



FIGURES 39–41.—Species of *Camissonia* sect. *Holostigma*, × 1: 39–40, *C. hirtella:* 39, small flowered plant (*Raven* 17473, DS); 40, large-flowered plant (*Raven* 17416, DS). 41 *C. robusta* (*Raven* 17043, DS).

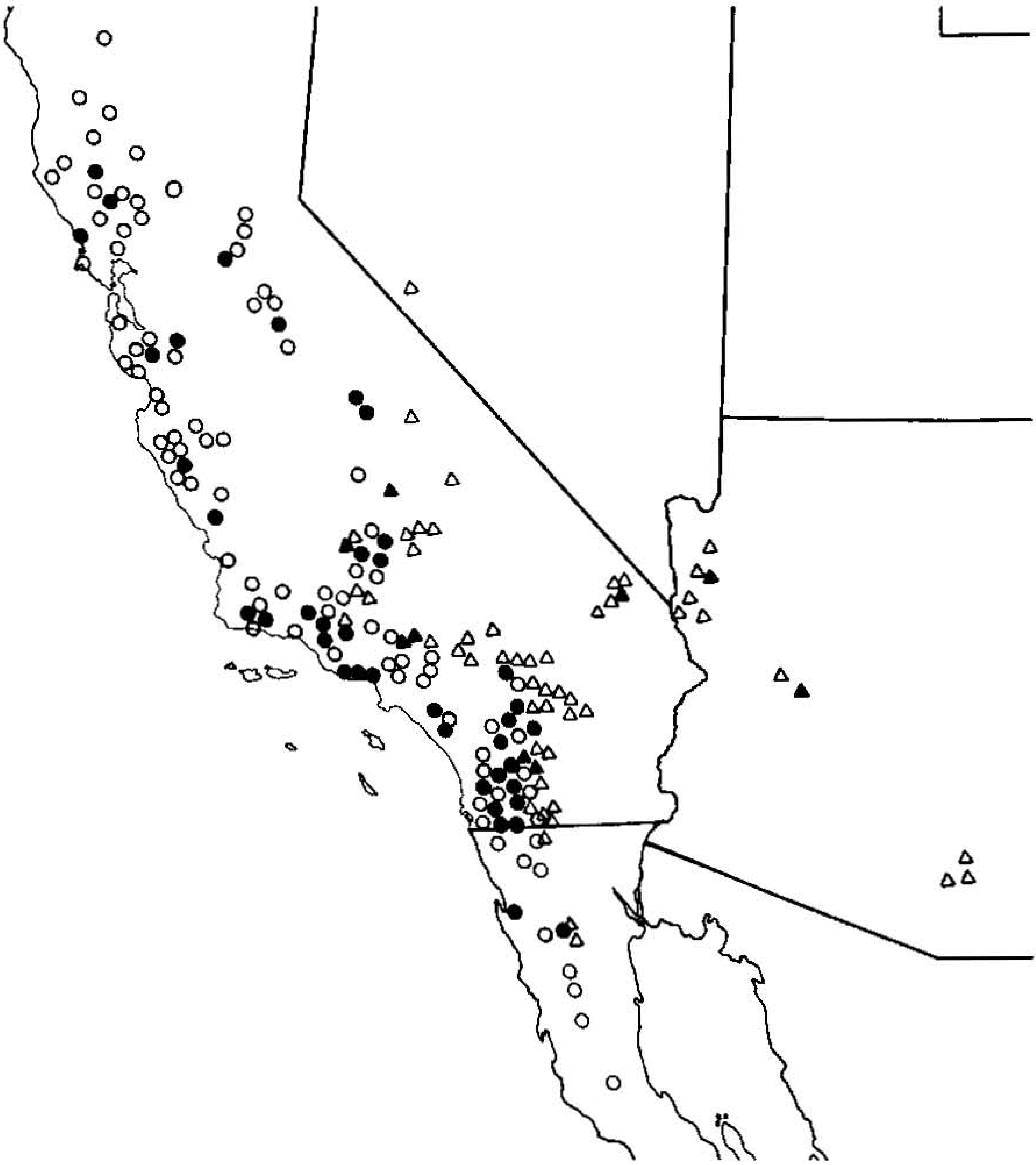


FIGURE 42.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia* sect. *Holostigma:* ○=*C. hirtella*, with ●=diploid chromosome counts ($n=7$); △=*C. pallida* subsp. *pallida*, with ▲=diploid counts ($n=7$).

in the Coast Ranges and Sierra Nevada of California to the Sierra Juárez and Sierra San Pedro Mártir (south to ca. 30°45′ N. lat.) of Baja California, as well as the hills to their west; usually away from the immediate coast and barely reaching the margins of the desert. From near sea level to 7,500 ft. alt.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: AMADOR CO.: 6 mi. N. of Jones Butte, 450 ft., *Roseberry* 121 (RSA, UC); Ione, *Hoover* 2416 (RSA, UC). CALAVERAS CO.: Cosumnes R., *Rattan* 6420; Mokelumne Hill, *Blaisdell* (CAS, GH, NY, US). ELDORADO CO.: Coloma, *Eastwood* 14168 (CAS). FRESNO CO.: Tehipite Valley, *Hall & Chandler* 508

(UC). GLENN CO.: Grade ca. 10 mi. E. of Alder Springs, *Heller* 11443 (CAS, DS, F, GH, NY, OSC, UC, WTU). KERN CO.: W. end of Teyuca Ridge, 6,800 ft. *Twisselmann* 9576 (DS); Breckenridge Mt., 7,400 ft., *Twisselmann* 4704 (CAS, LA); 1 mi. E. of Havilah, 3,600 ft., R17569 (DS); Erskine Creek, *Purpus* 5099 (GH, UC, US); 8–10 mi. E. of Caliente, *Thorne* 31714 (RSA); 5 mi. E. of Alta Sierra, ca. 5,000 ft., Greenhorn Mts., *Thorne* 31772 (RSA). LAKE CO.: W. base of Snow Mt., *Ackley* in 1965 (CAS); foot of Mt. Sanhedrin, *Reynolds* (CAS); Kelsey Creek, Kelseyville, *Benson* 2178 (POM); 2 mi. W. of Houghs Springs, *Abrams* 12483 (DS); Cobb Mt. to Adams Springs on the Binkley Ranch, *Jussel* 154 (CAS, POM, UC). LOS ANGELES CO.: Mandeville Canyon, Santa Monica Mts., *Anderson & Epling* in 1930 (F, LA, US); San Dimas Canyon, 1,500 ft. *Munz & Harwood* 3686 (POM, UC, WTUS); Soledad Canyon between Acton and Ravenna, *Craig* 480 (POM); Bear Canyon Trail to Mt. San Antonio, *Craig* 415 (POM, UC). MADERA CO.: State Hwy. 41, S. of junction with Bass Lake road, *Wedberg 441* (San Diego State College herb.). MARIN CO.: Mill Valley, *Bioletti* in 1892 (RM). MARIPOSA CO.: Mt. Bullion, 2,300 ft., *Jepson* 10722 (JEPS). MENDOCINO CO.: Anderson Valley, *Purdy* in 1882 (GH); summit on road between Ukiah and Boonville, 2,300 ft., *Swensen* 39 (UC). MONTEREY CO.: 3 mi. up Salinas R. from Monterey, *Peirson* 3793 (DS, RSA); Pajaro Hills, *Chandler* 436 (UC); Hanging Valley, Arroyo Seco Road, 3,000 ft., *Hardham* 10871 (DS, RSA); between Junipero Serra and Pinyon Peaks, 4,700 ft., *Howell* 30177 (CAS); Big Sur, *Baker* 7863 (CAS). NAPA CO.: Ridge W. of Oakville, ca. 500 ft., *Reed* 325 (UC, WTU); near Knoxville, *Jepson* in 1892 (UC); La Jota, Howell Mt., *Jepson* 17569 (JEPS). ORANGE CO.: Glen Ivy Trail to Santiago Peak, 4,000 ft., *Munz* 7064 (POM, UC). RIVERSIDE CO.: Junction Main Divide Truck Trail with Ortega Hwy., 2,300 ft., Santa Ana Mts., R17762 (DS); Chalk Hill, 5,000 ft., San Jacinto Mts., *Hall* 2089 (UC); W. of Lake Elsinore, 1,600 ft., *Munz* 5086 (POM). SAN BENITO CO.: Near Hernandez, *Dudley* in 1899 (DS); Chalone Creek, Pinnacles National Monument, *Burgess* 238 (UC); brushy slopes of San Benito Peak above New Idria Mine, 4,000 ft., *Lyon* 919 (UC). SAN BERNARDINO CO.: Devore, mouth of Cajon Canyon, 600 m, *Munz* 11054 (C, GH, POM, UC, US); near Big Bear L., 6,000 ft., *Goodman & Hitchcock* 1743 (NY); Fredalba, *Abrams* 2791 (DS, GH, LE, NMC, NY, PH, US). SAN DIEGO CO.: Above Henshaw Dam, Palomar Mts., 3,500 *Munz* 8334 (GH, NY, POM); Cuyamaca L., 4,700 ft., *Munz & Harwood* 7276 (POM); Laguna Junction, *Epling et al.* in 1932 (DS, LA, UC); 10 mi. W. of Campo, 3,000 ft., *Munz* 12633 (POM). SAN LUIS OBISPO CO.: 4.5 mi. NE. of Santa Margarita, R20158 (DS); Bryson, Santa Lucia Mts., *Hardham* 10728 (DS); Arroyo Grande, *Brewer* 443 (US); McChesney Peak, 3,500–4,000 ft., *Hardham* 11040 (DS). SANTA BARBARA CO.: Junction of Zaca Ridge and Catway roads, Figueroa Mt., San Rafael Mts., 4,200 ft., *Blakley* 4300 (CAS, RSA, SBEG); Carpinteria, *Jones* in 1929 (POM); S. slope of Santa Ynez Peak, Santa Ynez Mts., 3,700 ft., *Breedlove* 2696 (CAS); Cuyamaca Valley 55 mi. E. of Santa Maria, *Munz* 11417 (POM); Pelican Bay, Santa Cruz I., *Clokey* 5010 (DS, GH, NY, POM, SD, US). SANTA CLARA CO.: Sierra Azul Ridge near Loma Prieta, 3,600 ft., *Hichborn* in 1920 (DS); Rattan's Ranch, near San Jose, *Rattan* in 1885 (DS, RSA); Colorado Creek, Red Mts., 2,500 ft., Mt. Hamilton Range, *Sharsmith* 3800 (UC). SANTA CRUZ CO.: 1 mi. up Boulder Creek from town of Boulder Creek, *Thomas* 1780 (DS, OSC, RSA); Ben Lomond Mt., 2,500 ft., *Thomas* 3471 (DS, OSC, RSA). SOLANO CO.: Summit Vaca Mts. via Collins Camp, *Jepson* 14482 (JEPS). SONOMA CO.: Petrified Forest, *Eastwood* 4618 (CAS). SUTTER CO.: North Butte, Marysville Buttes, *Bacigalupi* 2241 (DS). TEHAMA CO.: W. of Paskenta along logging road, *Wagnon* 12659 (RSA). TRINITY CO.: The Knob, near Deer Lick Springs, *Kildale* in 1931 (DS). TULARE CO.: Road to Mineral King, ca. 5,000 ft., *Baker* 4195a

(DS). TUOLUMNE CO.: South Fork Bridge, Tuolumne R., *Grant* 843 (JEPS). VENTURA CO.: Upper Sespe Creek, N. of Wheelers Hot Springs, 3,500 ft., *Munz* 13189 (POM, UC); Goodenough Meadow, Mt. Pinos region, *Dudley & Lamb* 4698 (DS); between Nordhoff and Big Chief peaks, ca. 4,000 ft., *Pollard* in 1945 (CAS); burn near Kennedy Canyon, *Pollard* in 1946 (ARIZ, CAS, SBM).

BAJA CALIFORNIA. 13 mi. SE. of Tecate, *Munz* 9516 (POM); 50 mi. SE. of Tecate, *Munz* 9558 (POM, US); 9 mi. W. of La Rumorosa, 4,020 ft., *Hevly & Pitman* 2053 (ARIZ); 3.5 mi. E. of Rancho San José (Meling's Ranch), *Wiggins* 9787 (DS, UC, US); 19.5 km. SE. of San Vicente, 400 m, R12285 (DS); 10 mi. N. of La Huerta, pine-oak belt, 4,000 ft., *Wiggins* 11845 (DS, OSC, SD, UC); 1 mi. NE. of Santa Catarina, 64 mi. SE. of Ensenada, ca. 3,875 ft., *Broder* 683a (DS, UCSB); Los Emes, S. Sierra San Pedro Mártir, 3,500 ft., *Wiggins* 9903 (DS, UC, US).

As I conceive it, this taxon includes most of the populations generally referred to *Oenothera micrantha* var. *jonesii* (H. Lév.) Munz. As discussed under *Camissonia micrantha*, the tetraploid *C. intermedia* in part bridges the morphological hiatus between its two putative diploid parents, *C. micrantha* and *C. hirtella*, and thus renders the separation of all three taxa difficult. The chromosome number of *Camissonia hirtella* was determined in 84 individuals derived from 76 populations scattered throughout the range of this species (see Appendix).

This widely distributed species is extremely variable in flower size, some individuals having petals up to 9 mm. long. Even in a collection with such large flowers, like R19076 (grown from R17402) from San Diego County, California, the longer set of anthers surrounds the stigma and deposits pollen directly on it, and the plants are fully self-compatible, setting a full complement of seed even when protected from insects. Insects are in general very rare at the flowers of this species.

In addition to being one of the diploid parents of the tetraploid *C. intermedia*, *Camissonia hirtella* has very probably combined with the diploid *C. pallida* subsp. *pallida* to give rise to the tetraploid *C. confusa*, and with one of these two tetraploids to give rise to the hexaploid *C. luciae*. *Camissonia hirtella* occurs sympatrically with *C. bistorta*, *C. micrantha*, *C. ignota*, *C. pallida* subsp. *pallida*, *C. intermedia*, *C. confusa*, *C. hardhamiae*, *C. luciae*, and *C. robusta*.

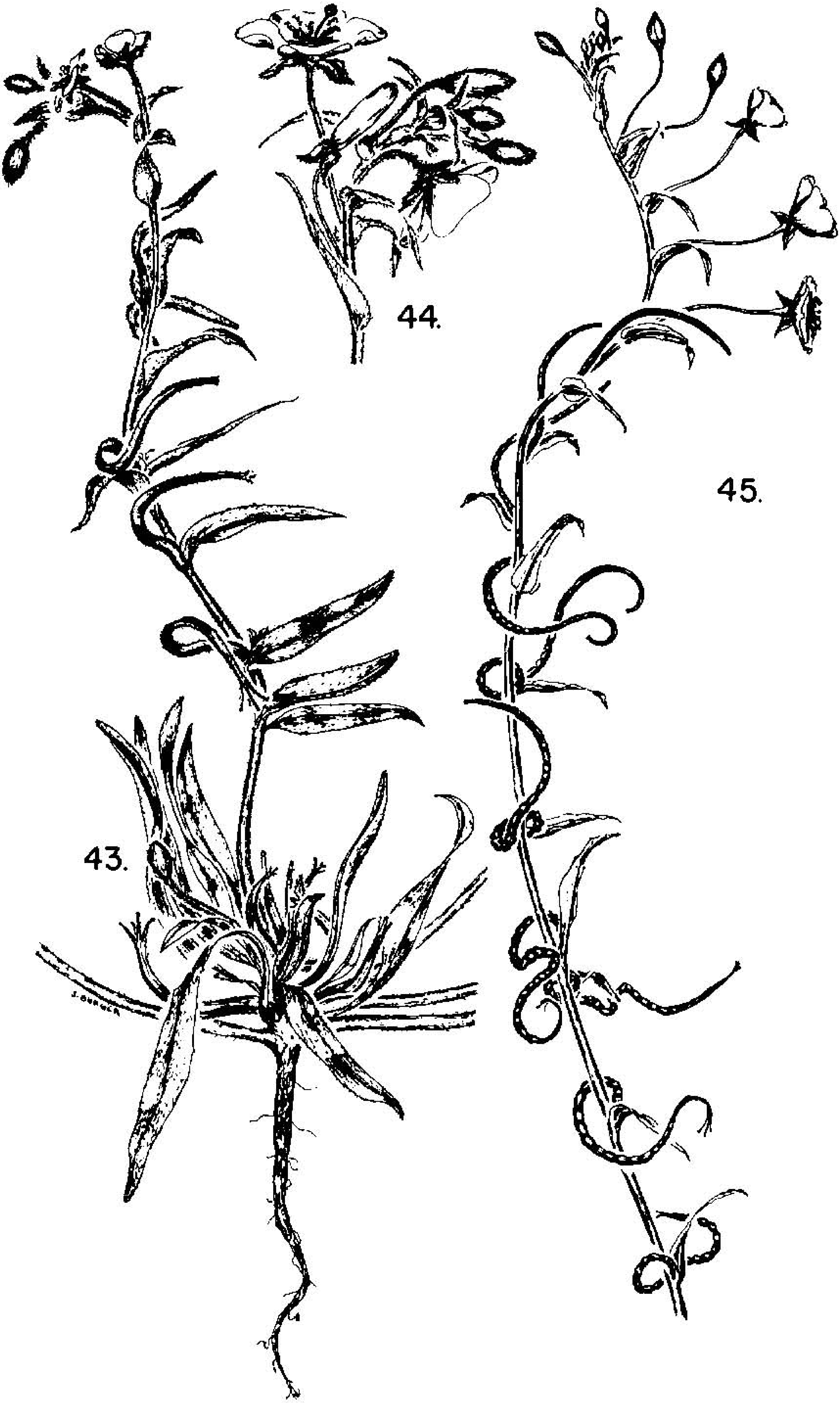
At times it is difficult to distinguish relatively narrow-leaved strains of this species from *C. intermedia*. For example, some populations from the central Sierra Nevada foothills of Calaveras County, California (e.g., *Quick* 52-01, CAS, 0.5 mile from Parrots Ferry bridge on road to Vallecito), temporarily referred here, might actually prove to be *C. intermedia* if their chromosome number could be determined. Similarly, *Heller* 7337 (DS, F, GH, LE, NY, OSC, PH, RM, UC, US), a widely distributed gathering from the foothills west of Los Gatos, Santa Clara County, California, might belong to either species.

Indeed, the existence of the tetraploid populations here referred to *C. intermedia* was the primary reason that plants as different as *C. micrantha* and *C. hirtella* could ever have been referred to a single species. Serious difficulty likewise exists in separating some of the large-flowered, southern California populations of *C. hirtella* from the geographically much more restricted tetraploid *C. confusa*. *Camissonia confusa* bridges the morphological hiatus between *C. hirtella* and *C. pallida* subsp. *pallida* in the same way that the other tetraploid known in the section, *C. intermedia*, bridges the gap between *C. hirtella* and *C. micrantha*. As *C. hirtella* is sometimes more similar to *C. pallida* subsp. *pallida* than it ever is to *C. micrantha*, the taxonomic problem can be even more serious, although the vast majority of populations can be assigned to one species or the other without difficulty. The three hexaploid species in the section can readily be separated from *C. hirtella* on the basis of the proportion of 4- and 5-pored pollen grains they possess.

A single plant that was apparently a natural F_1 hybrid between *C. hirtella* and *C. ignota* was found with the two parents in Lyons Valley, 8 miles northeast of Jamul, San Diego County, California. This plant had 6 pairs of chromosomes and 2 univalents in 2 cells and 5 pairs plus 4 univalents in 3 cells at diakinesis. It appeared to have set a full complement of seeds.

33. Camissonia ignota (Jeps.) Raven, Brittonia 16: 284. 1964. FIGURE 45
Oenothera micrantha var. *ignota* Jeps., Man. Fl. Pl. Calif. 684. 1925.
Oenothera hirta var. *ignota* (Jeps.) Munz, Bot. Gaz. 85: 263. 1928.
Oenothera ignota (Jeps.) Munz, N. Amer. Fl. II. 5: 161. 1965.

Erect, often subsucculent and reddish-tinged annual, similar to *C. micrantha*, with one or more ascending branches from the basal rosette; plants to 55 cm. tall, very finely strigulose with a sparse admixture of longer trichomes. Upper leaves very narrowly to narrowly elliptic, to 6 cm. long and 1.4 cm. wide, finely serrulate, the apex acute, the base attenuate; almost all leaves evidently petiolate, the petiole up to 2.5 cm. long. Bracts truncate at base, narrowly lanceolate or lanceolate. Inflorescence subglabrous or glandular-pubescent with a few longer erect trichomes, rarely entirely strigulose. Hypanthium (1.1–) 1.8–3 mm. long, 1.1–2 mm. across at the summit, glabrous within. Sepals 2.6–5.5 mm. long, 1–1.7 mm. wide. Petals (3–) 4–8 mm. long, (2–) 3–6 mm. wide, sometimes red-dotted near the base. Filaments of the episepalous stamens (1.2–) 2.5–3.6 mm. long, those of the epipetalous ones (1–) 1.3–2 mm. long; anthers (0.6–) 0.8–1.6 mm. long. Style (3–) 4.5–7 mm. long; stigma 0.8–1.2 mm. in diameter, surrounded by the anthers at anthesis. Capsule mostly 2–3 cm. long, 0.8–1 mm. thick, terete in living material, very slender and usually much contorted, coiled irregularly up to five times, or more



FIGURES 43–45.—Species of *Camissonia* sect. *Holostigma*, × 1: 43, *C. pallida* subsp. *pallida* (*Raven* 13995, DS); 44, *C. pallida* subsp. *hallii* (*Alexander & Kellogg* 2072, DS); 45, *C. ignota* (*Raven et al.* 12524, DS).

rarely simply flexuous. Seeds 1.2–1.3 mm. long, 0.5–0.6 mm. thick. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Jurupa Hills, west of Riverside, Riverside County, California, April 1905, *Mrs. C. M. Wilder* 90 (UC 69875).

DISTRIBUTION (Figure 46): Most common in clay fields and slopes at low elevations, but occasional on sandy soil and higher in the mountains in the Coast Ranges and bordering valleys from Yolo County, California, south to the southern end of the Sierra San Miguel, at about 30° N. lat., in Baja California, usually away from the immediate coast and barely reaching the margins of the desert; Santa Cruz Island, Santa Barbara County, California; collected once in the lowest foothills of the Sierra Nevada in Madera County, California.

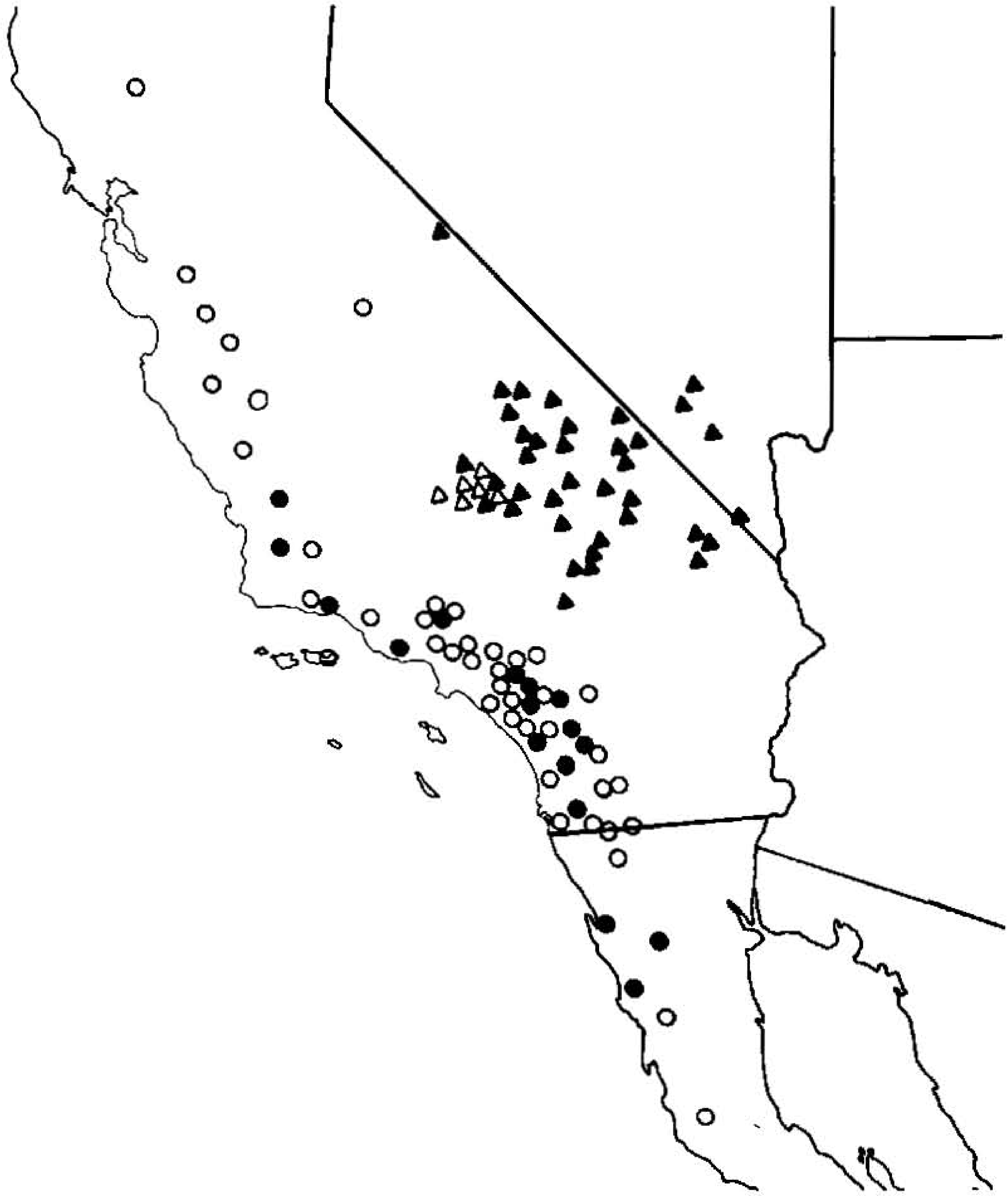


FIGURE 46.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia:* ○=*C. ignota*, with ●=diploid chromosome counts ($n=7$); ▲=*C. kernensis* subsp. *gilmanii;* △=*C. kernensis* subsp. *kernensis*.

From about 400 to 3,500 ft. alt. Most abundant in western Riverside and San Diego Counties, California, and generally local and sporadic elsewhere.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: FRESNO CO.: Alcalde, *Eastwood* 13549 (CAS). LOS ANGELES CO.: 1 mi. W. of Acton, Soledad Canyon, *Lewis* in 1954 (LA); 3 mi. S. of Boquet Canyon Guard Station, *Tavares & Brinson* 263 (DAO, RM, SD, UC); San Fernando wash, *Eastwood* in 1913 (CAS); Tujunga Canyon, 1,500 ft., *Peirson* 414 (JEPS, RSA); Griffith Park, *Davidson* 1451 (LAM); San Dimas Canyon, 1,500 ft., *Harwood* 3692 (POM); Johnson's Pasture, 3 mi. N. of Claremont, *Jones* in 1928 (CAS). MADERA CO.: San Joaquin R. ca. 5 mi. above Pollasky, *Heller* 8166 (CAS, DS, F, GH, NY, PH, UC, US). MERCED CO.: Ortigalita Peak, San Carlos Range, *Lyon* 1529 (RM, UC, WTU); Pacheco Pass, *Eastwood* 14092 (CAS). MONTEREY CO.: Lowes Canyon, *Hardham* 3317 (CAS, LA). ORANGE CO.: Trail to Santiago Peak from Trabuco Canyon, in Holy Jim Canyon, 3,500 ft., *Peirson* 3505 (RSA); 2.3 mi. above gate on Silverado Canyon Truck Trail, 2,500 ft., R17750 (DS); Anaheim plains, *King* in 1908 (JEPS). RIVERSIDE CO.: Temescal Canyon, ca. 12 mi. SE. of Corona, *Hitchcock & Muhlick* 22151 (DS, RM, UC, UT, WTU); Elsinore, *McClatchie* in 1892 (DS, NY); Temecula, *Cleveland* in 1882 (SD); Coldwater Trail, Santa Ana Mts., *Pequegnat* 2 (LA); Rattlesnake Mts., *Wilder* in 1905 (DS); Saunders Meadow, *Meyer* 161 (JEPS). SAN BENITO CO.: Pinnacles, *Sutliffe* in 1920 (CAS). SAN BERNARDINO CO.: Vicinity of San Bernardino, *Parish* 4756 (NY, US); near Colton, *Parish* 78 (DS, UC). SAN DIEGO CO.: Moro Hills near Fallbrook, *Abrams* 3326 (CAS, DS, GH, LA, LE, NY, PH, POM, UC, US); 2.3 mi. S. of Rincon Springs on road to Escondido, 1,100 ft., R17402 (DS); 1 mi. E. of Oak Grove, 2,700 ft., R17370 (DS); 2 mi. W. of Banner, *Gander* 173.3 (SD); Barrett, R16936 (DS); 1.1 mi. E. of Campo, R17445 (DS); Jacumba, *Gander* 181.6 (SD). SAN LUIS OBISPO CO.: Upper Navajo Creek, La Panza Range, *Hoover* 6904 (CAS, RSA); Cuyama Valley 44 mi. W. of Maricopa, 2,000 ft. *Benson* 5787 (POM). SANTA BARBARA CO.: Santa Ynez Mts., *Eastwood* in 1904 (CAS); Valley Anchorage, Santa Cruz I., *Hoffmann* in 1929 (POM). STANISLAUS CO.: Near head of Del Puerto Canyon, *Hoover* 4883 (UC). VENTURA CO.: Burn near Kennedy Canyon, Ojai Valley, *Pollard* in 1946 (RSA). YOLO CO.: Grade on Rumsey to Arbuckle road, *Hoover* 3199 (POM, RSA, UC, US).

Camissonia ignota as here constituted is, in general, a very distinctive entity that includes most of the populations referred by Munz (Bot. Gaz. 85: 263. 1928) to *Oenothera hirta* var. *ignota* and later to *Oenothera micrantha* var. *ignota*. Many of the populations here considered to belong to the tetraploid *C. confusa* were considered by Munz to belong to this taxon also. These differ in their more robust habit, broader leaves, abundant gray pubescence, less contorted capsules, and tetraploid chromosome number. At times, however, the separation of *C. confusa* from *C. ignota* can be very difficult, and it is not impossible that *C. ignota* has contributed to the origin of some of the tetraploid populations I have included with *C. confusa*. In general, however, it appears more probable that the diploid parents of the latter species are *C. hirtella* and *C. pallida* subsp. *pallida*. It does not appear likely that *C. ignota* has contributed to the formation of any other polyploid species, although at one time I thought that the tetraploid Baja California populations here referred to *C. intermedia* might have been derived from the diploids *C. proavita* and *C. ignota* (see discussion under *C. intermedia*). The chromosome number of *Camissonia ignota* has been determined in 22 individuals taken from 18 populations from throughout the range (see Appendix).

Camissonia ignota has been observed growing sympatrically with *C. bistorta, C. lewisii, C. proavita, C. hirtella, C. intermedia,* and *C. confusa.* A single F_1 hybrid with *C. hirtella* was found in San Diego County, California, and is discussed under that species.

34. Camissonia pallida (Abrams) Raven, **Brittonia 16: 284. 1964.**

Similar to *C. micrantha,* but covered with dense, strigose pubescence. Leaves entire or very sparsely denticulate, the upper ones undulate, mostly 1–3 cm. long, 0.35–0.7 cm. wide, with a short but distinct petiole up to 2 mm. long. Inflorescence occasionally with an admixture of glandular trichomes, usually conspicuously gray-pubescent. Hypanthium (1–) 1.8–4 mm. long, (0.7–) 1.2–3.5 mm. across at the summit. Sepals (1.5–) 2.5–8 mm. long, 0.6–3 mm. wide. Petals (2–) 3.5–13 mm. long, (1.3–) 3–14.5 mm. wide, occasionally with 1–3 red dots near the base. Filaments of the episepalous stamens (0.5–) 1.5–6.5 mm. long, those of the epipetalous ones (0.2–) 0.5–3.8 mm. long; anthers (0.4–) 0.8–2.2 mm. long. Style (2–) 3–10.5 mm. long; stigma 0.6–1.5 mm. in diameter, surrounded by at least the anthers of the longer stamens and often by both sets of anthers at anthesis. Capsule 1–1.2 mm. thick, more or less quadrangular in transection, straight or once or more coiled, rarely up to three times. Seeds 1–1.45 mm. long, 0.6–0.7 mm. thick. Gametic chromosome number, $n = 7$. Autogamous.

DISTRIBUTION (Figures 33, 42): Desert slopes and flats, often along washes, from the head of the San Joaquin Valley in Ventura and Kern Counties, California, across the Mojave and Colorado Deserts, north to the vicinity of Independence, Inyo County, California, and Esmeralda County, Nevada (the only member of the section in Nevada); east to Mohave and Yavapai Counties, Arizona, and also in the vicinity of Tucson, Pima County; and south along the eastern side of Baja California to the Sierra de San Borjas at about 29° N. lat.; from about 100–6,000 ft. alt.

Camissonia pallida consists of two subspecies: subsp. *hallii,* which is relatively large-flowered, and subsp. *pallida.* The former occupies a much more restricted range than the latter, and often grows with it. Numerous intermediate individuals are found in such localities, and the plants appear to differ only in flower size. No meiotic disturbances or evidences of sterility have been found in individuals with intermediate-sized flowers. Presumably the distinctness of these two species is maintained by their predominant autogamy. *Camissonia pallida* subsp. *hallii* was considered a variety of *Oenothera bistorta* (=*Camissonia bistorta*) by Munz (Bot. Gaz. 85: 267. 1928). Despite their similarity in flower size, however, *C. bistorta* is self-incompatible and the stigma is elevated above the anthers at anthesis, whereas *C. pallida* subsp. *hallii* is autogamous, the anthers shedding pollen directly on the stigma at anthesis. Vegetatively, these two entities are sharply distinct.

34a. Camissonia pallida subsp. **hallii** (Davids.) Raven, Brittonia 16: 284. 1964. FIGURE 44

Sphaerostigma hallii Davids., Muhlenbergia 3: 107. 1907.
Oenothera bistorta var. *hallii* (Davids.) Jeps., Man. Fl. Pl. Calif. 685. 1925.
Oenothera hallii (Davids.) Munz, N. Amer. Fl. II. 5: 160. 1965.

Hypanthium 3.8–4.2 mm. long, 2.2–3.5 mm. across at the summit. Sepals 4.8–8 mm. long, 1.2–3 mm. wide. Petals 6.5–13 mm. long, 5–14.5 wide, with 1–3 red dots near the base of each one. Filaments of the episepalous stamens 3–6.5 mm. long, those of the epipetalous ones 1.8–3.8 mm. long; anthers 1.5–2.2 mm. long. Style 6.5–10.5 mm. long, the longer stamens just equal to and their anthers shedding pollen directly on the stigma at anthesis. Gametic chromosome number, $n=7$. Autogamous, but clearly facultatively outcrossing.

TYPE: Banning, Riverside County, California, 17 April 1897, *H. M. Hall* 446 (UC).

DISTRIBUTION (Figure 33): Sandy washes in Riverside and San Bernardino Counties, California, ca. 100–4,300 ft. alt., from Banning east throughout the Little San Bernardino Mountains and their northern slopes and southeast to the vicinity of Mecca and Box Canyon.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S: CALIFORNIA: RIVERSIDE CO.: Big Oaks Canyon, Banning, 4,000 ft., *Cooper* 1645 (RSA); Whitewater Canyon 2 mi. N. of Banning-Indio boulevard, *Munz* 15660 (CAS, DS, GH, POM, UC, US, WS, WTU); near Mecca, *Winblad* in 1937 (CAS); Box Canyon, *Winblad* in 1937 (CAS). SAN BERNARDINO CO.: Just S. of Morongo Valley, 2,600 ft., R17532 (DS); E. of Quail Spring, *Moran* 844 (DS, POM, UC).

Camissonia pallida subsp. *hallii* has not been observed growing sympatrically with any other member of the section, except *C. pallida* subsp. *pallida*, with which it intergrades. Its chromosome number has been determined in 4 individuals from 3 different populations (see Appendix). The combination *Camissonia hallii*, attributed to me by Munz, N. Amer. Fl. II. 5: 160. 1965, has not been published elsewhere.

Relatively large-flowered plants similar to subsp. *hallii* are occasionally found elsewhere in the area of subsp. *pallida*. One such collection was made in the pinyon-juniper association of the Cerbat Mountains, Mohave County, Arizona, 5,000 ft. elevation, *Jaeger* in 1941 (POM); the petals of one plant are 11.5 mm. long and 8 mm. wide, and have red dots near the base similar to those usually found in subsp. *pallida*. One of the plants mounted on this sheet is typical of subsp. *pallida*, with petals ca. 3.5 mm. long. It would be highly desirable to have more material for study before extending the range of subsp. *hallii* to this disjunct station.

34b. Camissonia pallida subsp. **pallida** FIGURE 43

Sphaerostigma pallidum Abrams, Bull. Torrey Cl. 32: 539. 1905.

Sphaerostigma micranthum var. *exfoliatum* A. Nels., Bot. Gaz. 40: 59. 1905. Lectotype: Colorado Desert, probably in San Diego Co., Calif., April 1889, *C. R. Orcutt*.

Oenothera abramsi J. F. Macbride, Contr. Gray Herb. 65: 41. 1922.

Oenothera micrantha var. *abramsii* (J. F. Macbride) Jeps., Man. Fl. Pl. Calif. 684. 1925.

Oenothera hirta var. *exfoliata* (A. Nels.) Munz, Bot. Gaz. 85: 264. 1928.

Oenothera micrantha var. *exfoliata* (A. Nels.) Munz, Amer. Journ. Bot. 19: 778. 1932.

Hypanthium (1–) 1.8–3 mm. long, (0.7–) 1.2–2.5 mm. across at the summit. Sepals (1.5–) 2.5–5.5 mm. long, 0.6–2 mm. wide. Petals (2–) 3.5–6 (–8) mm. long, (1.3–) 3–5 (–6.5) mm. wide, very rarely with red dots at the base. Filaments of the episepalous stamens (0.5–) 1.5–4 mm. long, those of the epipetalous ones (0.2–) 0.5–2.2 mm. long; anthers (0.4–) 0.8–1.2 mm. long. Style (2.1–) 3–6.5 mm. long, the stigma surrounded at anthesis by both sets of anthers, or sometimes by only the longer set. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Near the station, Cabazon, Riverside County, California, 6 April 1903, *L. R. Abrams* 3228 (NY; isotypes, CAS, DS, GH, LA, LE, NY, RM, RSA, SBM, UC, US, WS, WTU).

DISTRIBUTION (Figure 42): That of the species.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: ARIZONA: MOHAVE CO.: 9 mi. NW. of Kingman, 3,300 ft., *Munz et al.* 22982 (DAO, RSA, UC). PIMA CO.: Bear Canyon, Santa Catalina Mts., *Mason et al.* in 1960. YAVAPAI CO.: 5.4 mi. NE. of Congress, 4,000 ft., R17367 (DS); Skull Valley, 4,300 ft., *Jones* in 1903 (POM). CALIFORNIA: IMPERIAL CO.: 0.5 mi. E. of Mountain Springs, *Ferris* 7078 (DS, NY). INYO CO.: North Fork of Oak Creek, Independence, 3,000 ft., *Train* in 1937 (ARIZ, DS, OSC); 2.5 mi. E. of Coso Hot Springs, Coso Range, 3,550 ft., *Alexander & Kellogg* 2768 (UC). KERN CO.: S. end of Soledad Mt., 2,775 ft., *Twisselmann* 4308 (CAS, LA); 9.7 mi. S. of Weldon, 3,100 ft., R17565 (DS); Poso Creek, slope on S. side, Greenhorn Mts., ca. 2,600 ft., *Smith* 299 (JEPS). LOS ANGELES CO.: N. of Pearblossom, *Wedberg* 250 (DS); 2 mi. N. of Saugus, *Munz* 10013 (POM, UC); Rock Creek to Big Pines, 4,500 ft., *Pierson* 7951 (RSA). RIVERSIDE CO.: Dos Palmos Spring, N. end of Santa Rosa Mts., 3,600 ft., *Munz* 15107 (CAS, GH, POM, UC); San Gorgonio Pass, 1 mi. W. of Whitewater, 1,200 ft., *Wolf* 8416 (ARIZ, GH, NY, RSA, WTU); Palm Canyon near Palm Springs, *Johnston* 1110 (DS, POM, US); Indio, *McGregor* in 1917 (DS); Fried Liver Wash, Pinto Basin, Joshua Tree

National Monument, R11863 (DS); 5 mi. S. of Gold Coin Mine, Little San Bernardino Mts., *Epling & Robinson* in 1933 (DS, LA, RSA). SAN BERNARDINO CO.: Cedar Canyon, Mid Hills, 5,000 ft., R17353 (DS); 3.5 mi. N. of Lake Arrowhead, 4,550 ft., *Axelrod* 273 (UC); Cajon Pass, 3,800 ft., *Jones* in 1903 (POM); Cactus Flat, San Bernardino Mts., 6,000 ft., *Munz* 10518 (POM); Granite Mts., N. of Amboy, *Jaeger* in 1939 (DS). SAN DIEGO CO.: Hell Hole Canyon, Borrego Valley, *Epling & Robinson* in 1932 (DS, F, LA, NY, RSA, UC); extreme SE. corner of the county, *Gander* in 1940 (SD); 11 mi. E. of Banner, *Gould* 2268 (RSA, UC); 5 mi. E. of Laguna Station, 1,090 m, *Bracelin* 5 (POM, UC). VENTURA CO.: Flood plain of Piru Creek, *Hoffmann* in 1930 (CAS, SBM); sandy field near Camulos, *Hoffmann* in 1929 (SBM). NEVADA: ESMERALDA CO.: 2 mi. E. of Bellville, *Purpus* in 1898 (UC).

BAJA CALIFORNIA. Vicinity of Japá, *Orcutt* 1191 (UC); 3 mi. W. of Santa Catarina, 64 mi. SE. of Ensenada, 3,755 ft., *Broder* 659 (DS, UCSB); Rancho San Matias, Sierra San Pedro Mártir, ca. 1,050 m, *Moran* 10844 (DS, SD); San Juan Mine, Sierra de San Borjas, ca. 1,200 m, *Moran* 8127 (RSA, SD, UC).

This extraordinarily variable taxon is at times difficult to separate from *C. hirtella* where the ranges of these two species approach one another along the margins of the desert. There is, however, no evidence of genuine intergradation, and most plants are easily referred to one species or the other. An even more difficult problem is the separation of *C. pallida* subsp. *pallida* from *C. confusa*, which is presumably an allotetraploid derived from the diploids *C. pallida* subsp. *pallida* and *C. hirtella*. In California, the problem is rarely a difficult one, but in Arizona further chromosome counts will clearly be necessary to elucidate the situation completely. All collections from the area of the Tonto National Forest in Gila and Maricopa Counties appear to be *C. confusa*, and this is documented by chromosome counts from the area. Collections from Paradise Valley and Avondale, farther west in Maricopa County, and the vicinity of Sacaton and Casa Grande Ruins, to the south in Pinal County, also are morphologically similar to the tetraploids of California. Populations in Yavapai and Mohave Counties, on the other hand, are known to be diploid. A series of populations from the vicinity of Tucson and the Santa Catalina Mountains in Pima County, Arizona, appears morphologically similar to the diploid and are tentatively referred here, even though they would, if this disposition is correct, represent a disjunct occurrence for *C. pallida* subsp. *pallida*. Unfortunately none of these populations has been examined cytologically.

The chromosome number of this subspecies has been determined in 26 individuals from 24 populations scattered throughout the range (see Appendix). *Camissonia pallida* subsp. *pallida* intergrades with *C. pallida* subsp. *hallii* and occurs sympatrically with *C. hirtella* and probably *C. ignota* (the latter in the vicinity of Santa Catarina, Baja California).

35. Camissonia intermedia Raven, sp. nov. FIGURE 48

Oenothera hirta var. *typica* sensu Munz, Bot. Gaz. 85: 261, 1928; pro parte.
Oenothera hirta var. *jonesii* sensu Munz, Bot. Gaz. 85: 262, 1928; pro parte.
Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 160. 1965; pro parte.

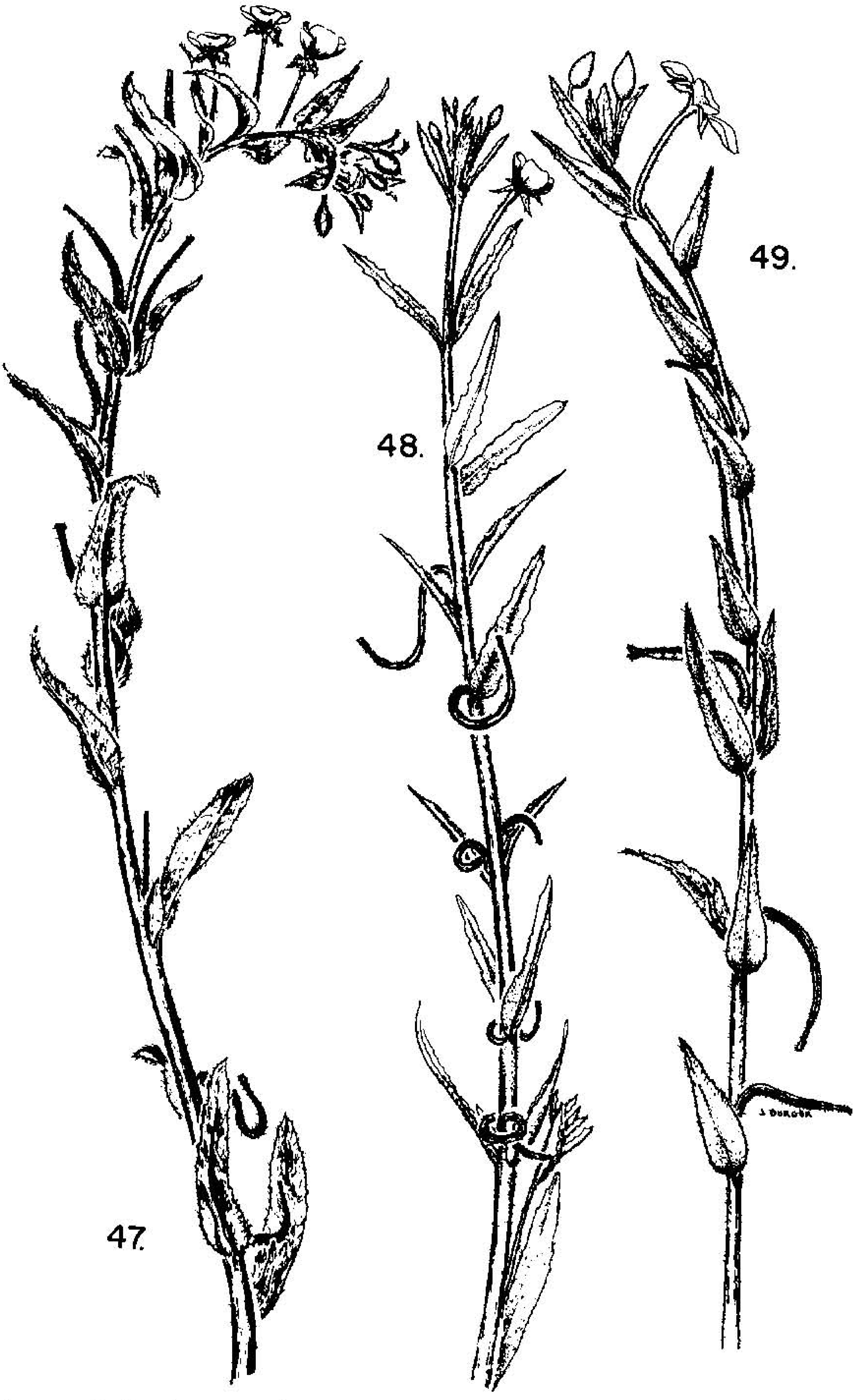
Herba annua dense villosa erecta, ad *C. micrantha* similis, usque ad 6 dm alta, ramis plurimis erectis e rosula centrali radiantibus, rariore caule singulari erecto. Folia his *C. micranthae* basi parum latiora. Inflorescentia plus minusve cano-villosa, persaepe pilis brevibus glandulosis pubescentes. Usque ad partem vicensimam pollinis granorum quadriporam, rariore ad partem dimidiam. Chromosomatum numerus gameticus, $n=14$. Autogama.

TYPE: Common along disturbed roadsides in chaparral, with *Adenostoma fasciculatum* and *Arctostaphylos glauca*, Mulholland Highway 2.6 miles east of Seminole Hot Springs, 1,800 ft. alt., Santa Monica Mountains, Los Angeles County, California, 1 May 1962, *P. H. Raven* 17517 (DS 514938; isotypes, RSA, US).

DISTRIBUTION (Figure 50): Mostly on disturbed brushy slopes, often common on burns, from Lake and Yolo Counties (where rare) south in the Coast Ranges of California to the western San Gabriel Mountains, western Riverside County, and San Diego County, and south in Baja California to the south end of the Sierra San Miguel at about 30° N. lat.; also on Santa Cruz and Santa Catalina Islands. From (500–) 1,000–2,500 ft. alt. Most abundant in Monterey County and from coastal Santa Barbara County to the Santa Monica Mountains of Los Angeles and Ventura Counties, California, and again in coastal Baja California.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: CONTRA COSTA CO.: W. slope of Mt. Diablo, ca. 900 ft. *Rose* 41229 (GH, NY, UC). LAKE CO.: Blue Lakes, *Baker* 264a (DS). LOS ANGELES CO.: Wilson's Trail, *Abrams* 1505 (DS); foothills near Sherman, *Braunton* 65 (US); Puddingstone Canyon, *Munz et al.* 2444 (POM); Liveoak Canyon Dam, San Gabriel Mts., 1,500 ft., *Wheeler* 2543 (LA); Mandeville Canyon, 1,200 ft., Santa Monica Mts., *Templeton & Clokey* 4458 (DAO, NY, POM, UC, US); Los Alisos Canyon, Santa Monica Mts., *Epling* in 1931 (CAS, F, LA, UC, US); Avalon Hill, Santa Catalina I., *Knopf* 428 (F). MONTEREY CO.: Priest Valley, 2,250 ft., *Howell* 39114 (CAS); limestone ridge above Posts, ca. 2,000 ft., Big Sur, *Hoffman* 1180 (UC). NAPA CO.: Oakville to Glen Ellen, ca. 900 ft., R2860 (CAS); Capell Valley, *Kamb & Chisaki* 1760 (UCSB). ORANGE CO.: Santiago Peak Trail, *Abrams* 1792 (NY); 5 mi. S. of Laguna, *Mason* 2926 (UC). RIVERSIDE CO.: 5 mi. NE. of Murietta, 1,500 ft., *Munz & Johnston* 5354 (POM). SAN BENITO CO.: 10.5 mi. from junction near Bitterwater on road to Hernandez, R9152 (CAS, LA, RSA, UC); Bear Valley, *Jepson* 12246 (JEPS). SAN DIEGO CO.: Near County line on U.S. Hwy. 395, *Gander* in 1937 (SD); Jamul, 1,500 ft., *Stokes* in 1895 (DS). SAN LUIS OBISPO CO.: Chimney Ranch, North Road to Adelaida, *Hardham* 3347 (LA, SBBG); east School Canyon, San Luis Obispo, *Condit* in 1908 (UC). SANTA BARBARA CO.: N. of Lompoc, *Chandler* 2570 (DS); Los Feliz School at end of Mission Canyon Road, 1,000 ft., *Smith* 920 (RSA); Gibraltar Road to El Camino



FIGURES 47–49.—Species of *Camissonia* sect. *Holostigma*, × 1: 47, *C. hardhamiae* (*Raven* 18315, holotype, DS); 48, *C. intermedia* (*Breedlove* 2305, DS); 49, *C. luciae* (*Raven* 18267, holotype, DS).

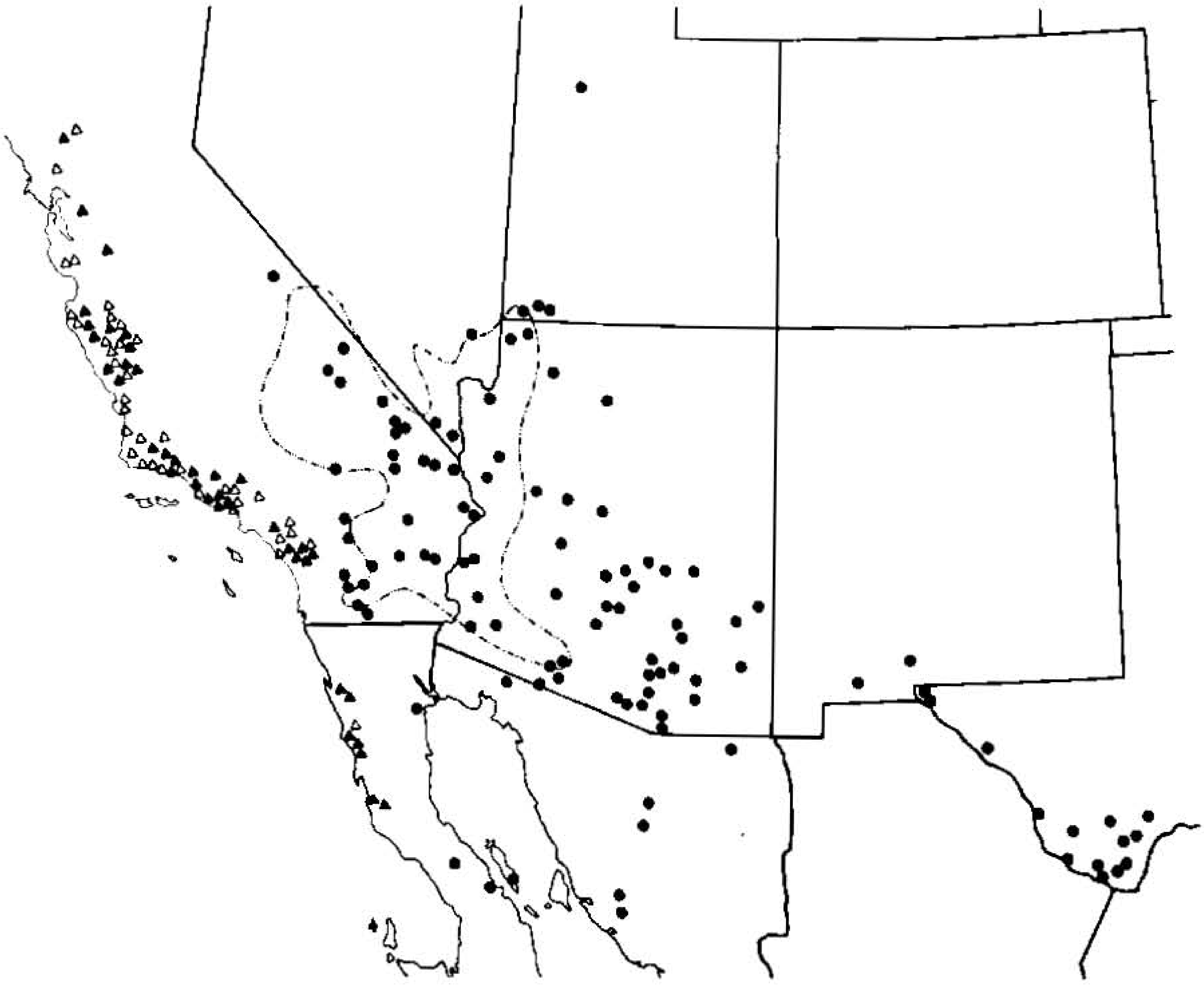


FIGURE 50.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia:* △=*C. intermedia*, with ▲=tetraploid chromosome counts ($n=14$); ●=*C. chamaenerioides;* the dotted-line outline indicates the range of the related, larger flowered, self-incompatible *C. refracta.*

Cielo, 2,000 ft., *Hardham* 10854 (DS); Sierra Blanca, Santa Cruz I., *Wolf* 2842 (POM, RSA); Coches Prietos Canyon to Alberts Anchorage, 400 ft., top of ridge, *Blakley* 3314 (SBBG). SANTA CLARA CO.: Evergreen, *Burtt Davy* 71 (UC); Loma Prieta, *Burtt Davy* 665 (UC). SANTA CRUZ CO.: Near summit of Santa Cruz to Los Gatos highway, *Covel* 323 (CAS). STANISLAUS CO.: Near head of Del Puerto Canyon, *Hoover* 4884 (RSA, UC). VENTURA CO.: Santa Susanna Pass, *Epling* in 1926 (LA); Foster Park burn, Ojai Valley, *Pollard* in 1945 (CAS, RSA, SBM). YOLO CO.: Grade on Rumsey-Arbuckle road, *Hoover* 3195 (POM, RSA, UC).

BAJA CALIFORNIA: 10 mi. S. of Ensenada, *Purer* 7140 (SD); near San Jacinto, *Gander* in 1939 (SD); near Refugio, *Cronemiller* 3083 (POM); 13.1 mi. S. of Santo Tomás, *Turner et al.* 2074 (DS); 9.3 mi. S. of San Vicente, R17045 (DS); 2.5 mi. S. of Ejido México, R17039 (DS).

Camissonia intermedia is almost certainly an allotetraploid, its two diploid ancestors being *C. micrantha* and *C. hirtella*. The difficulties of distinguishing it from these two diploids have been discussed in the sections dealing with each. At one time, I thought that the tetraploid populations of Baja California here referred to *C. intermedia* might have been derived from the diploids *C. ignota* and *C. proavita*, as mentioned under the latter species. Evidence for this view is the fact that *C. micrantha*, one of the parents of the northern populations of *C. intermedia*, ranges no farther south than northern San Diego County, California, where the main area of the tetraploid stops also. No tetraploids have been found in central San Diego County, despite intensive sampling, and the Baja California populations range north only to Jamul in the southernmost part of the county. In general, the plants found in Baja California seem to be somewhat more slender and glabrous than the ones from farther north; but this is far from an absolute difference, and I have found it difficult to quantify. It might be possible to elucidate this problem with a program of experimental hybridization, but at present it appears best to retain all of these obviously closely related tetraploid populations in a single species.

The chromosome number of this species has been determined in 60 individuals from 53 populations from throughout the range of the species including the type (see Appendix). *Camissonia intermedia* has been found growing sympatrically with *C. bistorta*, *C. lewisii*, *C. proavita*, *C. micrantha*, *C. hirtella*, *C. ignota*, *C. confusa*, and *C. robusta*. Individuals of this species were referred by Munz (Bot. Gaz. 85: 260–265. 1928) to *Oenothera hirta* var. *typica* and *O. hirta* var. *jonesii*, entities corresponding for the most part to the diploid parents of *C. intermedia*.

36. Camissonia confusa Raven, sp. nov. FIGURE 51

Oenothera hirta var. *ignota* sensu Munz, Bot. Gaz. 85: 263. 1928; pro parte.
Oenothera ignota sensu Munz, N. Amer. Fl. II. 5: 161. 1965; pro parte.

Herba annua robusta dense cinerero-villosa rare strigosa erecta, ad *C. micrantha* similis, usque ad 6 dm. alta, ramis plurimis erectis e rosula centrali radiantibus, rariore caule singulari erecto. Folia superiora lanceolata vel anguste ovata, 1–5 cm. longa, 0.4–2 cm. lata, basi rotundata vel truncata, sparse et exigue denticulata, undulata, apice longe acuminata. Inflorescentia glandulosa, rariore pilis longioribus admixta vel strigosa, rarissime subglabra. Hypanthium (1.8–) 2–3.8 mm. longum, ostio 1.2–2 mm. diametro. Sepala (1.5–) 3.2–8.5 mm. longa, 1.2–1.5 mm. lata. Petala (2.5–) 5–10.5 mm. longa, (1.5–) 2.8–6 mm. lata, plerumque prope basin puncto rubro uno vel duo. Filamenta staminum episepalorum (1.2–) 2.5–4.5 mm. longa, illa epipetalorum (0.8–) 1.5–2.5 mm. longa; antherae (0.4–) 0.8–1.5 mm. longae. Usque ad partem vicensimam pollinis granorum quadriporum. Stylus (2.5–) 4.5–7.5 mm. longus; stigma 1–1.2 mm. diametro, sub anthesi antheris saltem longioribus circumnexum. Capsula 0.9–1.2 mm. crassa surrecta vel in spiras 1 vel 2 contorta. Semina 1.2–1.35 mm. longa, 0.5–0.7 mm. crassa. Chromosomatum numerus gameticus, $n=14$. Autogama.

FIGURE 51.—*Camissonia confusa* (*Raven* 17388, DS), × 1.

TYPE: Common in coastal sage by edge of citrus orchard, along dirt road 2.3 miles west of Mill Creek Ranger Station, San Bernardino Mountains, 2,300 ft. alt., San Bernardino County, California, 28 April 1962, *P. H. Raven* 17466 (DS 515446; isotypes, RSA, US).

DISTRIBUTION (Figure 52): Dry slopes away from the coast, from the La Panza Range of central San Luis Obispo County south through the Coast Ranges to the San Bernardino Mountains and southern San Diego County, California; also in central Arizona (westernmost Gila, northern Pinal, and Maricopa Counties); from about 1,100–6,600 ft. alt.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: ARIZONA: GILA CO.: Tonto Hill, 690 m., *Collom* 265 (GH, NY); 12 mi. N. of Roosevelt, 2,300 ft., *Peebles & Smith* 11503 (ARIZ); Jana Gordo Wash, 1,800

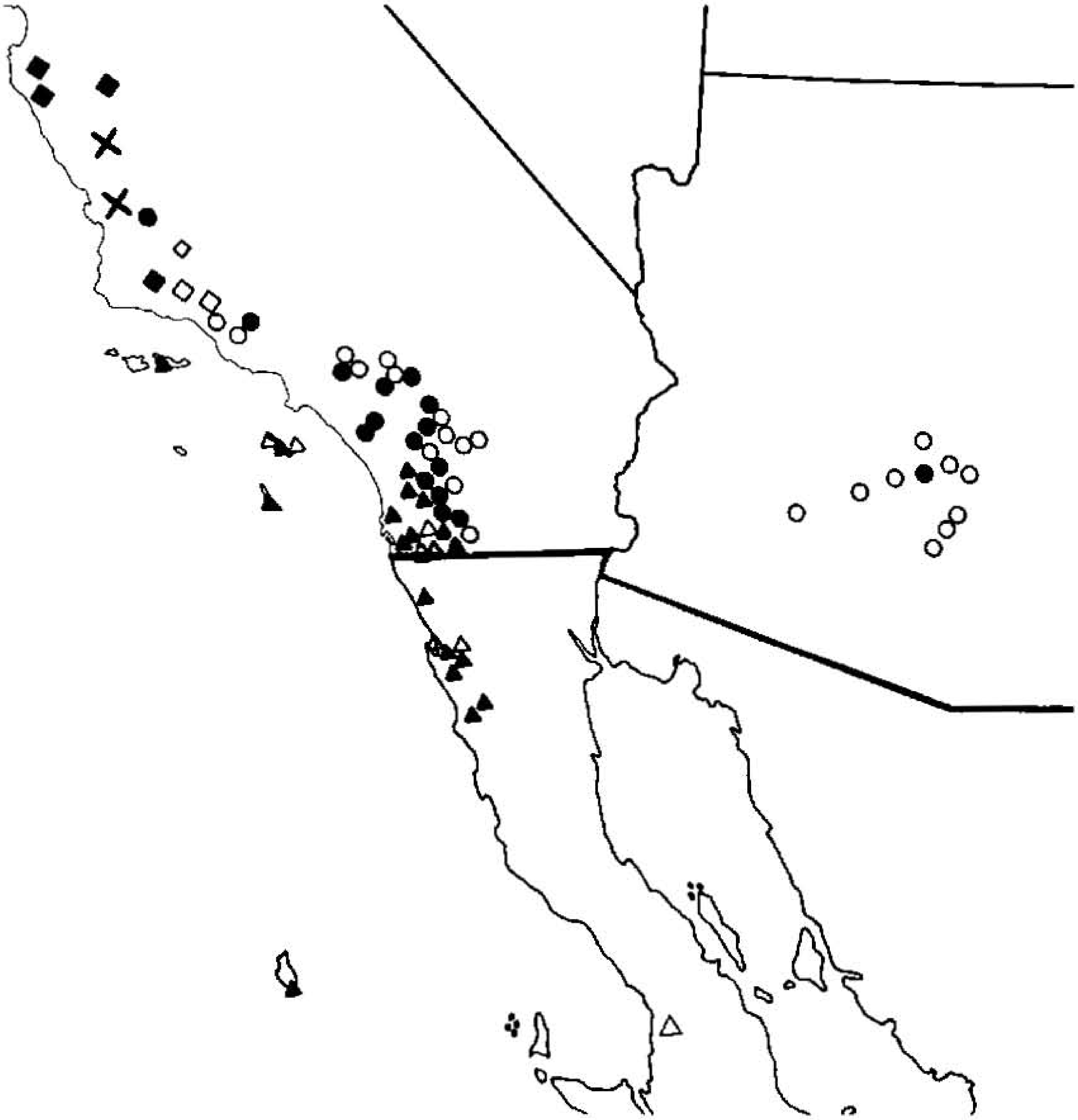


FIGURE 52.—Portion of the southwestern United States and northwestern Mexico, showing the ranges of species of *Camissonia* sect. *Holostigma:* ○=*C. confusa*, with ●=tetraploid chromosome counts ($n=14$); ×=*C. hardhamiae;* ◇=*C. luciae*, with ◆=hexaploid chromosome counts ($n=21$); △=*C. robusta*, with ▲=hexaploid counts ($n=21$).

ft., *Wittbank* 143 (US); Collom Camp, Mazatzal Mts., 1,200 m, *Collom* 268 (ARIZ, US). MOHAVE CO.: Tempe, *Gamong & Blaschke* in 1892 (US); 12.1 mi. SW. of Roosevelt on State Hwy. 88, 2,300 ft., *Gregory* 60B (DS, RSA, UC); Oak Flats, mountains between Miami and Superior, *A. & R. A. Nelson* 1858 (K, RM); 6 mi. SW. of Superior, *Russell* 11271 (OSC); Paradise Valley, 25 mi. N. of Phoenix, *Peebles et al.* 5102 (ARIZ, US); 25 mi. E. Scottsdale on Beeline Hwy., 1,160 ft., *Kennedy* 98 (DS); on canyon road 12 mi. from Apache Lodge, *Eastwood* 17161 (CAS). PINAL CO.: Superstition Mt., *Beckett* 10784 (ARIZ); Sacaton, *Peebles & Harrison* 1759 (US); sandy washes of the Gila R. near Casa Grande Ruins, *A. & R. A. Nelson* 1677 (RM). CALIFORNIA: ORANGE CO.: Lower San Juan Campground, *Bates* 2318 (DS). RIVERSIDE CO.: 3.6 mi. NE. of Aguanga, *Vestal* 63113.8 (DS); Main Divide Truck Trail at Ortega Hwy., Santa Ana Mts., 2,300 ft., R17763 (DS); ca. 4 mi. E. of Redlands, *Klein et al.* 265 (DS); 10 mi. S. of Hemet, *Munz* 10819 (POM, SBM); 18 mi. from Banning on road to Idyllwild, 5,000 ft., *Munz* 8142 (GH, POM). SAN BERNARDINO CO.: Oak Glen, *Munz & Hitchcock* 10916 (GH, POM); San Antonio Canyon, San Gabriel Mts., 5,500 ft., *Peirson* 2706 (POM, RSA); N. of Upland, *Breitung* 15060 (DAO); foothills, San Bernardino Mts., *Parish* in 1891 (NY). SAN DIEGO CO.: 3.1 mi. from U.S. Hwy. 80 on road to Morena L., 3,400 ft., R17439 (DS); Banner, *Keck et al.* 6089 (NY); 1 mi. E. of Warners Ranch, 3,400 ft., *McCully* 19 (POM); 6 mi. N. of Santa Ysabel, *Munz* 9808 (POM).

Camissonia confusa is a rather rare allotetraploid species which can readily be confused with certain populations of either of its presumed diploid parents, *C. hirtella* and *C. pallida* subsp. *pallida*. The problems of separating it from its two putative ancestors have been discussed under the treatments of the diploids, and it should be reemphasized at this point that further chromosome counts are badly needed from Arizona. As mentioned in the treatment of *C. ignota*, many of the collections of *C. confusa* have been confused with that diploid entity, and it is possible that *C. ignota* may have participated in the origin of some of the tetraploid populations here referred to *C. confusa*.

The chromosome number of *C. confusa* has been determined in 29 individuals from 22 populations, including the type collection (see Appendix). It has been observed growing sympatrically with *C. bistorta*, *C. micrantha*, *C. hirtella*, *C. ignota* and *C. intermedia*. North of San Bernardino County, California, populations are very scattered, but the following collection from Santa Barbara County may belong here: canyon of Mono Creek, 1,600 ft., upper Santa Ynez River watershed, *Chandler* 1460 (SBBG). The plants represented in this collection are immature, and the species is otherwise not known from Santa Barbara County.

37. **Camissonia hardhamiae** Raven, sp. nov. FIGURE 47

Herba annua robusta villosa pilis glandulosis brevioribus admixta, ad *C. intermedia* similis. Folia superiora lanceolata vel anguste ovata. Hypanthium 1.7–2 mm. longum, ostio 1.3–1.5 mm. diametro. Sepala 1.8–3.2 mm. longa, 0.8–1.2 mm. lata. Petala 2–4 mm. longa, 1.8–3.5 mm. lata, immaculata. Filamenta staminum episepalorum 1.5–2 mm.

longa, illa epipetalorum 1–1.5 mm. longa; antherae ca. 0.7 mm. longae. Pollinis granorum 70–80 per centum, 4– vel 5–porum. Stylus 3–4 mm. longus; stigma 0.7–1 mm. diametro, sub anthesi antheris circumnexum. Capsula 1.3–2.5 cm. longa, 1.3–1.6 mm. crassa surrecta vel in spiram unam contorta. Semina ca. 1.2 mm. longa, 0.6–0.7 mm. crassa. Chromosomatum numerus gameticus, $n=21$. Autogama.

TYPE: Calf Canyon, 3.7 miles northeast of Santa Margarita, San Luis Obispo County, California, 5 May 1963, *P. H. Raven* 18315 (DS 516765).

DISTRIBUTION (Figure 52): Very local, known only from a few localities in sandy soil in disturbed oak woodland, southernmost Monterey to central San Luis Obispo County, California; ca. 800–ca. 2,000 ft. alt.

SPECIMENS EXAMINED:

U.S.: CALIFORNIA: MONTEREY CO.: Sandy Valley, Big Sandy ca. 1.5 mi. NE. of intersection with Indian Valley Road, *Hardham* 10035A (DS). SAN LUIS OBISPO CO.: 4.5 mi. NE. of Santa Margarita, *Linsley & MacSwain* 59–87 (RSA), 59–88 (RSA), *Thorp* 62–33 (DS); 1.1 mi. N. of intersection with Parkhill Road on Calf Canyon Road, *Hardham* 2293 (LA); 1 mi. E. of Red Eagle Mine, 12 mi. S. of Shandon, *McMillan* 105 (CAS).

This local hexaploid species has almost certainly been derived from the diploid *C. micrantha* and the tetraploid *C. intermedia*, both of which grow in the area of *C. hardhamiae*. The hexaploid is quite similar to *C. micrantha*, but it can easily be distinguished by an examination of the pollen, *C. micrantha* having only an occasional 4-pored grain. *Camissonia hardhamiae* has broader leaves and thicker capsules than *C. micrantha* and is generally more robust. Its chromosome number has been determined in single plants from 3 populations, including the type collection (see Appendix). It has been found growing sympatrically with *C. micrantha* and *C. hirtella*.

Cammissonia hardhamiae is named in honor of Clare B. Hardham of Paso Robles, California, enthusiastic student of the flora of the area where it grows. Mrs. Hardham has contributed much to our knowledge of the flora of her area through her numerous collections.

38. Camissonia luciae Raven, sp. nov. FIGURE 49

Oenothera hirta var. *jonesii* sensu Munz, Bot. Gaz. 85: 262. 1928; pro parte.
Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 160. 1965; pro parte.

Herba annua erecta robusta villosa eglandulosa, ad *C. micrantha* similis. Folia superiora lanceolata, 1.3–5.5 cm. longa, 1.2–2.5 cm. lata, basi rotundata vel truncata, apice acuminata, sessilia, sparse denticulata. Inflorescentia plerumque cinereo-pubescens. Hypanthium 2–3 mm. longum, ostio 1.5–1.8 mm. diametro. Sepala 2.5–4.5 mm. longa, 1–1.8 mm. lata. Petala 4–7 mm. longa, 2.2–5 mm. lata, saepe mucronata, plerumque prope basin puncto rubro uno. Filamenta staminum episepalorum 1.2–6 mm. longa, illa epipetalorum 0.8–1.6 mm. lata; antherae 0.4–1 mm. longae. Pollinis granorum 25–60 percentum quadriporum. Stylus 3–6 mm. longus; stigma 1–1.2 mm. diametro, sub anthesi antheris staminorum longiorum vel rarissime et longiorum et breviorum circumnexum. Capsula ca. 1.5–2 cm. longa, 1.3–2 mm. crassa, transectione quadrangularis exsiccatis, subteretis in statu vivo non dessicata, in spiras 1.5–2+ contorta. Semina 1.3–1.5 mm. longa, 0.7–0.8 mm. crassa. Chromosomatum numerus gameticus, $n=21$. Autogama.

TYPE: Openings in *Adenostoma* chaparral, The Indians, 2,200 ft., Santa Lucia Mountains, Monterey County, California, 3 May 1963, *P. H. Raven* 18267 (DS 545885).

DISTRIBUTION (Figure 52): Locally common in openings in the chaparral, Santa Lucia Mountains, Monterey County, California, and scattered southward to San Benito, San Luis Obispo, and Santa Barbara Counties; 1,000–4,500 ft. alt.

SPECIMENS EXAMINED:

U.S.: CALIFORNIA: MONTEREY CO., SANTA LUCIA MTS.: Hastings Reservation, near Jamesburg, *Hoover* 2963 (POM, RSA, UC), 2964 (POM, RSA, UC), *Linsdale* 43 (CAS), 123 (COLO), in 1943 (CAS), *Cook & Cook* 842 (CAS, mix with *C. intermedia*), 680 (CAS); Conejo Creek 2 mi. below Jamesburg, *Bacigalupi* 1143 (DS, POM); road to Jamesburg 0.8 mi. from main road up Carmel Valley, R18226 (DS); The Indians, 2,200 ft., *Hardham* 5443a (CAS, RSA); trail to Ventana Double Cone between Pat Springs and Puerto Suelo, 4,000 ft., *Hardham* 10151 (DS, with *C. hirtella*); Tassajara Springs, *Kelley* in 1917 (CAS, with *C. intermedia*); Cachagua Creek, Santa Lucia Mts., *Howell* 30253 (CAS). SAN LUIS OBISPO CO.: Bill Hill Ranch at the foot of Caliente Mt., Caliente Range, 2,300 ft., *Twisselmann* 3489 (CAS); Crocker Grade, *Hardham* 12548 (DS). SANTA BARBARA CO.: "Santa Barbara," *Elmer* 3943 (DS, F, POM, RSA; probably from above Santa Barbara, in the mountains); upper Cuyama Valley, *Hoffmann* in 1929 (POM); Pine Corral Potrero near Salisbury Potrero, 4,500 ft., Sierra Madre Mts., *Muller & Blakley* 1014 (DS, SBBG); trail to Zaca Peak, *Eastwood* 616 (CAS); Miranda Pine Mt., 3,250 ft., *Graham* 545 (UC).

Camissonia luciae is a hexaploid species that parallels the widespread diploid *C. hirtella* in the variable notching of its petals. Presumably it has been derived from the diploid *C. hirtella* and the tetraploid *C. intermedia*, but it is rather easily separated from both by its relatively large flowers and pollen characteristics. The chromosome number of *C. luciae* has been determined in 7 individuals derived from as many populations, and including the type collection (see Appendix). It has been found growing sympatrically with *C. micrantha*, *C. hirtella*, and *C. intermedia*, especially often with the last-mentioned species.

39. Camissonia robusta Raven, sp. nov. FIGURE 41

Oenothera micrantha sensu Munz, N. Amer. Fl. II. 5: 160. 1965; pro parte.

Herba annua erecta robusta villosa, ad *C. micrantha* similis. Folia superiora latiora quam in *C. micrantha*, usque ad 12 cm. longa et 2 cm. lata. Inflorescentia semper pilis brevioribus glandulosis admixta. Hypanthium 1.8–3.7 mm. longa, ostio 1–2 mm. diametro. Sepala 2.6–4.2 mm. longa, 1.1–1.8 mm. lata. Petala 3.2–7 mm. longa, 2.5–6 mm. lata, plerumque prope basin puncto rubro uno vel punctis duabus. Filamenta staminum episepalorum 1.8–3 mm. longa, illa epipetalorum 1–1.5 mm. longa; antherae 0.8–1. 6 mm. longae. Pollinis granorum maximam partem 4-porum, rariore 5- vel 3-porum. Stylus 3–6.2 mm. longus; stigma 1–1.5 mm. diametro, sub anthesi antheris staminorum longiorum circumnexum. Capsula 1.4–2.5 cm. longa, 1.5–2 mm. crassa, transectione subquadrangularis in statu vivo, surrecta vel in spiram unam contorta. Semina 0.9–1.2 mm. longa, 0.6–6.7 mm. crassa. Chromosomatum numerus gameticus, $n=21$. Autogama.

TYPE: Disturbed soil along roadside, with *Orthocarpus purpurascens*, *Eschscholzia*, *Brassica*, near kilometer 201, 5.5 miles south of San Vicente, 950 ft., Baja California, 29 March 1962, *P. H. Raven* 17022 (DS 516799).

DISTRIBUTION (Figure 52): Coastal sage or chaparral, often in disturbed or open places, coastal San Diego County, California, and coastal northwestern Baja California, south to the vicinity of El Rosario at about 30° N. lat.; also on Santa Cruz, Santa Catalina, San Clemente, and Guadalupe Islands. From sea level to about 1,000 ft. alt. (to 3,500 ft. on Guadalupe Island).

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: LOS ANGELES CO. SANTA CATALINA I.: Avalon, *Trask* in 1896 (NY, UC, US). SAN CLEMENTE I.: Vicinity of Mosquito Harbor, *Abrams & Wiggins* 345 (DS, UC); N. coast, *Trask* 194 (NY, US); canyon S. of Lemon Tank, W. coast, *Munz* 6743 (POM). SAN DIEGO CO.: U.S. Hwy. 395, 2 mi. S. of turn to Lilac, R17458 (DS); 2 mi. E. of Pala, *Munz* 10364 (POM); 2 mi. E. of San Pasqual, R17408 (DS); Howard Canyon, La Jolla, *F. E. & E. S. Clements* 183 (COLO, F, GH, NY, PH, UC, UCSB); N. of Pt. Loma, *Stover* 149 (SD); bank of Dulzura Creek 3 mi. below Dulzura, *Wiggins* 2176 (CAS, DS, UC, WTU); Sweetwater R., base of San Miguel Mt., *Gander* 154.4 (POM, SD). SANTA BARBARA CO., SANTA CRUZ I.: Vicinity of Pelican Bay, *Abrams & Wiggins* 41 (F).

BAJA CALIFORNIA: Nachoguero Valley, *Schoenfeldt* 3409; Ensenada, *Bates* 2341 (DS); Todos Santos Bay, *Fish* in 1882 (F, UC); 6 mi. E. of El Rosario, *Wiggins* 17889 (DS); 6 mi. N. of Rancho Mesquital, *Wiggins* 16767 (DS). GUADALUPE I.: Near mouth of canyon at Northeast Anchorage, *Moran* 2891 (CAS, DS, GH, RSA); Northeast Anchorage, *Wiggins & Ernst* 222 (DS, UC), *Moran* 5661 (CAS, DS, RSA, SD, UC); near spring at top of island, N. end, ca. 1,200 m, *Lindsay* in 1948 (SD); Barracks Cove Cañon, *Copp* 151 (DS).

Camissonia robusta is one of the commoner species of its group throughout its mainland area, and the commonest species of the section on Santa Catalina Island. On Santa Cruz Island this species is very rare. On San Clemente and Guadalupe Islands, the only other species of the section is the very different *C. quadalupensis*, but the two species are ecologically different and not known to grow together. The pollen of *C. robusta* is absolutely diagnostic, and its stout capsules, which are evidently quadrangular but not nearly so sharply so in living material as are those of *C. lewisii*, and erect, robust habit make this species distinctive in gross morphology also. It has been collected growing sympatrically with *Camissonia bistorta*, *C. lewisii*, *C. micrantha*, *C. hirtella*, and *C. intermedia*.

The chromosome number of *Camissonia robusta* has been determined in 29 individuals derived from 24 populations from localities scattered throughout the range of the species, including the type collection (see Appendix). This hexaploid is almost certainly derived from two species with which it occurs nearly throughout its rather limited range, the diploid *C. lewisii* and the tetraploid *C. intermedia*. It is morphologically intermediate between these two entities in all respects, although on the average somewhat more robust.

Moran (Madroño 11: 160. 1951; as *Oenothera micrantha*) has suggested that this species might be introduced on Guadalupe Island, where it was first collected in 1948. He bases his argument largely on the fact that this species was not discovered by any of a succession of collectors who visited the island and inevitably landed in the same region where *C. robusta* is now fairly common. This may be true, but judging from the phytogeographic relationships of Guadalupe Island and the scarcity of this species on San Clemente Island, I believe that it is equally likely that the species may simply have gone undetected and become more common recently. It will probably not be possible to resolve this question definitely.

Section VI. *Camissonia*

Camissonia sect. *Camissonia*

Oenothera sect. *Sphaerostigma* Seringe, *in* DC., Prod. 3: 46. 1828.

Oenothera subg. *Sphaerostigma* (Seringe) Torr. & Gray, Fl. N. Amer. 1: 508. 1840.

Camissonia sect. *Sphaerostigma* (Seringe) Raven, Brittonia 16: 284. 1964.

Annuals, the plants caulescent, with no well-defined basal rosette, but the leaves sometimes clustered near the base, plants not flowering from the base. Leaves narrow, subsessile. Inflorescence nodding at anthesis, becoming erect in fruit. Flowers opening near sunrise. Ovary lacking a sterile projection. Sepals reflexed singly or in pairs. Petals yellow, often with one to several red dots near the base, fading reddish, with no contrasting pattern visible in ultraviolet light. Stamens, style, and inside of hypanthium yellow, the stigma yellow or greenish yellow. Capsule regularly loculicidal, straight or somewhat flexuous, subterete, more or less torulose, the seeds in one row in each locule, the friable central column much distorted by the seeds at maturity. Seeds with a scar at the micropylar end, blunt at the chalazal end, shining, dark brown, minutely lacunose, narrowly obovoid, more or less triangular in transection.

TYPE SPECIES: *Camissonia dentata* (Cav.) Reiche.

DISTRIBUTION: Brushy or open slopes and flats, southern Vancouver Island, British Columbia, southern Washington, southern Idaho, and western Wyoming south to western Colorado, central and northern Nevada, and throughout California to northernmost western Baja California (south to about 30°43′ N. lat.); said to have been collected once at Fort Huachuca, southern Arizona; also in western South America, mostly west of the Andes, from Arequipo (ca. 16° S. lat.), southern Peru to the vicinity of Lago Argentino and Santa Cruz (ca. 50° S. lat.), in Patagonia.

Camissonia sect. *Camissonia* is a close-knit group divided herein into 12 species with 4 additional subspecies. Two of these, *C. kernensis* and *C. campestris*, are self-incompatible diploids; two others, *C. pusilla* and *C. sierrae*, are self-compatible diploids; one is an autogamous hexaploid; and the remaining seven are autogamous tetraploids. One obviously closely interrelated group of species comprise the self-incompatible diploid *C. kernensis*, the autogamous diploid *C. pusilla*, and the two autogamous tetraploids *C. pubens* and *C. parvula*. These species differ from the others in their Great Basin habitat, and in having the sepals separating from one another when the flowers open. In the remaining species the sepals remain united in pairs. Relationships within this group are close, and the populations included here have generally been regarded as comprising only two species, the self-incompatible *C. campestris* (usually known, incorrectly, as *Oenothera dentata*) and the autogamous *C. contorta* (usually divided into *Oenothera contorta* var. *typica* and *O. contorta* var. *strigulosa*). The species that I have named *C. sierrae*, *C. benitensis*, and *C. integrifolia* have hitherto been too poorly represented in collections to attract attention; *C. lacustris* has been confused with *C. campestris* and *C. contorta* (sens. lat.); and the extremely closely related trio consisting of the tetraploid *C. strigulosa*, the hexaploid *C. contorta*, and the South American tetraploid *C. dentata* (some populations with $n=13$, the only instance of aneuploidy known in the genus) has in North America been regarded as comprising *Oenothera contorta* var. *strigulosa*, var. *epilobioides*, and var. *contorta*, the lines between these taxa not corresponding to those between the species recognized here. These might all conservatively be treated as *C. dentata* sens. lat., but I prefer to keep them separate for reasons that will be discussed in some detail below.

Camissonia kernensis subsp. *kernensis* was initially attributed to *Oenothera* subg. *Chylismia*, but I excluded it from that group in 1962 (Univ. Calif. Publ. Bot. 34: 115). On the other hand, *C. kernensis* subsp. *gilmanii* was first described as a variety of *C. campestris* ("*Oenothera dentata*"); I pointed out the conspecificity of the two taxa here grouped as *C. kernensis* to Dr. Munz in 1963, and he brought them together in 1965 (N. Amer. Fl. II. 5: 158–159). Part of what is here regarded as *C. kernensis* subsp. *gilmanii* was included by Munz (Bot. Gaz. 85: 259. 1928) in his concept of *Oenothera dentata* var. *johnstonii*, the type of which is *Camissonia campestris*. In the same 1928 treatment, Munz included all of the autogamous entities in this group in *Oenothera contorta*, with his var. *pubens* corresponding to *C. pubens*, his var. *flexuosa* to *C. pusilla* and *C. parvula*, his var. *typica* to much of *C. contorta*, and his var. *epilobioides* and var. *strigulosa* including the other autogamous taxa known to him.

Determinations of chromosome number, and in many cases pairing, have been made of 177 individuals from 166 populations of this section, including a few counts reported earlier by Lewis, Raven, Venkatesh, & Wedberg (Aliso 4: 73–86. 1958) and two reported by Gregory & Klein (Aliso 4: 505–521. 1960). The chromosome number for *Camissonia campestris* (as *Sphaerostigma dentatum* and var. *campestre*) was reported by Johansen (Proc. Nat. Acad. Sci. U.S. 15: 884. 1929; Amer. Journ. Bot. 16: 597. 1929), but without any indication of voucher specimens. As far as I know, these are all of the available reports for the section.

The degree of chromosomal structural heterozygosity in this section is low: of the 35 individuals of *Camissonia campestris* subsp. *campestris* examined, 3 had a ring of 4 chromosomes and 5 pairs and 1 had a chain of 3 plus a univalent and 5 pairs. Considering the two self-incompatible species in the section, *C. campestris* and *C. kernensis*, 49 individuals have been examined chromosomally, with the 4 just indicated being the only ones that were heterozygous—approximately 2 percent of the total. This is much lower than the more than 20 percent of 676 individuals of sect. *Chylismia* that were heterozygous for at least one reciprocal translocation, but significantly higher than in sect. *Holostigma*, where reciprocal translocations appear to play no role whatever in natural populations.

Several interploid natural hybrids, discussed in the following pages, shed light on the pattern of chromosomal evolution in sect. *Camissonia*. For example, in hybrids between the diploid ($n = 7$) *C. campestris* subsp. *campestris* and the hexaploid ($n = 21$) *C. contorta*, the maximum association of chromosomes observed was a chain of 8 chromosomes, a ring of 4, 2 chains of 4, 2 ring bivalents, and 2 rod bivalents. It is therefore obvious that the complete absence of multivalent configurations in the hexaploid is genetically controlled, and does not reflect any great degree of differentiation between the three genomes present in this species. No multivalents have been found in any polyploid in this section, and it would appear that even if the two diploid genomes present in a tetraploid would, on the basis of their homology, pair completely, they are prevented from doing this genetically. Natural hybrids between the tetraploids *C. integrifolia* and *C. strigulosa*, with up to 10 bivalents, and artificial hybrids between the North American tetraploid *C. strigulosa* and the South American tetraploid *C. dentata*, which show few multivalent associations despite their high degree of sterility, tend to support this hypothesis (Raven & Moore, MS.).

In sect. *Camissonia*, therefore, it appears that diploid genomes may be brought together in any way that will produce highly fit combinations for particular ecological situations, and that these polyploids will soon (perhaps initially) be pair-forming and highly fertile regardless of the degree of chromosomal divergence between their diploid antecedents. There appears to be a wide gap between the group of species consisting of *C. kernensis*, *C. pusilla*, *C. pubens*, and *C. parvula*, and the other species of the section; none of the polyploids appears to bridge the gap between these two groups.

The synonymous name *Onothera torulosa* H. Lév., Monogr. Onoth. 176. 1905, requires special mention here; this name was an illegitimate substitute for most of the species in this section published earlier, and it is not practical to cite it in the synonymy of all of these names or to attempt to typify it by one of these concepts; as far as I know, the concept has never been taken up by any author other than Léveillé.

40. Camissonia kernensis (Munz) Raven, Brittonia 16: 284. 1964.

Robust, erect annual, often well branched, from a prominent or poorly developed basal rosette, the plants 5–30 cm. tall, densely villous or glandular pubescent to subglabrous. Leaves very narrowly to narrowly elliptic, more rarely lanceolate, 1–3.8 (–5.5) cm. long, 0.2–0.5 cm. wide, sparsely serrate, the apex acuminate, the base narrowly cuneate, much reduced and bract-like in the inflorescence. Inflorescence usually densely glandular-pubescent, sometimes with an admixture of longer trichomes. Hypanthium 2.2–3.8 (–5) mm. long, 1.8–2.8 (–4) mm. across at the summit, villous within, with a red dot within at the base of each anther. Sepals 5–9 (–11) mm. long, 1.3–2 mm. wide, reflexed separately. Petals 8–15 (–18) mm. long, 5.5–12 (–16) mm. wide, with two large red dots at the base of each one. Filaments of the episepalous stamens 3.5–5.5 (–7) mm. long, those of the epipetalous ones 1.3–2 (–4.5) mm. long; anthers 1.8–2 (–3) mm. long. Style 7–10 (–14) mm. long, villous near the base; stigma 1–2 (–2.5) mm. in diameter, held well above the anthers at anthesis. Capsule 2.2–3.7 cm. long, 1.5–1.7 mm. thick, subsessile or on a pedicel up to 15 mm. long. Seeds 1.1–1.2 mm. long, 0.5–0.6 mm. thick. Gametic chromosome number, $n = 7$. Self-incompatible.

DISTRIBUTION (Figure 46): Desert washes and in canyons, northeastern Kern County to near Victorville and the Providence Mountains in San Bernardino County, southern Inyo County, and near Benton Station, southern Mono County, California; also in western Clark and Nye Counties, Nevada; 2,500–6,000 ft. alt.

Although most populations of the two subspecies comprising this species are easily assignable to one or the other, a number of others are intermediate and assignable only with great difficulty. Collectively, the species is sharply distinct from all others in its flower size, pubescence, and sepal characteristics.

40a. Camissonia kernensis subsp. kernensis

Oenothera kernensis Munz, Amer. Journ. Bot. 18: 737. 1931.
Oenothera kernensis subsp. *kernensis*; Munz, N. Amer. Fl. II, 5: 159. 1965.

Plants compact, 5–15 (–22) cm. tall, covered everywhere with long, white trichomes, the leaves clustered at the base. Capsule on a prominent pedicel 3–15 mm. long. Gametic chromosome number, $n = 7$. Self-incompatible.

TYPE: Sandy slopes and openings, east slope of Walker Pass, Freeman Canyon, 4,500 ft., Kern County, California, 13 May 1930, *F. W. Peirson* 8822 (POM; isotype, K).

DISTRIBUTION (Figure 46): Sandy slopes and flats, often with *Artemisia tridentata* and *Yucca brevifolia*, northeastern Kern County, California, from El Paso Peaks to the vicinity of Claraville and near Lake Isabella, north to Grapevine Canyon; 2,800–5,700 ft. alt. Often locally abundant.

Vouchers for chromosome number (4 individuals, 3 populations), $n = 7$:

U.S.: CALIFORNIA: KERN CO.: Walker Pass, W. slope, 5,000 ft., *Munz* 22581 (DS, RSA): 2.8 mi. W. of summit of Walker Pass, R12811; Freeman Canyon 3.4 mi. E. of summit of Walker Pass, R12763 (2 plants: ARIZ, DS, GH, SD, UC, US, WTU).

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: KERN CO.: Grapevine Canyon, 2,800 ft., *Twisselmann* 7117 (CAS, mixture with *C. campestris*); upper end of Short Canyon, *Linsley & MacSwain* 60–18 (RSA, UC); head of Indian Wells Canyon, 5,700 ft., *Twisselmann* 4525 (CAS, DS); NE. flank of Morris Peak, 4,175 ft., *Twisselmann* 7140 (CAS, DS, SBBG); Horse Canyon, Scodie (Kiavah) Mt., 5,300 ft., *Twisselmann* 8178 (CAS, DS, RSA); Weldon, 2,400 ft, R17559 (DS); 9.7 mi. S. of Weldon, 3,100 ft., R17563 (DS); 5 mi. NW. of Dove Well, *Rude* 408 (DS); divide between Kelso Canyon and Kelso Valley, 4,650 ft., *Twisselmann* 6912 (CAS, DS); Piute Mts., Harris Grade above Kelso Canyon, 3.1 mi. W. of Shorty's Place, 5,420 ft., *Twisselmann* 2799 (CAS); Erskine Creek, 4–5,000 ft., *Purpus* 5083 (UC, mixture with *C. hirtella*); Iron Canyon, El Paso Mts., ca. 3,300 ft., *Budgett* 30 (CAS); Dove Spring Canyon 25 mi. SW. of Inyokern, *Budgett* 54 (CAS).

First described as a member of *Oenothera* subg. *Chylismia* because of its stalked capsule, *Camissonia kernensis* subsp. *kernensis* is in the overwhelming majority of its characteristics obviously a member of sect. *Camissonia*. At the margins of its rather restricted range, it intergrades completely with *C. kernensis* subsp. *gilmanii* (*Oenothera dentata* var. *gilmanii*), an undoubted member of this group. Ten plants from the locality of R17559, cited above, were tested for self-incompatibility by caging the plants in the field and selfing and outcrossing them, with subsequent examination of pollen-tube growth. All were found to be self-incompatible. *Camissonia kernensis* subsp. *kernensis* is, at the head of Short Canyon, the principal pollen source of the large oligolectic bee *Andrena* (*Onagrandrena*) *mojavensis* Linsley & MacSwain, not known from any other locality (Linsley, MacSwain, & Raven, Univ. Calif. Publ. Entom. 33: 59–98. 1964). Other oligolectic species of *Onagrandrena* likewise visit the plant here and on Walker Pass and are undoubtedly important in the outcrossing of these self-incompatible individuals. The flowers of *Camissonia kernensis* subsp. *kernensis* open before sunrise, and considerably before those of *C. campestris* at most of its localities (Linsley et al., op. cit.).

Camissonia kernensis subsp. *kernensis* grows sympatrically with *C. campestris*, which like it is self-incompatible at a number of localities; no hybrids have been observed, even when, as at Short Canyon, Kern County, California, the plants grow intermixed and are known to be visited by the same species of bees. *Camissonia kernensis* subsp. *kernensis* likewise grows sympatrically with *C. pubens*, *C. strigulosa*, *C. integrifolia*, and *C. contorta*.

40b. Camissonia kernensis subsp. **gilmanii** (Munz) Raven, comb. nov.

Oenothera dentata var. *johnstonii* sensu Munz, Bot. Gaz. 28: 259. 1928; pro parte.

Oenothera dentata var. *gilmanii* Munz, Leafl. West. Bot. 2: 87. 1938. *Oenothera kernensis* subsp. *gilmanii* (Munz) Munz, N. Amer. Fl. II. 5: 159. 1965.

Oenothera kernensis subsp. *mojavensis* Munz, N. Amer. Fl. II. 5: 159. 1965. Type: 3 mi. W. of Pilot Knob, 900 m, western San Bernardino Co., Calif., 20 March 1947, *P. A. Munz* 11666 (RSA 38224; isotypes, ARIZ, CAS, COLO, SD, WTU).

Plants less compact, to 30 cm. tall, covered everywhere with short glandular pubescence, usually with a few scattered longer trichomes, or subglabrous, with few glandular trichomes, the leaves not markedly clustered at the base. Capsule subsessile or on a pedicel to 5 mm. (rarely to 15 mm.) long. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Bradbury Wash, 3,000 ft., Inyo County, California, 6 June 1937, *M. F. Gilman* 2587 (POM).

DISTRIBUTION (Figure 46): Desert washes and slopes, from the vicinity of Red Rock Canyon, Kern County and Victorville and the

Providence Mountains, San Bernardino County, California, north to westernmost Clark and Nye Counties, Nevada, and the southern half of Inyo County, California; also collected once near Benton Station, southern Mono County, California. From 2,500–6,000 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

U.S.: CALIFORNIA: INYO CO.: Trona to Death Valley Road, N. base of Panamint Mts., edge of Panamint Valley, *Lewis & Mosquin* 1119; 5.4 mi. from Emigrant Junction on road to Wildrose Station, *Lewis & Mosquin* 1123. SAN BERNARDINO CO.: Dawes Siding, between Cima and Kelso, R11926; road to Camp Irwin 26.6 mi. N. of U.S. Hwy. 466 at Barstow, R11944. NEVADA: NYE CO.: Wash below Cane Springs, R18947.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: INYO CO.: 10 mi. N. of Shoshone on road to Bradbury Well, ca. 3,000 ft., *Hitchcock* 6106 (DS NY, POM, RM, RSA, US, WS, WTU); Great Falls Canyon, Argus Mts., *Wheeler & Richardson* in 1930 (CAS, F, LA, LAM, UC, US); Mill Creek Canyon, Panamint Mts., 1,300–1,700 m, *Coville & Funston* 759 (C, DS, GH, PH, US); Epsom Salt Works, Hidden Spring region S. of Wingate Wash, 2,000 ft., *Train* 568 (ARIZ, COLO, DS, OSC, US); Cave Springs, *Jaeger* in 1927 (POM); Lee District (N. of Darwin), at Grape Vine Spring, *Austin* 539 (UC); 6 mi. NE. of Pilot Knob, Meerchaum Spring, *Miller* in 1920 (CAS). KERN CO.: U.S. Hwy. 395, 5 mi. N. of Johannesburg, 3,150 ft., *Campbell* 13406 (RSA); Red Rock Canyon, 2,800 ft., *Benson* 3411 (POM); Haiwee, *Davidson* 2820 (LAM); E. fork of Last Chance Canyon, El Paso Mts., 3,000 ft., *Peñalosa* 473A (CAS). MONO CO.: Benton Station, 5,500 ft., *Robinson & Linder* in 1935 (Fresno State College herb.). SAN BERNARDINO CO.: County road from Wheaton Springs to Nipton road S., ca. 11 mi. N. of Cima, *Ferris & Bacigalupi* 13293 (ARIZ, DS, RM, US, WS, WTU); 10 mi. SW. of Garlic Spring, *Munz & Keck* 7869 (GH, POM); 2 mi. N. of third summit out of Barstow, 8 mi. SW. of Bicycle Lake, 2,800 ft., *Wolf* 6532 (ARIZ, DS, LA, NY, RM, RSA, UT, WS); 5 mi. E. of Cima, *Munz* 13947 (DS, POM, UC); 5 mi. W. of Columbia Mine, Providence Mts., 1 mi. E. of Union Pacific R.R., 3,300 ft., *Wolf* 10649 (DS, RSA, WTU); 8 mi. E. of Victorville, *Jaeger* in 1932 (POM). NEVADA: CLARK CO.: Nipton, 3,000ft., *Jones* in 1907 (POM); 5 mi. below Deer Creek, 6,000 ft., Charleston Mts., *Raedar* 181 (COLO); Frenchman Flat 11 mi. N. of Mercury, R18854 (DS). NYE CO.: W. of Cane Springs, ca. 4,000 ft., *Rickard & Beatley* in 1959 (RSA, UC); W. Yucca Flat Drainage Basin, 4,800 ft., *Beatley* 2924 (DS, RSA).

Plants of *Camissonia kernensis* subsp. *gilmanii* in the vicinity of Cima, San Bernardino County, California, approach those of subsp. *kernensis* in their relatively low stature and unusually abundant eglandular pubescence. Closer to the restricted range of subsp. *kernensis*, the two subspecies intergrade completely. In general, plants from the southern part of the range of subsp. *gilmanii* are relatively lower and less glandular, and often with more obviously crisped leaves, than those from farther north; it was on this basis that Munz described a third subspecies, *Oenothera kernensis* subsp. *mojavensis*. Study of more abundant herbarium material has convinced me that these trends do not need to be reflected in the formal taxonomy of the group, especially since the geographical separation of the two sorts of plants is not complete.

Camissonia kernensis subsp. *gilmanii* has been found growing sympatrically with *C. campestris* at several localities without any evidence of hybridization, even though both entities consist entirely of self-incompatible individuals and are generally visited by the same bee species. Thus, 3 miles west of Pilot Knob, San Bernardino County, California, at an elevation of ca. 3,400 ft., P. A. Munz collected these two entities growing together; here *C. kernensis* subsp. *gilmanii* was restricted to the higher ground, and often grew in coarse gravelly soil, whereas *C. campestris* grew in the loose sandy soil of a wash. A mixed collection from Red Rock Canyon, Kern County, California (*Brown* in 1946, LA) suggests that the two species grow sympatrically at this locality also. Similar ecological relationships were observed near the head of Short Canyon, Kern County, California, where *C. campestris* grows in the sandy soil of the wash bottom, while *C. kernensis* subsp. *kernensis* is largely restricted to more stable slopes at the head of the wash.

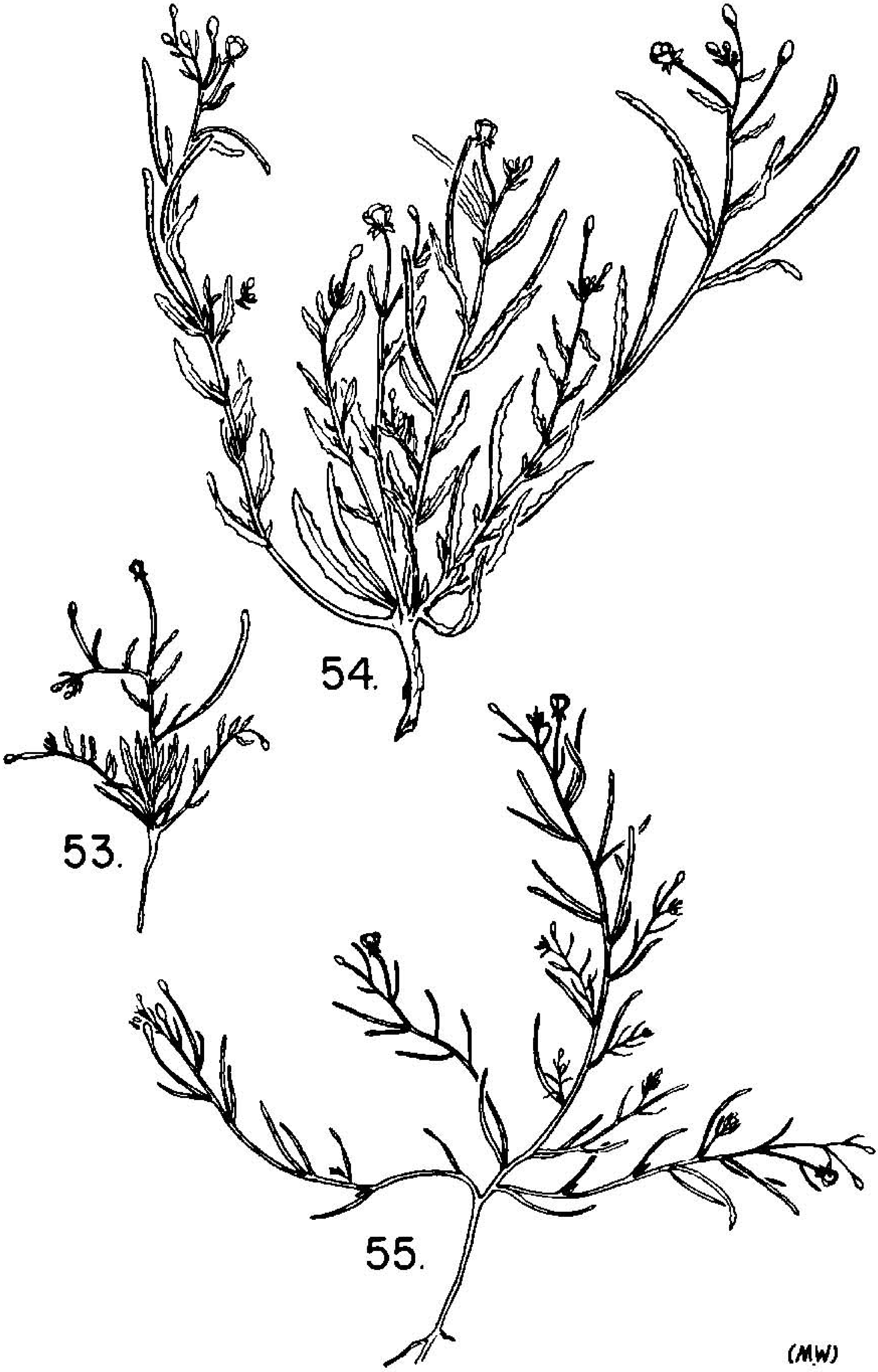
The self-incompatibility of *Camissonia kernensis* subsp. *gilmanii* was determined by pollen-tube growth following self- and cross-pollination in six individuals of R18947 from Nye County, Nevada, cited above.

41. Camissonia pusilla Raven, sp. nov. FIGURE 53

Oenothera contorta var. *flexuosa* sensu Munz, Bot. Gaz. 85: 253. 1928; and N. Amer. Fl. II. 5: 156. 1965; pro parte.

Herba annua tenuis 2–22 cm. alta, plerumque e basi ramis plurimis rosulaque bene evoluta. Plantae glanduloso-pubescentes, praecipue in inflorescentibus, et plerumque pilis longioribus eglandulosis admixtae, prope basin plantarum densiore. Folia linearia, 1–3 cm. longa, 0.4–1.8 mm. lata, plerumque purpureo-maculata, serrulata. Hypanthium 0.8–1.6 mm. longum, ostio 0.7–1.1 mm. diametro, intus glabrum. Sepala 1.2–2 mm. longa, 0.3–0.8 mm. lata, unumquidque sub anthesi discedens, alabastro apices sepalorum discreti. Petala 1.8–3.1 mm. longa, 0.8–1.5 mm. lata, rare prope basin punctibus duabus rubris maculata. Filamenta staminorum episepalorum 0.8–2 mm. longa, illa epipetalorum 0.4–0.9 mm. long; antherae 0.3–0.4 mm. longae. Stylus 1.6–3.2 mm. longus, glaber; stigma 0.5–1 mm. diametro sub anthesi antheris circumnexum. Capsula 1.8–3.2 cm. longa, 0.6–0.9 mm. crassa, subsessilis vel pedicelo usque ad 2 mm. longo, non rostrata. Semina 0.7–0.8 mm. longa, ca. 0.4 mm. crassa. Chromosomatum numerus gameticus, $n=7$. Autogama.

TYPE: On sagebrush (*Artemisia tridentata*) covered slopes 2.5 miles west of U.S. Hwy. 395 on U.S. Hwy. 50, 5,100 ft., Washoe County, Nevada, 28 May 1962, *P. H. Raven* 17867 (DS).



FIGURES 53–55.—Species of *Camissonia* sect. *Camissonia*, × ¾: 53, *C. pusilla* (*Raven* 17463, DS); 54, *C. pubens* (*Twisselmann* 7048, DS); 55, *C. parvula* (*Raven* 17864, DS).

Distribution (Figure 56): Scattered in sandy soil on open or brushy slopes, Franklin and Grant Counties, southeastern Washington, and Elmore and Payette Counties, west-central Idaho, south through the Great Basin to southern Inyo and the Providence Mountains of northeastern San Bernardino County, California; southern Nye County, Nevada; and Washington County, southwestern Utah;

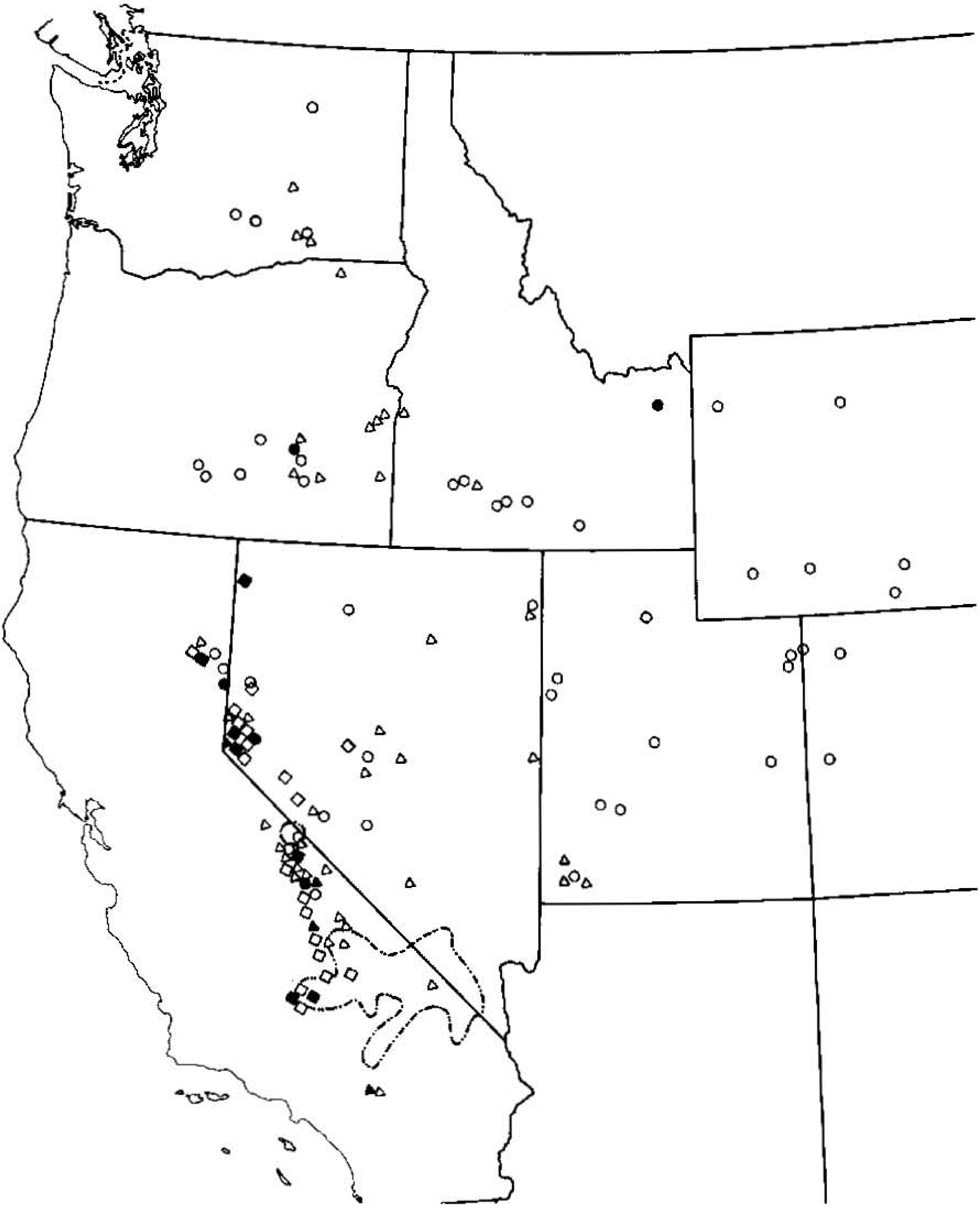


Figure 56.—Western United States, showing ranges of mainly autogamous species of *Camissonia* sect. *Camissonia*, the range of the related larger flowered, self-incompatible *C. kernensis* outlined by dotted line: △=*C. pusilla*, with ▲=diploid chromosome counts ($n=7$); ◇=*C. pubens*, with ◆=tetraploid counts ($n=14$); ○=*C. parvula*, with ●=tetraploid counts ($n=14$).

local in the eastern San Bernardino Mountains, San Bernardino County, California. From ca. 400–9,500 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

U.S.: CALIFORNIA: INYO CO.: Carroll Creek ca. 1 mi. above Mt. Whitney Pack Station, 5,900 ft., E. slope of the Sierra Nevada, R17541; ca. 4 mi. S. of Oasis, *Klein* 354 (RSA); near Black Ace Mine, just W. of summit of Westgard Pass, White Mts., *Lewis* 1091 (LA, RSA). SAN BERNARDINO CO.: Cactus Flat, San Bernardino Mts., 5,900 ft., R17463. NEVADA: WASHOE CO.: 2.5 mi. W. of U.S. Hwy. 395 on U.S. Hwy. 50, 5,100 ft., R17867 (type collection).

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: INYO CO.: 4 mi. W. of Lone Pine, 4,700 ft., *Alexander & Kellogg* 2786 (mixture with *C. parvula*); Lake Sabrina road, 8,500 ft., *Benson* 6020 (POM); Bishop Creek, 5,000 ft., *Hall & Chandler* 7244 (POM, UC); 0.5 mi. W. of Willow Spring, Last Chance Mts., 5,800 ft., *Roos* 6363 (CAS, DS, RSA, UC); Jackass Spring, Hunter Mt., Inyo Mts., 6,600 ft., *DeDecker* 1400 (RSA); Alabama Hills, 4,800 ft., *Howell* 33226; Lone Pine, 7,000 ft., *Jones* in 1897 (GH, NY, POM, US); Argus Mts., 5,800 ft., *Hall & Chandler* 7089 (UC); Wonoga Peak, 9,000–9,500 ft., *Howell* 25419 (CAS, RSA; with *C. pubens*); Mill Creek Canyon, Panamint Mts., 1,300–1,700 ft., *Coville & Funston* 762 (DS, NY, US); near Crystal Spring, Coso Mts., 1,850 m., *Coville & Funston* 938 (DS, NY, US). LASSEN CO.: 2 mi. N. of Susanville, *Gillespie* 9346 (DS). MONO CO.: Rock Creek, 6,700 ft., *Munz* 11785 (NY, RSA); near Benton, *Robinson & Linder* c26 (COLO, RSA, WTU), *Eastwood & Howell* 9547 (CAS, mixture with *C. parvula;* RSA); 5 mi. N. of Sherwin Grade, 1,750 m., *Munz* 11075 (C, GH, POM, UC, US); S. of Mono Lake, 4 mi. N. of Mono Mills, *Keck* 2882 (DS). SAN BERNARDINO CO.: 1 mi. SE. of Tecopa Pass, Kingston Range, *Alexander & Kellogg* 2365 (POM, UC); Cactus Flat, San Bernardino Mts., 6,000 ft., *Munz* 10519 (POM), *Jones* in 1926 (CAS, POM). IDAHO: ELMORE CO.: Glen's Ferry, *Davis* 85–36 (IDS). PAYETTE CO.: Willow Creek E. of Payette, *Christ* 9447 (NY) NEVADA: ELKO CO.: Cobre, 6,000 ft., *Jones* in 1906 (POM); Elko to Wendover road, *Hutchings* in 1932 (UT); Toana Range, 5 mi. E. of Shafter, *Maguire* 16892 (NY, mixture with *C. parvula*). ESMERALDA CO.: Candelaria, *Shockley* 247 (NY, mixture with *C. parvula*). EUREKA CO.: U.S. Hwy. 40, 2.9 mi. W. of Carlin, R18534 (DS). LANDER CO.: 3 mi. N. of Birch Creek, *J. M. & M. A. R. Linsdale* 780A (CAS). NYE CO.: Near Potts Ranch, near Potts, *Goodner & Henning* 330 (POM); 4 mi. S. of Millett, *J. M. & M. A. R. Linsdale* 694 (CAS); S. end of Rainier Mesa, 7,500 ft., *Beatley & Carl* 2616 (herb. Nevada Test Site, Mercury, Nev.). WASHOE CO.: 2 mi. SW. of Steamboat Springs, *Canby* 181 (POM); Truckee Pass, 4,500 ft., *Kennedy* 1306 (DS, RM, UC, US). WHITE PINE CO.: 2 mi. SW. of Baker, *Maguire* 20849 (UT). OREGON: Blue Mts., *Cusick* in 1897 (GH); eastern Oregon, *Howell* in 1880 (US). HARNEY CO.: Ca. 26 mi. S. of Folly Farm and near Manns Lake, *Hitchcock & Muhlick* 21131 (DS, RM, WS, WTU); 8 mi. W. of Riley, *Peck* 13840 (DS, F); Squaw Butte, *Gilkey* (OSC); 4.7 mi S. of Narrows, R18444 (DS). MALHEUR CO.: 4 mi. W. of Vale, *Peck* 20641 (UC); near Harper Ranch, 900 m., *Leiberg* 2221 (DS, F, GH, NY, POM, UC, US); ca. 15 mi. SW. of Vale, *Hitchcock* 20636 (WTU); Rome, *Peck* 21789 (UC). UTAH: IRON CO.: NE. of Enterprise, 5,500 ft., *Hall* EN16 (F, UT). WASHINGTON CO.: Anderson's Ranch, *Maguire & Blood* 1459 (POM, RM, UC); mountain meadows 50 mi. NW. of St. George, 1877, *Palmer* 166 (GH, NY). WASHINGTON: FRANKLIN CO.: Pasco, *Piper* 2965 (GH). GRANT CO.: Junction of Crab and Douglas Creeks, 2,000–3,000 ft., *Sandberg & Leiberg* 263 (C, CAS, DS, F, GH, NMC, NY, RM, UC, US, WS, WTU).

This diploid species is closely similar to the tetraploids *C. parvula* and *C. pubens,* differing from the former in its long, spreading trichomes and well-developed basal rosette and from the latter in its more slender habit, narrower leaves, and smaller flowers and seeds. At its type locality and elsewhere, *C. pusilla* grows sympatrically with *C. pubens,* and, as indicated above, it often grows sympatrically with *C. parvula;* at all such localities the entities are sharply distinct. On the other hand, northern populations of *C. pusilla* are occasionally somewhat difficult to distinguish from those of *C. parvula,* commoner northward, when the plants are relatively glabrous and depauperate, and chromosome counts from the northern localities of *C. pusilla* would be most helpful.

A collection said to be from Kramer, San Bernardino County, California, *K. Brandegee* in 1913 (UC), consists of a mixture of this species with *C. parvula;* the locality is very probably in error (cf. Raven, Univ. Calif. Publ. Bot. 34: 110. 1962).

Camissonia pusilla includes much of the material referred by Munz (Bot. Gaz. 85: 253–254. 1928; and subsequently) to *Oenothera contorta* var. *flexuosa,* that entity consisting of a mixture of this species, the tetraploid *C. parvula,* and misidentified specimens of the very different hexaploid *C. contorta.* In 1964 (Brittonia 16: 284. 1964), I considered *C. pusilla, C. parvula,* and *C. pubens* to be best regarded as comprising a single taxonomic species, *C. parvula;* I also annotated a number of specimens during the period when I held this view. On the other hand, Munz (N. Amer. Fl. II. 5: 156. 1965) recognized *C. pubens* as a distinct species, but unaccountably retained *C. parvula* and *C. pusilla* as *Oenothera contorta* var. *flexuosa* as he had done in 1928. As mentioned above, *C. contorta* is a very distinct hexaploid, in which the sepals are reflexed in pairs; however, depauperate individuals can sometimes be confused with those of *C. parvula.*

42. **Camissonia pubens** (S. Wats.) Raven, comb. nov. FIGURE 54

Chamissonia contorta var. *pubens* (S. Wats.) Kearney, Trans. N.Y. Acad. Sci. 14: 37. 1894.

Sphaerostigma contortum var. *pubens* (S. Wats.) Small, Bull. Torrey Cl. 23: 189. 1896.

Sphaerostigma pubens (S. Wats.) Rydb., Bull. Torrey Cl. 33: 146. 7 April 1906.

Sphaerostigma orthocarpum A. Nels. & Kennedy, Proc. Biol. Soc. Wash. 19: 155. 12 November 1906. Type: Pyramid Lake, Washoe Co., Nevada, 19 May 1905, *P. B. Kennedy* 1015a (RM).

Oenothera pubens (S. Wats.) Munz, N. Amer. Fl. II. 5: 156. 1965.

Similar to *C. pusilla,* but differing in the more robust habit, the stouter stems to 38 cm. long. Leaves narrowly lanceolate, 1.5–4.5 cm. long, 0.2–0.6 cm. wide, undulate-serrate, acuminate at the apex, narrowly cuneate at the base. Hypanthium 1.3–3 mm. long, 0.8–2 mm. wide at the summit, usually pubescent in lower half within, often with a small red dot at the base of each filament. Sepals 2.2–3.8 mm.

long, 0.8–1.3 mm. wide. Petals (2.2–) 3–4 mm. long, (1.3–) 1.8–3 mm. wide, often with one to several red dots near the base. Style 3.2–4.1 mm. long; stigma 1.2–1.4 mm. in diameter. Capsule (1.8–) 2.6–5 cm. long, 0.8–1.2 mm. thick. Seeds 1–1.1 mm. long, ca. 0.4 mm. thick. Gametic chromosome number, $n=14$.

Type: Carson City, Ormsby County, Nevada, May 1868, *S. Watson* (GH; isotype, US).

Distribution (Figure 56): Sandy, often sagebrush-covered slopes and flats from Lassen County, California, and northern Washoe County, Nevada, south to southwestern Lander and central Mineral Counties, Nevada, and southern Inyo and northeastern Kern Counties, California; 3,000–9,500 ft. alt.

Vouchers for chromosome number (9 individuals, 9 populations), $n=14$:

U.S.: California: KERN CO.: Weldon, R17537; 3.4 mi. E. of summit of Walker Pass, R12764. LASSEN CO.: 4.8 mi. N. of Milford, R17873. MONO CO.: 2.2 mi. S. of N. turn to Sherwin Grade, R14294. Nevada: ORMSBY CO.: U.S. Hwy. 50, 2 1 mi. W. of junction with U.S. Hwy. 395, R17862; 2 mi. S. of Carson City R18406. WASHOE CO.: 7.5 mi. S. of Vya, ca. 6,500 ft. R17883; 4.7 mi. W. of U.S. Hwy. 395 on road to Mt. Rose, 5,200 ft., R18410; 2.5 mi. W. of U.S. Hwy. 395 on U.S. Hwy. 50, 5,100 ft., R17866.

Representative specimens examined:

U.S.: California: INYO CO.: Wonoga Peak, 9,000–9,500 ft., *Howell* 25420 (CAS, RSA, US); near end of Mt. Whitney road, *Kerr* in 1937 (CAS); Carroll Creek, 5,500 ft., *Howell* 33378 (CAS); Olancha, *Hoffmann* in 1929 (CAS); Bishop Creek, 6,700 ft., *Howell* 33520 (CAS); 5 mi. W. of summit of Mountain Spring Canyon, *Hoffmann* in 1929 (POM); Onion Valley road, *Howell* 33430 (CAS); Sage Flat to Olancha Pass, ca. 7,000 ft., *Howell* 26701 (CAS); Taboose Creek, 6,500 ft., R9702 (CAS); Nine-mile Canyon, 5,000 ft., *Ripley & Barneby* 5867a (CAS); Snake Hill, 5 mi. W. of Independence, 5,000 ft., *Kerr* in 1937 (CAS). KERN CO.: 19 mi. above Weldon on road to Walker Pass, 4,500 ft., *Munz* 13357 (RSA, mixture with *C. strigulosa;* WTU); 1.9 mi. E. of summit of Walker Pass, R12814 (DS); W. slope of Walker Pass, near summit, *Twisselmann* 7048 (CAS, DS); Piute Mt. to Walker Basin road, 5,950 ft., *Twisselmann* 3650 (CAS); Weldon, R18790 (DS); Horn Brothers Sawmill 3.6 mi. W. of Claraville, Piute Mts., 6,200 ft., *Breedlove* 4008 (DS); Erskin Creek, 4,000–5,000 ft., *Purpus* 5365 (UC). LASSEN CO.: Honey Lake, *Brandegee* in 1892 (UC); between Susanville and Leavitt Lake, *Gillespie* 9351a (DS); vicinity of Doyle Station, 1,290 m, *Eggleston* 6741 (GH, NY, US). MONO CO.: Sonora Junction, 7,200 ft., *Ripley & Barneby* 5804 (CAS, NY). Nevada: DOUGLAS CO.: Clear Creek, 10 mi. SW. of Carson City, *Archer* 6055 (POM). LANDER CO.: Along roadside to Buzanes, ca. 25 mi. N. of Ione, *Goodner & Henning* 690 (DS, NY, POM). MINERAL CO.: E. slopes of Wassuk Range, near Big Indian Mt., 9,500 ft., *Archer* 7153 (ARIZ, POM); Hawthorne, *Jones* in 1882 (POM); 6–7 mi. from mouth, up Cory Creek, Wassuk Range, 7,400 ft., *Archer* 6951 (POM). ORMSBY CO.: Empire City, *Jones* 3870 (CAS, F, PH, UC); Carson City, 1,446 m, *Baker* 971 (CAS, F, GH, NMC, NY, POM, RM, UC, US). STOREY CO.: Virginia City, *Jones* in 1882 (POM); 1.8 mi. SE. of Five Mile House, 6,800 ft., *Adams* 31 (UC). WASHOE CO.: 5 mi. N. of Poeville, NW. of Reno, 5,000 ft., *Tillotson* 99 (RSA, UC); Reno, *Jones* in 1903 (POM);

Verdi, *Sonne* in 1889 (F); Lakeview, between Carson City and Franktown, *K. Brandegee* in 1913 (UC).

This distinctive tetraploid species occurs sympatrically with *C. pusilla*. It has also been found growing together with *C. parvula*, *C. kernensis* subsp. *kernensis*, *C. strigulosa*, *C. integrifolia*, and *C. contorta*, with no evidence of interspecific hybridization. The tetraploid chromosome voucher from northern Washoe County, Nevada, is rather doubtfully referred here, and more information is needed about the populations in the northern portion of the range of this species. This entity has generally been regarded as distinct and has rarely been confused with any other species since it was first described in 1873, as can readily be seen from the synonymy.

43. Camissonia parvula (Nutt. ex Torr. & Gray) Raven, Brittonia 16: 284. 1964.

FIGURE 55

Oenothera parvula Nutt. ex Torr. & Gray, Fl. N. Amer. 1: 511. 1840.

Sphaerostigma parvulum (Nutt. ex Torr. & Gray) Walp., Rep. 2: 78. 1843.

Sphaerostigma contortum var. *flexuosum* A. Nels., Bot. Gaz. 40: 58. 1905. Type: Point of Rocks, Sweetwater Co., Wyo., 16 June 1898, *A. Nelson* 4760 (RM; isotypes, GH, US).

Sphaerostigma filiforme A. Nels., Bot. Gaz. 40: 57. 1905. Type: New River (Reese's River), Utah, 28 May 1889, collector not known (MO).

Sphaerostigma flexuosum (A. Nels.) Rydb., Fl. Rocky Mts. 601. 1917.

Oenothera contorta var. *flexuosa* (A. Nels.) Munz, Bot. Gaz. 85: 253. 1928.

Slender annuals closely similar to *C. pusilla*, but differing as follows: basal rosette absent, with one or more wiry, naked stems arising from the base; pubescence strigulose, dense or wanting, or very rarely spreading, the plants usually with a sparse admixture of glandular trichomes, especially in the inflorescence, but often subglabrous; flowers sometimes larger, the hypanthium up to 2 mm. long; sepals to 2.2 mm. long and 1.1 mm. wide; petals to 3.6 mm. long.

TYPE: Probably from southern Idaho ("toward Lewis' River"), July or August 1834, *T. Nuttall* (NY; isotype, BM).

DISTRIBUTION (Figure 56): Sandy slopes, often under sagebrush, from Okanagan and Yakima Counties, Washington; Elmore and Fremont Counties, Idaho; and Teton, Washakie, and Carbon Counties, Wyoming, south through westernmost Colorado (Moffat and Mesa Counties), throughout Utah, to westernmost Nye and southern Mineral Counties, Nevada and central Inyo County, California; from ca. 400 (in southern Washington) to 6,600 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=14$:

U.S.: CALIFORNIA: INYO CO.: 2.5 mi. N. of Big Pine, R17860. LASSEN CO.: U.S. Hwy. 395, 32 mi. S. of Milford, R17870. IDAHO: FREMONT CO.: 4.8 mi. E. and 2.5 mi. N. of St. Anthony, R19561. NEVADA: ORMSBY CO.: Just E. of New Empire, R17864. OREGON: HARNEY CO.: 12.9 mi. S. of Narrows, R18449.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S. California: INYO CO.: 2.8 mi. N. of Big Pine, R13825 (DS); 4 mi. W. of Lone Pine, 4,700 ft., *Alexander & Kellogg* 2786 (UC, mixture with *C. pusilla*); head of Division Creek road, 6,500 ft., *Kerr* in 1938 (CAS); foothills W. of Bishop, *Heller* 8288 (CAS, DS, F, GH, NY, PH, UC, US, WS). LASSEN CO.: Secret Valley, *Applegate* 8930 (DS, RSA); 10 mi. S. of Amadee, 4,000 ft., *Jones* in 1897 (POM). MONO CO.: Long Valley, *Noldecke* in 1938 (CAS); near Benton, *Eastwood & Howell* 9547 (CAS, mixture with *C. pusilla*). Colorado: MESA CO.: Grand Junction, *Eastwood* in 1892 (OSC). MOFFAT CO.: 5 mi. W. of Maybell along Cedar Springs draw, *Weber* 5450 (COLO, DS). Idaho: COUNTY UNKNOWN: Lannans Spur, *Henderson* 5339 (DS). CASSIA CO.: Raft R., *Davis* 8–37 (IDS). GOODING CO.: 3 mi. S. of Hagerman, *Davis* 1950 (IDS, POM, UC). JEROME CO.: Blue lakes 1893, *Palmer* 74 (US). OWYHEE CO.: N. of Bruneau, *Ripley & Barneby* 6503 (CAS); Indian Cove near Hammett, *Christ* 9533 (NY); Bruneau, *Christ* 4483 (NY). TWIN FALLS CO.: W. of Buhl, *Piemeisel* 40–211 (WTU). Nevada: ELKO CO.: 2 mi. S. of Contact, *Holmgren* 949 (WS); Toana Range, 5 mi. E. of Shafter, *Maguire* 16892 (NY, mixture with *C. pusilla*). ESMERALDA CO.: Candelaria, *Shockley* 247 (DS; F, mixture with *C. pusilla*; JEPS). HUMBOLDT CO.: 10 mi. N. of Winnemucca, 4,500 ft., *Breene* 185 (POM). NYE CO.: Tonopah, *Shockley* 147 (DS, POM), Twin R., 6,000 ft., *J. M. & M. A. R. Linsdale* 858 (CAS); 10 mi. S. of Calloway, 4,900 ft., *Ripley & Barneby* 3633 (CAS). ORMSBY CO.: Carson City, 5,000 ft., *Jones* in 1897 (POM); Steamboat Springs, *Stokes* in 1903 (UC). WASHOE CO.: 2.1 mi. NE. of Pyramid, 4,100 ft., *Simontacchi* 553 (RSA, UC). Oregon: HARNEY CO.: 21 mi. N. of Frenchglen, *Hitchcock & Muhlick* 21204 (WTU); Narrows, *Peck* 6963 (GH); Squaw Butte, *Steward* in 1956 (OSC); 3 mi. S. of Frenchglen, *Peck* 25205 (UC). LAKE CO.: Alkali L., *Peck* 19440 (CAS); near Summer L., 1,360 m, *Eggleston* 6861 (NY, US). MALHEUR CO.: Near Harper Ranch, 900 m, *Leiberg* 2108 (UD). Utah: BEAVER CO.: Beaver Mts., near Milford, 4,900 ft., *Stokes* in 1903 (US). GRAND CO.: Thompsons Spring, *Jones* in 1891 (POM). SALT LAKE CO.: Antelope I., 4,300 ft., *Watson* in 1869 (GH, NY, US). SANPETE CO.: Sevier Bridge, *Jones* in 1880 (POM, US). TOOELE CO.: Gold Hill, *Jones* in 1891 (F, NY, POM, RM); Deep Creek, *Jones* in 1891 (F, GH, POM, UC, US). UINTAH CO.: 2 mi. S. of Jensen, 4,700 ft., *Graham* 9019 (POM); between Dinosaur National Monument and Green River, 4,800 ft., *Graham* 7739 (POM). WASHINGTON CO.: Silver Reef, 2,500 ft., *Jones* 5149n (POM). Washington: FRANKLIN CO.: Pasco, *Piper* 2965 (WS, mixture with *C. pusilla*; GH specimen is all *C. pusilla*). OKANAGAN CO.: Nespelem Road at Hopkins Canyon, *Fiker* 1874 (WS). YAKIMA CO.: Near North Yakima, *Henderson* in 1892 (WTU); Donald Pass, Rattlesnake Hills, *Hoover* 5789 (UC). Wyoming: CARBON CO.: Sierra Madre, *Nelson* in 1907 (RM); Ft. Steele, 6,500 ft., *Tweedy* 4432 (NY, US). SWEETWATER CO.: Granger, *Nelson* 4760 (NY), 4698 (RM, US); Point of Rocks, 6,550 ft., *Ripley & Barneby* 7922 (CAS). TETON CO.: Pacific Creek, *Merrill & Wilcox* 602 (GH, NY, RM, US). WASHAKIE CO.: W. of Worland, 4,100–4,300 ft., *Nichols* 380 (RM).

Camissonia parvula is closely related to *C. pusilla* and *C. pubens* and grows sympatrically with both species. It is the only species of sect. *Camissonia* in Wyoming and Colorado and the most widespread one in Idaho and Utah. It can usually be distinguished readily by its linear leaves, lack of a definite basal rosette, and strigose pubescence, but the plants are occasionally subglabrous or very rarely have a few spreading longer trichomes, in which cases they are difficult to distinguish from the diploid *C. pusilla* that occurs in the same general areas in northern Nevada and eastern Washington and Oregon. *Camissonia parvula* has also been found growing sympatrically with *C. contorta.*

44. Camissonia campestris (Greene) Raven, Brittonia 16: 284. 1964.

Slender, erect or decumbent annual, usually well branched, with wiry stems and no definitely defined basal rosette, the plants 5–25 (–50) cm. tall, glabrous, hirsutulous, strigulose, or glandular-pubescent; stems with a conspicuously exfoliating white rhytidome. Leaves linear to narrowly elliptic or narrowly oblanceolate, 0.5–2.5 (–3) cm. long, 0.1–0.15(–0.5) cm. wide, sparsely serrulate to coarsely serrate, the apex acuminate, the base attenuate. Inflorescence glandular-pubescent, sometimes very sparsely so or glabrous, or with an admixture of longer eglandular trichomes, or strigulose, sometimes densely so, or sparsely short-villous. Hypanthium 1.5–5.5 mm. long, 2.5–6 mm. across at the summit, more or less densely villous in lower half within, often with a red dot at the summit within at the base of each filament. Sepals 3–8 (–12) mm. long, 1.3–3 mm. wide, reflexed in pairs. Petals (3.5–) 5–15.5 mm. long, (3–) 5–13 mm. wide, usually with two (or one) red dots at the base of each one. Filaments of the episepalous stamens (1.4–) 2.1–5.5 mm. long, those of the epipetalous ones (0.7–) 1.2–3.2 mm. long; anthers 1–2.4 mm. long. Style (3.2–) 4–12 (–15) mm. long, glabrous or sparsely hirsutulous near the base; stigma 0.7–3 mm. in diameter, held well above the anthers at anthesis. Capsule 2–4.3 cm. long, 0.7–1.5 (–2) mm. thick, subsessile. Seeds 0.8–1.6 mm. long, 0.4–0.6 mm. thick. Gametic chromosome number, $n=7$. Self-incompatible.

Distribution (Figure 57): Open sandy flats, endemic to California; often abundant and covering large areas, from the vicinity of Antioch, Contra Costa County, San Joaquin County and northern Stanislaus County, California, south in the San Joaquin Valley, inner Coast Ranges, and Sierra Nevada foothills to Santa Barbara, Ventura, the northern half of Los Angeles, and western Riverside County; near Campo, San Diego County (*Eastwood* 9447, CAS); and western borders of the Mojave Desert from the vicinity of Twentynine Palms and the Little San Bernardino Mountains in northern Riverside and southern San Bernardino Counties northwest to the vicinity of Daggett and Calico, east of Barstow, San Bernardino County, the area about Red Mountain, in westernmost San Bernardino and easternmost Kern Counties, and the southwesternmost corner of Inyo County, where it extends north almost to Olancha. Not found near the coast, and occurring from near sea level on the lower San Joaquin River to about 6,400 ft. alt., in the Sierra Nevada of Kern County. I have also seen a collection from Painted Canyon, in the northwestern corner of the Colorado Desert, Riverside County (*Randall* 219 SD); the occurrence of *Camissonia campestris* at this locality should be confirmed by additional collections, as should the following: Santa Cruz Mountains, 2,300 ft., *Pendleton* 945 (UC); Panamint Mountains, Inyo County, *Winblad* in 1937 (CAS). Collections of this species cited from the Sacramento Valley and bordering mountains are all polyploid and here referred to *C. lacustris* and *C. contorta*; otherwise all material cited by Munz (Bot. Gaz. 85:258–260. 1928) under *Oenothera dentata* var. *campestris*, var. *johnstonii* (except for collections cited above as *Camissonia kernensis* subsp. *gilmanii*), and var. *parishii* belongs here, and specifically to *Camissonia campestris* subsp. *campestris*.

This species has usually been referred to the South American *Camissonia dentata*, and consequently known as *Oenothera dentata* Cav.; all South American populations, however, are tetraploid ($n=14$ or 13) and self-compatible, the stigma being surrounded by at least the anthers of the longer stamens at anthesis.

44a. Camissonia campestris subsp. **campestris**

Oenothera dentata sensu auct. Amer. bor. mult.; non Cav. 1798.

Oenothera campestris Greene, Fl. Francisc. 216. 1891.

Sphaerostigma campestre (Greene) Small, Bull. Torrey Cl. 23: 189. 1896.

Sphaerostigma campestre var. *parishii* Abrams, Fl. Los Angeles 272. 1904. Type: Plains, San Bernardino, San Bernardino Co., Calif. May 1900, *S. B. Parish* (DS).

Oenothera torulosa race *helianthemiflora* H. Lév., Monogr. Onoth. 178, *pl.* 1905. Lectotype: Mojave Desert, Calif., May 1882, *S. B. & W. F. Parish* 1304 (MO).

Sphaerostigma campestre var. *helianthemiflorum* (H. Lév.) A. Nels., Bot. Gaz. 40: 57. 1905.

Oenothera torulosa f. *permixta* H. Lév., Monogr. Onoth. 180. 1905. Type: Fresno, Fresno Co., Calif., 21 March 1889, collector unknown (presumably MO).

Oenothera dentata var. *campestris* (Greene) Jeps., Man. Fl. Pl. Calif. 685. 1925.

Oenothera dentata var. *parishii* (Abrams) Munz, Bot. Gaz. 85: 259. 1928.

Oenothera dentata var. *johnstonii* Munz, Bot. Gaz. 85: 259. 1928. Type: Near Mojave, Kern Co., Calif., 5 May 1920, *I. M. Johnston* (POM 8844).

Sphaerostigma dentata subsp. *campestris* (Greene) Johansen, Amer. Journ. Bot. 16: 597. 1929.

Oenothera campestris subsp. *campestris* Munz, N. Amer. Fl. II. 5: 158. 1965.

Oenothera campestris subsp. *parishii* (Abrams) Munz, Fl. N. Amer. II. 5: 158. 1965.

Oenothera cruciata sensu Munz, N. Amer. Fl. II. 5: 157. 1965; pro parte.

Plants usually erect; leaves linear to narrowly elliptic or narrowly oblanceolate, serrulate. Gametic chromosome number, $n=7$. Self-incompatible.

LECTOTYPE: California, 1831–2, *D. Douglas* (GH); cf. Munz, Bot. Gaz. 85: 258. 1928.

DISTRIBUTION (Figure 57): That of the species.

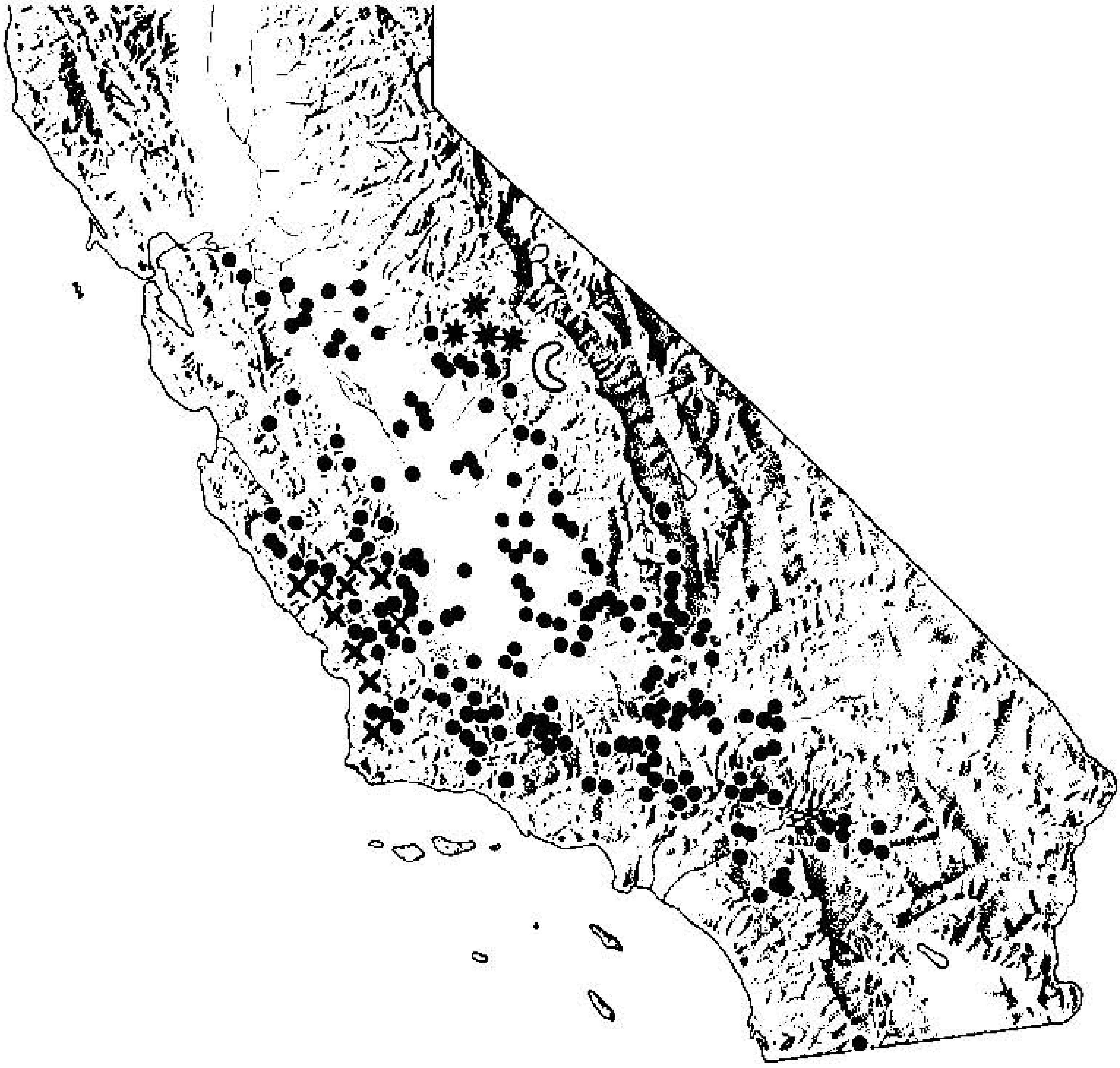


FIGURE 57.—California, showing ranges of species of *Camissonia* sect. *Camissonia:* ●=*C campestris* subsp. *campestris;* ×=*C. campestris* subsp. *obispoensis;* ✳=*C. sierrae* subsp. *sierrae; C. sierrae* subsp. *alticola*, area outlined by heavy black line.

Vouchers for chromosome number (35 individuals, 32 populations), $n=7$ (all with 7 pairs, except where noted):

U.S.: CALIFORNIA: FRESNO CO.: 3.3 mi. N. of Selma, R17064; 7 mi. SW. of Tollhouse, *Breedlove* 5199. KERN CO.: Jawbone Canyon, *Munz & Gregory* 23310 (RSA); 1.2 mi. SE. of Blackwells Corner, 650 ft., R16982; 0.7 mi. S. of Taft, 800 ft., *Breedlove* 1947; Wheeler Ridge, E. of Maricopa, *Lewis* 1684 (LA); 7.3 mi. N. of Bakersfield, R17078; S. of Arvin, 450 ft., R17089; near mouth of Kern R. canyon, *Lewis et al.* 1675 (LA; 5 pairs + ring of 4); W. of mouth of Kern R. canyon, *Lewis* 1683 (LA; 5 pairs + ring of 4); Kern R. canyon, 8.2. mi above road to Redwood Meadow, *Lewis & Wedberg* 1109 (LA, RSA; two plants, 7 pairs; one, 5 pairs + ring of 4); 8.9 mi. S. of Weldon, R12802; Miracle Hot Springs, R18804; ca. 5 mi. S. of Walker Basin on road to Caliente, *Lewis* 1253; 10 mi. N. of Red Rock Canyon, *Munz & Gregory* 23313 (RSA); Black Mt. burn, Greenhorn Mts., 3,500 ft., R18765; head of Short Canyon, R13985. LOS ANGELES CO.: 0.5 mi. E. of Pearblossom, *Lewis* 1691 (5 pairs + chain of 3 + univalent); 3.7 mi. W. of Littlerock, *Theobald* 88; 1 mi. W. of Littlerock, R13994. MADERA CO.: 7.6 mi. S. of Coarsegold, 1,300 ft., R18330; San Joaquin Experimental Range, between Coarsegold and O'Neals, *Lewis* 1296 (2 plants). MONTEREY CO.: 6 mi. N. of Mission San Antonio, *Breedlove* 5579; 1.5 mi. W. of Bradley, R18205. SAN BERNARDINO CO.: 0.3 mi. N. of junction of Hwy. 138 with Hwy. 395, *Wedberg* in 1957 (LA); Barstow, R11894. SAN LUIS OBISPO CO.: 0.4 mi. S. of San Juan Creek S. of Shandon, 1,150 ft., R16973; 5.5 mi. S. of Shandon on San Juan Creek, 1,200 ft., R16967; 8.6 mi. W. of Simmler, 1,800 ft., *Breedlove* 2061; W. edge of Carrizo Plain, *Breedlove* 2085. SANTA BARBARA CO.: 11.8 mi. W. of New Cuyama, 2,100 ft., *Breedlove* 1939. TULARE CO.: 2 mi. S. of Tipton, 500 ft., R17063.

Two early reports of chromosome number in this species were made by Johansen (Proc. Nat. Acad. Sci. U.S. 15: 884. 1929) but no localities or vouchers were cited.

Plants of this taxon are abundantly visited by oligolectic bees, especially *Andrena* spp. The following populations were found to consist of self-incompatible individuals: 7.6 miles south of Coarsegold, 1,300 ft., Madera County, R18330 (nine plants, tested in field); Black Mountain burn, Greenhorn Mountains, 3,500 ft., Kern County, R18765 (one plant, in greenhouse); 1.5 miles west of Bradley, Monterey County, R18205 (12 plants, tested in field); 3 miles southwest of Livingston, Merced County, R18809 (12 plants, tested in field).

Populations of *Camissonia campestris* from the foothills of the Sierra Nevada tend to have relatively small flowers; but these plants are probably all self-incompatible, judging from the results with the Madera County population mentioned above. Some populations from relatively high elevations in the Greenhorn and Tehachapi Mountains of Kern County consist of plants with relatively broad leaves, but the leaves are attentuate at the base and the plants do not closely resemble *C. sierrae* from farther north. Such collections are (all from Kern County, California): Black Mountain burn, Greenhorn Mountains, 3,500 ft., R18765 (self-incompatible; see above); Wagy Creek Fire Road, east side of Greenhorn Mountains, *Hardham* 3682a (LA); east slope of Bear Mountain, Tehachapi Mountains, 6,200 ft., *Twisselmann* 9633 (DS). The status of these plants should be further investigated.

Oenothera cruciata, as recognized by Munz (N. Amer. Fl. II. 5: 157. 1965), consists of a mixture of late-season plants of *Camissonia campestris* subsp. *campestris*, whence the chromosome count, $n=7$; relatively large-flowered plants of the hexaploid *C. contorta;* and the Clear Lake, Lake County, California, populations of the tetraploid *C. lacustris*.

Hybridization between *Camissonia campestris* and the hexaploid *C. contorta* was studied 1.5 miles due west of Bradley, Monterey County, California, on April 20, 1963. Here both parents were common on a sunny, west-facing hillside in open oak woodland, with *C. campestris* predominant in the more sandy localities and *C. contorta* everywhere. Widely scattered intermediate individuals made up a very small proportion of the population, with some 15 collected among many thousands of the parents. Ten of these were studied cytologically, with observations of meiosis possible in eight. Of these, five had

$2n=28$ chromosomes and were presumably F_1 individuals. The maximum configuration observed was a chain of 8 chromosomes, a ring of 4, two chains of 4, and 4 pairs, two of which were ring bivalents and two heteromorphic rod bivalents. Less extensive chromosome configurations were observed in most cells of most plants, with trivalents rather frequent and univalents occasional. These observations clearly show that the complete lack of multivalent formation in the hexaploid is under genetic control, which breaks down in the hybrids. Pollen stainability in these presumed F_1 individuals was as follows (samples of 200 grains): 0 percent (one plant), 15.5 percent, 20.5 percent, 22.5 percent, 42 percent.

The remaining three plants on which chromosomal observations were made had $2n=21$ and were presumably backcross individuals with *C. campestris* as the recurrent parent. One of these had a ring of 4 chromosomes, a chain of 4, 6 pairs (including 3 ring pairs), and a univalent, with 7 percent stainable pollen; the second had a chain of 4, a chain of 3, 6 pairs, and 2 univalents, with 0.5 percent stainable pollen; and the third had 2 chains of 3, 7 pairs, and a univalent, with 4 percent stainable pollen. The petals in these plants were 5–5.5 mm. long, instead of 4–4.5 mm. as in the presumed F_1 individuals. Despite their low fertility, these individuals strongly suggest the possibility of interspecific hybridization enhancing the variability of *C. campestris*. It is not surprising that no backcrosses with *C. contorta* were obtained in this small sample, for *C. contorta* is largely autogamous, *C. campestris* self-incompatible and outcrossing. Thus backcrossing to *C. campestris* is far more likely than to *C. contorta*.

Another apparent F_1 hybrid plant was studied from 2.9 miles east of Paso Robles, San Luis Obispo County, California, *Keck* 2110 (DS). This completely pollen-sterile individual was mounted on a herbarium sheet with plants of the putative parents. Another similar mixed collection with one apparent F_1 hybrid was collected about 1 mile southeast of Havilah, Kern County, California, 975 m., *Coville & Funston* 1082 (US).

An unusual individual that was presumably not of hybrid origin is *S. B. & W. F. Parish* 1304A (GH), collected with normal individuals of *C. campestris* (1304). In this plant, the petals are narrowed greatly in their upper two-thirds, thus resembling an exaggerated form of the sort of petals found occasionally in *C. hirtella* (sect. *Holostigma*).

Camissonia campestris subsp. *campestris* grows sympatrically with *C. kernensis* subsp. *kernensis*, *C. kernensis* subsp. *gilmanii*, *C. strigulosa*, *C. integrifolia*, and *C. contorta*. It is one of the only two diploid species in that part of sect. *Camissonia* in which the sepals are reflexed in pairs, and thus may have contributed to the origin of the tetraploids *C. lacustris*, *C. benitensis*, *C. strigulosa*, *C. dentata*, and *C. integrifolia*;

these species have very likely had a common origin at the tetraploid level. Judging from the fact that the hexaploid *C. contorta* occupies the hot, dry San Joaquin Valley of California, almost to the exclusion of the tetraploid *C. strigulosa*, which is restricted to the foothills and margins of the valley, it appears likely that *C. contorta* (at least in this area) is an allohexaploid combining genomes from the diploid *C. campsteris* (abundant with it in the valley) and the tetraploid *C. strigulosa*. Whether the hexaploid populations found north and east of the area of *C. campestris* originated in this way or by the functioning of an unreduced gamete in a tetraploid plant cannot at present be determined. It is likely, however, considering the sort of pairing observed in natural hybrids between the diploid *C. campestris* and the hexaploid *C. contorta*, that a hexaploid formed by the functioning of such an unreduced gamete would be pair-forming, and therefore probably fertile, from the time of its origin.

44b. Camissonia campestris subsp. **obispoensis** Raven, subsp. nov.

A subsp. *campestri* differt: foliis anguste ellipticis, grosse serratis; ramis persaepe decumbentibus. Chromosomatum numerus gameticus, $n=7$.

TYPE: Opening in chaparral on sandy soil, 1.8 miles west of Bee Rock, San Luis Obispo County, California, 5 May 1963, *P. H. Raven* 18301 (DS 520310).

DISTRIBUTION (Figure 57): Marine sand deposits in openings in chaparral and oak woodland, endemic to central coastal California from southern Monterey County through northern and western San Luis Obispo County to northwesternmost Santa Barbara County; from ca. 300–1,600 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

U.S.: CALIFORNIA: MONTEREY CO.: E. edge of San Antonio Valley, Santa Lucia Mts., 1,350 ft., *Breedlove* 2268; Bradley, R18306; Big Sandy Valley 2 mi. N. of Indian Valley Road, R18290. SAN LUIS OBISPO CO.: 1.8 mi. W. of Bee Rock, R18301; Atascadero, R18278.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: MONTEREY CO.: Big Sandy, N. of San Miguel, *Hardham* 10823 (DS); Big Sandy, 3 mi. NE. of Indian Valley, N. of San Miguel, *Hardham* in 1962 (DS); Lowes Canyon, 15 mi. N. of San Miguel, *Hardham* 3332 (CAS, LA), R18296 (DS); ca. 3 mi. N. of summit of Hog Canyon Road S. of Parkfield, R18300 (DS); Cholame Creek (upper end), *Jepson* 15903 (JEPS); 28.1 mi. NE. of San Miguel, Big Sandy to Parkfield road, *Hardham* 10773 (DS, RSA). SAN LUIS OBISPO CO.: Nacimiento Dam to Bradley-Pleyto road, *Hardham* 4582 (SBBG); Cantinas Creek, near N. end of Nacimiento L., *Hardham* 4567 (LA, SBBG); sand dunes on top of Tierra Redonda, *Hardham* 1859 (LA, SBBG); 1.6 mi. W. of Bee Rock, *Hardham* 2259 (LA); 5 mi. ESE. of Bryson, 1,500 ft., *Graham* 379 (UC); Oak Flat Road intersection with road to Adelaida, *Hardham* 2058 (LA); upper

Navajo Creek, *Hoover* 6898 (CAS); Yaro Creek district N. of Pozo, *Hoover* 6993 (CAS); Chimney Rock Ranch, South Road to Adelaida, *Hardham* 829 (LA); Santa Margarita, *Summers* in 1886 (ARIZ, POM), *Wall* in 1933 (CAS, POM); upper Arroyo Grande, *Hoover* 6860 (CAS, RSA); road from Arroyo Grande to Huasna, *Eastwood* 14988 (CAS). SANTA BARBARA CO.: 3 mi. NE. of Mt. Solomon, 800 ft., *Lee* 241 (UC); Cuyama Valley, *Pollard* in 1953 (CAS, RM).

This distinctive local endemic intergrades completely with subsp· *campestris* wherever the ranges of these two taxa approach one another. A series of hybrids between *C. campestris* subsp. *obispoensis* and *C. strigulosa* is represented by *Hardham* 3240 (LA, RSA, SBBG), from a damp grain field at Bee Rock, northern San Luis Obispo County, California. The fertility of four representative putative F_1 hybrids, based on the stainability of a sample of 200 pollen grains from each in cotton blue in lactophenol was, respectively, 11, 1.5, 6.5, and 9 percent. A similar population is represented by *Hardham* 10823 (DS), from the Big Sandy, north of San Miguel, 21.2 miles north of the Salinas River bridge, Monterey County, California, where it grew on the borders of the road. This collection includes two plants of *C. campestris* subsp. *obispoensis*, one of *C. strigulosa*, and two hybrids, one of which had a pollen stainability of 0.5 percent, based on a sample of 200 pollen grains.

An apparent backcross to this subspecies from a hybrid between it and the hexaploid *C. contorta* was found with the presumed parents at Atascadero, San Luis Obispo County, California (R18281). This individual had 7 pairs of chromosomes, 3 univalents, and a chain of 4; it was not setting any seed.

45. **Camissonia sierrae** Raven, sp. nov.

Herba annua hirsutulosa humilis, plerumque ramis multis e basi; caules tenuissimi, ad 15 cm. longi. Folia lanceolata vel anguste ovata, aliquando elliptica, 0.5–1.8 cm. longa, 0.2–0.5 cm. lata, subintegria, apice acuta, basi rotundata vel obtusa. Inflorescentia pilis glandulosis brevioribus admixta. Hypanthium 1.3–2.2 mm. longum, ostio 1.2–2.2 mm. diametro, intus in dimidio inferiore hirsutulosum, summum puncto rubro prope basin omnium filamentorum. Sepala 3–4.2 mm. longa, 1–1.3 mm. lata, binatim reflexa. Petala 4–7 mm. longa, 3.5–5 mm. lata, unumquidque prope basin punctis duabus rubris maculatum. Filamenta staminorum episepalorum 2.4–3.2 mm. longa, illa epipetalorum 1.2–2 mm. longa; antherae 0.6–1.2 mm. longae. Stylus 4.5–7 mm. longus; sub anthesi insuper antheribus minime portatum vel antheris staminorum longiorum stigma 0.6–0.8 mm. diametro, circumnexum. Capsula tenuissima, 2–3 cm. longa, ca. 0.5–0.7 mm. crassa, sessilis. Semina his *C. campestris* similia. Chromosomatum numerus gameticus, $n=7$. Plus minusve autogama.

TYPE: Meadow in forest dominated by *Pinus ponderosa*, 0.7 miles west of junction in Oakhurst on road to Mariposa, 2,400 ft., Madera

County, California, 7 May 1963, *P. H. Raven* 18343 (DS; isotypes, BM, GH, NY, RSA, US).

DISTRIBUTION (Figure 57): Carpeting the ground locally in open forest of *Pinus ponderosa* and at the upper limits of the *Pinus sabiniana–Quercus douglasii* forest, from 1,800–4,000 ft. alt., Sierra Nevada foothills of central California, in central Mariposa and Madera Counties.

Vouchers for chromosome number (2 individuals, 2 populations) $n=7$.

U.S.: CALIFORNIA: MADERA CO.: 0.7 mi. W. of Oakhurst, R18343 (type collection); 4.3 mi. W. of Oakhurst, R18345.

ADDITIONAL SPECIMENS EXAMINED:

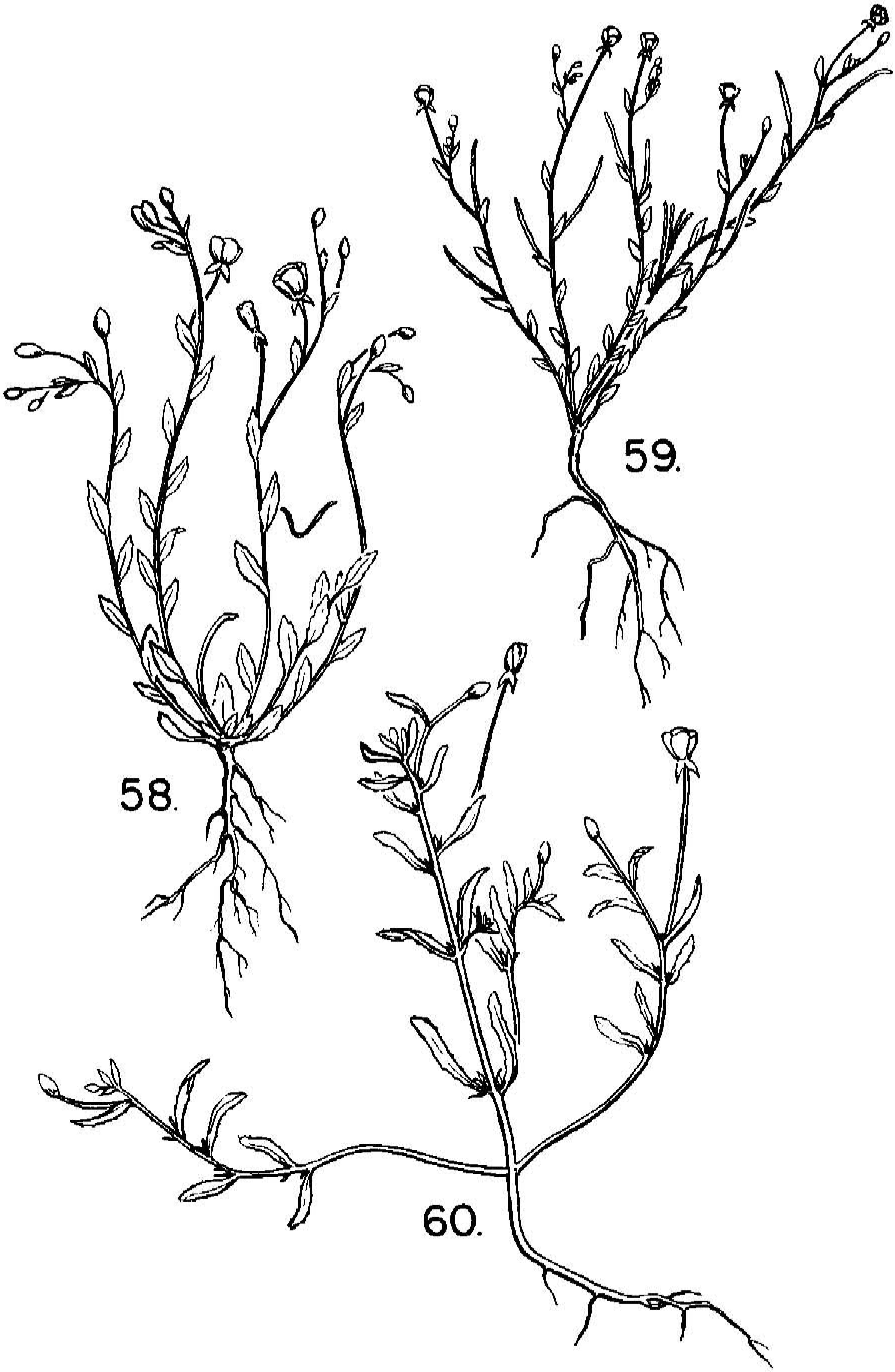
U.S.: CALIFORNIA: MADERA CO.: 3.7 mi. W. of Oakhurst, *Thorp* 63–10 (DS); S. end of Oakhurst, *Thorp* 63–12 (DS); the Falls, Bass Lake, 3,450 ft., *H. & M. Dearing* 5955 (DS, SBBG); Bass Lake, *H. & M. Dearing* 6018 (SBBG, UCSB). MARIPOSA CO.: Yosemite Valley, *Corring* in 1884 (GH), *Bioletti* in 1900 (NY), *Head* in 1906 (CAS), 4,000 ft., *Wright & Patchett* in 1917 (JEPS); Royal Arches, Yosemite Valley, *Jepson* 10478 (DS, JEPS); Little Yosemite, *Flinn* in 1925 (F); 2 mi. off state highway, 7 mi. below Mariposa on road to Ben Hur, 1,800 ft., *Wolf* 4836 (COLO, POM, RSA, SD, WS, WTU).

Camissonia sierrae is a delightful and distinctive endemic found above the upper limits of *C. campestris*, its closest relative, in the central Sierra Nevada of California. The latter species occurs locally in much drier habitats. Eighteen plants of *Thorp* 63–10, cited above, were tested for pollen-tube growth and found to be self-compatible, in contrast to all known populations of *C. campestris*. Despite this, *C. sierrae* is probably outcrossed to a large extent, and is abundantly visited by bees, including a large species of *Andrena* (*Onagrandrena*). Its stigma is often held above the anthers and this, together with the red markings at the summit of the hypanthium and on the petals, is highly correlated with outcrossing in *Camissonia*, as is the abundant pubescence in the lower half of the hypanthium within and near the base of the style.

This species is very probably a derivative of *C. campestris*, but is usually easily distinguished by its habit (cf. fig. 58) and much broader, relatively shorter leaves. The populations from Mariposa County have narrower leaves and a laxer habit than those from Madera County, but form a distinctive morphological and ecological unit with them. *Camissonia sierrae* has been observed growing sympatrically with *C. contorta* at the type locality of the former.

45a. Camissonia sierrae subsp. **sierrae** FIGURE 58

All of the preceding remarks apply to this subspecies. It has been necessary in this instance to depart from the usual format of this paper, as both subspecies are being described as new at this time.



FIGURES 58–60.—Species of *Camissonia* sect. *Camissonia*, × ¾: 58, *C. sierrae* subsp. *sierrae* (*Raven* 18343, holotype, DS); 59, *C. sierrae* subsp. *alticola* (*Russell* 75, DS); 60, *C. benitensis* (*Raven* 15084, holotype, DS).

45b. Camissonia sierrae subsp. **alticola** Raven, subsp. nov. FIGURE 59

A subsp. *sierrae* differt: floribus parvioribus; hypanthio 1–2.2 mm. longo, ostio 0.9–2.2 mm. diametro, intus subglabro; sepalis 1.2–3 mm. longis, 0.8–1.5 mm. latis; petalis 2.2–4 mm. longis, 1.8–2.2 mm. latis, immaculatis; filamentis staminorum episepalorum 1.8–2.8 mm. longis, illis epipetalorum 0.8–1.8 mm. latis; antheris 0.6–0.9 mm. longis; stylo 2.8–5 mm. longo, glabro; stigmate 0.6–0.8 mm. diametro, sub anthesi antheris circumnexo. Chromosomatum numerus gameticus, $n=7$. Autogama.

TYPE: Grassy pocket of soil in seepage over granite ledge 100 yards north of Mono Hot Springs Campground, in yellow pine forest, 6,500 ft., Fresno County, California, 8 June 1963, *D. E. Breedlove* 5212 (DS; isotypes, BM, GH, NY, RSA, US).

DISTRIBUTION (Figure 57): Shallow soil on granite outcrops, yellow pine forest, in the Sierra Nevada of northeastern Fresno County, California, from 6,500–7,700 ft. alt.

Voucher for chromosome number (1 individual, 1 population), $n=7$:

U.S.: CALIFORNIA: FRESNO CO.: Mono Hot Springs, *Breedlove* 5212 (type collection).

ADDITIONAL SPECIMENS EXAMINED:

U.S.: CALIFORNIA: FRESNO CO.: Near Bear Dam, 7,300 ft., R7157 (CAS); Mono Hot Springs, 6,500 ft., R6217 (CAS), *S. & C. H. Quibell* 2326 (DS), *Ferguson* 430 (DS, JEPS); between Florence L. and Blaney Meadows, 7,500 ft., R4284 (CAS); Florence L., *Russell* 75 (DS); 3/8 mi. above E. end of Vermillion Valley, ca. 7,700 ft., *C. H. & E. M. Quibell* 2670 (herb. Fresno State College).

A distinctive local race, *Camissonia sierrae* subsp. *alticola* is obviously very closely related to *C. sierrae* subsp. *sierrae* but is highly autogamous and occurs at much higher elevations. I have seen a collection from Lake Merced on the Merced River of Mariposa County, 7,200 ft., *Jepson* 3181 (JEPS), which is very similar to Fresno County plants of subsp. *alticola;* additional collections from the Merced River drainage basin would make it possible to evaluate the relationship between these two series of populations.

46. Camissonia lacustris Raven, sp. nov. FIGURE 61

Oenothera dentata var. *campestris* sensu Munz, Bot. Gaz. 85: 258. 1928; pro parte.

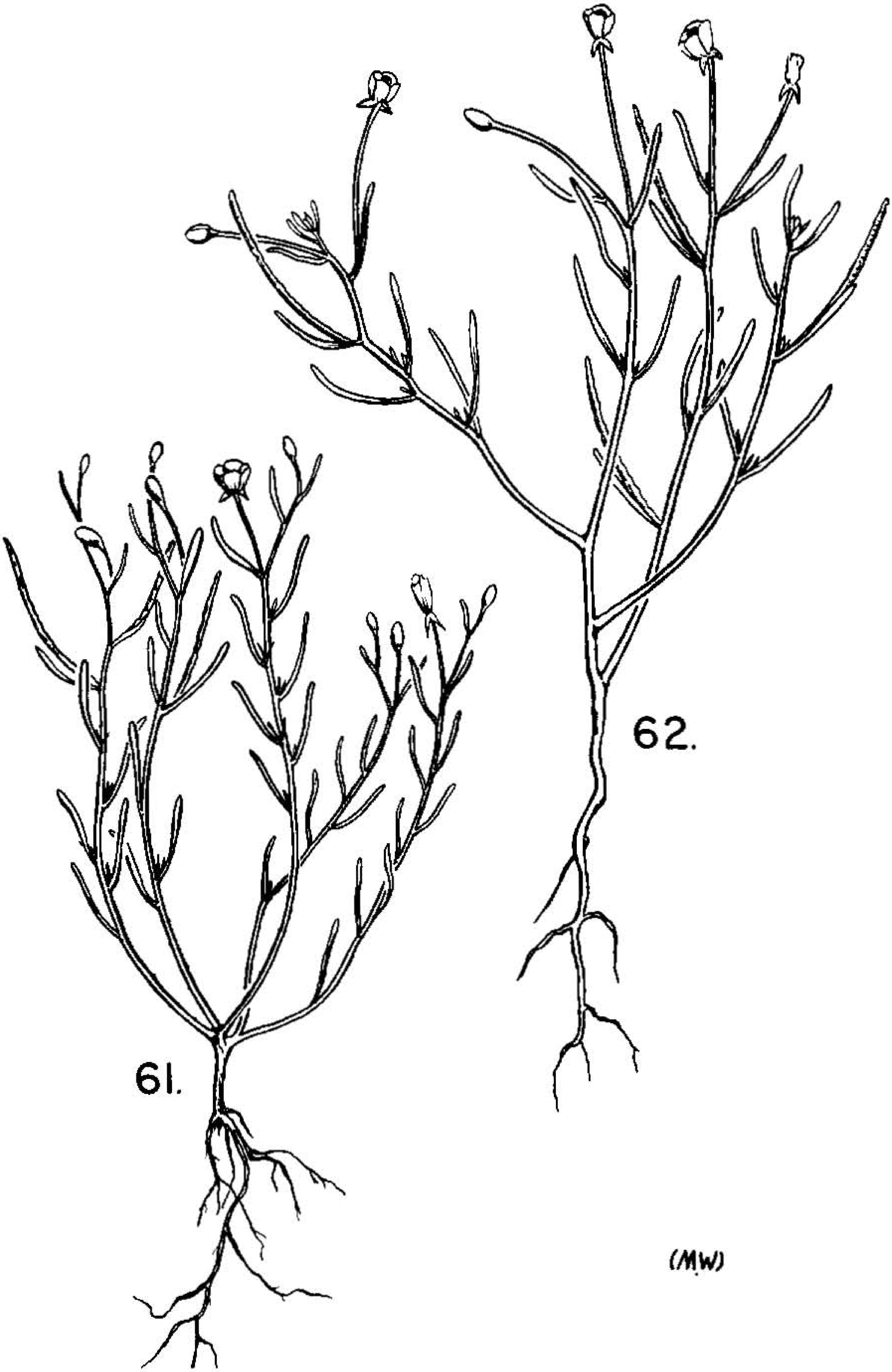
Oenothera contorta var. *epilobioides* sensu Munz, Bot. Gaz. 85: 256. 1928; pro parte.

Oenothera dentata sensu Munz, N. Amer. Fl. II. 5: 157. 1965; pro parte.

Oenothera cruciata sensu Munz, Amer. Fl. II. 5: 157. 1965; pro parte.

Oenothera campestris subsp. *campestris* sensu Munz, N. Amer. Fl. II. 5: 158. 1965; pro parte.

Herba annua *C. strigulosae* persimilis. Plantae pilis longis erectis dense vestitae; inflorescentia glanduloso-pubescens. Hypanthium intus in partem dimidiam pubescens. Sepala (3–) 3.8–5.5 mm. longa.



(MW)

FIGURES 61–62.—Species of *Camissonia* sect. *Camissonia*, × ¾: 61, *C. lacustris* (*Raven* 18164, holotype, DS); 62, *C. integrifolia* (*Raven* 12806, holotype, DS).

Petala (4–) 4.5–7 mm. longa, (2.8–) 3–6.5 mm. lata, plerumque unumquidque prope basin punctis duabus rubris maculatum. Filamenta staminorum episepalorum 2.5–3.5 mm. longa, illa epipetalorum 1.7–2.5 mm. longa; antherae 0.8–1.3 mm. longae. Stylus (3.5–) 4–7 mm. longus, prope basin pubescens. Chromosomatum numerus gameticus, $n=14$. Autogama.

TYPE: In open grassland of serpentine hill 0.2 mile west of State Highway 29 near Lakeport, Lake County, California, 13 April 1963, *P. H. Raven* 18164 (DS).

DISTRIBUTION (Figure 63): Open grassland of central California, in two disjunct areas: serpentine soil along the northwest side of Clear Lake, Lake County, 1,400–1,800 ft. alt.; Sierra Nevada foothills from Eldorado to Fresno County, 600–5,000 ft., scattered.

Vouchers for chromosome number (5 individuals, 4 populations), $n=14$:

U.S.: CALIFORNIA: LAKE CO.: 0.2 mi. W. of Lakeport, R18164 (type collection), *Breedlove* 4546. MARIPOSA CO.: Bootjack Road at Chowchilla School, 2,900 ft., R18346. TUOLUMNE CO.: 1 mi. NE. of Tuolumne City, *Breedlove* 4817; Carnegie Institution Field Station, Mather, *Lewis* 1665 (LA, RSA).

FIGURE 63.—California, showing ranges of some tetraploid ($n=14$) species of *Camissonia* sect. *Camissonia:* northern limits of the widespread *C. strigulosa* indicated by a dotted line; ○ = *C. lacustris*, with ● = tetraploid chromosome counts; ✳ = *C. benitensis;* △ = *C. integrifolia*, with ▲ = tetraploid chromosome count.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: CALAVERAS CO.: Mokelumne Hill, *Blaisdell* (GH, US). ELDORADO CO.: N. fork of the Cosumnes R. NW. of Youngs, R9107 (CAS, RM). FRESNO CO.: Pine Flat, 600 ft., *C. H. & E. Quibell* 1712 (NY, RSA); 4 mi. W. of Pine Ridge, *Breedlove* 5275 (DS). LAKE CO.: Cold Creek Canyon, 1,800 ft., *Schulthess* in 1928 (POM); near Lakeport, *Baker* 3067 (CAS, NMC, POM, UC); Kelseyville, *Blankinship* in 1923 (RSA). MARIPOSA CO.: Near Leconte Memorial, Yosemite Valley, 4,000–4,500 ft., *Abrams* 4426 (DS, GH, NY); Camp Curry, *Stone* in 1915 (PH); Little Yosemite, *Smith* in 1908 (ARIZ, PH). TUOLUMNE CO.: Hog Ranch, Hetch-Hetchy Valley, 4,700 ft., *Grant* 974 (POM); Phoenix L., *Grant* 946 (JEPS).

Camissonia lacustris is very closely related to and probably derived from the widespread tetraploid *C. strigulosa*. The latter occurs in the Sierra Nevada north only to Kern County and in the North Coast Ranges only on the immediate coast to the vicinity of Bodega Bay. Thus *C. lacustris* occupies a series of widely scattered enclaves in the area now within the range of the hexaploid *C. contorta*. It is of interest that the northernmost population of tetraploids in this section in the Coast Ranges, that near Clear Lake, Lake County, occurs on serpentine: marginal populations of plants often occur on substrates unusual for the species as a whole, and such a situation is ideal for the derivation of edaphically restricted endemics (cf. Raven, Evolution 18: 336–338. 1964). In *Camissonia contorta*, the hexaploid which occurs in the same areas, often a third or more of the pollen grains are 4-pored, whereas in *C. lacustris* and other tetraploids of sect. *Camissonia* it is rare for as many as 5 percent of the pollen grains to be 4-pored. The long, spreading trichomes on the stems of *C. lacustris* and its relatively large flowers are likewise useful in its recognition.

In the vicinity of Clear Lake, Lake County, California, *Camissonia lacustris* occurs on serpentine soils and the hexaploid *C. contorta* nearby on the nonserpentine soils now under moderately heavy cultivation. The records of *C. campestris* (*Oenothera dentata* auct.) from Lake County apply to *C. lacustris*, as do some of the populations included in Munz' (N. Amer. Fl. II. 5: 157. 1965) concept of *Oenothera cruciata* (S. Wats.) Munz, a diverse assemblage of unrelated elements with several different chromosome numbers. Twelve individuals from the type locality were selfed in the field and found to be self-compatible by pollen-tube growth; the stigma is surrounded by at least the anthers of the four longer stamens even in the largest flowered individuals of this species.

47. Camissonia benitensis Raven, sp. nov. FIGURE 60

Herba annua *C. strigulosae* persimilis. Plantae 3–18 mm. altae, plus minusve purpurascentes, ramis secondariis tenuibus numerosis ad angulum 90° patentibus, pilis longis 0.2–0.3 mm. longis erectis dense vestitae; inflorescentia glanduloso-pubescens et villosa. Folia angustissime elliptica, sparsa, 0.7–2 cm. longa, 0.15–3 cm. lata, apice acuta. Hypanthium ca. 1.2 mm. longum ostioque diametro, intus in partem dimidiam dense brevipubescens. Sepala 3.2–3.5 mm. longa, ca. 1.5 mm. lata. Petala 3.5–4 mm. longa, ca. 3 mm. lata, unumquidque prope basin punctis duabus rubris maculatum. Filamenta staminorum episepalorum ca. 2 mm. longa, illa epipetalorum ca. 1.2 mm. longa, unumquidque basi puncto rubro. Stylus 2.1–2.5 mm. longus, glaber; stigma sub anthesi antheribus circumnexum. Chromosomatum numerus gameticus, $n=14$. Autogama.

TYPE: On serpentine by small stream 5.4 miles from Hernandez on road to New Idria, along Clear Creek, San Benito County, California, 19 April 1960, *P. H. Raven* 15084 (DS; isotype, US).

DISTRIBUTION (Figure 63): Clay soils derived from serpentine, lower Clear Creek Drainage, San Benito County, California, at an elevation of ca. 2,000 ft.

ADDITIONAL SPECIMEN EXAMINED:

U.S.: CALIFORNIA: SAN BENITO CO.: Along wash of Clear Creek 1.8 mi. from Hernandez on road to New Idria, R15094 (DS).

This distinctive species is apparently an endemic of serpentine soils in the vicinity of the type locality. Nonserpentine soils in the vicinity are occupied by populations of the hexaploid *Camissonia contorta*, which species tends to occur in light sandy soil, and expecially along washes. Both of the collections of *C. benitensis* cited above were tetraploid, with 14 pairs of chromosomes at meiotic metaphase I. Like *C. lacustris*, it occupies an enclave in an area that is now dominated by the hexaploid, and, also like *C. lacustris*, it was probably derived from *C. strigulosa*.

48. **Camissonia strigulosa** (Fisch. & Mey.) Raven, comb. nov.

Sphaerostigma strigulosum Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 50. 1835.
Oenothera strigulosa (Fisch. & Mey.) Torr. & Gray, Fl. N. Amer. 1: 512. 1840.
Oenothera strigulosa var. *epilobioides* Greene, Fl. Francisc. 216. 1891. Lectotype: Near Los Angeles, Los Angeles Co., Calif., 1890, *A. Davidson* (ND).
Sphaerostigma contortum var. *greenei* Small, Bull. Torrey Cl. 23: 189. 1896; nom. subs.
Oenothera contorta var. *strigulosa* (Fisch. & Mey.) Munz, Bot. Gaz. 85: 255. 1928.
Oenothera contorta var. *epilobioides* (Greene) Munz, Bot. Gaz. 85: 256. 1928.
Oenothera dentata sensu Munz, Fl. N. Amer. II. 5: 157. 1965; pro parte.

Erect or sometimes decumbent annual, to 5 dm. tall, usually well branched, with wiry stems and no well-defined basal rosette, the stems white or later brown, with exfoliating rhytidome; plants strigulose and often also glandular-pubescent, especially in the inflorescence, or occasionally glandular-pubescent only and then subglabrous;

hirsute pubescence sometimes present near the base, but this almost always accompanied by strigulose pubescence higher on the stems. Leaves linear to very narrowly elliptic, 0.8–3.5 cm. long. 0.1–0.3 cm. wide, sparsely serrulate. Hypanthium 1.6–2.7 mm. long, 1.1–2.4 mm. across at the summit, moderately to very sparsely pubescent within in lower half, or more rarely glabrous. Sepals 1.6–4 mm. long, 1–1.65 mm. wide, reflexed in pairs, the short tips of the sepals subterminal and distinct in bud. Petals 2.1–4.2 (–4.5) mm. long, 1.4–3.1 mm. wide, sometimes with two red dots at the base of each one. Filaments of the episepalous stamens 0.9–2 (–2.2) mm. long, those of the epipetalous ones 0.5–1.3 mm. long; anthers 0.3–0.6 mm. long. Usually less than 10 percent of the pollen with four pores. Style 2.3–4.8 mm. long, pubescent or rarely glabrous near the base; stigma 0.8–1.4 mm. in diameter, surrounded by the anthers of both sets of stamens at anthesis, and these shedding pollen directly on the stigma. Capsule straight or somewhat flexuous, 1.5–4.5 cm. long, 0.8–1.3 mm. thick, subsessile, with a sterile beak usually 1.5–3 mm. long. Seeds 0.6–0.8 mm. long, 0.3–0.4 mm. thick. Gametic chromosome number, $n=14$. Autogamous.

LECTOTYPE: Sphaerostigma strigulosum F. M. California. Cult.—C. A. Meyer" (ex herb. Ledebour), LE. This specimen closely matches a modern collection from the dunes between the town of Bodega Bay and Bodega Head, Sonoma County, California, *Raven* 18246, which is known to be tetraploid. It was probably grown from seeds gathered in the vicinity of Fort Ross, Sonoma County, California, at the northern limit of the species.

DISTRIBUTION (Figure 64): Widespread in open sandy grassland, vicinity of Bodega Bay, Sonoma County, California, south through the Coast Ranges to the vicinity of Santa Eulalia, at about 30°43′ N. lat. in Baja California; common in cismontane southern California, and in the Tehachapi Mountains, through which it reaches the southern Sierra Nevada of Kern County, California; Santa Rosa Island. A single collection supposed to be from Fort Huachuca, Arizona, has been seen, but the presence of this species in Arizona should be confirmed; this collection might represent a short-term introduction, for example. From sea level to 6,700 ft. alt.

Vouchers for chromosome number (54 individuals, 50 populations), $n=14$:

U.S.: CALIFORNIA: KERN CO.: Near Havilah, R18802; 1 mi. S. of Havilah, *Lewis* 1345, 3.4 mi. S., R20251; 0.5 mi. W. of Weldon, R18799 (sympatric with *C. contorta*); Weldon, R18777 (sympatric with *C. integrifolia*), 18796 (sympatric with *C. contorta*); 5 mi. S. of Weldon, R18793 (sympatric with *C. integrifolia*); 9.7 mi. S. of Weldon, 3,100 ft., R17561; NE. of Lake Isabella, 2,600 ft., *Howell* 37164 (CAS; progeny = R18844, 19750); Black Mt. burn, Greenhorn Mts., 3,500 ft., *Howell* 38215 (CAS; progeny = R18784; sympatric with *C. campestris* and

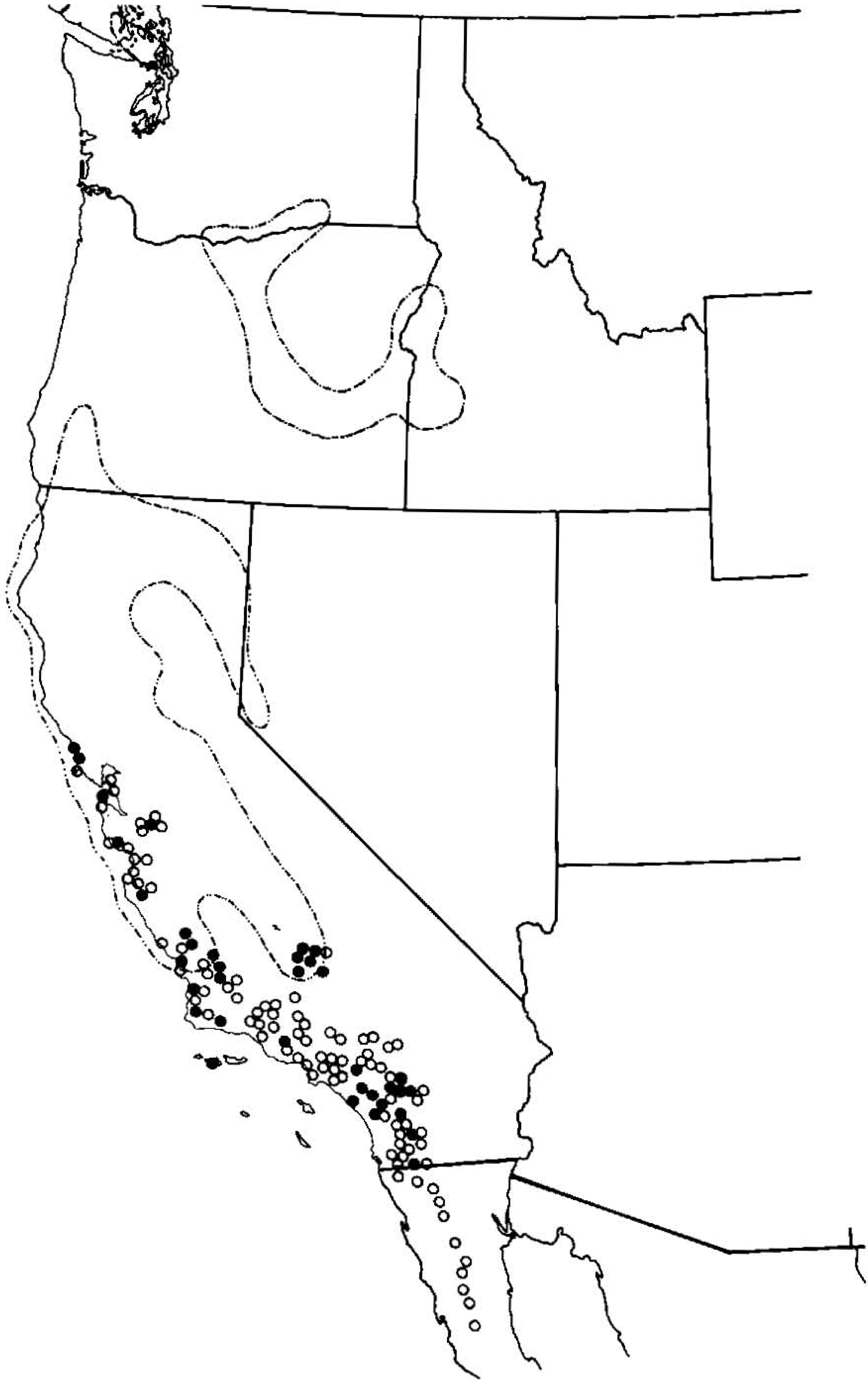


FIGURE 64.—Western United States and a portion of northwestern Mexico: ○=range of *Camissonia strigulosa,* with ●=tetraploid chromosome counts ($n=14$); area of the closely related hexaploid *C. contorta* is outlined with dotted line.

C. contorta). MARIN CO.: Dillons Beach, R18244. MONTEREY CO.: Paloma Creek, road from Arroyo Seco to Jamesburg, R18217; Big Sandy Valley, R18282. ORANGE CO.: 5.6 mi. NE. of Mission San Juan Capistrano, *Wedberg* 179. RIVERSIDE CO.: Reche Canyon, *Wedberg* 228; 4.1 mi. W. of Dripping Springs, R14022; Cajalco Road 0.1 mi. W. of Mockingbird Canyon Road, *Wedberg* 197; Machado Road near Elsinore, *Wedberg* 192; 7.7 mi. E. of Hemet, *Wedberg* 199 (herb. San Diego State College); 1.8 mi. S. of Hemet, *Wedberg* 201 (herb. San Diego State College); San Jacinto River wash 2.1 mi. SW. of Cranston Ranger Station, San Jacinto Mts., *Lewis* 1250; Hemet Meadows, San Jacinto Mts., R14245; Lake Fulmor, San Jacinto Mts., R14234; Vanderbilt Flat, San Jacinto Mts., *Wedberg* in 1957 (LA, RSA). SAN DIEGO CO.: Warner Hot Springs, *Kuijt* in 1958 (progeny); Dodge Valley, *Wedberg* 225 (herb. San Diego State College); 2.5 mi. W. of Julian, *H. & M. Lewis* 1672 (LA); 2.4 mi. N. of Pala, R16919; 2.2 mi. W. of Campo R16925. SAN FRANCISCO CO.: Sunset District, *Breedlove* 4907. SAN LUIS OBISPO CO.: 4.5 mi. E. of Santa Margarita, R20159; 8.6 mi. W. of Simmler, La Panza Range, 1,800 ft., *Breedlove* 2059; Morro Bay, R17935; Nipomo Mesa, *Breedlove* 2099, 4267, R17956; Camatti Creek, R18322; 2.9 mi. E. of San Miguel, R18311; Simmler to Creston Road, 3.6 mi. W. of junction with Pozo to Simmler Road *H. & M. Lewis* 1609 (LA); summit of road between Arroyo Grande and Edna, *Lewis et al.* 1664 (LA). SANTA BARBARA CO.: 4 mi. N. of Lompoc, R15509; Juncal Campground, upper Santa Ynez Valley, 1,800 ft., *Breedlove* 2234; E. of Torrey Pines, Santa Rosa I., R15000. SANTA CLARA CO.: Upper Arroyo del Puerto, Mt. Hamilton Range, R18231, *Breedlove* 4890. SANTA CRUZ CO.: Summit of Quail Hollow Road near Ben Lomond, R18184; 1 mi. S. of Ben Lomond, *Breedlove* 4636. SONOMA CO.: Between town of Bodega Bay and Bodega Head, R18246. VENTURA CO.: Cow Spring Campground, 17.6 mi. N. of Fillmore, Topatopa Mts. 3,500 ft., *Breedlove* 2645.

BAJA CALIFORNIA: 7.5 mi. N. of Santo Tomás, R17048.

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: ALAMEDA CO.: Alameda, *Jepson* in 1891 (JEPS, NY, UC US); Oakland, *Brewer* 2735 (US). CONTRA COSTA CO.: West Berkeley, *Tidestrom* in 1893 (POM). FRESNO CO.: Priest Valley to Parkfield Junction, *Thomas* 497 (DS; all pollen 3-pored). KERN CO.: Miracle Hot Springs, *Buckalew* 23 (RSA); Cuddy Valley, near Mt. Pinos, 5,500 ft., *Hall & Chandler* 6356 (UC); W. end of Tecuya Ridge, 6,800 ft., *Twisselmann* 9577 (CAS, DS); Black Bob Canyon, 4,200 ft., *Twisselmann* 8339 (CAS, DS); Kernville, 2,650 ft., *Howell* 37114 (CAS); Temblor Range W. of McKittrick, *Eastwood & Howell* 4099 (CAS). LOS ANGELES CO.: Browns Flat, San Gabriel Mts., 4,300 ft., *Wheeler* 915 (CAS, LA, UC); near Inglewood, *Abrams* 3237 (DS, GH, LE, NMC, NY, PH, POM, UC, US); vicinity of Elizabeth Lake, 2,750 ft., *Hall* 3051 (DS, NY, POM, RM, UC, US; possibly *C. contorta*, and one individual with 40 percent 4-pored pollen); summit Mt. Wilson, 6,000 ft., *Grant* in 1906 (DS); Tuna Canyon, Verdugo Hills, *MacFadden* in 1931 (GH, NY, RM, UC); Santa Monica Mts., 800 ft., *Abrams* 1261 (DS, NY, POM); Tujunga Creek at Barley Flats Trail crossing, 4,046 ft., *Ewan* 7271 (POM). MARIN CO.: Dunes near the radio station, Pt. Reyes Peninsula, *Howell* 21755 (CAS). MONTEREY CO.: Tassajara Hot Springs, 1,550 ft., *Ferris* 8314 (DS, GH, UC); Pacific Grove, *Patterson & Wiltz* in 1907 (DS); near Soledad, *Howitt* 1510 (CAS); San Simeon, *T. S. Brandegee* in 1888 (UC). ORANGE CO.: Rancho Santa Ana, 500 ft., *Howell* 900 (RSA). RIVERSIDE CO.: Banning, 2,300 ft., *Jones* in 1903 (DS, POM); Temescal Canyon, 8 mi. SE. of Corona, *Hitchcock & Muhlick* 22136 (DS, UC, WS, WTU); Idyllwild, San Jacinto Mts., 5,400 ft., *Spencer* 2201 (POM). SAN BENITO CO.: San Juan Bautista, *Brewer* 715 (UC). SAN BERNARDINO co.: San Bernardino Valley, *S. B. & W. F. Parish* 81 (DS, F, GH, NY, UC, US); N. of Cajon Pass, 3,600 ft., *Peirson* 4514 (RSA); Mojave R. at Deep Creek, 3,000 ft., *Lewis* 1428 (LA); Redlands, *Lewis* in 1937 (LA); Baldwin Lake, 6,700 ft., *Munz* 10745 (POM, UC). SAN DIEGO CO.: 2 mi. E. of Pala, *Munz* 10371 (POM); Warner Springs, 3,132 ft., *Rose* 49097 (COLO, RSA); Palomar Mt., 6,000 ft., *Cooper* 1494 (NY); pasture between Middle and South Peaks, Cuyamaca Mts., 5,000 ft., *Munz* 9792 (DS, POM); Descanso, *Munz & Harwood* 7137 (GH, POM, RM, UC); Jacumba, *Munz* 8091 (POM); Campo, *Eastwood* 9383 (CAS); base of San Miguel Mt., *Gander* in 1935 (POM). SAN FRANCISCO CO.: Presidio, Lake Merced, *Rose* 41282 (ARIZ, C, CAS, COLO, DS, GH, LA, NMC, NY, OSC, PH, POM, RM, UC, US, WS); Sutter St., San Francisco, *Rattan* in 1878 (DS). SAN LUIS OBISPO CO.: Salinas R. 5 mi. N. of Paso Robles, *Wiggins* 3421 (DS); Queen Bee Public Camp, La Panza Range, 2,300 ft., *Munz* 16325 (NY, RSA, WTU); Price Canyon, *Hoover* 9171 (CAS); Pismo Beach, *Abrams* 6513 (DS); foothills of Caliente Mt., Carissa Plains, *Hardham* 1786 (LA); Black Lake, S. of Arroyo Grande, *Hoover* 7069 (CAS, RSA). SAN MATEO CO.: South San Francisco, *Eastwood* in 1894 (GH); Colma, *K. Brandegee* in 1905 (UC). SANTA BARBARA CO.: Santa Barbara, *Elmer* 4001 (CAS, COLO, DS, F, GH, NY, POM, US); 10 mi. W. of Buellton, *Munz* 10297 (C, POM); base of Figueroa Mt., *Breedlove* 209 (UCSB); Big Pine, San Rafael Mts., *Hoffmann* in 1929 (CAS); E. fork of Lion Canyon, below Pine Corral Potrero, Sierra Madre Mts., 4,500 ft., *Blakley & Muller* 3425 (CAS, DS, JEPS, SBBG, UCSB; might be *C. contorta*); near edge of Pine Corral Potrero, near Salisbury Potrero, 4,500 ft., *Muller & Blakley* 1015 (DS, SBBG; might be *C. contorta*—22 percent 4-pored pollen); Santa Rosa I., *Brandegee* in 1888 (UC). SANTA CLARA CO.: Mt. Hamilton, *Elmer* 4625 (ARIZ, CAS, DS, NY, OSC, POM, UC, US, WS). SANTA CRUZ CO.: Swanton, *Rick* in 1912 (DS); Sunset Beach State Park, *Thomas* 3073 (DS); near Boulder Creek, ca. 650 ft., *Thomas* 1781 (DS). SONOMA CO.: Bodega Bay, *Heller & Brown* 5613 (COLO, DS, F, GH, NY, PH, POM, RM, US); "Colon Ross," *Wrangell* (LE). STANISLAUS CO.: Head of Adobe Creek, Adobe Valley, 1,600 ft., Mt. Hamilton Range, *Sharsmith* 3564 (RSA, UC). VENTURA CO.: North Fork of Ventura R. 1.7 mi. above Wheelers Hot Springs, 1,900 ft., *Wolf* 6898 (CAS, DS, GH, NY, RSA, UC, WS, WTU); Red Reef Canyon, Topatopa Mts., 2,800–3,500 ft., *Abrams & McGregor* 155 (DS, GH, NY, US); Matilija Canyon area above dam, *Pollard* in 1947 (CAS); Dry Lakes Ridge, Matilija-Sespe Divide, ca. 4,700 ft., *Pollard* in 1962 (CAS).

BAJA CALIFORNIA: 1.5–2.5 mi. upstream from Rincón, 4.5 mi. NE. of Santa Catarina, 64 mi. SE. of Ensenada, ca. 4,100 ft., *Broder* 716 (DS, UCSB); 9 mi. SE. of Tecate, *Munz* 9477 (POM, UC); 15 mi. NNW. of Rosarito, 3,780 ft., *Wiggins* 10009 (DS, US); Laguna Hansen, 5,450 ft., Sierra Juárez, *Gander* 3294 (SD); Rancho San José (Meling's Ranch), 2,300 ft., *Wiggins* 9771 (DS, UC, US); Rancho San Matias, 31°17′N. lat., 115°33′W. long., ca. 1,050 ft., *Moran* 10843 (DS, SD); Santa Eulalia, 30°43′N. lat., 115°20′W. long., ca. 1,850 m, *Moran* 11135 (DS, SD).

Camissonia strigulosa is a tetraploid species very closely related to the South American tetraploid *C. dentata* and at times distinguishable from it only with difficulty. Hybrids between these two species are, however, highly sterile (Raven & Moore, MS.), and most individuals can be distinguished by their habit and flower size, which is often larger in the South American populations. *Camissonia strigulosa* is likewise very closely related to the North American hexaploid *C. contorta*, although the latter can usually be distinguished by its possession of more than 10 percent 4-pored pollen grains, a character which is of course directly correlated with its higher chromosome number. In Kern County, California, in the southern Sierra Nevada, where the ranges of the two overlap, tetraploid individuals (=*C. strigulosa*) have appressed pubescence on the stems, hexaploid individuals (=*C. contorta*), spreading pubescence. This distinction does not always hold true in the Coast Ranges, but is sometimes useful.

Despite the undoubtedly close relationship between these three species, I prefer to maintain them as distinct, particularly in view of the other closely related but more easily distinguishable entities that are accorded taxonomic recognition in this revision. It is likely that differentiation at the tetraploid level has given rise to the local endemics *C. benitensis* and *C. integrifolia*, and the relatively local *C. lacustris* in North America, and to *C. dentata* following the introduction of a seed of this tetraploid group to South America (cf. Raven, Quart. Rev. Biol. 38: 151–177. 1963). The three relatively uncommon North American tetraploids are now at the margins of the range of the common tetraploid, *C. strigulosa*, and in two cases completely surrounded by populations of the hexaploid. As mentioned in the discussion of the diploid *C. campestris*, it is likely that some populations of the hexaploid *C. contorta* (those in the San Joaquin Valley of California, especially) have originated following hybridization between the diploid *C. campestris* and the tetraploid *C. strigulosa;* others have very probably originated by the occasional functioning of unreduced gametes in tetraploid populations.

Hybridization between *C. campestris* subsp. *obispoensis* and *C. strigulosa* has been mentioned in the account of the former taxon, above. From a bud collection made at Miracle Hot Springs, Kern County, California (R17567), I obtained a meiotic chromosome configuration of ca. 5 weakly joined pairs, a chain of 3 chromosomes, and 22 univalents ($2n=35$), suggesting hybridization between the hexaploid *C. contorta* and the tetraploid *C. strigulosa* at this locality; unfortunately, the individual from which these buds were taken was not identified in the collection. Another individual from the same collection had 5 pairs, a chain of 3 chromosomes, and 8 univalents, suggesting hybridization between *C. campestris* subsp. *campestris*, also present at this locality, and the tetraploid *C. strigulosa*. In addition to the three taxa just mentioned, *C. strigulosa* also has been observed growing sympatrically with the tetraploids *C. pubens* (*Munz* 13357, RSA) and *C. integrifolia*; hybridization with the latter is discussed under the treatment for that species, and with the diploid *C. kernensis* subsp. *kernensis*.

A single collection of what appears to be this species is supposed to have been made at Fort Huachuca in southern Arizona (May

1892, *Wilcox*, NY; Trans. N.Y. Acad. Sci. 14: 37. 1894). If the collection is properly labeled, the plant may have been a temporary introduction at this locality, perhaps with feed for animals; it is not otherwise known from Arizona.

49. **Camissonia dentata** (Cav.) Reiche, Fl. Chile 2: 264. 1898.[3]

South American plants very similar to the North American *C. strigulosa*, but differing in most cases by a combination of the following characteristics. Plants ascending, decumbent, or prostrate. Leaves linear to broadly elliptic, 0.3–2.8 cm. long, 0.07–0.45 cm. wide, usually denticulate but more rarely subentire. Hypanthium 0.8–3 mm. long. Sepals 1–4(–5) mm. long, 0.7–2 mm. wide. Petals 1.5–6(–8) mm. long. Filaments of the episepalous stamens 0.5–1.8 mm. long, those of the epipetalous ones 0.5–1.3 mm. long; anthers 0.5–1.3 mm. long. Style 0.8–5 mm. long; stigma 0.5–0.8 mm. thick, usually surrounded by the anthers in anthesis, but elevated above them in the plants with the largest flowers. Capsule 0.8–3.5 cm. long, 0.6–1.3 mm. thick. Seeds 0.8–1.1 mm. long, 0.3–0.5 mm. thick. Gametic chromosome numbers, $n=14$, 13. Self-compatible and usually autogamous.

DISTRIBUTION: In South America, from Arequipa, Peru, southward west of the Andes to Concepción Province, Chile, and southeastward in Argentina to Lago Argentino and Deseado in Gobernación de Santa Cruz. From sea level to ca. 3,500 ft. alt. throughout most of its area, but in northernmost Chile and southern Peru mostly between ca. 9,500 and 12,500 ft. alt. A map of the range of this species will be given by Raven and Moore (MS.).

The extreme variability of this complex species, which occupies a north-south range of some 2,500 miles in South America, has been the basis of a great deal of taxonomic confusion. The two recent treatments of the South American members of *Camissonia* (Munz, Physis 11: 266–292. 1933; Farm. Chil. 3–12. 1934) divide the populations here assigned to this species into five taxa: *Oenothera contorta* var. *divaricata* (Gay) Munz, *O. contorta* var. *epilobioides* (Greene) Munz, *O. dentata* Cav. (var. *dentata*), *O. dentata* var. *campestris* (Greene) Jeps., and *O. micrantha* var. *acuminata* (Phil.) Munz. *Camissonia cheiranthifolia*, erroneously reported from Chile in its protologue by Gay (Fl. Chile 2: 330. 1846) and by Reiche (Fl. Chile 2: 263. 1898), was correctly excluded from the flora of South America by Munz (Farm. Chil. 10. 1934; Rev. Univ. Cat. Santiago 22: 275. 1937). Munz distinguished *Oenothera dentata* from *O. contorta* on the basis of the larger flowers of the former, with petals 4–7 mm. long, those of

---

[3] The treatment of this species is by P. H. Raven and D. M. Moore, Department of Botany, The University, Leicester, England. Moore's fieldwork in Chile and Argentina was supported by grants from the National Science Foundation to Harlan Lewis and from the Royal Society of London to Moore.

the latter given as 2.5–3.5 mm. long. In our study of a wide range of Chilean material, however, we have found a complete range of flower size, the petals ranging from 1.5–6 or even 8 mm. long. With one exception, this variation does not appear to be geographically correlated. Collections from the central part of Concepción Province tend to have larger flowers than those from elsewhere, although plants with petals longer than 3 mm. are scattered from Coquimbo to Concepción. Sample measurements of petal length are given in the list of cited specimens.

Munz (1933–34, 1937) separated *Oenothera contorta* var. *divaricata* from var. *epilobioides* on the basis of the larger size and longer capsules of the latter, which often had a sterile tip at the apex. We have been unable, however, to confirm these relationships in our studies of South American material. Neither have we found the nature of the pubescence to be a reliable or geographically correlated characteristic. Many of the plants in this group have glandular pubescence in the inflorescence, but a large number have strigose pubescence, and these two types are sometimes found mixed in a single gathering. Other plants are subglabrous.

Oenothera dentata var. *campestris* was separated from *O. dentata* in Munz' treatment of the Chilean species (1934) by its narrower leaves. Such plants are sporadic throughout central Chile and ought not to be confused with the California diploid *Camissonia campestris* for reasons which will be made clear below.

Finally, as regards *Oenothera micrantha* var. *acuminata,* we have seen only a photograph made of the type in Santiago (GH). The plant shown is exceptional in its long-acuminate upper leaves, but in other respects there seems to be no reason why it could not be an unusual form of the complex so widespread throughout South America. It certainly seems unreasonable, on the basis of this single specimen, to credit the North American sect. *Holostigma* to South America. It is, however, highly desirable that similar plants be re-collected, and they may exist in Bíobío or neighboring provinces.

Despite the fact that all of the South American populations of this genus seem to belong to a single species, there are two distinctive geographical races within this species that deserve formal taxonomic recognition. The more local and uniform series of populations consists of a group of heavyset, broad-leaved plants with relatively large flowers and thick, heavy capsules found along the coast of Concepción and the neighboring provinces. This series is described as *C. dentata* subsp. *littoralis*.

We have grown 15 populations of this species, including 2 populations of subsp. *littoralis*, in the experimental garden. Of these, 13 had $n=14$, and 2, one belonging to the series of relatively large-flowered populations from Concepción mentioned above and the other to subsp. *littoralis*, had $n=13$. The two populations with $n=13$ represent the only naturally occurring aneuploid populations in the genus, but they are not strongly separated by sterility barriers from other South American populations with $n=14$. A summary of our cytogenetic and experimental studies with this group is given elsewhere (Raven & Moore, MS).

It appears likely that *Camissonia* may have reached South America only once, and relatively recently, by long-distance dispersal across the tropics (Raven, Quart. Rev. Biol. 38: 151–177. 1963), a phenomenon which has probably occurred twice in *Gayophytum*, once in *Clarkia*, and twice in *Boisduvalia*, three other genera of annual plants in the Onagraceae. *Camissonia dentata* is obviously most closely related to the North American tetraploid *C. strigulosa*, from which it may well have been derived, but the South American entity is far more variable, and most populations can easily be distinguished from those of North America. In these respects, the situation is closely similar to that in *Clarkia*. In view of this, the high degree of sterility between North and South American plants (Raven & Moore, MS) and the degree of morphological distinction between the species recognized in North America in this assemblage, it appears best to consider the North and South American plants as specifically distinct. If this is not done, the oldest name for the collective group would be *Camissonia dentata*, a name which (as *Oenothera dentata*) has usually been incorrectly applied to the diploid species here called *Camissonia campestris* in North America. Should *Camissonia dentata* be understood in this collective sense, it would probably be best to include the hexaploid *C. contorta* in the same species, but it would probably still be possible to maintain the more local tetraploids *C. benitensis* and *C. lacustris* as species distinct from this complex. *Camissonia integrifolia*, a third local tetraploid species, is so distinct morphologically that it does not really enter into this problem.

49a. Camissonia dentata subsp. **dentata**

Oenothera dentata Cav., Icon. 4: 67, *t. 398.* 1797, excl. verbis falsis "stigma . . . quadrifidum, laciniis ovatis minimis."

Camissonia flava Link, Jahrb. Gewachsk. 186. 1818.

Oenothera chamissonis Link, Enum. Pl. Hort. Berol. 1: 378. 1821. Type: Chile, presumably cultivated at Berlin, and probably destroyed (not seen).

Holostigma argutum Spach, Ann. Nat. Sci. Bot. Paris II. 4: 270. 1835; nom. subs.

Holostigma heterophyllum Spach, Ann. Sci. Nat. Bot. Paris II. 4: 271. 1835; nom. subs.

Sphaerostigma chamissonis (Link) Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 49. 1835.

Holostigma tenuifolium Spach, Ann. Sci. Nat. Bot. Paris II. 4: 270. 1835; non *Oenothera tenuifolia* Cav. 1797. Type: Chile, *Bertero* (P), not seen. The

Unio Itineraria distribution of Bertero's 466 and 1190 (BM, NY, S), from "Quintero, Quillota, in petrosis aridis planitiei fluvii Cachapual," is a mixture of large- and small-flowered plants, probably from two different localities; the small-flowered plants may be isotypes of this species, or the type collection may be *Bertero* 467 (BM), from Rancagua, Prov. O'Higgins.

Oenothera chilensis D. Dietr., Syn. Pl. 2: 1285. 1840; non Fisch. & Mey. 1835.

Oenothera heterophylla (Spach) Steud., Nom., ed. 2, 2: 206. 1841; non Spach 1835, nec Nutt. ex Hook. & Arn. 1838.

Oenothera minutiflora D. Dietr., Syn. Pl. 2: 1285. 1840. Type: Cultivated, from Chile, *C. A. Meyer* (isotype, LE).

Sphaerostigma dentatum (Cav.) Gay, Fl. Chil. 2: 326. 1846.

Sphaerostigma heterophyllum (Spach) Gay, Fl. Chil. 2: 327. 1846.

Sphaerostigma tenuifolium (Spach) Gay, Fl. Chil. 2: 327. 1846.

Sphaerostigma divaricatum Gay, Fl. Chil. 2: 238, *t. 22.* 1846. Type: Sandy places in the low mountains around Santiago, Chile (not seen).

Sphaerostigma ramosissimum Philippi, Linnaea 33: 68. 1864. Type: Near Concumen, Aconcagua, Chile, *Landbeck* (SGO, not seen; photographs, GH, POM).

Sphaerostigma acuminatum Philippi, Anal. Univ. Chile 84: 629. 1893. Type: Sandy places near Nacimiento, Bíobío, Chile, January 1877, *Philippi* (SGO; isotype, NY).

Chamissonia acuminata (Phil.) Reiche, Anal. Univ. Chile 98: 481. 1897.

Chamissonia tenuifolia (Spach) Reiche, Fl. Chile 2: 263. 1898.

Chamissonia paradoxa var. *divaricata* (Gay) Reiche, Fl. Chile 2: 264. 1898.

Oenothera torulosa f. *chilensis* (D. Dietr.) H. Lév., Monogr. Onoth. 180. 1905

Oenothera contorta var. *divaricata* (Gay) Munz, Physis 11: 288. 1933.

Oenothera micrantha var. *acuminata* (Phil.) Munz, Farm. Chil. 11. 1934.

Oenothera dentata var. *campestris* sensu Munz, Farm. Chil. 10. 1934.

Oenothera contorta var. *epilobioides* sensu Munz, Farm. Chil. 10. 1934.

Plants erect, decumbent, or prostrate. Leaves linear or very narrowly lanceolate. Capsules 0.6–0.9 mm. thick. Gametic chromosome numbers, $n = 14$, 13. Self-compatible and mostly autogamous.

TYPE: Near Coquimbo and Talcaguano, Coquimbo, Chile, Nov., *Ruiz & Pavon* (MA; photographs, CONC, F). Judging from the photographs I have seen, the flowers are probably shown a little too large in the illustration that accompanies the type description; the stigma was certainly not 4-lobed in this plant.

DISTRIBUTION: That of the species, except coastal Arauco and Cautín Provinces, Chile.

REPRESENTATIVE SPECIMENS EXAMINED:

ARGENTINA: BUENOS AIRES: Carmen de Patagones, *Miccio-Peralta* 67 (DS). CHUBUT: "Río Carren" (?), *Skottsberg* in 1908 (UPS); "Futalenfú," *Skottsberg* in 1908 (S, UPS); Lago Colue Huapi, *Riggs* 67 (F, GH). COMODORO RIVADAVIA: 50 km. W. of town of Lago Buenos Aires, *Eyerdam et al.* 24491 (GH, K, UC). NEUQUÉN: Neuquén, 240 m, *Comber* 37 (K); Río Caliefu, *Cabrera* 5109 (F, POM); Piedra de Águila, 40°02'S. lat., 70°01' W. long., *Senn* 4244 (RSA); Cerro Lotena, 900 m, *Ammann* 83 (F). Río NEGRO: San Carlos de Bariloche, 800 m, *Buchtein* in 1905 (US); General Roca, 250–360 m, *Fischer* 85 (BM, F, GH, K, NY, US); shore of Lago Nahuel Huapi, *Cordini* 155 (POM, US). SANTA CRUZ: Deseado, *Darwin* 129 (K); Tehuelches, 300 m, *Donat* 87 (BM, F, GH, K, S, UC); 160 km.

S. of Deseado on road to San Julian, *Eyerdam et al.* 23912, (GH, UC); San Julian, 50 m, *Blake* 318 (K); 78 km. S. of San Julian on road to Santa Cruz, Río Chico, *Eyerdam et al.* 23994 (GH, UC); S. shore of Lago Argentino 3 km. E. of Calefate, 270 m, *Eyerdam et al.* 24279 (GH, K, UC).

CHILE: Aconcagua: Papudo, *E. W. D. & M M. Holway* 65 (GH, US); Los Andes, *Mancilla* in 1952 (CONC). Arauco: Isla Santa Maria, *Beck* 75 (K). Atacama: Sandy washes around El Morro, ca. 14 km. ENE. of Caldera, *Worth & Morrison* 16165 (GH, UC); La Varilla, ca. 25 km. N. of Vallenar on road to Capiapó, *Worth & Morrison* 16262 (GH, K, UC); Cachiyuyo, *Ricardi & Marticorena* 4885/1270 (CONC). Bíobío: Candelaria, Arenales de Los Setenta, *Junge* in 1935 (CONC; petals 5 mm long). Colchagua: La Rufina, Río Claro, *Ricardi* in 1951 (CONC); Talcarihue, San Fernando, *Ricardi* in 1950 (CONC). Concepción: Puente Itata, road from Concepción to Bulnes, *Pfister* 810 (CONC; petals 6.5 mm long); Quilacoya, *Pfister* 298 (CONC; petals 6 mm long); between Yumbel and Estación Yumbel, *Marticorena et al* in 1959 (CONC; petals 4.5 mm long); Pangal del Laja, W. of Yungay, *Marticorena et al.* in 1959 (CONC; petals 3.5 mm long), *Ricardi & Marticorena* 4991/1375 (CONC; petals 5 mm long). Coquimbo: Punta Colorado, *Rose & Rose* 19340 (NY, US); Paihuano, Valle del Cochiguaz, 1,120 m. *Behn* in 1948 (CONC); Parque Lambert, ca. 6 km. NW. of La Serena on road to Islon, 30 m, *Worth & Morrison* 16337 (GH, K, UC); Coquimbo, 30 m, *Elliot* 548 (K; petals 4.5 mm long); Fray Jorge, *Muñoz* B112 (GH); Los Vilos, *Behn* (CONC; petals 3–4 mm long); ca. 5 km. above Los Molles, *Moore* 215 (DS). Curico: Los Queñes, *Milner* 45 (CONC). Malleco: Fundo Tambillo near Nacimiento, *Hempel* 7422 (CONC; petals 6–8 mm long), *Pfister* in 1934 (CONC; petals 2 mm long). Maule: Caquenes, *Reid* (K, NY; some plants with petals 2.5 mm long, others 5.5–6 mm). Ñuble: Fundo Santa Ana, *Behn* in 1937 (CONC); Río Cholguan, road from Yungay to Huépil. *Pfister* in 1946 (CONC). O'Higgins: Callanas, Río Pangal valley, *Moore* 263 (DS). Santiago: Batuco, over 500 m, *Looser* 3652 (GH); San Antonio, coast, *Claude-Joseph* 1449 (US); Esmeraldar, Departmento Melpilla, *Reed* 1867/10 (GH). Talca: Talca, *Claude-Joseph* 1692 (US). Tarapacá: Road from Azapa to Chapiquiña, Episcacha, Km. 94, 3,500 m, *Ricardi & Marticorena* 4760/1145 (CONC). Valparaíso: Limache, Cuesta La Dormida, 1,200 m, *Behn* in 1940 (CONC); Valparaíso, 60 m, *Sandeman* 202 (BM, K); Viña del Mar, *Buchtein* in 1895 (S). Without definite locality: *Gay* (GH, K, NY, RSA; "*Sphaerostigma tenuifolium* Spach").

PERU: Arequipa: Chachani, 3,350 m, *Stafford* 607 (BM, K); near Chiguata, 3,100 m., *Várgas* 8093 (RSA); Pampa de Arrieros, 3,750 m., *Pennell* 13327 (F, GH, NY, PH); lower slopes of Misti, 3,050 m, *Sandeman* 4002 (K); Tiabaya, 2,100–2,200 m., *Pennell* 13096 (PH). Without definite locality: *Dombey* 726 (F).

49b. Camissonia dentata subsp. **littoralis** Raven & Moore, subsp. nov.

A subsp. *dentata* differt: foliis latioribus, 0.5–1.8 cm. longis, 0.2–0.45 cm. latis, crassioribus; plantis prostratis; capsulis crassioribus, 1.2–2.5 cm. longis, 1.1–1.3 mm. latis. Numerus chromosomatum gameticus, $n=14$, 13. Autogama.

Type: Near Concepción, Concepción, Chile, 1855, *P. H. Germain* (GH; isotypes, BM, F, K). An isotype is illustrated in H. Lév., Monogr. Onoth., facing p. 175. 1905.

Distribution: Sandy soil and dunes on the coast of Concepción, Arauco, and Cautín Provinces, Chile; from sea level to a few hundred feet alt.

SPECIMENS EXAMINED:

CHILE: ARAUCO: Laraquete, *Moore* 290 (DS). CAUTÍN: Bajo Imperial, *Moreton Middleton* in 1906 (BM, S). CONCEPCIÓN: San Vicente, *Scott Elliott* 197 (BM), *Junge* in 1934 (CONC): Concepcíon, *Jaffuel* 2906 (GH), *Cuming* 116 (BM): mouth of the Bíobío, *Ricardi* 8520 (CONC); N. side, mouth of the Bíobío, *Junge* in 1935 (CONC), *Pfister* 297 (CONC), in 1941 (CONC), in 1948 (CONC), *Ramírez* in 1959 (CONC); Tomé, *Junge* in 1935 (CONC); Coronel, *Hill* 167 (K); Coronel, Mina Schwager, *Sparre* 10111 (CONC); Lengua, in mouth of Estero Lengua in Bahía San Vicente, *Moore* 276 (DS). PROVINCE UNKNOWN: Taliahua, *Philippi* (US); I. Quiriquina, *Gunckel* 2805 (GH).

This distinctive and fairly localized entity occupies the southern part of the coastal range of this species in Chile. It has relatively large flowers, the petals ranging from 3–5.5 mm. long.

A specimen from Concepción (*Elliot* 549, GH, K) is spreading in habit but does not have the broad leaves of subsp. *littoralis;* one from San Pedro, Concepción (*Sparre* 14229, CONC) is closer to *littoralis* but intermediate. Likewise, a single collection that has been examined from farther north (Santo Domingo, south of Llolleo, Santiago, *Looser* 1455 GH) approaches subsp. *littoralis*, as does one from Linares, Playa de Pelluhue, *Aravena* 61 (UC, US).

For some unknown reason, Hector Léveillé (Monogr. Onoth. 175. 1905) considered this taxon a species distinct from his *Onothera torulosa*, in which he included all other members of sect. *Camissonia*. He called this species *Onothera hyssopifolia* Molina, Saggio Chile, ed. 2, 134. 1810, but Molina says of his species "fiore . . . terminale violetto, di più d'un pollice di diametro . . ."; it seems likely that, as suggested by Munz (Farm. Chil. 7. 1934), this name refers to some form of *Clarkia tenella* (Cav.) H. & M. Lewis (*Godetia tenuifolia* (Cav.) Spach). *Onothera hyssopifolia*, however, was not mentioned by Moore and Lewis in the most recent revision of the South American species of *Clarkia* (Bol. Soc. Arg. Bot. 10: 332–340. 1965).

50. Camissonia integrifolia Raven, sp. nov. FIGURE 62

Herba annua *C. strigulosae* persimilis. Inflorescentia dense cinererostrigulosa; plantae sparse strigulosa vel subglabrae. Folia linearia, integria, rare dentibus parvulis obscuris 1–2. Hypanthium intus in partem dimidiam pubescens. Stylus prope basin pubescens vel glaber. Capsula stricta, erecta, 4.5–6 cm. longa. Semina 1–1.2 mm. longa, 0.4–0.5 mm. crassa. Chromosomatum numerus gameticus, $n=14$. Autogama.

TYPE: On bank covered with *Artemisia tridentata*, Weldon, Kern County, California, 3 May 1958, *P. H. Raven* 12806 (DS).

DISTRIBUTION (Figure 63): Dry, often deserty slopes along the Kern River from Miracle Hot Springs to the vicinity of Weldon, Kern County, California; 2,450–3,000 ft. alt.

Vouchers for chromosome number (1 population, 1 individual), $n=14$:

U.S.: CALIFORNIA: KERN CO.: Weldon, R18776 (grown in experimental garden).

ADDITIONAL SPECIMENS EXAMINED:

U.S.: CALIFORNIA: KERN CO.: Weldon, 2,450 ft., R17536 (DS), 18791 (DS); mouth of Kelso Canyon at State Hwy. 178, 2,800 ft., *Twisselmann* 7041 (CAS, DS, SBBG); 5 mi. S. of Weldon, R18792 (DS); 6 mi. from Weldon on road to Kelso Valley, 3,000 ft., *Weatherby* 1158 (RSA); 8.3 mi. S. of Weldon on road to Kelso Valley, 2,900 ft., R17560 (DS); Miracle Hot Springs, ca. 2,500 ft., *Buckalew* 23 (RSA).

Camissonia integrifolia is a narrow endemic of a portion of the upper Kern River drainage. It is distinctive in its entire leaves, long, erect capsules, and distribution of its pubescence. *Raven* 17536, cited above, is predominantly this species but includes two plants of *C. strigulosa* and one probable hybrid. A chromosome determination was made of one plant of this collection, which had an extremely irregular polyploid meiosis, suggesting hybridity. Progeny of this collection was grown at Stanford, yielding R18776 (*C. integrifolia*, $n=14$), R18777 (*C. strigulosa*, $n=14$), and R18778, a single obvious hybrid between these two species. The hybrid had variable meiotic configurations ranging from 8 univalents and 10 pairs of chromosomes to 1 chain of 3, 13 univalents, and 6 pairs. It had 11 percent stainable pollen, based on a sample of 200 grains in lactophenol. Thus *C. integrifolia* appears amply distinct from *C. strigulosa*, from which it may have been derived, and grows sympatrically with it, with the occasional formation of sterile hybrids. These two species were also observed growing sympatrically at the locality of R18792, cited above. *Camissonia integrifolia* has also been observed growing sympatrically with *C. kernensis* subsp. *kernensis*, *C. pubens*, *C. campestris*, and *C. contorta*.

51. Camissonia contorta (Dougl.) Kearney, Trans. N.Y. Acad. Sci. 14: 37. 1894.

Oenothera contorta Dougl., *in* Hook., Fl. Bor. Amer. 1: 214. 1834.

Sphaerostigma contortum (Dougl.) Walp., Rep. 2: 78. 1843.

Oenothera dentata var. *cruciata* S. Wats., Proc. Amer. Acad. 8: 594. 1873. Lectotype: Sandy places in the Sacramento Valley, Calif., *Hartweg* 1733 (GH, NY).

Oenothera campestris var. *cruciata* (S. Wats.) Greene, Fl. Francisc. 216. 1891.

Sphaerostigma campestre (Greene) Small var. *minus* ("minor") Small, Bull. Torrey Cl. 23: 189. 1896.

Oenothera cheiranthifolia var. *contorta* (Dougl.) H. Lév., Monogr. Onoth. 216. 1905.

Oenothera torulosa f. *cruciata* (S. Wats.) H. Lév., Monogr. Onoth. 180. 1905.

Oenothera torulosa f. *mixta* H. Lév., Monogr. Onoth. 180. 1905. Type: Possibly at MO; cf. A. Nelson, Bot. Gaz. 40: 57. 1905.

Sphaerostigma campestre var. *mixtum* (H. Lév.) A. Nels., Bot. Gaz. 40: 57. 1905.

Oenothera contorta var. *typica* Munz, Bot. Gaz. 85: 253. 1928.

Oenothera contorta var. *strigulosa* sensu Munz, Bot. Gaz. 85: 255. 1928; pro parte.
Oenothera contorta var. *epilobioides* sensu Munz, Bot. Gaz. 85: 256. 1928; pro parte.
Oenothera contorta var. *contorta*; Munz, N. Amer. Fl. II. 5: 156. 1965.
Oenothera cruciata (S. Wats.) Munz, N. Amer. Fl. II. 5: 157. 1965.
Oenothera dentata sensu Munz, N. Amer. Fl. II. 5: 157. 1965; pro parte.

Very similar to *C. strigulosa*, but almost always with hirsute pubescence near the base and often with only hirsute pubescence or a limited admixture of glandular trichomes in the inflorescence, very rarely entirely strigulose and glandular-pubescent. Leaves often broader, to narrowly elliptic, the foliage often more bluish green than that of *C. strigulosa*. Flowers often larger, the petals to 5 mm. long and 3.3 mm. wide. Longer filaments to 2.6 mm. long, the shorter to 1.5 mm. long; anthers to 0.8 mm. long. Often more than 30 percent of the pollen with 4 or 5 pores. Style to 5.1 mm. long. Seeds 0.7–0.9 mm. long. Gametic chromosome number, $n=21$. Autogamous.

TYPE: On barren sandy soils of the interior parts of the Columbia River, Washington or Oregon, 1825–6, *D. Douglas* (K; isotype, BM).

DISTRIBUTION (Figure 65): Open or grassy slopes and flats, usually on sandy soil: southern Vancouver Island, British Columbia, and San Juan and Whidbey Islands, northwesternmost Washington; Klickitat and Walla Walla Counties, southern Washington, and Adams and Ada Counties, Idaho, south through east-central Oregon to the vicinity of Reno, western Nevada, and from southwestern Oregon (Douglas, Jackson, and Josephine Counties) south nearly throughout California to the southern San Joaquin Valley and bordering foothills in Kern County; generally away from the coast from Sonoma County, California, southward, where replaced by *C. strigulosa*. From sea level to 7,500 ft. alt.

Vouchers for chromosome number (42 individuals, 40 populations), $n=21$:

U.S.: CALIFORNIA: CONTRA COSTA CO.: Antioch, R18142; ca. 1 mi. S. of Oakley, R18144. FRESNO CO.: 1.6 mi. S. of Easton, R18328· Fresno, R17067; 3.3 mi. N. of Selma, R17065. HUMBOLDT CO.: Near Arcata, R18373; 1 mi. E. of Dinsmores, R18367. KERN CO.: West of mouth of Kern River canyon, *Wedberg & Lewis* 1671 (LA); Miracle Hot Springs, R17567 (progeny = R18773), R18805; Isabella, R18800; 0.5 mi. W. of Weldon, R18798 (sympatric with *C. strigulosa*); Weldon, R18795 (sympatric with *C. strigulosa*); Havilah, R17568; Black Mt. burn, Greenhorn Mts., 3,500 ft., *Howell* 38215 (CAS; progeny = R18785; sympatric with *C. campestris* subsp. *campestris* and *C. strigulosa*). LAKE CO.: 3 mi. S. of Kelseyville, *Breedlove* 5143; 2 mi. NE. of Lower Lake, *Breedlove* 4540; 9.9 mi. N. of Lower Lake, R18240; Lakeport R18239. LASSEN CO.: 4.8 mi. N. of Milford, R17872. MADERA CO.: 7.6 mi. S. of Coarsegold, R18340; 0.7 mi. W. of Oakhurst, R18344. MERCED CO.: Ca. 20 mi. W. of Merced, *Klein* 444 (RSA; progeny, DS). MONTEREY CO.: 1.5 mi. W. of Bradley, R18206: 4.1 mi. N. of Mission San Antonio,

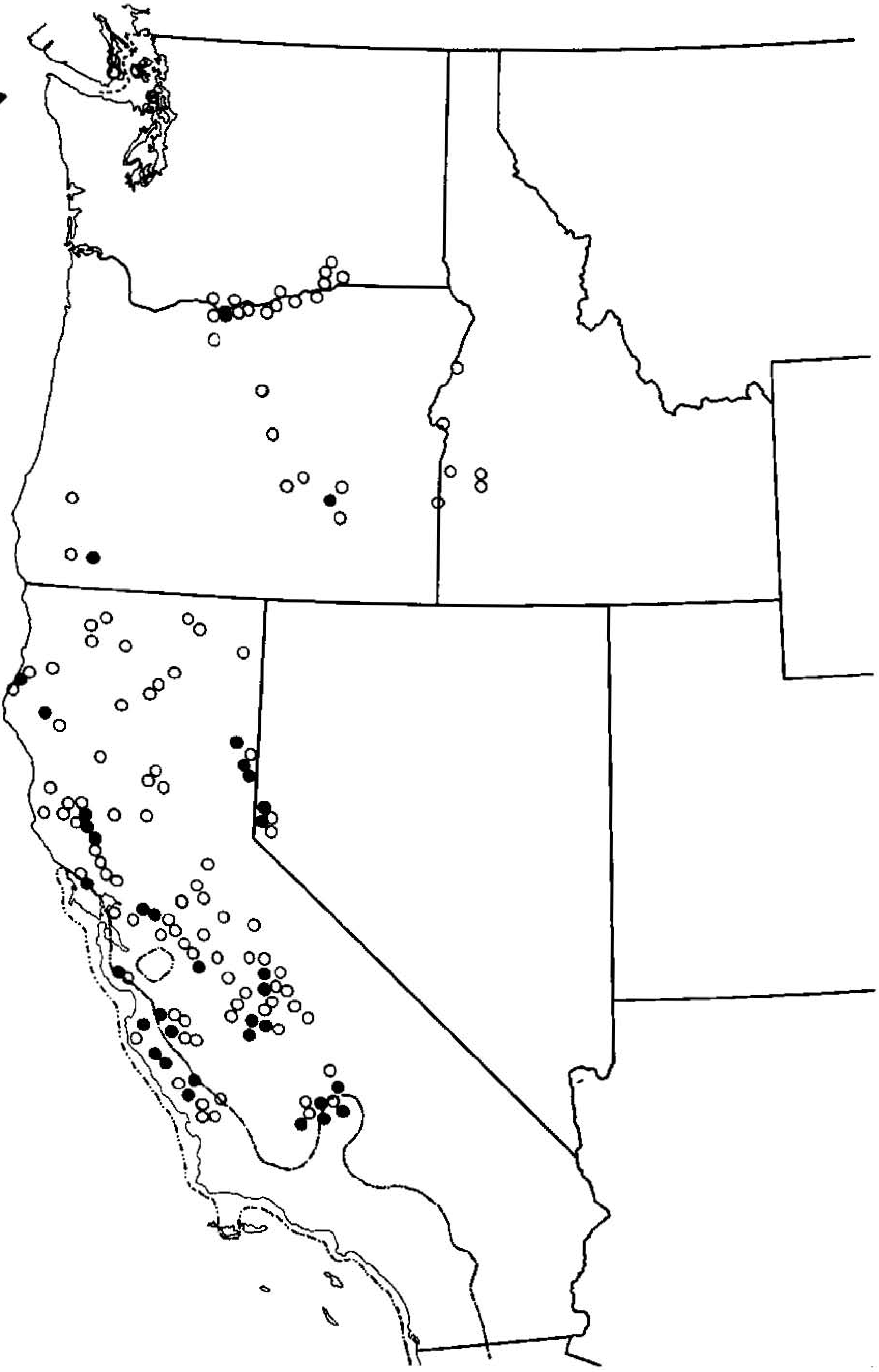


FIGURE 65.—Western United States: ○=range of *Camissonia contorta,* with ●=hexaploid chromosome counts ($n=21$). Northern limits of the closely related tetraploid *C. strigulosa* indicated by dotted line.

Breedlove 2278; 1.6 mi. N. of junction to Jamesburg, Carmel Valley, R18149; Jolon, R18154; 10 mi. N. of Hunter Liggett Military Reservation Headquarters on road to The Indians, R18272. PLUMAS CO.: 3.1 mi. W. of Vinton, R18418; 4.8 mi. W. of Vinton, R18420. SAN BENITO CO.: Panoche Creek Campground, Pinnacles, *Breedlove* 2182; 1.1 mi. S. of Cienaga School, near Hollister, R18199. SAN LUIS OBISPO CO.: 1.8 mi. W. of Bee Rock, R18302, 18303; Atascadero, R18280. SONOMA CO.: 3 mi. S. of Sebastopol, *Breedlove* 3706. TULARE CO.: Posey to White River, R20239; Kern River Canyon 6 mi. S. of Roads End P.O., 3,100 ft., *Howell* 33134 (CAS; progeny = R18770). NEVADA: STOREY CO.: 4.7 mi. N. of Carson City, R18544. WASHOE CO.: Ca. 5 mi. N. of Reno, *Mosquin & Gillett* 5310 (DAO; progeny = R18780). OREGON: HARNEY CO.: 5.3 mi. N. of Narrows, R18455. JACKSON CO.: Just N. of Central Point, R18381. WASCO CO.: 2.2 mi. W. of Sherman Co. line along Columbia R., R18385.

REPRESENTATIVE SPECIMENS EXAMINED:

CANADA: Saanich Spit, *Eastham* in 1942 (NMC, UBC); Cedar Hill, near Victoria, *Macoun* in 1887 (NMC).

U.S.: CALIFORNIA: AMADOR CO.: 2 mi. NNE. of Buena Vista, ca. 300 ft., *Howell* 29808 (CAS). BUTTE CO.: Chico, *Copeland* 3033 (POM); hills 8 mi. N. of Oroville, *Heller* 11330 (CAS, DS, GH, NY, OSC, PH, UC, US, WTU). CALAVERAS CO.: 2 mi. W. of Camanche, 400 ft., *Belshaw* 1978 (UC); Mokelumne Hill, *Blaisdell* (CAS). CONTRA COSTA CO.: Alhambra Valley, *Rattan* in 1887 (DS); Nortonville, *Bacigalupi* 4977 (JEPS). ELDORADO CO.: Coloma, *Reed* in 1941 (UC). FRESNO CO.: Hwy. 180 just below 4,000 ft. marker, *Quibell* 1963 (RSA); Shaver, 5,200 ft., *Hall & Babcock* 292 (UC); Millwood Meadow, near Sequoia Lake, 5,100 ft., *Simonian* 482 (herb. Fresno State College); Clovis, *Thompson* in 1902 (DS, POM). HUMBOLDT CO.: Klamath R. at mouth of Slate Creek, 400 ft., *Tracy* 16244 (UC). KERN CO.: Cedar Canyon just below mouth of Fulton Creek, Greenhorn Range, 3,250 ft., *Twisselmann* 8495 (DS); Walker Basin, 3,400 ft., *Twisselman*, 9518 (CAS, DS, RSA); 16 mi. S. of Bodfish, *Thorne* 31736 (DS, RSA); Poso Creek, *Hall & Babcock* 5012 (DS, GH, PH, UC). LAKE CO.: Dashiels, Mt. Sanhedrin, *Eastwood* in 1925 (CAS); W. base of Snow Mt., *Ackley* in 1965 (CAS); Jordan Park, *Jussel* in 1932 (POM). LASSEN CO.: Milford, *Baker* in 1890 (UC); Chat, 5,000 ft., *Jones* in 1897 (POM). MADERA CO.: N. side of Millerton L., 550 ft., *Bacigalupi* 7672 (JEPS); Bass Lake, 3,300 ft., *Quibell* 2452 (POM); 5 mi. NE. of Madera, *Howell* 41073 (CAS). MARIPOSA CO.: Just S. of Mormon Bar, 1,800 ft., *Howell* 40571 (CAS). MENDOCINO CO.: Sand in the Russian R., Ukiah, *Bolander* 3857 (F, NY); Navarro, *Byxbee* in 1895 (JEPS); near Longvale, 1,500 ft., *Tracy* 9924 (UC, WTU). MERCED CO.: Delhi, *Howell* 35293 (CAS); 2 mi. SW. of Livingston, *Stage* 59–59 (RSA, UC); Merced R. bottom between Snelling and Hopeton, *Howell* 1049 (CAS). MODOC CO.: Parker Creek SE. of Alturas, 5,200 ft., *Payne* 637 (JEPS); sink along highway between Malin and Canby, several miles N. of quarantine station, *Baker* 8309 (POM). MONTEREY CO.: Trail to Ventana Double Cone, 4,000 ft., *Hardham* 10127 (DS); 3 mi. NE. of Pleyto Well, SW. of Bradley, 550 ft., *Graham* 266 (RSA, UC). NAPA CO.: Howell Mt., *Jepson* 14478 (JEPS); Capell Valley, 700 ft., *Kamb & Chisaki* 1761 (UCSB). PLUMAS CO.: Near Beckwourth, 4,880 ft., *Howell* 37800 (CAS). SAN BENITO CO.: 5.4 mi. S. of Willow Creek School on road to the Pinnacles, *Ferris* 8347 (CAS, DS, GH, POM, UC); Panoche Pass, *Abrams & Borthwick* 7984 (DS, NY, POM); 3.7 mi. from Hernandez on road to New Idria, R15088 (DS). SAN JOAQUIN CO.: 8.8 mi. S. of Stockton, R9132 (CAS); Mokelumne, 200 ft., *Roseberry* 160 (UC); Tracy, *Baker* 2775 (CAS, F, GH, NY, POM, RM, UC, US). SAN LUIS OBISPO CO.: Palo Prieto

Canyon, *Ferris* 12816 (DS); Atascadero, *Hardham* 3054 (LA, SBBG). SANTA CLARA CO.: Stanford University, *Elmer* 2368 (NY, US). SANTA CRUZ CO.: Bielawski Look Out Station, 3,270 ft., *Thomas* 1514 (DS, OSC); Deer Ridge Farm, summit of Santa Cruz Mts., 2,800 ft., *Pendleton* 371 (POM, UC). SHASTA CO.: Near McArthur, *Eastwood & Howell* 7955 (CAS, POM); Hat Creek ca. 20 mi. W. of Fall River Mills, *Hitchcock* 6554 (POM, WTU); near Redding, *Heller* 7888 (GH, NY, PH, US). SISKIYOU CO.: French Creek Logging Road W. of Callahan, 3,500–4,000 ft., *Ferris & Lorraine* 11757 (DS, RSA, UC, WTU); Scott Valley, 2,900 ft., *Parker* 406 (NMC, UC); Yreka Creek, Siskiyou Mts., 2,800 ft., *Wheeler* 3527 (POM, RSA, UC); near Yreka, *Greene* in 1876 (F). SONOMA CO.: Pitkin Marsh near Forestville, *Rubtzoff* 1027 (UC). STANISLAUS CO.: 8 mi. E. of Oakdale, *Hoover* 3956 (UC); Turlock, *Fosberg* in 1927 (POM); Modesto, *Hoover* 889 (UC). SUTTER CO.: South Peak, Marysville Buttes, *Jepson* 14478 (JEPS, UC). TEHAMA CO.: 6 mi. W. of Paskenta, *Bailey* in 1938 (JEPS). TRINITY CO.: Three Forks of Mad River, 2,900 ft., *Tracy* 10175 (DS, UC). TULARE CO.: Sand along Tule R., *Dudley* in 1897 (DS); Johnsondale, 4,670 ft., *Howell* 37343 (CAS). TUOLUMNE CO.: Tuolumne R. just below junction of Middle and South Forks, R8234 (CAS). IDAHO: ADA CO.: Boise, 2,880 ft., *Clark* 38 (DS, F, GH, NY, POM, RM, UC, US, WS, WTU). CANYON CO.: New Plymouth, 2,200 ft., *Nelson & Macbride* 777 (RM); Big Willow, 3,000 ft., *Macbride* 158 (GH, NY, RM, US). OWYHEE CO.: Jump Creek Canyon, R13391 (DS). WASHINGTON CO.: Weiser, 2,200 ft., *Jones* in 1900 (POM). NEVADA: STOREY CO.: Carson City, 5,000 ft., *S. Watson* in 1868 (NY). WASHOE CO.: Reno Hot Springs to Steamboat Springs, 5,200 ft., *Train* 3557 (NY, UC). OREGON: CROOK CO.: Hay Creek, 730 mi., *Leiberg* 204 (F, GH, NY, ORE, UC, US, WS). DOUGLAS CO.: Bluffs of the Umpqua R. opposite Roseburg, *Constance & Rollins* 2959 (DS, GH, NMC, NY, RM, RSA, UC, US, WS, WTU). GILLIAM CO.: 6 mi. E. of Arlington, R18390 (UC, WS, WTU). HARNEY CO.: 28 mi. from Burns on road to Lakeview, *Howell* 28697 (CAS); 12 mi. N. of Frenchglen, *Peck* 25262 (OSC, UC). HOOD RIVER CO.: Hood River, *Suksdorf* in 1895 (WS). JACKSON CO.: 2 mi. N. of Central Point, *Peck* 14968 (US). JOSEPHINE CO.: Grants Pass, *Henderson* in 1886 (DS). MORROW CO.: 0.5 mi. E. of Boardman, *Cronquist* 6239 (NY, OSC, RSA, US, WS, WTU). SHERMAN CO.: Mouth of John Day R., *Hitchcock* 20435 (WTU). UMATILLA CO.: Umatilla, *Jones* in 1902 (POM). WASCO CO.: The Dalles, *Sheldon* 10263 (DS, F, GH, NY, POM, US, WS); Tygh Valley, *Flinn* in 1913 (ORE). WHEELER CO.: 2 mi. SW. of the Painted Hills, ca. 10 mi. NW. of Mitchell, 2,300 ft., *Cronquist* 7269 (NY, OSC, RSA, US, WS, WTU). WASHINGTON: BENTON CO.: Collidge, *ZFR* in 1910 (WS). FRANKLIN CO.: Pasco, *Piper* 2965b (WS). ISLAND CO.: Whidbey I., *Gardner* (POM, UC). KLICKITAT CO.: Carley to Roosevelt, *Pickett et al.* 1433 (WS); near Rockland, *Suksdorf* 5098–5101 (DS, F, US, WS). SAN JUAN CO.: Cattle Point, San Juan I., *Peck* 12711 (WS, WTU). WALLA WALLA CO.: Wallula, *Booth* in 1944 (WS).

As mentioned in the discussions of the preceding species of this section, some populations of *Camissonia contorta*, the only hexaploid species of the group, are very difficult to distinguish from those of the tetraploid *C. strigulosa*. *Camissonia contorta* probably arose, at least in part, following hybridization between the diploid *C. campestris* subsp. *campestris* and the tetraploid *C. strigulosa*, but some populations referred to this species may also have originated following the functioning of an unreduced gamete in a tetraploid plant. *Camis-*

sonia contorta has been found growing sympatrically with *C. kernensis* subsp. *kernensis*, *C. pubens*, *C. parvula*, *C. campestris* subsp. *campestris*, *C. campestris* subsp. *obispoensis*, *C. sierrae*, *C. lacustris* (populations in near vicinity), *C. strigulosa*, and *C. integrifolia*. Hybrids have been observed with *C. campestris* subsp. *campestris*, *C. campestris* subsp. *obispoensis*, and *C. strigulosa*, but these were highly sterile, and there is no evidence of intergradation between *C. contorta* and any other species. Whether the northern and southern populations of this hexaploid differ from one another enough to merit formal taxonomic recognition (particularly in view of the large gaps in the range) remains to be seen; I cannot identify any consistent differences between them at present.

Hexaploid populations were referred by Munz (Bot. Gaz. 85: 251–257. 1928) to *Oenothera contorta* var. *typica* (virtually all of this taxon), var. *epilobioides*, and var. *strigulosa* (a few northern populations only; mostly=*C. strigulosa*). In his more recent treatment of the group (N. Amer. Fl. II. 5: 156–157. 1965) he presented a very confusing treatment, recording *Oenothera contorta* var. *contorta* as diploid, which, so far as I am aware, it never is; placing some hexaploid populations with his *Oenothera dentata*, which name I now restrict to South American plants; and recognizing as a species *Oenothera cruciata*, said to have $n=7$, and consisting of a mixture of late-season plants of *Camissonia campestris* subsp. *campestris* ($n=7$), the Clear Lake, Lake County, California, populations of *C. lacustris* ($n=14$), and some relatively large-flowered plants of *C. contorta* ($n=21$).

Section VII. *Eremothera*

Camissonia sect. *Eremothera* Raven, Brittonia 16: 285. 1964.

Oenothera subg. *Sphaerostigma* sensu Munz, Bot. Gaz. 85: 234. 1928; pro parte.

Oenothera sect. *Eremothera* (Raven) Munz, N. Am. Fl. II. 5: 148. 1965.

Annuals, the plants caulescent, with no well-defined basal rosette, but the leaves sometimes clustered near the base; plants usually with conspicuous exfoliating white rhytidome, often reddish; plants flowering from the base or not. Leaves subsessile or petiolate, sometimes purple-dotted. Inflorescence erect or nodding at anthesis and becoming erect in fruit. Flowers opening near sunset. Ovary lacking a sterile projection. Petals white, only rarely reddish initially but always fading reddish after fertilization, without any dots or markings. Anthers yellow; stigma and inside of hypanthium greenish; filaments and style white. Capsule sessile regularly but sometimes tardily loculicidal, straight or much contorted, often somewhat torulose, the seeds in one row in each locule, the friable central column much distorted by the seeds at maturity. Seeds either of two kinds, those of the body of the capsule sharply angular, truncate-ellipsoid, dark brown, coarsely papillose, those of the beak narrowly obovoid or narrowly oblanceolate, smooth or finely lacunose, or all of the second type (figs. 71, 72).

TYPE SPECIES: *Camissonia refracta* (S. Wats.) Raven.

DISTRIBUTION: Mainly in the interior deserts and bordering areas, from east-central Washington, central and southern Idaho, and western Wyoming south through western Colorado to trans-Pecos Texas, northern Sonora, northeastern and central Baja California, and the deserts of California, whence north in the inner Coast Ranges to Alameda and San Joaquin Counties; loose, sandy, or clay soil, on brushy or open slopes and flats.

The clearly related species of *Camissonia* sect. *Eremothera* can easily be divided into four distinctive groups: The first consists of the self-incompatible *C. refracta* and its more widely distributed autogamous derivative, *C. chamaenerioides;* second, the polymorphic, self-incompatible *C. boothii*, here divided into six subspecies, and its two autogamous, smaller flowered derivatives, *C. pygmaea* and *C. gouldii;* third, *C. nevadensis*, a localized endemic of clay soil in west-central Nevada which is very likely an outcrosser and may or may not be self-incompatible; and fourth, the highly autogamous, widespread *C. minor*, which does not appear to be closely related to any of the other groups. In contrast to sect. *Holostigma* and sect. *Camissonia*, which contain majorities of polyploid species, sect. *Eremothera* resembles sect. *Chylismia* and sect. *Eulobus* in being almost exclusively diploid, the one exception being one of the two strains of the autogamous *C. pygmaea* that was examined cytologically; this plant was tetraploid ($n=14$). I cannot make any useful suggestions as to whether *C. refracta* or *C. boothii* is more primitive within this group, but it is clear that the autogamous species have all been derived from self-incompatible ancestors. *Camissonia nevadensis* is comparable with *Boisduvalia cleistogama* Curran, an annual species of another tribe of the family (Epilobieae), in inhabiting heavy clay soil and having decumbent branches with tardily dehiscent capsules which shed their seed only following rains and many months after the flowers were open and the plants were green. As pointed out earlier in this paper, *Camissonia graciliflora* and *C. palmeri* also share this unusual habit; I do not know of any comparable species of Onagraceae, although a number of genera in other families that occur in the same places have produced one or more species that are somewhat comparable.

In general, the outcrossing species of *Eremothera* are visited and pollinated by small moths in the evening after they open and sometimes also by bees early the following morning. At a few, widely scattered localities, *Camissonia boothii* subsp. *decorticans* opens its flowers about an hour before sunset and is visited and pollinated by the large, oligolectic bee *Andrena* (*Onagrandrena*) *vespertina* Linsley & MacSwain. Most populations of this subspecies, and most (if not all) other populations of the section open their flowers at or shortly after sunset, and there is generally not enough time for visitation by bees before darkness.

In his revision of this group, Munz (Bot. Gaz. 85: 233–270. 1928) recognized *C. refracta*, *C. chamaenerioides*, *C. nevadensis*, and *C. minor* with the same limits accepted in the present paper. No problems have arisen subsequently concerning the delimitation of these distinctive species. *Camissonia pygmaea* was considered a variety of *C. boothii*, but I raised it to specific rank in 1964 (Raven, Brittonia 16: 285) because of its nonoverlapping pattern of variation. This entity is autogamous, in contrast to the self-incompatible and much larger flowered *C. boothii;* the separation of these two taxa at the specific rank was subsequently accepted by Munz (N. Amer. Fl. II. 5: 154. 1965). *Camissonia gouldii* is described in the present revision from material that was not available to Munz at the time of his 1928 paper; like *C. pygmaea*, it is evidently an autogamous derivative of *C. boothii.*

The populations here grouped as *C. boothii* were separated by Munz (Bot. Gaz. 85: 233–270. 1928) into three species: *Oenothera decorticans*, with four intergrading varieties; *O. boothii;* and *O. alyssoides*. Three of the four varieties of *O. decorticans* are here regarded as subspecies of *Camissonia boothii;* the fourth, var. *rutila*, is regarded as a series of unrelated populations with relatively small flowers in which the petals are red from the time the flowers first open. Intermediate populations are found joining the three species recognized by Munz in 1928, and this is the reason that I considered them best treated as subspecies in 1964. In his 1965 monograph, Munz followed this treatment, describing an additional subspecies, subsp. *intermedia*, which occurs in central Nevada and adjacent easternmost California and links subsp. *boothii* with subsp. *alyssoides*. Dr. Munz and I thought earlier that an additional subspecies, which he described in 1965 as subsp. *inyoensis*, should be recognized; but I have since come to believe that this entity is best treated as part of subsp. *desertorum* as delineated here. At any rate, we both agree that this complex series of populations is best regarded as a single, polytypic species.

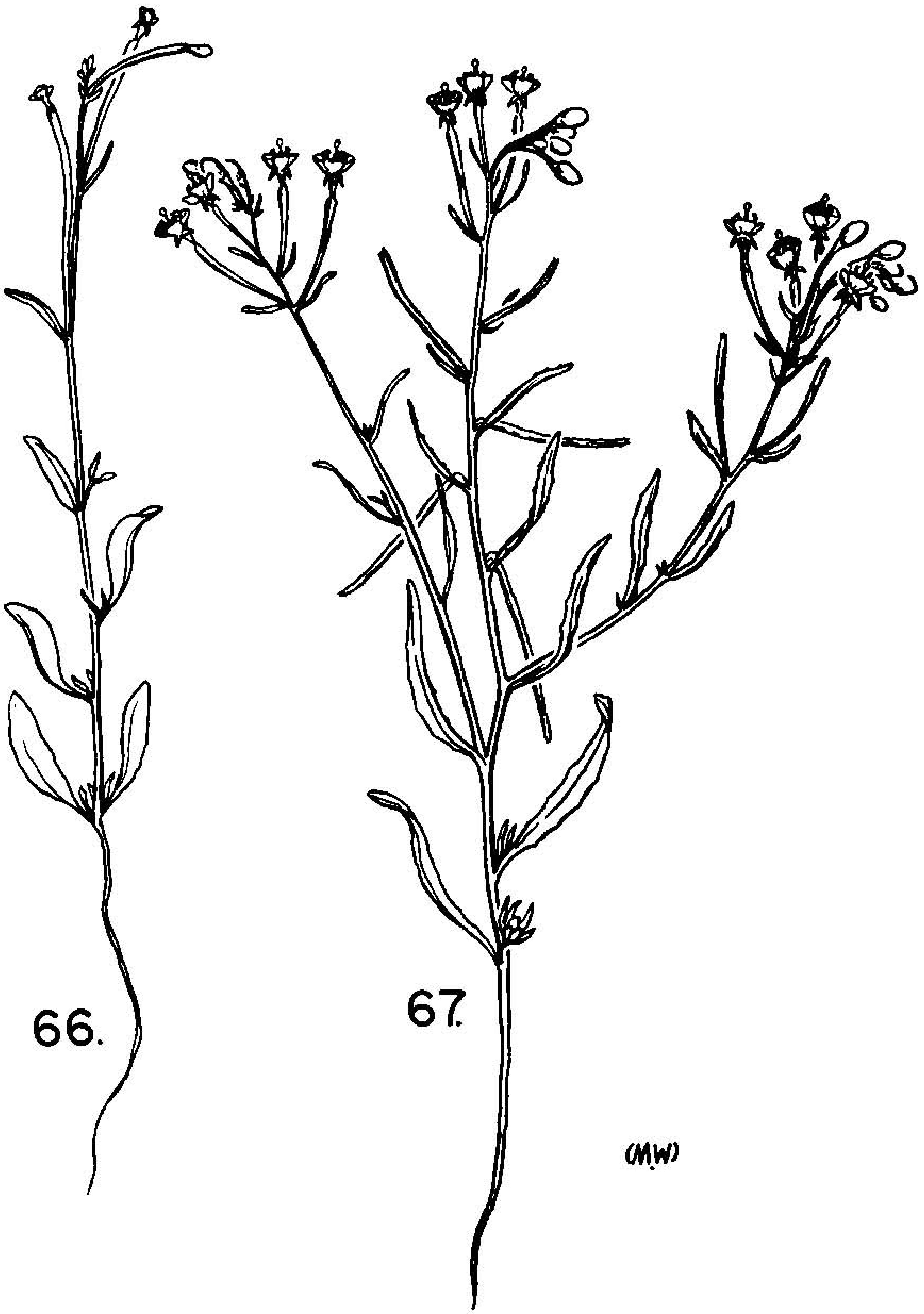
52. Camissonia refracta (S. Wats.) Raven, Brittonia 16: 285. 1964. FIGURE 67

Sphaerostigma refractum (S. Wats.) Small, Bull. Torrey Cl. 23: 192. 1896.

Oenothera deserti M. E. Jones, Contr. West. Bot. 12: 15. 1908. Type: Needles, San Bernardino Co., Calif., 5 May 1884, *M. E. Jones* 3828 (POM: isotypes, DS, GH, US).

Sphaerostigma deserti (Jones) Heller, Muhlenbergia 9: 68. 1913.

Erect, 6–45 cm. tall, often well branched at the base and above, not flowering near the base, sparsely strigulose or with an admixture



FIGURES 66–67.—Species of *Camissonia* sect. *Eremothera*, × ¾: 66, *C. chamaenerioides* (*Gould* 1473, DS); 67, *C. refracta* (*Hitchcock & Muhlick* 22246, DS).

of glandular trichomes in the inflorescence or all over. Leaves very narrowly elliptic to very narrowly lanceolate, the basal ones largest, to 6 cm. long and 0.8 cm. wide, often withered by the time of flowering; leaves sparsely and weakly denticulate; apex acuminate, the base attenuate; basal leaves with a petiole up to 2 cm. long, the upper ones subsessile. Inflorescence nodding before anthesis. Hypanthium 4–6 mm. long, 1.6–2 mm. across at the summit, villous in lower half within. Sepals 4–6 mm. long, 1.2–2 mm. wide. Petals 3.5–7 mm. long, 2–6 mm. wide. Filaments of the episepalous stamens 2–4.5 mm. long, those of the epipetalous ones slightly shorter; anthers 1.5–2.5 mm. long. Style 9–13 mm. long, the lower portions villous; stigma 1–1.5 mm. in diameter, held well above the anthers at anthesis. Capsule 2–5 cm. long, 0.7–1 mm. thick, straight to contorted, erect, spreading, or reflexed, terete. Seeds all of one type, 0.9–1.5 mm. long, 0.45–0.5 mm. thick, gray, finely lacunose, the lacunae in lines. Gametic chromosome number, $n=7$. Self-incompatible.

Lectotype: Gravelly hills near the Colorado River, Arizona or California, 17 February 1854, *J. Bigelow* (GH); cf. Munz, Bot. Gaz. 85: 237. 1928.

Distribution (Figure 68): Sandy desert slopes and flats from southernmost Esmeralda, southern Nye, and Clark Counties, Nevada, and Washington County, southwestern Utah, south throughout the Mojave and Colorado Deserts of Inyo, San Bernardino, Imperial, central and eastern Riverside, and eastern Kern and San Diego Counties, California; Mohave, Yuma, and western Pima Counties, Arizona. A single collection has been seen from Hidalgo County, New Mexico (east of Lordsburg, *Jones* in 1930, POM), but this is from some 250 miles out of the usual range. I have not mapped it and feel that the locality should be reconfirmed by further collections. From about 100 ft. below sea level to 4,500 ft. alt.

Vouchers for chromosome number (15 individuals, 12 populations), $n=7$:

U.S.: Arizona: Yuma Co.: Ca. 20 mi. E. of Yuma, *H. & M. Lewis* 1640 (LA; 2 pairs + ring of 10); 20 mi. N. of Yuma, R14837 ($n=7$); 4.3 mi. E. of Ehrenburg, R11597 (2 plants, both with 5 pairs + ring of 4). California: Imperial Co.: 23 mi. N. of Ogilby, *Klein* 119 (7 pairs). Inyo Co.: Sheppard Canyon, Panamint Valley, *T. & L. Mosquin* 4312 (4 pairs + ring of 6); Harrisburg Flats, Panamint Mts., *Gregory* 399 (RSA; 5 pairs + ring of 4). Riverside Co.: Box Canyon, *Lewis* 1623 (LA; 5 pairs + ring of 4), 1633 (LA; 3 pairs + 2 rings of 4); Corn Springs, Chuckwalla Mts., R11577 (2 plants, both with 5 pairs + ring of 4); Fargo Canyon, R11439 (2 plants, both with 7 pairs). San Bernardino Co.: Near Whipple Mts., *Klein* 1394 (7 pairs). Nevada: Clark Co.: Ranger Mts., R18916 ($n=7$).

Camissonia refracta is distinctive and has rarely been confused with any other entity. It often grows sympatrically with *C. chamaenerioides*, *C. boothii* subsp. *condensata*, and *C. boothii* subsp. *desertorum*, but no hybrids have been observed in nature. The high degree of chromosomal heterozygosity in this species is striking and could well be investigated further; of the 13 individuals in which chromosome association has been observed, 4 had 7 pairs; 6 had 5 pairs and a ring of 4; 1 had 3 pairs and 2 rings of 4; 1 had 4 pairs and a ring of 6;

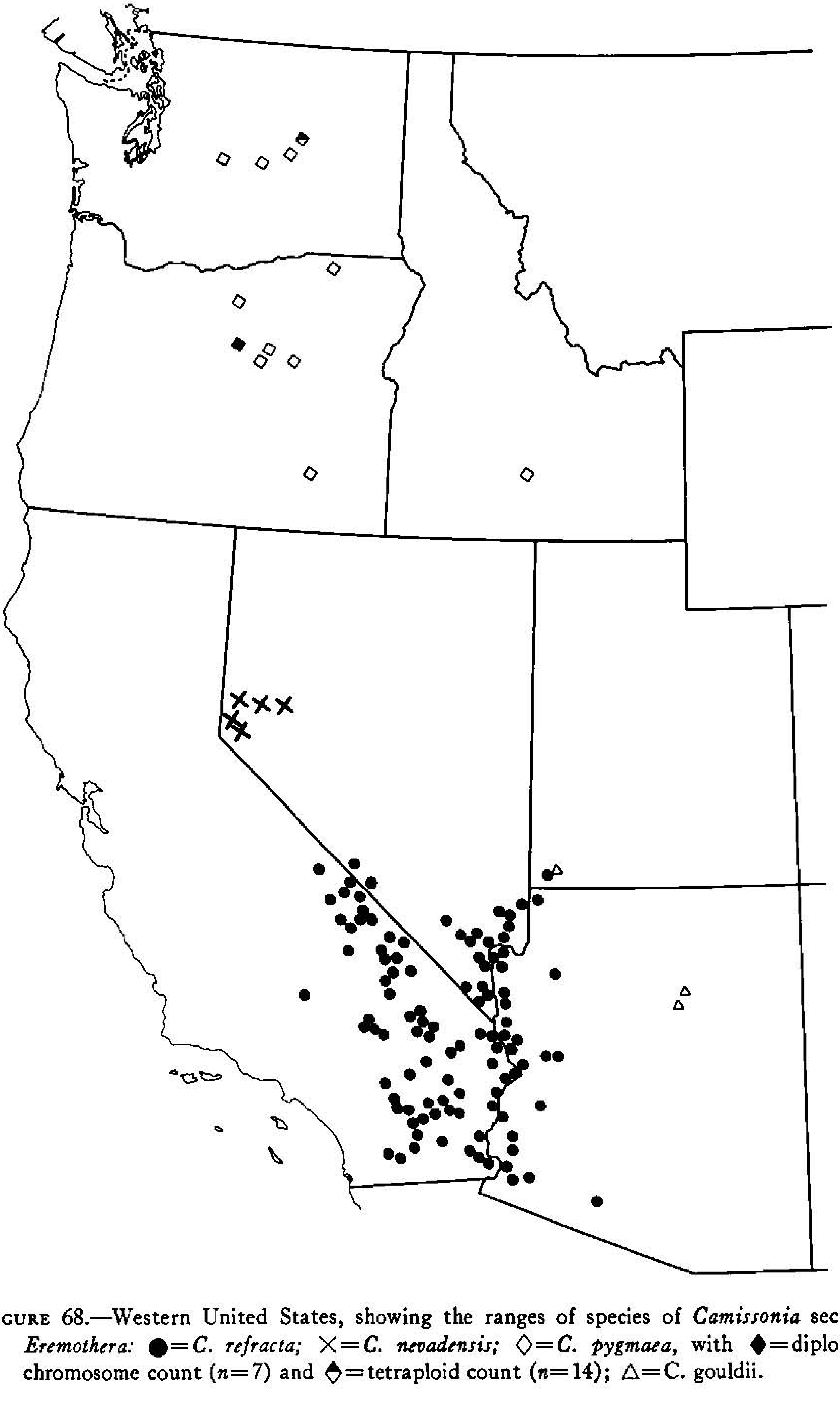


FIGURE 68.—Western United States, showing the ranges of species of *Camissonia* sect. *Eremothera:* ●=*C. refracta;* ×=*C. nevadensis;* ◇=*C. pygmaea,* with ◆=diploid chromosome count ($n=7$) and ⬘=tetraploid count ($n=14$); △=C. gouldii.

and 1 had 2 pairs and a ring of 10. There is no evidence that any of these configurations is associated with balanced lethals as in certain species of *Oenothera*, *Gayophytum*, *Calylophus*, and *Gaura;* but it would seem on the basis of our present limited amount of evidence that well over half of the individuals of this species are heterozygous for at least one reciprocal translocation, a situation unknown elsewhere in *Camissonia*. Six individuals from the Nevada population cited above were found to be self-incompatible by pollen-tube growth.

53. Camissonia chamaenerioides (A. Gray) Raven, Brittonia 16: 285. 1964.

FIGURE 66

Sphaerostigma chamaenerioides (A. Gray) Small, Bull. Torrey Cl. 23: 189. 1896.

Sphaerostigma erythrum A. Davids., Bull. S. Calif. Acad. Sci. 1: 118, *pl. 9.* 1902. Type: Dry hill slopes, south of Clifton, Greenlee Co., Ariz., 10 April 1899, *A. Davidson* 244 (LAM; isotypes, DS, UC).

Oenothera erythra (A. Davids.) Macbride, Contr. Gray Herb. 65: 41. 1922.

Erect, 8–50 cm. tall, usually branched near the base, not flowering near the base, glandular-pubescent with an admixture of strigulose pubescence in and near the inflorescence. Leaves very narrowly elliptic, more rarely narrowly elliptic, the basal ones largest, to 8 cm. long and 2.5 cm. wide; leaves entire to very sparsely denticulate; apex acute or acuminate, the base attenuate; petioles of basal leaves 1–3.5 cm. long, the upper leaves subsessile. Inflorescence nodding before anthesis. Hypanthium 1.6–2.3 mm. long, 0.9–1.4 mm. across at the summit, pubescent in lower half within. Sepals 1.5–2.5 mm. long, 0.7–1.3 mm. wide. Petals 1.8–3 mm. long, 1–1.8 mm. wide. Filaments of the episepalous stamens 0.7–1.5 mm. long, those of the epipetalous ones very slightly shorter; anthers 0.5–1.1 mm. long. Style 2.3–4.5 mm. long, the lower portions pubescent; stigma 0.7–1 mm. in diameter, surrounded by the anthers at anthesis. Capsule 3.5–5.5 cm. long, 0.8–0.9 mm. thick, spreading, terete. Seeds similar to those of *C. refracta*, 0.9–1 mm. long, ca. 0.3 mm. thick. Gametic chromosome number, $n = 7$. Autogamous.

TYPE: El Paso, El Paso County, Texas, 1852, *C. Wright* 1377 (GH; isotypes, BM, K, PH, US).

DISTRIBUTION (Figure 50): Sandy desert slopes and flats from northern Inyo County, California, Nye and Lincoln Counties, Nevada, and Washington County, Utah (also known from Dugway, Tooele County, *Jones* 1891, POM), south to the vicinity of Bahía de los Angeles in northeastern Baja California, in Sonora to the vicinity of Luja midway between Hermosillo and Guaymas, throughout Arizona except for the northeastern corner, rare in New Mexico (Dona Ana and Luna Counties), and in trans-Pecos Texas east to Brewster County; also known from Isla Angel de la Guarda in the Gulf of California. Not known from, but to be expected in, Chihuahua. From about 150 ft. below sea level to 4,600 ft. alt.

Vouchers for chromosome number (10 individuals, 5 populations), $n = 7$:

U.S.: ARIZONA: PIMA CO.: 3 mi. N. of headquarters, Organ Pipe National Monument, *H. & M. Lewis* 1639 (3 plants; LA). YUMA CO.: 4.3 mi. E. of Ehrenburg, R11596 (DS); 1 mi. S. of Ehrenburg, R11593 (DS). CALIFORNIA: RIVERSIDE CO.: Corn Springs, Chuckawalla Mts., *Mosquin* 3209 (4 plants; DAO).

BAJA CALIFORNIA: Bahia de los Angeles, *Moran* 12422.

Camissonia chamaenerioides is distinctive and has rarely been confused with any other species. It is similar to *C. refracta* and probably derived from populations relatively similar to that species, but differs not only in flower size but also in leaf shape, pubescence, and seed size. *Camissonia chamaenerioides* is the only species of the genus that occurs in Texas. This species occurs sympatrically with *C. refracta*, *C. boothii* subsp. *condensata*, and *C. boothii* subsp. *desertorum;* no natural hybrids have been observed.

54. **Camissonia boothii** (Dougl.) Raven, Brittonia 16: 285. 1964.

Erect, 12–65 cm. tall, often well branched at the base and above, usually not flowering near the base, subglabrous, strigulose, villous, or glandular-pubescent. Leaves very narrowly elliptic to narrowly ovate, the basal ones largest, 2–10 cm. long, 0.5–3.8 cm. wide, often withered by time of flowering, sparsely denticulate, the apex acuminate or acute, the base narrowly cuneate to attenuate; basal leaves with a petiole 0.4–6 cm. long, the upper ones subsessile. Inflorescence nodding before anthesis. Hypanthium 4–7 (–8) mm. long, 1.7–2.5 mm. across at the summit, villous in lower half within. Sepals (2.7–) 4–8 mm. long, 1.4–2.3 mm. wide. Petals (3–) 4–7.5 mm. long, (1.75–) 2.6–7 mm. wide. Filaments of episepalous stamens (1.5–) 2–5.8 mm. long, those of the epipetalous ones slightly shorter; anthers (1–) 1.8–2.3 mm. long. Style (6.5–) 8.2–13.5 (–15) mm. long, villous near the base; stigma 1.2–2 mm. across, depressed-globose, held well above the anthers at anthesis. Capsule slightly curved outward to contorted, 0.8–3.5 cm. long, 1–3.8 mm. thick at the base, terete, held on the dried plant and shedding seeds tardily. Seeds all of one type or of two types, the relatively smooth kind (which may be the only kind) 1.4–2.1 mm. long, 0.5–0.7 mm. thick, more or less triangular in transection, light brown, those of the body 0.5–0.9 mm. thick, dark brown, coarsely papillose. Gametic chromosome number, $n = 7$. Self-incompatible.

DISTRIBUTION (Figure 69): Deserty, often brushy or open slopes and flats, from Klickitat, Adams, and Whitman Counties, eastern Washington, and southwestern Idaho, south to eastern California (whence north in the inner Coast Ranges to Alameda and San Joaquin counties), northeastern Baja California, northwestern Sonora, and through western Utah to western Arizona, south to Pima and Pinal Counties. From about 200 ft. below sea level to 6,600 ft. alt.

As explained in the introductory remarks for the section, *Camissonia boothii* is here treated as a polytypic species with six subspecies that replace one another geographically. The seeds are apparently always monomorphic in subsp. *alyssoides* but very rarely so in populations of the other subspecies.

Of the 21 individuals of this species for which meiotic chromosome association was observed, 2 had a ring of 4 chromosomes and 5 pairs, 1 had a ring of 6 and 4 pairs, and 18 had 7 pairs. This suggests the presence of translocation heterozygosity of about the same order of magnitude (about 20 percent) as found in sect. *Chylismia*, but much less than characteristic of *C. refracta*.

54a. Camissonia boothii subsp. **decorticans** (Hook. & Arn.) Raven, Brittonia 16: 285. 1964.

Gaura decorticans Hook. & Arn., Bot. Beechey Voy. 343. 1838.

Oenothera gauraeflora Torr. & Gray, Fl. N. Amer. 1: 510. 1840.

Sphaerostigma gauraeflorum (Torr. & Gray) Walp., Rep. 2: 78. 1843.

Oenothera decorticans (Hook. & Arn.) Greene, Fl. Francisc. 217. 1891.

Oenothera rutila A. Davids., Erythea 2: 62. 1894. Type: Big Rock Creek, San Gabriel Mts., Los Angeles Co., Calif., 8 July 1894, *A. Davidson* (LAM).

Sphaerostigma decorticans (Hook. & Arn.) Small, Bull. Torrey Cl. 23: 191. 1896.

Sphaerostigma rutilum (A. Davids.) Parish, Erythea 6: 89. 1898.

Oenothera alyssoides var. *decorticans* (Hook. & Arn.) Jeps., Man. Fl. Pl. Calif. 686. 1925.

Oenothera decorticans var. *typica* Munz, Bot. Gaz. 85: 245. 1928.

Oenothera decorticans var. *rutila* (A. Davids.) Munz, Bot. Gaz. 85: 245. 1928.

Oenothera boothii subsp. *decorticans* (Hook. & Arn.) Munz, N. Amer. Fl. II. 5: 152. 1965

Oenothera boothii subsp. *rutila* (A. Davids.) Munz, Fl. N. Amer. II. 5: 153. 1965.

Stems 12–65 mm. long, hollow, with conspicuous, exfoliating white or somewhat pinkish or brownish rhytidome. Plants subglabrous, with strigulose or glandular trichomes in the inflorescence. Capsule nearly straight, curved outward, swollen at base, 1.7–2.3 mm. thick near the base, rapidly tapering upward. Seeds dimorphic, 1.4–2.1 mm. long, 0.5–0.7 mm. (smooth type) or 0.8 mm. (papillose type) thick. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: California, 1833, *D. Douglas* (K; isotypes, BM, GH, NY).

DISTRIBUTION (Figure 69): Open, usually steep slopes, often on shale or other loose rocky substrates, endemic to California: inner south Coast Ranges from Alameda and southwestern San Joaquin Counties south to Santa Barbara and Ventura Counties and the San Gabriel Mountains and easternmost Santa Monica Mountains of Los Angeles County, whence north through the Tehachapi Mountains to the western slopes of the southern Sierra Nevada in Kern and southernmost Tulare Counties; from near sea level to 6,000 ft. alt.

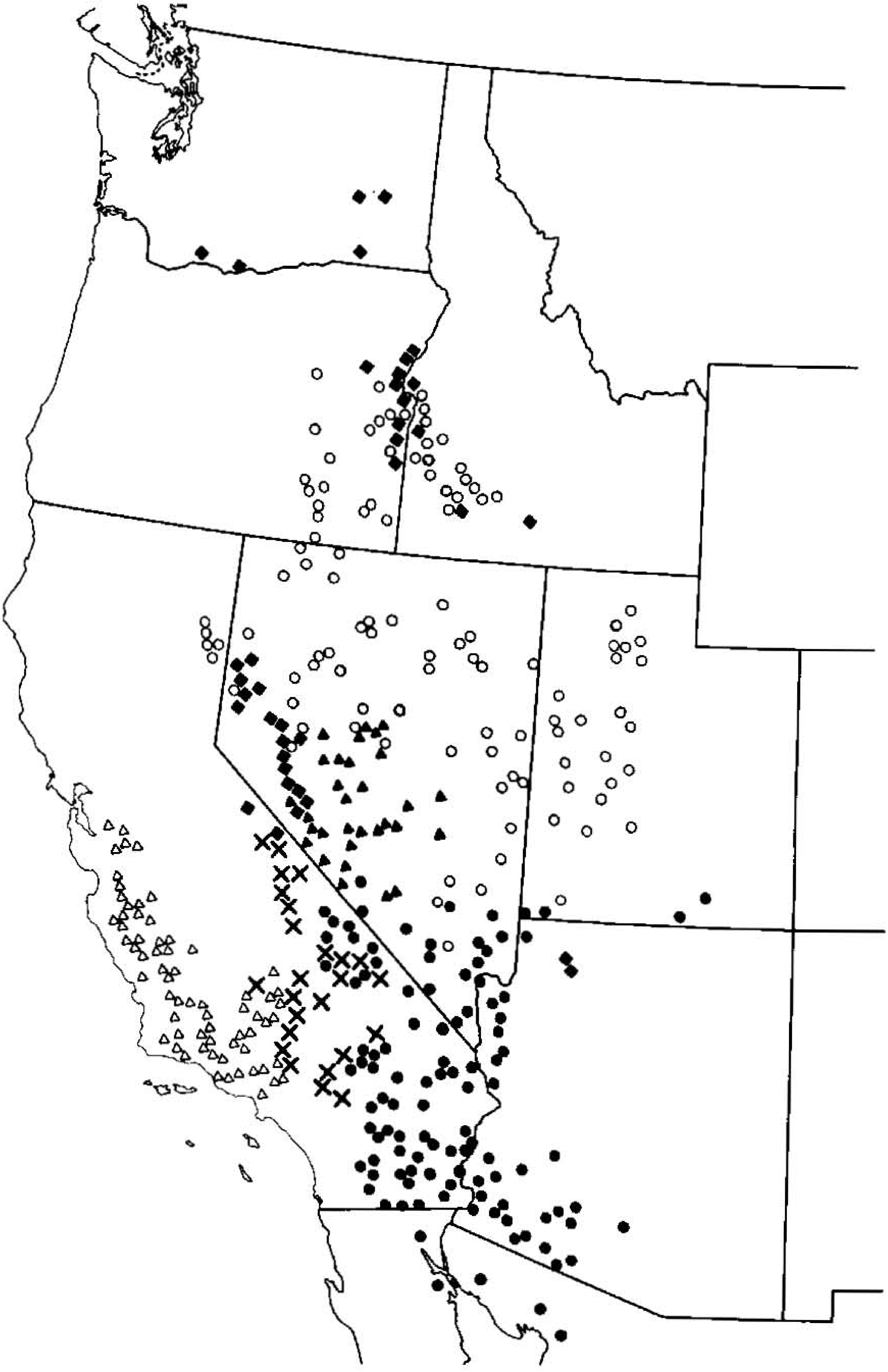


FIGURE 69.—Western United States and a portion of northwestern Mexico, showing the range of *Camissonia boothii:* △=*C. boothii* subsp. *decorticans;* ×=subsp. *desertorum;* ●=subsp. *condensata;* ▲=subsp. *intermedia;* ○=subsp. *alyssoides;* =◆subsp. *boothii.*

Vouchers for chromosome number (19 populations, 10 individuals), $n=7$ (7 pairs in plants marked with an asterisk):

U.S.: CALIFORNIA: KERN CO.: Grocer Grade 5 mi. W. of Maricopa, 2,000 ft., *Breedlove* 2395*; near Havilah, *Lewis* 1106 (2 plants, 1*; LA, RSA, UC). MONTEREY CO.: 4.9 mi. E. of King City, *Breedlove* 2175*. SAN LUIS OBISPO CO.: Carrizo Plain at S. end of Soda Lake, *Bates* 2407; 8.6 mi. W. of Simmler, *Breedlove* 2062; N. road to Adelaida near junction to Nacimiento Dam, R18326; Paso Robles, *Lewis & Thompson* 1101* (LA). SANTA BARBARA CO.: 4.3 mi. W. of Pendola Flats Guard Station, upper Santa Ynez R., 1,600 ft., *Breedlove* 2241. STANISLAUS CO.: Arroyo del Puerto, *Breedlove* 5579.

Camissonia boothii subsp. *decorticans* is the only member of sect. *Eremothera* to occur off the deserts, but it still occurs in related, highly xeric communities. Twenty plants of R18326, cited above, were tested for pollen-tube growth following self- and cross-pollination and found to be self-incompatible, as have four from east San Luis Obispo County, California, *Kyhos* 65–173. This subspecies has not been found growing sympatrically with any other member of the section, but it intergrades with subsp. *desertorum* at the margins of its range. It is usually found away from the coast, but has been found on the bluffs at Taylor Ranch, 1.5 miles east of the mouth of the Ventura River, *Pollard* in 1963 (CAS, SBBG).

Occasional populations of this subspecies at relatively high elevations in the southern part of its range have somewhat smaller flowers and reddish petals; they have been distinguished as *Oenothera rutila* or, more recently, *Oenothera boothii* subsp. *rutila*. In my opinion, there is no evidence that the various populations with this combination of characteristics had a common origin, and, even if they did, they do not appear to constitute a major geographical race comparable with the other subspecies recognized here.

54b. Camissonia boothii subsp. **desertorum** (Munz) Raven, Brittonia 16: 285. 1964.

Oenothera decorticans var. *desertorum* Munz, Bot. Gaz. 85: 246. 1928.

Oenothera boothii subsp. *desertorum* (Munz) Munz, Fl. N. Amer. II. 5: 153. 1965.

Oenothera boothii subsp. *inyoensis* Munz, Fl. N. Amer. II. 5: 153. 1965. Type: Willow Creek, Saline Valley, 800 m, Inyo Co., Calif., 25 April 1942, *A. M. Alexander & L. Kellogg* 2702 (RSA, 41213).

Similar to subsp. *decorticans* but shorter, usually less than 35 cm. tall. Capsule flexuous-contorted, the beak often directed downward, 1–1.6 mm. thick near the base. Gametic chromosome number, $n=7$.

TYPE: 10 miles southwest of Garlic Springs, San Bernardino County, California, 8 April 1924, *P. A. Munz & D. D. Keck* 7881 (POM 48926).

DISTRIBUTION (Figure 69): Desert slopes and washes, endemic to California: from vicinity of Benton Station, Mono County, south in the deserts and east slope of the Sierra Nevada to eastern Kern, northern Los Angeles, and western San Bernardino Counties; also in the upper Kern River drainage, west to the vicinity of Kernville, and in southeasternmost Tulare County. From 1,500–6,500 ft. alt.

Vouchers for chromosome number (5 individuals, 5 populations), $n=7$:

U.S.: CALIFORNIA: INYO CO.: 3 mi. N. of Big Pine, R14258; road to Westgard Pass, *Lewis* 1085 (LA, RSA, UC; 7 pairs); Marble Canyon, Inyo Mts., R17551 (7 pairs). KERN CO.: Road from Randsburg to Red Rock Canyon, *Wedberg* in 1957 (LA; 5 pairs+ring of 4). MONO CO.: Sherwin Grade, 5,000 ft., *Lewis* 1673 (LA).

As here conceived, *Camissonia boothii* subsp. *desertorum* occupies a position intermediate between subsp. *decorticans* and subsp. *condensata,* both geographically and morphologically. Populations of subsp. *desertorum* from the northern portion of its range are in general more pubescent than those from farther south and were referred by Munz (Bot. Gaz. 85: 241–247. 1929; N. Amer. Fl. II. 5: 151–154. 1965) to subsp. *alyssoides.* They may represent intermediates with that taxon, but do not agree with it in habit, being much more lax, and have much more appressed pubescence. In my view, the only populations of subsp. *alyssoides* in California are those in eastern Lassen County, and the nearest populations to those of subsp. *desertorum* are in the Sheep Range of northern Clark County, Nevada, and in Churchill County, Nevada. I have also included in subsp. *desertorum* those populations from the Panamint Mountains Inyo, County, California, listed by Munz (Bot. Gaz. 85: 245. 1929) as approaching *Oenothera decorticans* var. *rutila;* these were apparently also included in subsp. *desertorum* by Munz in his more recent work on the group (N. Amer. Fl. II. 5: 153–154. 1965).

Populations from the eastern slope of the Inyo Mountains and elsewhere in Inyo County, California, where they grow on limestone, have relatively small flowers and lax inflorescences, which make them appear quite distinct in appearance. They were named *Oenothera boothii* subsp. *inyoensis* by Munz in 1965, and at the time, I too thought that they deserved formal taxonomic recognition. Intergradation with other populations more typical of subsp. *desertorum* is so broad and complete that it is often impossible to assign particular plants to one or the other with confidence. Therefore I now consider that they are best assigned to subsp. *desertorum,* despite the fact that their inclusion makes subsp. *desertorum* quite heterogeneous.

A few collections made within the range of subsp. *condensata* on the western Colorado Desert of California appear to be this subspecies; for example, *Parish* in 1882 (JEPS) from Whitewater, Riverside County. These may be extreme variants of subsp. *condensata* or may represent relict populations of subsp. *desertorum* in an area now largely occupied by subsp. *condensata,* which may be of relatively recent derivation.

54c. Camissonia boothii subsp. **condensata** (Munz) Raven, Brittonia 16: 285. 1965.

Oenothera decorticans var. *condensata* Munz, Bot. Gaz. 85: 247. 1928.

Oenothera boothii subsp. *condensata* (Munz) Munz, N. Amer. Fl. II. 5: 154. 1965.

Similar to subsp. *desertorum*, but shorter, 5–20 (–30) cm. tall, the stems very thick, the inflorescence more crowded. Capsules 2–3.8 mm. thick near the base, more or less quadrangular, tapering abruptly, the midribs of the valves very prominent, yellowish. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Dos Palmos Spring, Riverside County, California, 31 January 1926, *P. A. Munz* 9960 (POM 98708).

DISTRIBUTION (Figure 69): Desert slopes and washes, in sandy soil, from the vicinity of Death Valley, Inyo County, California, south to the region around Barstow, San Bernardino County, and throughout the Colorado Desert of Riverside, Imperial, and eastern San Diego Counties, to the region about the head of the Gulf of California in Baja California and Sonora (south to about 31°30′ N. lat.); eastward to Esmeralda, southern Nye and Lincoln, and Clark Counties, Nevada, and Washington County, Utah, and western Mohave, Yuma, Maricopa, southwesternmost Pinal, and westernmost Pima Counties, Arizona; also in Glen Canyon, San Juan County, Utah (*Gaines* 927, 1011, WS). From about 250 ft. below sea level to 4,000 ft. alt.

Vouchers for chromosome number (8 individuals, 7 populations), $n=7$:

U.S.: ARIZONA: MARICOPA CO.: Near Sentinel, R14826. MOHAVE CO.: 48 mi. NW. of Kingman, *Munz et al.* 22985 (5 pairs + ring of 4). CALIFORNIA: IMPERIAL CO.: Coyote Wells, *Breedlove* 1847; 1 mi. N. of U.S. Hwy. 80 on road to Ogilby, *Klein* 94 (2 plants, 7 pairs). RIVERSIDE CO.; Box Canyon, *Lewis* 1663 (LA; 7 pairs). SAN DIEGO CO.: Borrego Valley, *Lewis* 1624 (LA; 7 pairs), *Wedberg* in 1957 (LA).

As noted by Munz in the protologue of this taxon (Bot. Gaz. 85: 247. 1928), it is very distinctive in fruit, the plants persisting in a dried condition for a long time and shedding their seeds tardily. *Camissonia boothii* subsp. *condensata* intergrades broadly with subsp. *desertorum* where their ranges approach one another. Twelve plants from Frenchman Flat, Nye County, Nevada (R18853), were found to be self-incompatible by pollen-tube growth following cross- and self-pollination.

54d. Camissonia boothii subsp. **alyssoides** (Hook. & Arn.) Raven, Brittonia 16: 285. 1964.

Oenothera alyssoides Hook. & Arn., Bot. Beechey Voy. 340. 1838.

Holostigma alyssoides (Hook. & Arn.) Hook., Icon. 4: 339. 1840.

Sphaerostigma alyssoides (Hook. & Arn.) Walp., Rep. 2: 78. 1843.

Oenothera alyssoides var. *villosa* S. Wats., Proc. Amer. Acad. 8: 591. 1873. Type: Near Salt Lake, Utah, *Capt. H. Stansbury* (GH; isotype, NY).

Sphaerostigma utahense Small, Bull. Torrey Cl. 23: 191. 1896. Lectotype: Milford, Beaver Co., Utah, June 1880, *M. E. Jones* (NY).
Sphaerostigma alyssoides var. *macrophyllum* Small, Bull. Torrey Cl. 23: 192. 1896; nom. subs.
Oenothera gauraeflora var. *hitchcockii* H. Lév., Monogr. Onoth. 226. 1905. Type: Simpson's Park, Utah, 6 July 1859, collector not known (MO).
Sphaerostigma hitchcockii (H. Lév.) A. Nels., Bot. Gaz. 40: 226. 1905.
Oenothera utahensis (Small) Garrett, Spring Fl. Wasatch Reg. 64. 1911.
Sphaerostigma implexum A. Nels., Bot. Gaz. 52: 267. 1911. Type: Falk's Store, 2,200 ft., Canyon Co., Idaho, 17 May 1910, *J. F. Macbride* 27 (RM; isotypes, GH, UC, US, WS, WTU).
Sphaerostigma macrophyllum Rydb., Bull. Torrey Cl. 40: 66. 1913.
Oenothera alyssoides var. *typica* Munz, Bot. Gaz. 85: 242. 1928.
Oenothera boothii subsp. *alyssoides* (Hook. & Arn.) Munz, N. Amer. Fl. II. 5: 154. 1965.

Similar to subsp. *desertorum*, the plants 3–35 cm. tall, sometimes flowering near the base, with leafier stems and a less prominent basal rosette, the leaves relatively small. Plants strigulose, often densely so, especially in the inflorescence, or more rarely villous or with an admixture of glandular trichomes. Capsule 1–1.4 mm. thick, usually very contorted and crowded. Seeds monomorphic, smooth. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: Pine Creek, Snake River plains, southern Idaho, probably in July 1830, *D. Douglas* (K; isotype, GH).

DISTRIBUTION (Figure 69): Sandy slopes and flats, often with *Artemisia tridentata*, from Grant and northern Malheur Counties, eastern Oregon and Payette, Ada, and Elmore Counties, southwestern Idaho, south to eastern Lassen County, California, and Churchill, northernmost Nye, Lincoln, and northern Clark Counties, Nevada, and throughout western Utah, south to Piute and Washington Counties. From 2,000 to 5,500 ft. alt.

Vouchers for chromosome number (8 individuals, 8 populations), $n=7$ (7 pairs in those collections marked with an asterisk):

U.S.: CALIFORNIA: LASSEN CO.: 19 mi. S. of Ravendale, R13273. NEVADA: CHURCHILL CO.: 28.9 mi. SW. of Lovelock, *Kyhos* 65–253.* EUREKA CO.: 2.9 mi. W. of Carlin, R18535*. HUMBOLDT CO.: 3.5 mi. W. of Golconda Summit, R18537*. LINCOLN CO.: E. of Panaca, R11255 (CAS, LA, RSA). PERSHING CO.: 20 mi. NE. of Lovelock, R18540. OREGON: LAKE CO.: 3.4 mi. E. of Headquarters, Hart Mt. Antelope Refuge, R13347*. UTAH: MILLARD CO.: 62 mi. SW. of Delta, *Mathias* 3025* (COLO, LA, RSA, UC).

The number of synonyms listed with this taxon attests to its wide range rather than to any extraordinary degree of variability. Self-incompatibility was demonstrated by pollen-tube growth in 21 plants from the locality of R18540, cited above, and three from 28.9 miles southwest of Lovelock, Churchill County, Nevada, *Kyhos* 65–253. *Camissonia boothii* subsp. *alyssoides* intergrades broadly with subsp. *intermedia* and is very similar to subsp. *desertorum*. Certain populations cited by Munz (Bot. Gaz. 85: 241–244. 1928) are here regarded as belonging to *C. boothii* subsp. *desertorum*, as noted in the treatment of that subspecies.

In general, the last three subspecies of this species consist of plants that persist and flower over a much longer season than the first three, which flower chiefly following the winter rains.

54e. Camissonia boothii subsp. **intermedia** (Munz) Raven, comb. nov.

Oenothera alyssoides var. *villosa* sensu Munz, Bot. Gaz. 85: 243. 1928: pro parte.

Oenothera boothii var. *typica* sensu Munz, Bot. Gaz. 85: 248. 1928: pro parte.

Oenothera boothii subsp. *intermedia* Munz, Fl. N. Amer. II. 5: 152. 1965.

Similar to subsp. *alyssoides*, but densely villous with a dense admixture of glandular trichomes in the inflorescence, the plants usually 5–20 cm. tall, the leaves mostly less than 2.5 cm. long. Seeds dimorphic. Gametic chromosome number, $n=7$.

TYPE: Dry sandy gravel wash, 4 miles south of Cloverdale Ranch on Reese River to Tonopah road, Nye County, Nevada, 16 September 1939, *P. Train* 3455 (RSA 56046; isotypes, UC, WTU).

DISTRIBUTION (Figure 69): Sandy washes and flats, often with *Artemisia tridentata*, in Nevada from southeastern Churchill and southern Lander Counties south throughout Nye and Esmeralda Counties and in southern Mineral County, and in northeastern Inyo County, California; also in the Kingston Range, northeastern San Bernardino County, California. From 5,000–7,000 ft. alt.

Vouchers for chromosome number (2 individuals, 2 populations), $n=7$ (7 pairs observed in 1 plant of population marked with asterisk):

U.S.: CALIFORNIA: INYO CO.: Ca. 4 mi. S. of Oasis, Fish Lake Valley, *Klein* 353 (RSA). NEVADA: NYE CO.: 10 mi. W. of Lockes, *Thompson & Mathias* 1692* (ARIZ, LA, RSA, UC, WTU).

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: CALIFORNIA: INYO CO.: Deep Springs Valley, *Ferris* 1357 (DS): 2 mi. NE. of Willow Spring, Last Chance Mts., 6,000 ft., *Roos* 6396 (DS, RM, RSA, UC). SAN BERNARDINO CO.: Kingston Mts., 0.1 mi. E. of summit of grade between Horse (Thief) and Beck Springs, ca. 5,000 ft., *Wolf* 10515 (RSA). NEVADA: CHURCHILL CO.: 2 mi. E. of Frenchman, *Mills & Beach* C–20 (UC): vicinity of East Gate, 5,100 ft., *Allen* 349 (DS, NY, POM). ESMERALDA CO.: 3 mi. W. of Lida, Silver Peak Range, *Maguire & Holmgren* 25625 (GH, NY, UC, US, WTU); Montezuma Mt. W. of Goldfield, 2,000 m, *Tidestrom* 9764 (GH, US): Icehouse Canyon, W. slope of Silver Peak Range, 5,300 ft., *Alexandria & Kellogg* 5682 (DS, RM, UC, US, WTU); wash leading to summit between Fish Lake Valley and Basalt, *Ferris* 6681 (DS, POM). LANDER CO.: Austin to Big Creek, 6,000 ft., *Kennedy* 4507 (CAS, DS, GH, PH, RM); Austin, 6,000 ft., *Hitchcock & Martin* 5626 (DS, NY, POM, UC, WS, WTU); 18.5 mi. E. of Austin, *Goodner & Henning* 836 (DAO, F, POM, UC). NYE CO.: Warm Springs Valley, *Maguire & Holmgren* 25458 (GH, NY, UC, WTU); Smoky Valley, *Maguire & Holmgren* 25365 (ARIZ, DS, GH, NMC, NY, OSC, UC, US, WS, WTU); 2 mi. NW. of Penelas Mill, 15 mi. NW. of Ione, *Beach* 865 (ARIZ, DS, IDS, NMC, NY, POM, RM, UC, US, WS, WTU); pass over Pancake Mts., 84 mi. SW. of Ely, 6,000 ft., *Rollins & Chambers* 2497 (DS, GH, RM, UC, US); foothills of Pahute Mesa, N. Forty Mile Drainage, 6,000 ft., *Beatley* 1694 (DS). MINERAL CO.: 10 mi. N. of Basalt, *Tidestrom* 10040 (GH); Candelaria, 6,000 ft., *Shockley* 324 (DS, UC).

This entity bridges the morphological and geographical gap between subsp. *boothii* and subsp. *alyssoides* in Nevada completely. Nevertheless, it consists of a large number of morphologically relatively uniform populations that occupy a sizable range in central Nevada.

54f. Camissonia boothii subsp. **boothii**

Oenothera boothii Dougl., *in* Hook., Fl. Bor. Amer. 1: 213. 1834.

Sphaerostigma boothii (Dougl.) Walp., Rep. 2: 77. 1843.

Oenothera gauraeflora race *boothii* (Dougl.) H. Lév., Monogr. Onoth. 226. 1905.

Sphaerostigma senex A. Nels., Proc. Biol. Soc. Wash. 18: 173. 29 June 1905. Type: Pyramid Lake, Washoe Co., Nev., 9 June 1903, *G. H. True* 750 (RM).

Sphaerostigma lemmoni A. Nels., Bot. Gaz. 40: 61. 1905. Type: "East flank of the Sierra Nevada," presumably in Nevada, 1875, *J. G. Lemmon* 103 (MO; probable isotype, US).

Oenothera boothii var. *typica* Munz, Bot. Gaz. 85: 248. 1928.

Oenothera boothii subsp. *boothii* Munz, N. Amer. Fl. II. 5: 151. 1965.

Similar to subsp. *intermedia*, but often more robust, and the leaves broader, lanceolate or narrowly ovate, the cauline ones especially proportionately broader, 0.8–6 cm. long, 0.6–2.2 mm. broad, more coarsely serrulate, the plants mostly 15–60 cm. tall. Gametic chromosome number, $n=7$. Self-incompatible.

TYPE: On high sandy and gravelly hills near the junction of the Snake and Clearwater Rivers, vicinity of Lewiston, Idaho (either in Washington or in Idaho), approximately 24 July 1826, *D. Douglas* (K; isotype, BM).

DISTRIBUTION (Figure 69): Sandy flats or steep, loose slopes, in Adams, Whitman, and Walla Walla Counties, southeastern Washington, west along the Columbia River to Klickitat County and Hamilton Island, Skamania County, Washington; Washington, Canyon, Owyhee, and Jerome Counties, southwestern Idaho; south through eastern Oregon (Grant, Harney, and Malheur Counties); and again in west-central Nevada (southern Washoe, western Churchill, easternmost Lyon, and Mineral Counties) and adjacent Mono County, California, in the vicinity of Mono Lake and Benton. Indistinguishable populations occur in the vicinity of Toroweap Valley, Mohave County, Arizona (e.g., *Cottam* 13936, CAS, UT). From 2,000–7,500 ft. alt.

Vouchers for chromosome number (3 individuals, 3 populations), $n=7$:

U.S.: NEVARA: MINERAL CO.: W. side of Walker L., R11246 (7 pairs). WASHOE CO.: Pyramid L., 18.8 mi. N. Sutcliffe, R13197 (7 pairs); ca. 15 mi. N. of Nixon, ca. 3,500 ft., *Ornduff* 4203 (LA; 4 pairs + ring of 6).

Camissonia boothii subsp. *boothii* occurs in three disjunct areas, intergrading completely with subsp. *intermedia* and subsp. *alyssoides* in the Nevada portion of its range. A few collections from two areas on the Mojave Desert of California, within the range of subsp. *desertorum*, resemble subsp. *boothii* closely in their glandular pubescence, habit, and summer blooming:

U.S.: CALIFORNIA: INYO CO.: 10 mi. N. of Little Lake, 1931, *Hoffmann* 576 (POM). SAN BERNARDINO CO.: Brown's Crossing of the Mohave R., 1882, *S. B. & W. F. Parish* 1504 (DS, F, GH); Hesperia, 1901, *Abrams* 2166; near Victorville, 1916, *Peirson* 792 (RSA).

Plants of this sort have not been collected in these areas for nearly 40 years. The relationship of these populations to the other subspecies should be investigated when additional material becomes available. It is possible, but seems unlikely, that the plants were introduced in these areas. A similar specimen has been seen from Fort Mojave, Mohave County, Arizona, 1860–1861, *Cooper* (GH).

Self-incompatibility was demonstrated in 40 plants from the locality of R11246, cited above, by examining pollen-tube growth in selfed and outcrossed stigmas.

55. Camissonia pygmaea (Dougl.) Raven, Brittonia 16: 285. 1964.

FIGURES 71–73

Oenothera pygmaea Dougl., *in* Hook., Fl. Bor. Amer. 1: 213. 1834.

Oenothera boothii var. *pygmaea* (Dougl.) Torr. & Gray, Fl. N. Amer. 1: 510. 1840.

Sphaerostigma boothii var. *pygmaeum* (Dougl.) Walp., Rep. 2: 78. 1843.

Very similar to *C. boothii* subsp. *boothii*, the plants 1.5–35 cm. tall. Flowers smaller, the hypanthium 1.7–2.2 (–4) mm. long, 0.8–1 (–1.5) mm. across at the summit; sepals 1.8–2 mm. long, 0.9–1 mm. wide; petals 1.5–2.5 mm. long, 0.8–1.3 (–2) mm. wide; filaments of episepalous stamens 1–2.2 mm. long, those of the epipetalous ones slightly shorter, the anthers 0.45–0.5 (–0.7) mm. long; style 3.2–4 mm. long, the stigma 0.5–0.8 mm. thick, surrounded by the anthers at anthesis. Gametic chromosome numbers, $n=7$, 14. Autogamous.

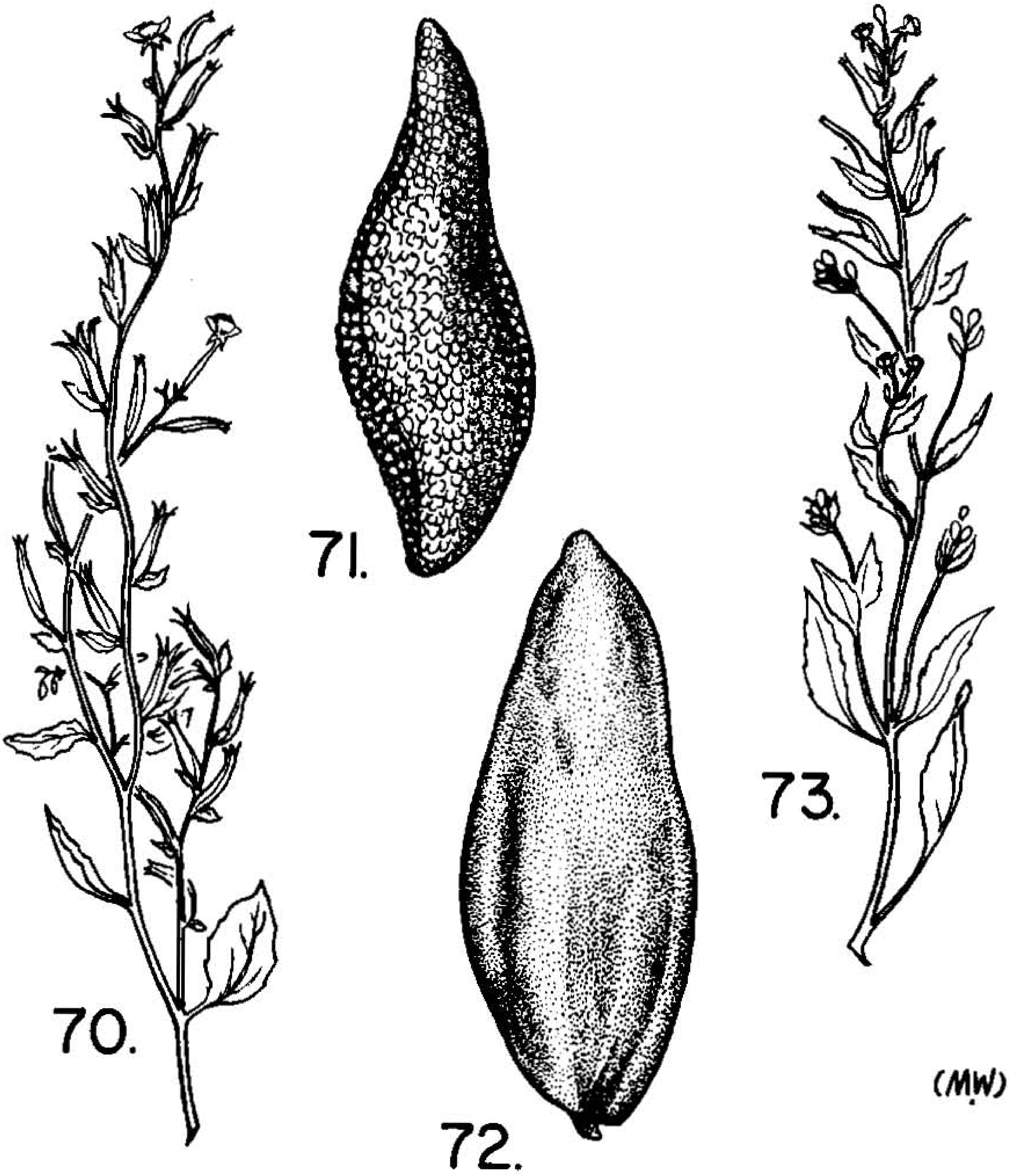
TYPE: On the barren sands of the interior near the Umatilla ("Utalla") River, east of Pendleton, Umatilla County, Oregon, June 1826, *D. Douglas* (K; isotype, BM).

DISTRIBUTION (Figure 68): Rare and local on steep, loose slopes, often in scree, sometimes on gravelly flats, at scattered localities in eastern Washington (Douglas, Grant, and Kittitas Counties), eastern Oregon, and at one locality in adjacent southern Idaho (Jerome County). From 1,200–4,000 ft. alt.

Voucher for chromosome number (1 individual), $n=7$:

U.S.: OREGON: WHEELER CO.: 10 mi. NW. of Mitchell, R18474.

Voucher for chromosome number (1 individual), $n=14$:



FIGURES 70–73.—Species of *Camissonia* sect. *Eremothera:* 70, *C. gouldii*, × ¾ (*Gould* 1423, holotype, POM). 71–73, *C. pygmaea* (*Henderson* 5411, DS): 71–72, Seeds, × 36: 71 dark papillose seed from lower part of capsule; 72, lighter, smoother seed from upper part of capsule. 73, Flowering branch, × ¾.

U.S.: WASHINGTON: GRANT CO.: Dry Falls, R18489 (12 pairs + ring of 4).

ADDITIONAL SPECIMENS EXAMINED:

U.S.: IDAHO: JEROME CO.: Blue Lakes, Snake Plains, 1893, *Palmer* 71 (CAS, UC), 523 (CAS, UC; these two collections with relatively large flowers and doubtfully referred here). OREGON: GILLIAM CO.: Near camp on Pine Creek, 1470 m, *Leiberg* 199 (F, GH, NY, ORE, UC, US). GRANT CO.: Muddy Station, John Day Valley, *T. Howell* in 1885 (F, GH, NY, ORE, PH, US, WS, WTU); John Day Valley NW. of Dayville, *Ripley & Barneby* 6628 (CAS, NY); Squaw Creek, Humphreys Ranch, *Henderson* 5411 (CAS, DS, GH, ORE); 5 mi. W. of Mt.

Vernon, Peck 19880 (CAS). HARNEY CO.: Base of Steens Mt., *T. Howell* in 1885 (NY). WHEELER CO.: Dry gravelly washes between Sutton Mt. and Bridge Creek, 10 mi. NW. of Mitchell, 2,200 ft., *Cronquist* 7239 (CAS, DAO, DS, GH, NY, RM, UBC, UC, WS, WTU); 17 mi. E. of Mitchell, *Peck* 21056 (UC); 22 mi. E. of Mitchell, R18480 (DS). WASHINGTON: DOUGLAS CO.: Rock Island, *Sandberg & Leiberg* 441 (CAS, GH, LE, NMC, ORE, PH, POM, UC, US, WS, WTU). GRANT CO.: Dry Falls, *Thompson* 9105 (DS, GH, NY, POM, RSA, UC, US, WTU); Grand Coulee near Park Lake, *Thompson* 11657 (WTU); Soap Lake, *Eyerdam* 642 (UC). KITTITAS CO.: Above Blue Lake, near Cle Elum, *McCalla* 4438 (UBC).

This rarely collected species is obviously an autogamous derivative of populations similar to those of the much larger flowered, self-incompatible *C. boothii* subsp. *boothii*. As mentioned in the list of cited specimens, the occurrence of *C. pygmaea* in Idaho is somewhat doubtful and needs to be confirmed. I have been unable to separate diploid and tetraploid populations of this species morphologically or by any character of the pollen. It is likely that the tetraploid individual examined was of autopolyploid origin, and the observation of a ring of four chromosomes in it tends to confirm this view. This plant was the only tetraploid invidudual found in the section.

56. Camissonia gouldii Raven, sp. nov. FIGURE 70

A *C. pygmaea* persimilis, differens pilis omnibus glandulosis; foliis ellipticis; capsulis 8–12 mm. longis, 1.7–1.8 mm. latis; seminis omnibus sublaevibus, nullis papillosis. Autogama.

TYPE: Associated with *Phacelia palmeri*, on steep slope of volcanic cone among loose cinders, Diamond Valley, 12 miles north of St. George, 3,500 ft., Washington County, Utah, 15 October 1941, *Frank W. Gould* 1423 (POM; isotypes, ARIZ, CAS, F, GH, NY, UC, US).

DISTRIBUTION (Figure 68): Volcanic scree or cinder flats, rare and local; south-central Washington County, Utah, and east-central Coconino County, Arizona; 3,500–5,400 ft. alt.

ADDITIONAL SPECIMENS EXAMINED:

U.S.: ARIZONA: COCONINO CO.: Cinder flats E. of San Francisco Peaks, 1,700 m., *Leiberg* 5808 (US); San Francisco Mt., *Knowlton* 200 (US). WUPATKI NATL. MONUMENT (COCONINO CO.): Deadmans Wash below Wupatki Ruin, occasional on volcanic ash, ca. 4,800 ft., *Whiting & Jones* 1089/5213 (US); Wupatki Rim, *Jones* 337 (ARIZ); E. slope of Doney Mt., 2 mi. W. of Wupatki, deep cinder soil, 5,200 ft., *Jones* in 1939 (ARIZ); deep cinder near Hall Canyon, 5,400 ft., *Whiting* 1089/5274 (ARIZ, POM).

Camissonia gouldii is obviously autogamous and, like *C. pygmaea*, probably a derivative of populations similar to those of the self-incompatible *C. boothii* subsp. *boothii*. The monomorphic seeds and entirely glandular pubescence of *C. gouldii* (fig. 70) set it off from *C. pygmaea*, the nearest stations of which are some 500 miles to the northwest. In addition, its reddish color and relatively broad leaves give *C. gouldii* a very distinctive aspect. The chromosome number of *C. gouldii* is unknown.

It is a pleasure to name this distinctive local endemic in honor of Prof. Frank W. Gould of Texas A. & M. University, student of the grasses, who has collected widely and critically in the western United States, in Mexico, and elsewhere in Latin America. It adds another to the long list of edaphically sharply restricted endemics of its region, one of which is *Camissonia parryi.*

57. Camissonia nevadensis (Kell.) Raven, Brittonia 16: 285. 1964. FIGURE 74

Oenothera nevadensis Kell., Proc. Calif. Acad. 2: 224, *fig. 70.* 1863.

Sphaerostigma tortuosa A. Nels., Proc. Biol. Soc. Wash. 17: 95. 1904. Type: Truckee Pass, Virginia Mts., Washoe Co., Nev., 16 June 1902, *P. B. Kennedy* 766 (RM; isotypes, DS, UC).

Oenothera gauraeflora var. *caput-medusae* H. Lév., Monogr. Onoth. 226. 1905. Lectotype: Foothills, Reno, 5,500 ft., Washoe Co., Nev., 10 June 1897, collector unknown (MO; isotypes, POM, UC, US).

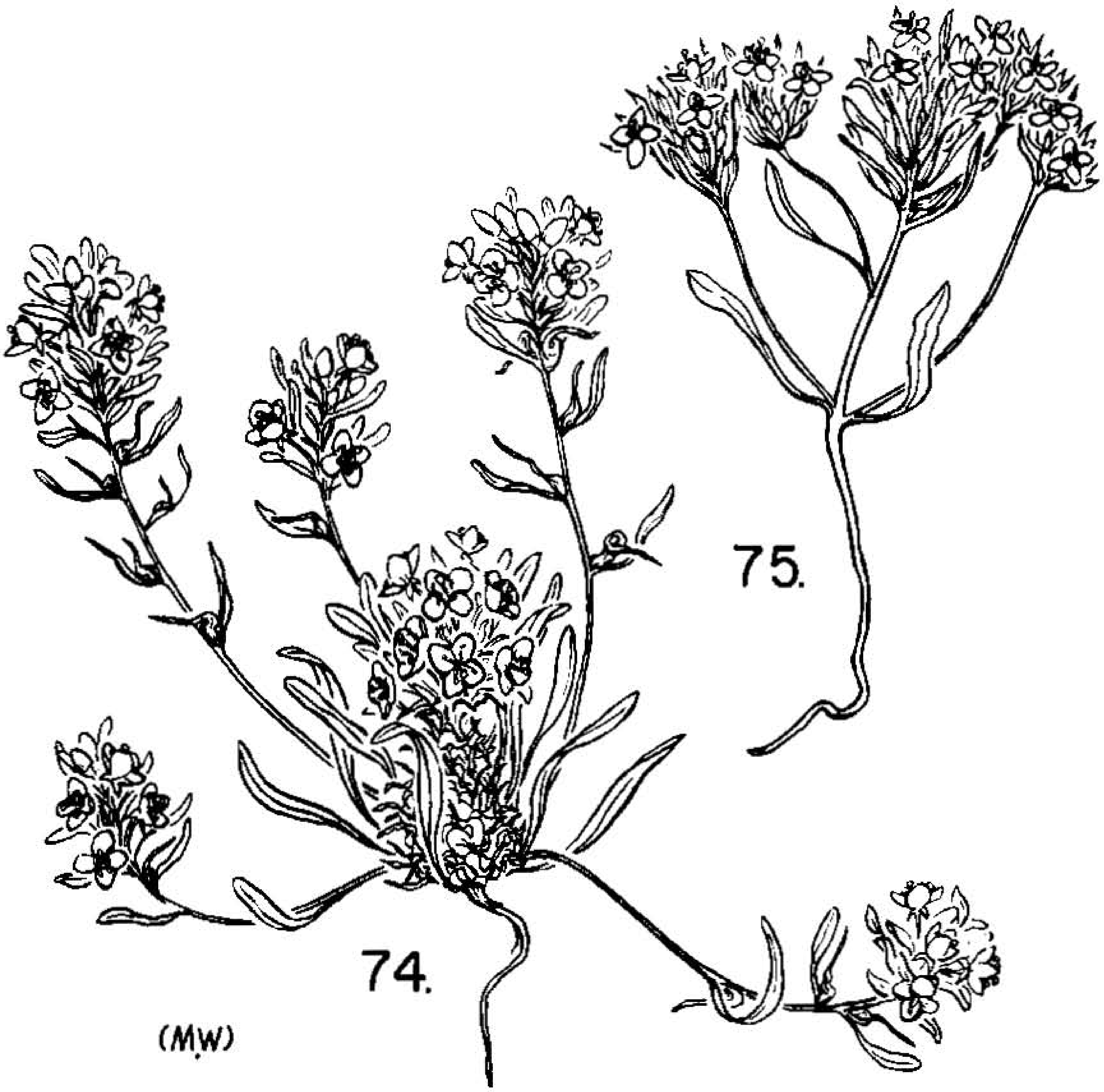
Oenothera gauraeflora var. *vermiculata* M. E. Jones, Contr. West. Bot. 12: 16. 1908.

Sphaerostigma nevadense (Kell.) Heller, Muhlenbergia 6: 51, with cover illustration. 1910.

Erect, densely flowering from the base, the central stem 1–5 cm. tall, the larger individuals with slender decumbent branches to 18 cm. long radiating from near the base of the plant, these naked below and with a dense tuft of leaves and flowers at the ascending end; plants subglabrous, the inflorescence strigulose. Leaves oblanceolate or narrowly oblanceolate, the blades 1–3.5 cm. long, 2–7 mm. wide, entire, acuminate at the apex, attenuate at the base; petioles 1–3 cm. long. Inflorescence erect. Hypanthium 2.2–3.2 mm. long, 1.2–1.3 mm. across at the summit, glabrous within. Sepals 3.2–3.5 cm. long, 1–1.1 mm. wide. Petals 3–5 mm. long, 2.2–4.2 mm. wide. Filaments of the episepalous stamens 4.5–4.8 mm. long, those of the epipetalous ones 3–4 mm. long; anthers 0.4–1.5 mm. long. Style 6–7 mm. long, glabrous; stigma 0.5–0.8 mm. thick, held somewhat above the anthers at anthesis. Capsule highly contorted, 0.8–1.4 cm. long, 1–2 mm. thick near the base, quadrangular in transection, tapering strongly from the swollen base, with a prominent pale brown midrib running down the center of each valve, held on the dead plant and shedding seeds very tardily. Seeds monomorphic, 1.2–1.5 mm. long, 0.3–0.4 mm. thick, gray, finely lacunose, much distorted by the walls of the capsule. Gametic chromosome number, $n=7$. Probably outcrossing, and possibly self-incompatible.

TYPE: From an unknown locality (doubtless the vicinity of Reno, Washoe County, Nevada), CAS 838 in part (fragment).

DISTRIBUTION (Figure 68): Local and colonial on vernally moist clay flats in west-central Nevada, southernmost Washoe, Ormsby,



FIGURES 74–75.—Species of *Camissonia*, × ¾: 74, *C. nevadensis* (*Raven* 17869, DS); 75, *C. hilgardii* (*Raven* 18485, DS).

Storey, northernmost Lyon, and western Churchill Counties; 3,900–4,600 ft. alt.

Voucher for chromosome number (1 individual), $n=7$ (7 pairs):

U.S.: NEVADA: WASHOE CO.: 2 mi. N. of Sparks, R17869 (DS).

REPRESENTATIVE SPECIMENS EXAMINED:

U.S.: NEVADA: CHURCHILL CO.: Fallon, *Ross* in 1914 (JEPS); ca. 8 mi. NW. of Fallon, toward Soda L., *Mills & Beach* C–108 (RSA, UC). LYON CO.: 5 mi. S. of Fernley on U.S. Hwy. 95A, *Mason* 15189 (UC). ORMSBY CO.: Empire City, *Jones* 3862 (CAS, GH, NY, POM, RM, UC, US); hills N. of Carson City, *Stretch* in 1865 (NY). STOREY CO.: 13 mi. E. of Sparks, *Goodner & Henning* 4 (POM). WASHOE CO.: University Heights, Reno, 4,550 ft., *Heller* 9697 (DS, GH, PH, UC); 12 mi. N. of Reno on road to Pyramid Lake, 4,000 ft., *Ripley & Barneby* 4492 (CAS, NY); Truckee Pass E. of Reno, 4,500 ft., *Heller* 8647 (DS, GH, NY, PH, US), *Kennedy* 1592 (NY, UC, US); near Wadsworth, *Kennedy* 2053 (DS); 9 mi. N. of Poeville, 5,200 ft., *Tillotson* 120 (RSA, UC); 2.6 mi. NW. of Spanish Spring, 4,500 ft., *Hendrix* 823 (RSA, UC); 6 mi. SW. of Reno, *Canby* 99 (POM); 2 mi. N.

of Sparks on Pyramid L. road, 4,700 ft., *Archer* 5077 (POM); near Pyramid L., Lemmon 239 (F; locality may be only an approximation).

Mature plants of this species are unmistakable; occasionally younger ones are identified as *Camissonia boothii* subsp. *alyssoides*. The habitats of these two taxa are distinct, and *C. nevadensis* is not known to occur sympatrically with any other member of its section. Floral morphology suggests that *C. nevadensis* is outcrossed, but it is not known whether this species is self-incompatible. It probably is not, judging from what is known of the other local entities within the genus and the tribe. *Camissonia nevadensis*, one of the two species of its genus endemic to Nevada (the other *C. megalantha*), is relatively rare, and a number of its localities are being destroyed by urban expansion in the vicinity of Reno. A few collections made by J. G. Lemmon suggest the occurrence of this species in adjacent California, but Lemmon's localities are notoriously inaccurate, and it would seem to be much more probable that he obtained this material in the vicinity of Reno or Pyramid Lake, where he is known to have collected the species.

58. **Camissonia minor** (A. Nels.) Raven, Brittonia 16: 285. 1964. FIGURE 76

Oenothera alyssoides var. *minutiflora* S. Wats., Bot. King Rep. 111. 1871. Lectotype: Stansbury I., 2,300 ft., Tooele Co., Utah, June 1869, *S. Watson* (US: isotype, NY); non Fisch. & Mey. 1835.

Sphaerostigma minus ("*minor*") A. Nels., Bull. Torrey Cl. 26: 130. 1899.

Sphaerostigma nelsonii Heller, Muhlenbergia 1: 1. 1900, nom. subs.

Oenothera chamaenerioides var. *torta* H. Lév., Monogr. Onoth. 230. 1905. Lectotype: Granger, Sweetwater Co., Wyo., 3 June 1898, *A. Nelson* 4691 (MO; isolectotypes, F, GH, NY, RM, UC, US).

Sphaerostigma tortum (H. Lév.) A. Nels., Bot. Gaz. 40: 60. 1905.

Sphaerostigma tortum var. *eastwoodae* A. Nels., Bot. Gaz. 40: 61. 1905. Type: Grand Junction, Mesa Co., Colo., May 1892, *A. Eastwood* (MO; isotypes, GH, NMC, NY, OSC, UBC, US).

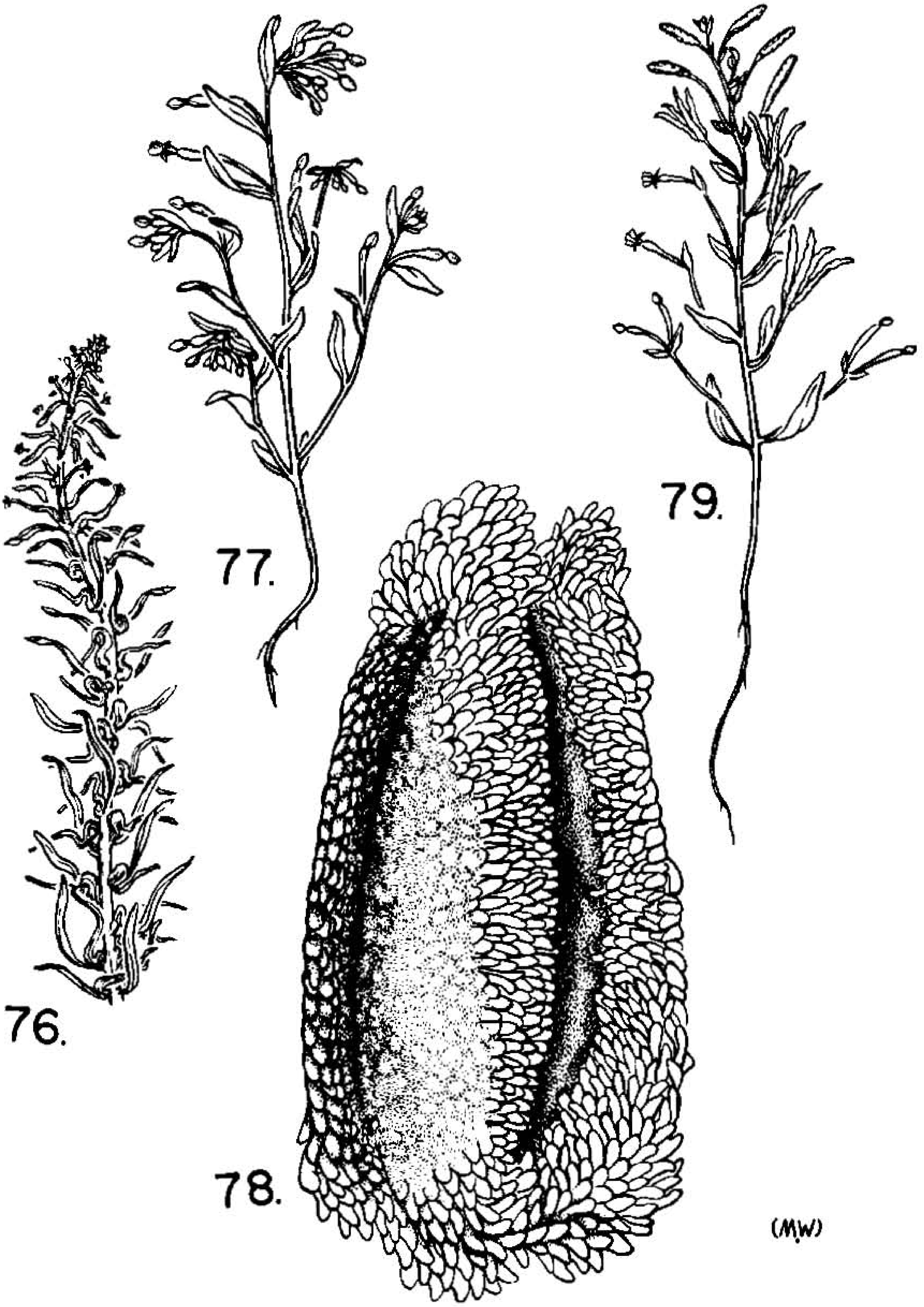
Sphaerostigma alyssoides var. *minutiflorum* (S. Wats.) Small, Bull. Torrey Cl. 33: 146. 1906.

Oenothera minor (A. Nels.) Munz, Bot. Gaz. 85: 238. 1928.

Oenothera minor var. *typica* Munz, Bot. Gaz. 85: 239. 1928.

Oenothera minor var. *cusickii* Munz, Bot. Gaz. 85: 240. 1928. Type: Malheur R. and adjacent hills, Malheur Co., Oreg., 6 June 1901, *W. C. Cusick* 2545 (UC 35348; isotypes, F, GH, K, NY, POM, RM, UC, US).

Erect, flowering from the base, and often well branched from below, the stems 3–30 cm. long; plants densely strigulose, often grayish, the inflorescence often with a more or less evident admixture of glandular trichomes. Leaves oblanceolate or narrowly oblanceolate, the blades of the basal leaves 0.5–2.5 cm. long, 0.3–1.5 cm. wide, the petioles 5–20 mm. long; leaves acuminate at the apex, attenuate at the base. Inflorescence erect. Hypanthium 0.5–1.9 mm. long, 0.5–1.2 mm. across at the summit, pubescent in lower half within. Sepals 0.8–1.8 mm. long, 0.35-0.7 mm. wide. Petals 0.8–1.3 mm. long, 0.4–1.3 mm. wide. Filaments 0.3–1.3 mm. long, the epipetalous ones



FIGURES 76–79.—Species of *Camissonia:* 76, *C. minor,* × ¾ (*Train* 191, DS). 77–79, *C. pterosperma:* 77, Habit, × ¾ (*Leiberg* 2075, DS); 78, ventral view of winged seed, × 65 (*Heller* 8376, DS); 79, habit of fruiting plant, × ¾ (*Heller* 8376, DS).

shorter than the episepalous ones and sometimes apparently abortive; anthers 0.5–0.8 mm. long. Style 1.2–3.2 mm. long, pubescent near the base; stigma 0.5–0.6 mm. thick, surrounded by the anthers at anthesis. Capsule contorted, 1–2.5 cm. long, 0.8–1.2 mm. thick, subterete, not tapering sharply. Seeds monomorphic, 1.1–1.2 mm. long, 0.4–0.45 mm. thick, gray, finely lacunose. Gametic chromosome number, $n=7$. Autogamous or rarely cleistogamous.

TYPE: Green River, Sweetwater County, Wyoming, 31 May 1897, *A. Nelson* 3047 (RM; isotypes, GH, NY, US).

DISTRIBUTION (Figure 80): Occasional on sandy slopes and flats, often with *Artemisia tridentata*, from Douglas and Lincoln Counties, eastern Washington; Payette, Lehmi, Butte, and Bannock Counties, southern Idaho; and Wyoming (Big Horn, 12 miles north of Graybull, 4,050 ft., *Hamner* 43, RM; Washakie, west of Worland, 4,100–4,300 ft., *Nichols* 374, RM; Sweetwater; and Carbon Counties) south through southeastern Oregon (Lake, Harney, and Malheur Counties), Utah (south to Beaver, Sevier, San Pete, Duchesne, and Uintah Counties), and westernmost Colorado (Moffat and Mesa Counties) to northern and central Nevada (Humboldt, White Pine, Eureka, Elko, Pershing, Lander, Nye, and Washoe—near Verdi, *Stokes* in 1903, US—Counties), and northeastern California (valley east of Cedarville, 4,000 ft., Modoc County, *Ripley & Barneby* 6006, CAS).

Vouchers for chromosome number (3 individuals, 3 populations), $n=7$ (all 7 pairs):

U.S.: NEVADA: EUREKA CO.: Near Lone Mt., cultivated at Los Angeles, R15418. OREGON: HARNEY CO.: 4.7 mi. S. of Narrows, R18443; 12.9 mi. S. of Narrows, R18448.

This species is here taken in the same sense in which it was constituted by Munz (Bot. Gaz. 85: 238–240) in 1928. Some of the populations from the western portions of the range of this species consist of relatively small-flowered individuals, but these do not constitute the sort of well-marked geographical race that I consider to merit formal taxonomic recognition. Thus I do not recognize the taxon described as *Oenothera minor* var. *cusickii.*

In some of the plants of *Hitchcock & Muhlick* 21200 (DS), from 21 miles north of French Glen, Harney County, Oregon, the epipetalous stamens are extremely reduced, the apparently abortive anthers being subsessile. It is conceivable that some plants of this species might be found which lack this set of anthers completely, as is the case in some populations of *C. andina* and in both known populations of *C. exilis*. In these cases, it would appear that the drastic reduction or loss of the smaller set of anthers is associated with autogamy; in the other genus of the tribe Onagreae containing species in which there has been a loss of the epipetalous stamens, namely *Clarkia,* this is certainly not the case.

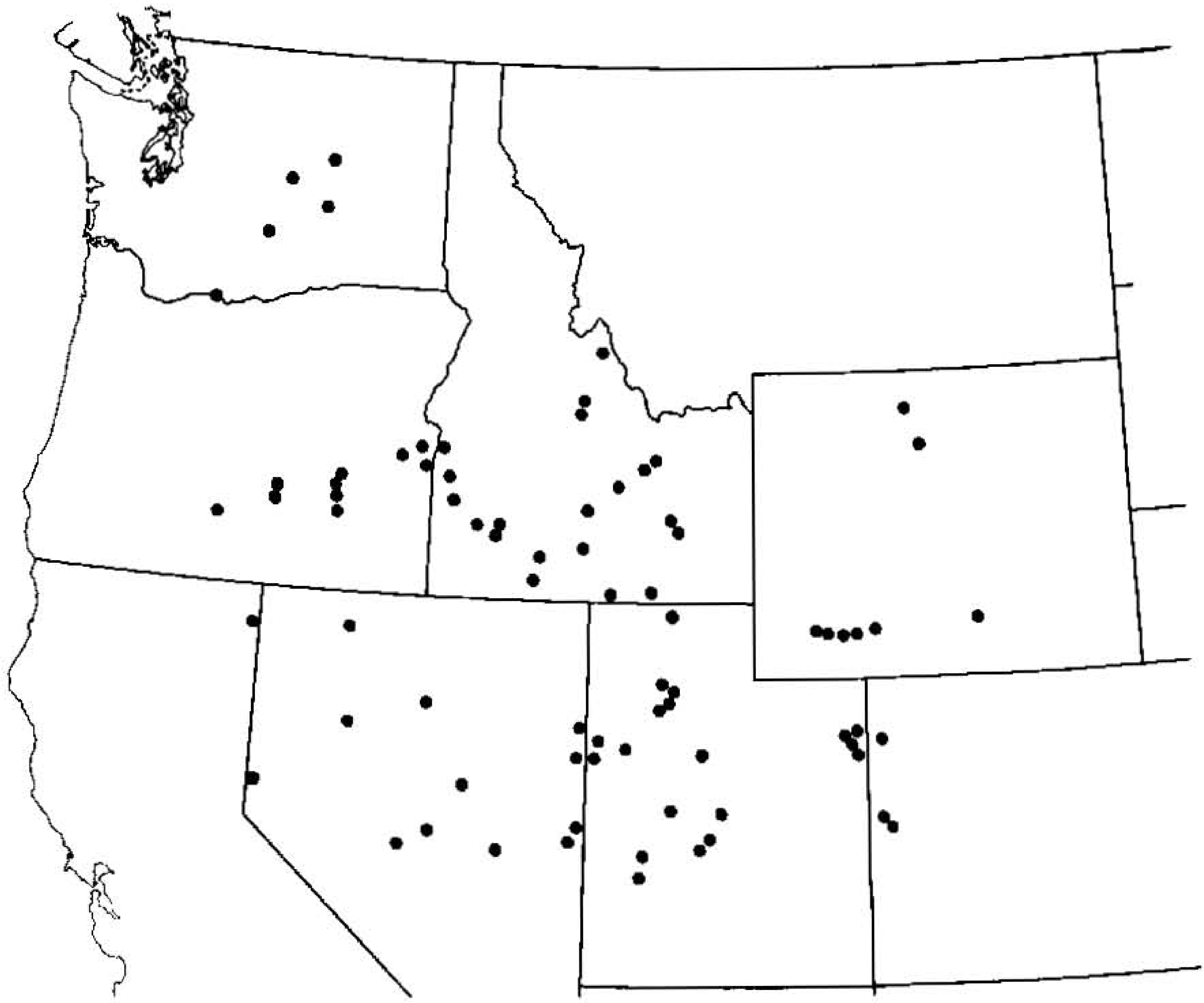


FIGURE 80.—Western United States, showing range of *Camissonia minor*.

Section VIII. *Chylismiella*

Camissonia sect. *Chylismiella* (Munz) Raven, Brittonia 16: 282. 1964.
Oenothera sect. *Chylismiella* Munz, Amer. Journ. Bot. 15: 224. 1928.
Oenothera subg. *Chylismia* sensu Munz, Amer. Journ. Bot. 15: 224. 1928.

Annuals, the plants caulescent, not flowering at the basal nodes, the leaves cauline; plants with exfoliating white rhytidome. Leaves subsessile, sometimes purple-dotted. Inflorescence nodding at anthesis, becoming erect in fruit. Flowers opening near sunrise. Ovary lacking a sterile projection. Petals white, yellow at the base, fading purplish after fertilization, without any dots or other markings. Stamens, style, and inside of hypanthium yellow. Pollen shed singly. Capsule stalked, regularly and promptly loculicidal, straight, or slightly curved, somewhat torulose, terete, the seeds in two rows in each locule, appearing as one by crowding. Seeds monomorphic, brown, with a convex side and a concave side, the concave side surrounded by a thick wing, this and the back densely covered with glassy, clavate trichomes.

TYPE SPECIES: *Camissonia pterosperma* (S. Wats.) Raven.

DISTRIBUTION: Southeastern Oregon, south through Nevada and western Utah to Inyo County, California, and northern Coconino and Mohave Counties, Arizona.

The single species of this section is extremely distinctive and cannot be allied with any other group of the genus with confidence. There is no reason to consider it related to sect. *Chylismia,* the only common feature being the prominently stalked capsule. The color of the petals, white with a yellow band near the base, is unique in *Camissonia* but widespread in the related genus *Gayophytum* and found nowhere else in the tribe Onagreae.

59. Camissonia pterosperma (S. Wats.) Raven, Brittonia 16: 282. 1964.
FIGURES 77–79

Oenothera pterosperma S. Wats., Bot. King Rep. 112, *pl. 14.* 1871.
Chylismia pterosperma (S. Wats.) Small, Bull. Torrey Cl. 23: 193. 1896.
Sphaerostigma pterospermum (S. Wats.) A. Nels., Bot. Gaz. 40: 63. 1905.

Slender and branching freely, 2–14 cm. tall; stems and leaves entirely covered with hispid pubescence. Leaves narrowly lanceolate to oblanceolate, 0.3–3 cm. long, 0.1–0.6 cm. wide, entire, with a single prominent vein, acute or acuminate at the apex, the base narrowly cuneate or attenuate. Inflorescence glandular pubescent. Hypanthium 1–2 mm. long, 1–1.2 mm. across at the summit, glabrous within. Sepals 1.5–2.5 mm. long, 0.8–1.2 mm. wide. Petals 1.5–2.5 mm. long, 1–1.9 mm. wide. Filaments of the episepalous stamens 1–1.7 mm. long, those of the epipetalous ones 0.5–1 mm. long; anthers 0.3–0.4 mm. long. Style 2.2–4 mm. long, glabrous; stigma 1–1.5 mm. thick, surrounded by the anthers at anthesis. Capsule 1.2–1.8 cm. long, 1.2–1.6 mm. thick, ascending or spreading; pedicel 4–8 mm. long, spreading. Seeds 1–1.5 mm. long, 0.6–0.8 mm. thick, broader at one end, and truncate at each end (where contacting next seed in row), the trichomes longer at one end than at the other and shortest in the middle, the two areas of trichomes (back and wings) separated by a narrow glabrous band running around the seed. Gametic chromosome number, $n=7$. Autogamous.

TYPE: Growing under sagebrush, Trinity Mountains, 5,000 ft. (probably Churchill County), Nevada, May 1868, *S. Watson* (US 47918; isotypes, GH, NY).

DISTRIBUTION: Well-drained slopes, often of volcanic orgin, with *Pinus edulis, Juniperus,* and *Artemisia tridentata,* from south-eastern Oregon (Lake and Malheur Counties) south through Nevada and western Utah to Inyo County, California, and northern Mohave and Coconino (upper end of House Rock Valley, *Goodding* 112–49, RM) Counties, Arizona; widely distributed but rare. From 2,500–8,000 ft. alt. See Univ. Calif. Publ. Bot. 34: *fig. 2.* 1962.

Section IX. *Nematocaulis*

Camissonia sect. *Nematocaulis* Raven, Brittonia 16: 285. 1964.
Oenothera subg. *Sphaerostigma* sensu Munz, Bot. Gaz. 85: 234. 1928; pro parte.
Oenothera sect. *Nematocaulis* (Raven) Munz, N. Amer. Fl. II. 5: 155. 1965.

Annuals, the plants caulescent, flowering from near the base, but the lower stem usually naked, the leaves cauline and densely tufted, nearly every one bearing a flower in its axil; many slender branches often arising from near the base, these naked below, the leaves and flowers tufted near the end of each as on the main stem. Leaves subsessile. Inflorescence erect. Flowers opening near sunrise. Ovary lacking a sterile projection. Petals yellow, not fading purplish after fertilization, without any dots or other markings. Stamens, style, and inside of hypanthium yellow. Stamens eight, the epipetalous ones sometimes greatly reduced, or four. Pollen shed singly. Capsule sessile, regularly loculicidal, straight or nearly so, somewhat torulose, strongly flattened, the central axis falling free at maturity, the seeds in one row in each locule, crowded. Seeds monomorphic, narrowly obovoid, light to dark brown, smooth and shining.

TYPE SPECIES: *Camissonia hilgardii* (Greene) Raven.

DISTRIBUTION: Southern British Columbia and Alberta, south through westernmost Montana, western Wyoming, eastern Washington, and eastern Oregon to northern and central Utah and Nevada and northeastern California, east of the Cascade axis.

The two species assigned to this section are very closely related but entirely distinct within the genus; they are not similar to any other group with which I am familiar. The smaller flowered tetraploid and hexaploid populations, comprising *Camissonia andina*, have an extremely wide distribution, whereas the larger flowered diploids, *C. hilgardii*, have a relatively narrow range almost entirely in eastern Washington. On the basis of present knowledge of the group, it would appear likely that the tetraploids have had an autopolyploid origin, and that the hexaploids may have been derived directly from them by the functioning of an unreduced gamete. Such a hypothesis would if true postulate the existence of strict genetic control of pairing in this group, as no multivalents have been observed at diakinesis and metaphase I in the polyploids; but this must be true of the members of sect. *Holostigma* and sect. *Camissonia*, so it may also apply here. As there is only one series of diploid populations known in this extremely distinct group, no alternative seems to suggest itself.

Occasional plants of the highly autogamous, sometimes even cleistogamous, member of sect. *Nematocaulis*, *Camissonia andina*, have 3-merous flowers; these have been named *Oenothera andina* f. *tripetala* by Léveillé and *O. andina* var. *anomala* by M. E. Peck. Such flowers are unknown elsewhere in the genus but appear again in another genus of the tribe, *Gaura*, where they characterize one autogamous entity, *G. hexandra* Gómez Ortega subsp. *hexandra*, and are found very frequently in another autogamous species, *G. angustifolia* Michx. Elsewhere in the family 3-merous flowers occur regularly only in the highly autogamous (sometimes cleistogamous) African *Ludwigia* sect. *Prieurea*, consisting of a single variable species. Thus there appears to be a strong correlation between autogamy and the reduction in number of flower parts in the family Onagraceae. The same may be said of the loss of epipetalous stamens, which occurs in occasional plants (perhaps entire populations?) of *Camissonia andina* (e.g., two from Blaine County, Idaho: *Macbride & Payson* 3056, POM; *Macbride* 806, DS). As noted above, there is a strong tendency toward this condition in some individuals of the highly autogamous *Camissonia minor*, and it is a consistent feature in the two known populations of *C. exilis*. On the other hand, there is certainly no connection between autogamy and the loss of the epipetalous stamens in *Clarkia* or in *Ludwigia*, with a single exception in the latter: relatively small-flowered (and presumably more highly autogamous) individuals and populations of *L. inclinata* (L. f.) Raven tend to have only four stamens and have been named *L. verticillata* and placed in another section of the genus by Munz.

60. Camissonia hilgardii (Greene) Raven, Brittonia 16: 285. 1964. FIGURE 75

Oenothera hilgardi Greene, Bull. Torrey Cl. 10: 41. 1883.

Sphaerostigma hilgardi (Greene) Small, Bull. Torrey Cl. 23: 188. 1896.

Sphaerostigma andinum var. *hilgardii* (Greene) A. Nels., Bot. Gaz. 40: 56. 1905.

Oenothera andina var. *hilgardii* (Greene) Munz, Bot. Gaz. 85: 251. 1928.

Similar to *C. andina*, but the flowers larger. Hypanthium 1.5–2 mm. long, ca. 1.2 mm. across at the summit, sparingly pubescent in lower portions within. Sepals 2–3 mm. long, 0.9–1.1 mm. wide. Petals 2.5–5 mm. long, 2.2–3.5 mm. wide. Filaments of the episepalous stamens 2–4 mm. long, those of the epipetalous ones 1.5–2.8 mm. long; anthers of the longer stamens 0.7–0.8 mm. long, those of the shorter 0.5–0.6 mm. long. Style 4.5–6 mm. long, sparsely pubescent near the base; stigma 0.7–0.8 mm. thick, held at or slightly above the anthers of the longer stamens at anthesis. Gametic chromosome number, $n=7$. Probably self-compatible but outcrossing.

TYPE: Moist alkaline soil of the Klickitat Swale, Klickitat or Yakima County, Washington, July 1882, *E. Hilgard* (GH).

DISTRIBUTION (Figure 81): Sandy or clay slopes under *Artemisia tridentata*, scattered but locally common, occasionally growing with *C. andina*, in Okanagan, Chelan, Douglas, Grant, Kittitas, and Yakima Counties, Washington; collected twice along the lower Columbia River, at Bingen, Klickitat County, Washington, and Hayden Island, Multnomah County, Oregon. From near sea level to ca. 1,600 ft. alt.

Vouchers for chromosome number (2 individuals, 2 populations), $n=7$ (7 pairs in each):

U.S.: WASHINGTON: KITTITAS CO.: 16.7 mi. W. of Ginkgo Petrified Forest, R18485. YAKIMA CO.: 2.3 mi. S. of L. Wenas, R18483.

61. Camissonia andina (Nutt.) Raven, Brittonia 16: 285. 1964.

Oenothera andina Nutt., *in* Torr. & Gray, Fl. N. Amer. 1: 512. 1840.

Sphaerostigma andinum (Nutt.) Walp., Rep. 2: 79. 1843.

Oenothera andina f. *tripetala* H. Lév., Monogr. Onoth. 182. 1905. No specimens cited.

Oenothera andina var. *typica* Munz, Bot. Gaz. 85: 250. 1928.

Oenothera andina var. *anomala* M. E. Peck, Torreya 32: 151. 1932. Type: Dry slope 6 mi. NW. of Paisley, Lake Co., Oregon, 15 July 1927, *M. E. Peck* 15176 (WILLU).

Plants finely strigulose throughout, more densely so in the inflorescence, especially on the ovaries. Branches 1–15 cm. long. Leaves very narrowly oblanceolate, 1–3 cm. long, 0.1–0.25 cm. wide, entire, acuminate at the apex, attenuate at the base. Hypanthium 0.8–2 mm. long, 0.75–1.1 mm. across at the summit, glabrous or more rarely sparsely pubescent in lower half within. Sepals 0.8–2 mm. long, 0.5–1.1 mm. wide. Petals 0.8–2.3 mm. long, 0.6–1.2 mm. wide. Filaments of the episepalous stamens 0.45–2.2 mm. long, those of the epipetalous ones 0.1–0.45 mm. long, the epipetalous stamens rarely lacking; anthers of the longer stamens 0.2–0.45 mm. long, those of the shorter ones 0.08–0.2 mm. long. Style 1.7–3 mm. long, glabrous or more rarely sparsely pubescent near the base; stigma 0.4–0.6 mm. thick, surrounded by the anthers at anthesis. Capsule (0.5–)0.8–1 cm. long, 1–1.3 mm. thick along the wider axis, ascending. Seeds 0.7–1.3 mm. long, 0.3–0.35 mm. thick. Gametic chromosome numbers, $n=14$, 21. Autogamous, more rarely cleistogamous.

TYPE: Dry plains near the Blackfoot River, Bingham or Caribou County, Idaho, 10–12 July 1834, *T. Nuttall* (BM; isotypes, GH, K, NY, PH).

DISTRIBUTION (Figure 81): Vernally moist flats, often in clay soil under *Artemisia tridentata* or in pinyon-juniper association, inconspicuous and often overlooked, from the vicinity of Lake Osoyoos, British Columbia, and Medicine Hat, Alberta, south to Missoula County, Montana (Missoula, *Hitchcock* 2326, CAS, POM, RSA, WS); the western half of Wyoming; Cache, Wasatch, and Beaver Counties, Utah; Elko, Eureka, Humboldt, northern Nye, and Ormsby Counties, Nevada; and from Sierra County, California, north along the east side of the Cascades throughout eastern Oregon and Washington, and west along the Columbia River to Skamania County, Washington; from ca. 1,600–ca. 6,500 ft. alt. I have seen a specimen labeled "Golden City, etc., Colorado," *Greene* in 1873 (US), but the occurrence of *Camissonia andina* in that state needs confirmation.

Vouchers for chromosome number (4 individuals, 4 populations), $n=14$:

U.S.: CALIFORNIA: LASSEN CO.: Near Eagle L., *Ornduff* 4205 (LA). IDAHO: FREMONT CO.: Near St. Anthony, R19560. OREGON: LAKE CO.: W. of Lakeview,

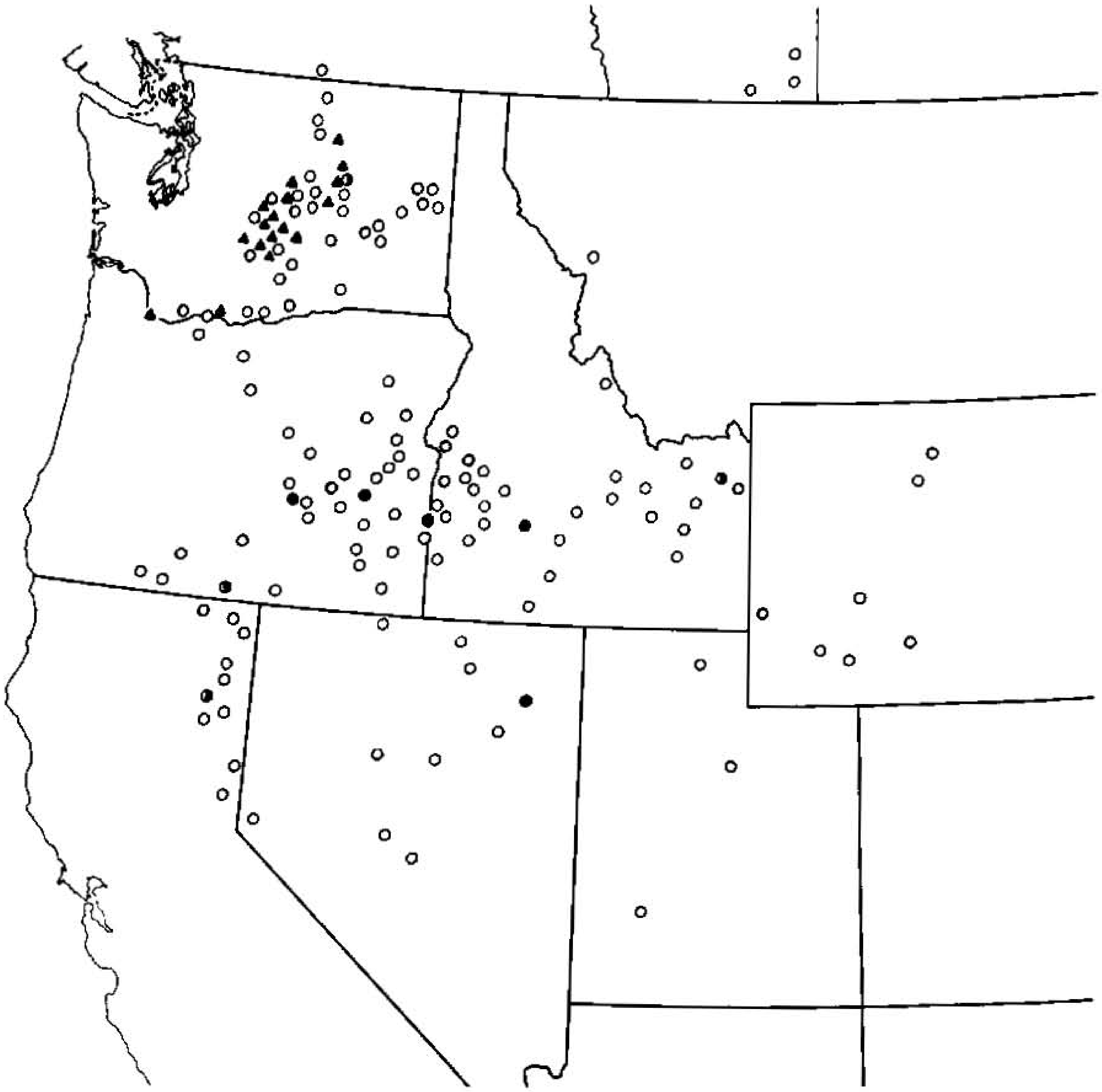


FIGURE 81.—Western United States, showing range of species of *Camissonia* sect. *Nematocaulis*: ▲=*C. hilgardii*; ○=*C. andina*, with ◑=tetraploid chromosome counts ($n=14$) and ●=hexaploid chromosome counts ($n=21$).

R18429. WASHINGTON: DOUGLAS CO.: State Hwy. 10, 4.6 mi. N. of junction with U.S. Hwy. 2, R18495.

Vouchers for chromosome number (5 individuals, 5 populations), $n=21$:

U.S.: IDAHO: ELMORE CO.: 19 mi. E. of Dixie, R18524 (54 percent of pollen 4-pored). NEVADA: ELKO CO.: East Humboldt Mts., R13456. OREGON: HARNEY CO.: 3.4 mi. E. of Buchanan, R18458 (46 percent of pollen 4-pored); 14 mi. NE. of Wagontire, R13356. MALHEUR CO.: Idaho State line on U.S. Hwy. 95, R19581.

Camissonia andina grows sympatrically with its diploid relative, *C. hilgardii*, at a number of localities within the range of the latter. With the accumulation of additional chromosome number determinations from *C. andina*, it should become possible to develop a method for distinguishing tetraploids and hexaploids. Whether it will then become desirable to accord formal taxonomic recognition to tetratploid and hexaploid populations remains to be seen. In general, it now appears that hexaploids often have 40–90 percent 4-pored pollen grains, tetraploids mostly 10 percent or fewer (often none). Several of the collections examined (without chromosome number determinations) had 10–40 percent 4-pored pollen, and more chromosome counts will be necessary to draw a clear line between plants at the two different polyploid levels. At any rate, it is virtually certain that the type collections of this species is hexaploid ($n=21$), as an isotype (NY) had 27 of the 50 pollen grains examined 4-pored.

The limited amount of evidence now available suggests that tetraploid races occupy the margins of the range of this species and are infrequent in the main portion of its range, where hexaploids appear to predominate. I have thus far been unable to discover any morphological distinctions between the two races other than the pollen difference just discussed.

Excluded Species

Sphaerostigma andinum var. *minutum* A. Nels., Bot. Gaz. 40: 56. 1905=*Gayophytum* sp. (Type: without data, MO).

Oenothera micrantha Presl, Rel. Haenk. 2: 31. 1827; non Hornem. ex Spreng. 1825. Type: Chile, *Haenke* (PR). *Holostigma paradoxum* Spach, Nouv. Ann. Mus. Paris III. 4: 334. 1835. *Sphaerostigma paradoxum* (Spach) Gay, Fl. Chil. 2: 329. 1846. *Chamissonia paradoxa* (Spach) Reiche, Anal. Univ. Chile 98: 482. 1897=*Gayophytum micranthum* Hook. & Arn. (cf. Lewis & Szweykowski, Brittonia 16: 389. 1964).

Appendix

Chromosome numbers of *Camissonia* sect. *Holostigma*[4]

In the following lists are grouped the vouchers for chromosome counts in *Camissonia* sect. *Holostigma.* Collections made by Raven are preceded by *R*, those by Breedlove by *B*, and those by Wedberg by *W*. As usual throughout this paper, vouchers are presumed to be deposited at DS unless some other indication of place of deposit is made. In this section, "SDSC" is used for the herbarium of San Diego State College, where some of the vouchers are deposited; abbreviations for other herbaria are standard. In general, Wedberg counted his own collections and Raven counted the others, often with the assistance of Breedlove.

In addition to the original counts reported here, we have also included 34 counts reported for plants of this group by Lewis, Raven, Venkatesh, & Wedberg (Aliso 4: 73–86. 1958). The only earlier chromosome number determinations for the group appear to be those by Johansen (Amer. Journ. Bot. 16: 595–597. 1929; Proc. Nat. Acad. Sci. U.S. 15: 882–885. 1929) of $n=7$ in "*Sphaerostigma veitchianum*" and "*S. spirale*" (= *Camissonia bistorta* and *C. cheiranthifolia*, respectively), but without any indication of the source of the materials examined.

Including the 34 earlier counts for which voucher specimens are available, a total of 389 individuals from 335 populations have been examined cytologically. These populations represent all 17 taxa recognized for the section, including 14 species and 3 additional subspecies. Cytogenetically, the most striking characteristic of these counts is the almost complete lack of rings of chromosomes such as are associated with the presence of reciprocal translocations. Lewis et al. (1958, p. 80) reported 12 pairs and a ring of 4 chromosomes in one plant of *Camissonia confusa* (*Lewis & Lewis* 1669, LA; as *Oenothera micrantha* var. *ignota*). This ring of 4 chromosomes may have resulted from the presence of a reciprocal translocation, or it may have been because of homology between the pairs of chromosomes involved in it. At any rate, it was the only individual, out of 389 examined, in which such a ring of chromosomes was found. In contrast, reciprocal translocations occurred in over 20 percent of the 676 individuals of *Camissonia* sect.

---

[4] This work was done in cooperation with Dennis E. Breedlove and Hale L. Wedberg (San Diego State College).

Chylismia that were examined cytologically (Raven, Univ. Calif. Publ. Bot. 34: 20–43, 1962), and similar percentages probably occur in sect. *Eremothera* and are characteristic of other groups of the tribe Onagreae, such as the genus *Clarkia*. In view of the complete absence of reciprocal translocations in natural populations of sect. *Holostigma*, it is also of considerable interest that not one of the 389 individuals of this section (with the possible exception noted above) examined cytologically had a supernumerary chromosome, as compared with the 26 of the 676 individuals of sect. *Chylismia*. This would appear to lend considerable weight to Lewis' (Evolution 5: 142–157, 1951) suggestion of a causal relationship between reciprocal translocation (presumably by occasional misdivision of rings of chromosomes) and supernumerary chromosomes in Onagreae.

It is also noteworthy that little evidence of autopolyploid pairing has been found in the two tetraploids and three hexaploids of this section, even though the diploid species contributing to their formation are obviously extremely closely related. This subject is discussed further on p. 176.

Camissonia bistorta (Nutt. ex Torr. & Gray) Raven, (29 individuals, 22 populations), $n=7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Point Dume, W13, in 1958, 169 (SDSC), in 1957 (LA), *H* (LA), *Lewis* 1634 (LA); Playa del Rey, WI (LA), 562 (SDSC); Mulholland Drive, Santa Monica Mts., W260 (SDSC). ORANGE CO.: Corona del Mar, W172; 6.5 mi. E. of San Juan Capistrano, R17491 (progeny=R18782); 5.6 mi. NE. of San Juan Capistrano, W178; Dana Point, W176; lower edge of Cleveland National Forest just above San Juan Guard Station, 850 ft., R18783. RIVERSIDE CO.: 6.5 mi. SE. of Hemet, B1896; 5 mi. N. of Alberhill, W3; Upper San Juan Campground, W188 (SDSC); Lake Mathew Road, W196; 5.1 mi. W. of Dripping Springs, R14023; 0.5 mi. NW. of Alberhill, WB (LA); Temescal Canyon, *Lewis* 1630 (2 plants; LA); ca. 2 mi. N. of Aguanga, *Klein* 1300 (RSA). SAN BERNARDINO CO.: U.S. Hwy. 70–99, 0.15 mi. W. of Etiwanda Ave., W26 (LA). SAN DIEGO CO.; La Mesa, W922 (SDSC); 2.2 mi. W. of Campo, R16926; Torrey Pines Park, W211 (SDSC); Balboa Park, San Diego, W213 (SDSC).

BAJA CALIFORNIA. 3 mi. S. of Ensenada, *Klein & Gregory* 1272.

Camissonia cheiranthifolia (Hornem. ex Spreng.) Raimann subsp. **cheiranthifolia** (8 individuals, 8 populations), $n=7$:

U.S.: CALIFORNIA: HUMBOLDT CO.: 8.8 mi. N. of Big Lagoon, *T. & L. Mosquin* 4489. LOS ANGELES CO.: San Clemente I., R17627 (progeny). SACRAMENTO CO.: Brannan I. State Park, near Rio Vista, R20178. SANTA BARBARA CO.: Jalama Beach, R14040; San Miguel I., *Blakley* 5099 (the form called *Oenothera nitida* Greene, at its type locality); Santa Cruz I., Fraser Point, R15312; Santa Rosa I., R14995. SONOMA CO.: Bodega Bay to Bodega Head, R18247.

Camissonia cheiranthifolia subsp. **suffruticosa** (S. Wats.) Raven (7 individuals, 7 populations), $n=7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Point Dume, R13855 (LA, RSA). SAN DIEGO CO.: S. of Carlsbad, R14027; Torrey Pines State Park, W210 (SDSC). SANTA BARBARA CO.: Devereaux Point, B1766 (UCSB); Goleta Point, R14044. VENTURA CO.: Ventura, R13999.

BAJA CALIFORNIA: 3 mi. S. of Ensenada, R17009 (2 plants).

Camissonia confusa Raven (29 individuals, 22 populations), $n=14$:

U.S.: ARIZONA: MARICOPA CO.: 12.6 mi. E. of Tortilla Flat on State Hwy. 88, 2,700 ft., R17373, 12.9 mi. E., R17375. CALIFORNIA: LOS ANGELES CO.: Native to Rancho Santa Ana Botanic Garden, Claremont, R15535, 17748, 18139. ORANGE CO.: Lower San Juan Campground, Santa Ana Mts., *Lewis* 1642 (LA), W183. RIVERSIDE CO.: Upper San Juan Campground, Santa Ana Mts., W187 (SDSC); Ortega Hwy. 3.9 mi. above its E. base, Santa Ana Mts., 2,400 ft., R17488; Reche Canyon, Loma Linda, 1,900 ft., R17471, 18766; 7.7 mi. E. of Hemet, WO (LA), 198; 10.3 mi. S. of Hemet, W204 (SDSC); 6.6 mi. from Banning on Idyllwild road, *Lewis* 1667 (LA); 7.4 mi. from Banning on Idyllwild road, W303 (SDSC); Hwy. 74 ca. 11 mi. W. of Elsinore, Santa Ana Mts., W191 (SDSC). SAN BERNARDINO CO.: Oak Glen Road 2.5 mi. E. of junction with road from Yucaipa to Mill Creek, San Bernardino Mts., 3,300 ft., R17469; 2.3 mi. W. of Mill Creek Ranger Station, 2,300 ft., R17466 (type collection). SAN DIEGO CO.: 2.7 mi. SE. of Aguanga, 2,400 ft., R17388; 0.6 mi. W. of Banner Queen Store, 3,000 ft., R17422; State Hwy. 79, 2.2 mi. S. of junction with State Hwy. 76, N. of Santa Ysabel, 3,300 ft., R17395; road to Mt. Palomar 3.9 mi. NW. of turn to L. Henshaw, 4,000 ft., R17397; L. Henshaw, 2,800 ft., R17396; 2.5 mi. W. of Julian, *H. & M. Lewis* 1669 (2 plants; LA). SAN LUIS OBISPO CO.: La Panza Campground, 2,000 ft., R16968, 18323. VENTURA CO.: Cow Spring Campground, 17.6 mi. N. of Fillmore, Topatopa Mts., 3,500 ft., B2643.

Camissonia guadalupensis (S. Wats.) Raven subsp. **clementina** (Raven) Raven (3 individuals, 3 populations), $n=7$:

U.S.: CALIFORNIA: SAN CLEMENTE I., LOS ANGELES CO.: Eel Point, R17125 (type collection); beach due W. of Wall 2, R17260; W. side of island opposite Wilson Cove, R17628 (progeny=R18176).

Camissonia guadalupensis subsp. **guadalupensis** (2 individuals, 1 population), $n=7$:

BAJA CALIFORNIA: Arroyo Melpomone, Guadalupe I., *Moran & Ernst* 6737 (2 plants in progeny=R17530, 18175).

Camissonia hardhamiae Raven (3 individuals, 3 populations), $n=21$:

U.S.: CALIFORNIA: SAN LUIS OBISPO CO.: 3 mi. E. of Santa Margarita, R18313; Calf Canyon, 3.7 mi. NE. of Santa Margarita, R18315 (type collection); 4.2 mi. NE. of Santa Margarita, at junction to Parkhill District, R18318.

Camissonia hirtella (Greene) Raven (84 individuals, 76 populations), $n=7$:

U.S.: CALIFORNIA: AMADOR CO.: 1.5 mi. N. of Buena Vista, R18351. FRESNO CO.: Copper Creek Trail, Kings Canyon, 5,500 ft., *Howell* 34332 (progeny=R19082, 19748); Simpson Meadow, Middle Fork of Kings R., *Howell* 33793 (progeny=R18989, 19755); 8 mi. N. of Pine Ridge, B15277. KERN CO.: Black Mt. burn, Greenhorn Mts., *Howell* 18779 (progeny=R18779, 19746); Breckinridge Mt., 7,400 ft., *Twisselmann*, 4704 (progeny=R19080); 3.5 mi. E. of Alta Sierra, Greenhorn Mts., R20249; ca. 1 mi. S. of Havilah, *Lewis* 1344. LAKE CO.: 4 mi. E. of Clear Lake, B5150; 4 mi. NW. of Lower Lake, B4542; 2 mi. NE. of Lower Lake, B4539; Lower Lake, R18241. LOS ANGELES CO.: Santa Monica Mts.: Latigo Canyon Road 0.4 mi. from Mulholland Hwy., W287 (SDSC); Corral Canyon, R17512A; Topanga Canyon, W308; Piuma Road 5.1 mi. NW. of Rambla Pacifica, 700 ft., R15369; Mulholland Hwy. just E. of junction with Decker Road, 1,600 ft., R17516; Saddle Peak Road 0.9 mi. above Stuntz Canyon Road, 2,200 ft., R17510; 0.6 mi. above junction of La Tuna Canyon on road to Saddle Peak, 2,050 ft., R17506; Soledad Canyon, *Lewis* 1677 (LA). MARIPOSA CO.: 3.7 mi. NW. of Coulterville, 2,000 ft., R18347. MONTEREY CO.: Hanging Valley, NW. side of Junipero Serra Peak, B5599. RIVERSIDE CO.: 2 mi. S. of Banning, WM (LA); west of Mountain Center, San

Jacinto Mts., W304, 305 (SDSC); Upper San Juan Campground, Santa Ana Mts., *Lewis* 1655 (LA); Upper San Juan Campground to Hwy. 74, W190 (SDSC); 10.3 mi. S. of Hemet on Hwy. 79, W202 (SDSC); Dripping Springs Campground, 1,700 ft., R17384; Ortega Hwy. 1 mi. above E. base, 1,600 ft., R17487, 3.9 mi. above, R17489; Main Divide Truck Trail at Ortega Hwy., 2,300 ft., R17762 (progeny = R18845); Main Divide Truck Trail 8.1 mi. S. of Santiago Peak, Santa Ana Mts., 4,050 ft., R17760; Vandeventer Flat, San Jacinto Mts., WN-1(LA). SAN BERNARDINO CO.: 1.5 mi. W. of Mill Creek Ranger Station, 2,300 ft., R17467; State Hwy. 30, 2 mi. N. of National Forest Boundary, 2,000 ft., R17465, 4.5 mi. N. of boundary, 2,800 ft., R17464; road to Barton Flats 6.5 mi. N. of Mill Creek, R17926 (cleistogamous). SAN DIEGO CO.: 1 mi. from Santa Ysabel road to Julian, 3,000 ft., W928 (SDSC); Lake Wohlford, R20169; 0.9 mi. from U.S. Hwy. 395 on Deer Springs Road to San Marcos, 700 ft., R17473; State Hwy. 94, 1.5 mi. W. of turn to Tecate, 1,600 ft., R17449; 0.5 mi. E. of Santa Ysabel, 3,300 ft., R17339, 17392, 17393; 1.1 mi. E. of Campo, 2,900 ft., R17444; 1.1 mi. E. of Campo, 2,900 ft., R17442, 17443; 3.7 mi. N. of Cameron Corners on road to Pine Valley, 3,500 ft., R17441; 3.1 mi. from U.S. Hwy. 80 on road to Morena Lake, 3,400 ft., R17440; 1.0 mi. E. of Oak Grove, 2,700 ft., R17389; County Road S6 just S. of turn to Felicita County Park, R16948; 5.6 mi. W. of Campo, 2,600 ft., R17448; 3.8 mi. from turn to Escondido on road to Mt. Palomar, 4,100 ft., R17398; 2.3 mi. S. of Rincon Springs on road to Escondido, cultivated at Stanford, R19076; 3.5 mi. NE. of Lake Wohlford, 1,700 ft., R17404; 8.6 mi. E. of Ramona, 2,800 ft., R17413; 2.5 mi. W. of Santa Ysabel, 3,100 ft., R17416; 2.1 mi. E. of Santa Ysabel 3,700 ft., R17418; 0.6 mi. above Banner Queen Store, R16922, 1.3 mi. W., 3,000 ft., R17419, 0.8 mi. E., R16924; Jamul-Lyons Valley road 0.7 mi. NE. of turn to Camp Barrett, 2,200 ft., R17432; U.S. Hwy. 80, 0.7 mi. W. of Guatay Summit, 4,000 ft., R17436. SAN LUIS OBISPO CO.: S. road to Adelaida 6.4 mi. from its junction with Oak Flat Road, *Lewis & Thompson* 1099 (LA, RSA, UC). SANTA BARBARA CO.: 1.5 mi. W. of Juncal Campground, upper Santa Ynez Valley, 1,750 ft., B2236; 4.4 mi. E. of Santa Ynez Peak along El Camino Cielo, 3,300 ft., B2689; Tunnel Road 2.5 mi. N. of U.S. Hwy. 150, Mission Canyon, 800 ft., B1902; above Mono Debris Dam, upper Santa Ynez Velley, 1,500 ft., B2244. SANTA CLARA CO.: 1.5 mi. E. of Red Mt. near summit of Del Puerto Road, Mt. Hamilton Range, B4889; upper Arroyo del Puerto 2.4 mi. E. of junction in San Antonio Valley, R18230; summit of Loma Prieta, Santa Cruz Mts., B4675, 5011. VENTURA CO.: Cow Spring Campground, 17.6 mi. N. of Fillmore, Topatopa Mts., 3,500 ft., B2644; U.S. Hwy. 399 at turn to Rose Valley, 3,600 ft., R17499; just N. of Wheeler Gorge Guard Station, 1,950 ft., R17498; 1.2 mi. S. of Wheeler Springs, 1,400 ft., R17496A; Camp Ozena, Ozena Valley, 3,800 ft., B2436; Sespe Creek 7.6 mi. S. of Sandstone Camp, 3,700 ft., R17500.

BAJA CALIFORNIA: 10.9 mi. N. of Santo Tomás, 600 ft., R17014; Santa Catarina, *Broder* 436 (progeny = R18992, 19754).

Camissonia ignota (Jeps.) Raven (22 individuals, 18 populations), $n = 7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Soledad Canyon, *Lewis* 1676 (3 plants; LA, RSA). ORANGE CO.: Lower San Juan Campground, Santa Ana Mts., W180 (SDSC). RIVERSIDE CO.: 5 mi. NW. of Alberhill, *W* in 1967 (2 plants; LA); State Hwy. 74, 1.6 mi. NE. of junction with State Hwy. 71, near Elsinore, R16914; 5.7 mi. SE. of U.S. Hwy. 395 on State Hwy. 74, road to Hemet, 1,600 ft., B1898; Reche Canyon, R17472; Dripping Springs Campground, 1,700 ft., R17385; Lake Mathews road 14.7 mi. W. of U.S. Hwy. 395, R16909. SAN DIEGO CO.: NW. of Fallbrook, W206 (SDSC); 2.3 mi. S. of Rincon Springs on road to Escondido, 1,100 ft., R17402 (progeny = R18787, 19751); 2.7 mi. SE. of Aguanga, 2,400 ft., R17387; Lyons Valley along road 8 mi. NE. of Jamul, 1,800 ft., R17434. SAN LUIS OBISPO CO.: 1.2 mi. S. of Santa Margarita to Simmler road on road to Navajo Camp, La Panza Range, 2,000 ft., R16970. SANTA BARBARA CO.: Juncal Campground, upper Santa Ynez Valley, 1,800 ft., B2229; S. bank of Cuyama R. on State Hwy. 166, 1.6 mi. E. of Tepusquet Canyon Road, 1,800 ft., B1930. VENTURA CO.: Boney Ridge, Santa Monica Mts., grown at Stanford, R18173.

Camissonia intermedia Raven (60 individuals, 53 populations), $n=14$:

U.S.: CALIFORNIA: CONTRA COSTA CO.: Mt. Diablo, B4698. LAKE CO.: 4 mi. W. of Reiff, R20213. LOS ANGELES CO.: Soledad Canyon, *Lewis & Thompson* 1616 (LA); near Bird Park, Memorial Canyon, Avalon, Santa Catalina I., R17857, 18171. SANTA MONICA MTS., LOS ANGELES CO.: just S. of Agoura, 850 ft., R17520; Corral Canyon, 1,900 ft., R17512 (progeny=18756); 0.9 mi. W. of Seminole Hot Springs, 800 ft., R17518; 2.6 mi. E. of Seminole Hot Springs, R17517 (type collection); Mulholland Hwy. just E. of junction with Decker Road, 1,600 ft., R17515; Stuntz Canyon Road 3.1 mi. below junction to Saddle Peak, 1,200 ft., R17511; Saddle Peak Road 0.9 mi. above Stuntz Canyon Road, 2,200 ft., R17509; Saddle Peak Road 2.4 mi. above junction of La Tuna Canyon Road, 2,400 ft., R17507; La Tuna Canyon 3.6 mi. N. of Coast Highway, 1,800 ft., R17504. MONTEREY CO.: Big Sandy Valley 2 mi. N. of Indian Valley Road, R18289; Hastings Reservation, R18220, 18218; just N. of Hastings Reservation, R18225; road to Jamesburg 0.8 mi. from main road up Carmel Valley, R18227; W. edge of San Antonio Valley, Santa Lucia Mts., 1,350 ft., B2267; 2.1 mi. SW. of Arroyo Seco Guard Station, 1,250 ft., B2305; 6 mi. W. of Priest Valley on State Hwy. 198, 2,500 ft., B2376; 0.6 mi. SW. of San Benito Co. line on road from Bitterwater to King City, R18201; The Indians, Santa Lucia Mts., R18213, 18264, 18268; Lowes Canyon, R18293, 18298. RIVERSIDE CO.: Machado Road 1 mi. SW. of U.S. Hwy. 71, W193, 194 (SDSC); 3.3 mi. W. of Dripping Springs Campground, 1,500 ft., R17382. SAN BENITO CO.: 3.7 mi. from Hernandez on road to New Idria, R15087. SAN DIEGO CO.: 2.7 mi. W. of De Luz on road to Fallbrook, 600 ft., R17483; 2.4 mi. from Fallbrook on road to De Luz, R17477 (progeny=R18758); road to Fallbrook at junction with U.S. Hwy. 395, 950 ft., R17484. SAN LUIS OBISPO CO.: 1.2 mi. W. of Bee Rock, R18305; near junction 1.8 mi. W. of Paso Robles, R18327. SANTA BARBARA CO.: Head of Buckhorn Canyon, summit of San Rafael Mts., 2,600 ft., B2779; Alamo Pintado Creek, 7–8 mi. N. of Los Olivos, Birbent Canyon, base of Figueroa Mt., ca. 1,400 ft., B2498; Little Agua Caliente Hot Springs, 1.5 mi. NE. of Mono Debris Dam, 1,700 ft., B2230; 0.9 mi. N. of State Hwy. 150 on San Roque Road, Santa Barbara, 800 ft., B2228; Portazuela Grade, Santa Cruz I., R15197; Prisoners Harbor, Santa Cruz I., R18172. STANISLAUS CO.: 12 mi. W. of Patterson on road to Mt. Hamilton, B4856. VENTURA CO.: Cow Springs Campground, 17.6 mi. N. of Fillmore on Cow Springs Road, Topatopa Mts., 3,500 ft., B2617; 0.3 mi. S. of Camp Comfort, S. of Ojai, R17493 (progeny=18755); 1.2 mi. S. of Wheeler Springs, R17496 (progeny=18768); Little Sycamore Canyon, Santa Monica Mts., *Lewis* 1666 (LA, RSA).

BAJA CALIFORNIA: 10 mi. S. of Ensenada, R17053; 15.2 km. N. of San Vicente, R12308; 5.5 km. S. of San Vicente, R17019; 19.5 km. SE. of San Vicente, R12263; 2.5 mi. S. of Ejido México, R17040; 4 km. S. of Ejido México, R12234; 11.3 mi. N. of Colonia Guerrero, R17037; 8.5 km. E. of El Rosario, R12429; Summit of Aguajito Grade, 2 km. E. of Rancho Aguajito, R12523.

Camissonia lewisii Raven (23 individuals, 19 populations), $n=7$:

U.S.: CALIFORNIA: LOS ANGELES CO.: Point Dume, W13, 170; Playa del Rey, W273. ORANGE CO.: Lower edge Cleveland National Forest, just above San Juan Guard Station, R17490 (progeny=R18764, 19079). SAN DIEGO CO.; 2.7 mi. from

Fallbrook on road to De Luz, R17478, W207; Carlsbad, R14032; Switzers Canyon, San Diego, W212; Balboa Park, San Diego, W859 (SDSC); Otay Lakes Road 1.8 mi. E. of Bonita Road, R16971.

BAJA CALIFORNIA: 2.1 mi. S. of El Descanso, *Klein & Gregory* 1186; ca. 3 mi. S. of Ensenada, *Klein & Gregory* 1273, R17011; 7.5 mi. N. of Santo Tomás, R17017, 17050; 5.5 mi. S. of San Vicente, 950 ft., R17021; 1.1 mi. N. of Colonia Guerrero, R17035 (type collection); 2 km. N. of Colonia Guerrero, R12135; San Quintín, R12362; 3 mi. S. of San Quintín, *Gregory* 335 (RSA, US); 14 mi. S. of San Quintín, R17030; 5 mi. NE. of El Rosario, *Klein & Gregory* 1266; ca. 13 mi. SE. of El Rosario, *Klein & Gregory* 1249.

Camissonia luciae Raven (7 individuals, 7 populations), $n=21$:

U.S.: CALIFORNIA: MONTEREY CO., SANTA LUCIA MTS.: Road to Jamesburg 0.8 mi. from main road up Carmel Valley, R18150; shale roadbank 7.8 mi. SW. of Arroyo Seco Guard Station on road to Jolon, B2299; Hastings Reservation, near Jamesburg, R18221; The Indians, R18267 (type collection). SAN BENITO CO.: 3.1 mi. W. of Fresno Co. line on road from Coalinga to Hernandez, *Lewis et al.* 1342–1. SANTA BARBARA CO., SAN RAFAEL MTS.: 1.3 mi. N. of Cachuma Guard Station, *Lewis* 1678 (LA); Davy Brown Campground, *Lewis* 1647 (LA).

Camissonia micrantha (Hornem. ex Spreng.) Raven (47 individuals, 39 populations), $n=7$:

U.S.: CALIFORNIA: CONTRA COSTA CO.: Antioch, R18141; 1 mi. S. of Oakley, R18143. LOS ANGELES CO.: Claremont, W271 (SDSC), R17120, 17121; Point Dume, W13 (SDSC), 171. MONTEREY CO.: Hastings Reservation, R18224; Big Sandy Valley, R18283; 3 min. N. of summit of Hog Canyon Road, S. of Parkfield, R18299; Bradley, R18307. RIVERSIDE CO.: 11 mi. W. of Riverside, *Snow & Mosquin* in 1957 (LA). SAN BENITO CO.: Pinnacles National Monument, B2183, *Lewis* 1340; 1.1 mi. S. of Cienaga School, R18198; 5.1 mi. N. of Cienaga School, R18196. SAN BERNARDINO CO.: Alta Loma, R16987. SAN DIEGO.: U.S. Hwy. 395, 2 mi. S. of turn to Lilac, R16950, 17457. SAN FRANCISCO CO.: Lake Merced, R18160. SAN LUIS OBISPO CO.: Near mouth of Arroyo de la Cruz, *Hardham* in 1963; 2 mi W. of Nipomo, B4269; 1.2 mi. N. of Simmler-Creston road on road to Shandon, R16972, 18321; near Atascadero, R18277; 1.8 mi. W. of Bee Rock, R18034; 2.9 mi. E. of San Miguel, R18310; 1.2 mi. E. of Santa Margarita, R18312, 3.8 mi. E., B2026, 3 mi. E., R18314, 3.7 mi. NE., R18316, 4.2 mi. NE., R18317, 18.6 mi. NE., R18319, 18320; Nipomo Valley 1.5 mi. N. of Santa Barbara Co. line, R16955; S. road to Adelaida 6.4 mi. W. of junction with Oak Flat Road, near Paso Robles, *Lewis & Thompson* 1100 (LA). SANTA BARBARA CO.: 1 mi. W. of Goleta, B1967; Jalama Beach, R14039; 4 mi. N. of Lompoc, R15510; 1.7 mi. N. of Santa Ynez R. on State Hwy. 1, B2556; San Miguel I., R18178; Cherry Canyon, Santa Rosa I., R14962. SANTA CRUZ CO.: Sunset Beach, R18187; near Ben Lomond, R18183, B4637. SONOMA CO.: Bodega Bay, R18245.

CULTIVATED: Seeds from Copenhagen Botanic Garden as *Oenothera hirta*, R18242.

Camissonia pallida (Abrams) Raven subsp. **hallii** (Davids.) Raven (4 individuals, 3 populations), $n=7$:

U.S.: CALIFORNIA: RIVERSIDE CO.: Jumbo Rocks Campground, Joshua Tree National Monument, R17116; Whitewater Canyon 2.7 mi. from U.S. Hwy. 70–99, R17109; Morongo Canyon, *Lewis* 1682 (LA, RSA); Morongo Canyon, ca. 8 mi. from U.S. Hwy. 60–70–999, W231 (SDSC).

Camissonia pallida subsp. **pallida** (26 individuals, 24 populations), $n=7$:

U.S.: ARIZONA: MOHAVE CO.: 9 mi. N. of Kingman, 2,950 ft., R17359. YAVAPAI CO.: 5.4 mi. NE. of Congress, R18367 (progeny = R18767, 19752).

U.S.: CALIFORNIA: KERN CO.: Kern R. 6 mi. S. of Roads End P.O., 3,100 ft., *Howell* 33144 (progeny = R19081, 19747); W. of the mouth of Kern R. Canyon, *Lewis* 1670 (LA, RSA). LOS ANGELES CO.: Big Rock Creek, San Gabriel Mts. R11961; 0.5 mi. N. of Pearblossom, 2,800 ft., R17104; 0.2 mi. E. of Pearblossom, *Lewis & Wedberg* 1692 (LA); 1 mi. W. of Littlerock, R13995. RIVERSIDE CO.: Whitewater Canyon, *W* in 1957 (LA); near San Bernardino Co. line in Morongo Canyon, W232; Pinyon Crest Road 2.5 mi. from Palms-to-Pines Hwy., *Theobald* 62. SAN BERNARDINO CO.: Cushenbury Grade 0.5 mi. below Cactus Flat, San Bernardino Mts., 5,900 ft., R17461; Bonanza King Mine, Providence Mts., R17358 (progeny = R18769, 19753). SAN DIEGO CO.: 8.7 mi. S. of Scissors Crossing on road to Vallecito Valley, R16902, 9.1 mi. SE., R11536, 6.8 mi. S., R16900; San Felipe Creek wash 2 mi. E. of road to Yaqui Pass, R16895, 2.2 mi. W. of road W219 (SDSC), in 1957 (LA); Vallecito Valley just outside Anza-Borrego State Park boundary, R16904; N. end of Vallecito Valley, W222; 0.8 mi. E. of Banner Queen Store, Banner Grade, R16923; 2.5 mi. inside Anza-Borrego State Park on road from Scissors Crossing, W221; 3 mi. from Banner on road to Borrego Valley, W216 (SDSC); Ensign Ranch, Borrego Valley, *H. & M. Lewis* 1637A (LA), 1637B (LA).

Camissonia proavita Raven (4 individuals, 4 populations), $n=7$:

BAJA CALIFORNIA: 5.5 mi. S. of San Vicente, R17020 (type collection); 19.5 km. SE. of San Vicente, R12264; 1.2 mi. N. of Colonia Guerrero, R17034; San Quintín, R12363.

Camissonia robusta Raven (29 individuals, 24 populations), $n=21$:

U.S.: CALIFORNIA: LOS ANGELES CO.: SANTA CATALINA I.: Haypress, R17807 (progeny = 18170). SAN CLEMENTE I.: *Piehl* 62387 (progeny = R18174). SAN DIEGO CO.: U.S. Hwy. 395, 2 mi. S. of turn to Lilac, R17458 (progeny = 18846); 4.8 mi. W. of Pala, R17061; 1.6 mi. E. of Pala, R16921, 17062; 4.6 mi. E. of San Pasqual, R17407; 2.3 mi. E. of Ramona, R17411; 0.3 mi. from U.S. Hwy. 395 on Deer Springs Road to San Marcos, R17474; 0.7 mi. N. of Felecita County Park, R17453; Balboa Park, San Diego, W214 (SDSC); Sweetwater Road, San Diego, W860 (SDSC); Descanso to Lyons Valley road 3.2 mi. NE. of turn to Camp Barrett, R17431; 2 mi. E. of Chula Vista on road to Bonita, B1809; Barrett, R16937 (3 plants). SANTA BARBARA CO., SANTA CRUZ I.: Top of Ridge between Coches Prietos Canyon and Alberts Anchorage, 400 ft., *Blakley* 3314 (progeny = R18756, 19077).

BAJA CALIFORNIA: Above La Misión, between Tijuana and Ensenada, R17056; 10 mi. S. of Ensenada, R17054; ca. 16 mi. S. of Ensenada, *Klein & Gregory* 1195; 10.9 mi. N. of Santo Tomás, R17012; 7.5 mi. N. of Santo Tomás, R17016, 17051A; 5.5 mi. S. of San Vicente, R17022 (2 plants); 7.4 mi. N. of Ejido México, 500 ft., R17043. GUADALUPE I.: NE. side of Barracks Cove Canyon, *Copp* 151 (progeny = R18759); Northeast Anchorage, *Wiggins & Ernst* 222 (progeny = R18754, 19078).

Index

(Synonyms and page numbers of figures in *italics*. Page numbers of principal entries in **boldface.**)

- *Agassizia*, 179, 253
- *Agassizia cheiranthifolia*, 179, 265
- Andrena, 323
  - subg. Diandrena, 270
  - subg. Onagrandrena, 266, 270, 310, 327
  - chalybea, 242
  - eulobi, 190
  - mojavensis, 310
  - oenotherae, 261
  - parachalybea, 261
  - raveni, **247**
  - vespertina, 352
- Anthophora urbana, 231
- Boisduvalia, 341
- Boisduvalia cleistogama, 351
- *Burragea*, 161
- Calylophus, 161, 162, 163, 356
- Calylophus hartwegii, 161
- Camissonia
  - Sect. Camissonia, 165, 169, 171, *172*, 173, 174, *175*, 176, 177, 181, 186, 201, **305**, *313*, *314*, 319, *322*, 324, *328*, *330*, *331*, 332, 339, 344, 351, 376
  - Sect. Chylismia, 168, 169, 171, *172*, 173, 174, *175*, 176, 177, 180, 181, 182, **202**, 233, 234, 307, 310, 351, 358, 375, 382
  - Sect. Chylismiella, 168, 169, *172*, 173, 174, *175*, 180, 181, 189, **374**
  - Sect. Eremothera, 169, 171, *172*, 173, 174, *175*, 176, 177, 181, 188, 203, **350**, *353*, *355*, *367*, 382
  - Sect. Eulobus, 168, 169, 170, 171, *172*, *175*, 176, 177, 180, 181, 188, **189**, *193*, *195*, 233, 234, 351
  - Sect. Holostigma, 165, 169, 171, *172*, 173, 174, *175*, 176, 177, 179, 181, 185, 189, 201, **253**, *262*, *270*, *274*, *278*, *283*, *284*, *288*, *296*, *300*, 307, 324, 340, 351, 376, 381, 382
- Camissonia—Continued
  - Sect. Lignothera, 168, 169, 171, *172*, 174, *175*, 180, 181, 184, **233**
  - Sect. Nematocaulis, 169, *172*, 173, 174, *175*, 176, 181, 189, 203, **375**, *379*
  - Sect. *Sphaerostigma*, 305
  - Sect. *Tetranthera*, 202, 203
  - Sect. Tetrapteron, 169, 171, *172*, 173, 174, *175*, 176, 180, 181, 184, **237**, *239*, *240*, *241*, *246*, *252*
  - *acuminata*, 342
  - andina, 168, 169, 174, 189, 203, 229, 373, 376, 377, **378**
  - angelorum, 182, 190, **192**, *193*, *195*, 196, 200
  - arenaria, 184, *228*, 233, **236**
  - benitensis, 188, 306, 324, 328, *331*, **332**, 338, 341
  - bistorta, 174, 185, 254, 255, *262*, 263, 264, **267**, *268*, 276, 277, 281, 286, 291, 292, 298, 301, 305, 381, 382
  - boothii, 172, 351, 352, **357**, *359*
  - boothii subsp. alyssoides, 166, 189, 352, 358, *359*, 361, **362**, 364, 365, 366, 371
  - boothii subsp. boothii, 188, 352, *359*, **365**, 366, 368
  - boothii subsp. condensata, 188, 354, 357, *359*, 361, **362**
  - boothii subsp. decorticans, 188, 351, **358**, *359*, 360, 361
  - boothii subsp. desertorum, 166, 188, 354, 357, *359*, **360**, 361, 362, 363, 364, 366
  - boothii subsp. intermedia, 188, *359*, 363, **364**, 365, 366
  - breviflora, 168, 169, 173, 174, 180, 184, 237, 238, *239*, *241*, 244, *246*, 247, 248, **249**

Camissonia—Continued
  - brevipes, 184, 202, **204**, 209, 213, 219
  - brevipes subsp. arizonica, 205, 206, **207**, 220, 222
  - brevipes subsp. brevipes, 178, **205**, 206, 209, 211, 216, 217, 218, 222, 232
  - brevipes subsp. pallidula, 205, **206**, 209, 211, 218, 219, 222
  - californica, 169, 171, 176, 180, 182, 189, 190, 196, **197**, *199*, 200, 271
  - campestris, 306, 307, 309, 310, 312, **320**, 321, 323, 324, 326, 327, 334, 338, 340, 341, 345
  - campestris subsp. campestris, 187, 307, **321**, *322*, 325, 326, 338, 346, 347, 350
  - campestris subsp. obispoensis, 187, *322*, **325**, 338, 350
  - cardiophylla, 233, **234**, 236
  - cardiophylla subsp. cardiophylla, 184, **234**, 237
  - cardiophylla subsp. cedrosensis, 168, 184, **236**
  - cardiophylla subsp. robusta, 184, **235**
  - chamanerioides, 169, 174, 188, 203, *297*, 351, 352, *353*, 354, **356**
  - cheiranthifolia, 171, 179, 254, 255, **258**, *260*, 281, 339, 381
  - cheiranthifolia subsp. cheiranthifolia, 172, 185, 259, *260*, *262*, **265**, 270, 274, 281, 382
  - cheiranthifolia subsp. suffruticosa, 172, 185, 258, **259**, *260*, *262*, 266, 267, 270, 277, 279, 382
  - claviformis, 173, 174, 202, 205, **212**, 213
  - claviformis subsp. aurantiaca, 183, 205, 207, 209, 213, 216, **217**, 218, 219, 220, 222
  - *claviformis* subsp. *citrina*, 213
  - claviformis subsp. claviformis, 183, 205, 213, 215, **216**, 218, 226, 231
  - claviformis subsp. cruciformis, 183, 212, **213**, 226
  - claviformis subsp. funerea, 183, 205, 213, **216**, 217, 218, 222, 232
  - claviformis subsp. integrior, 183, 205, 213, 214, **215**, 218, 226, 232
  - claviformis subsp. lancifolia, 183, 213, **214**, 232

Camissonia—Continued
  - claviformis subsp. peeblesii, 169, 175, 183, 205, 207, 213, **218**, 220, 222
  - claviformis subsp. peirsonii, 183, 213, 218, **219**, 220, 221
  - claviformis subsp. rubescens, 183, 207, 213, 219, **221**
  - claviformis subsp. wigginsii, 169, 183, 213, **221**
  - claviformis subsp. yumae, 183, 207, 213, 218, **220**
  - confertiflora, 169, 172, 175, 184, 202, **203**, 204
  - confusa, 186, 255, 271, 281, 286, 287, 290, 291, 294, **298**, *299*, *300*, 381, 383
  - contorta, 168, 187, 306, 307, 310, 316, 318, 320, 321, 323, 324, 325, 326, 327, 332, 333, 334, *335*, 336, 337, 338, 341, **345**, *347*, 350
  - *contorta* var. *pubens*, 316
  - crassifolia, 170, 171, 181, **190**, 194, *195*, 196, 200
  - dentata, 164, 169, 175, 179, 180, 306, 308, 321, 324, 337, 338, **339**
  - dentata subsp. dentata, 175, 188, **341**, 343
  - dentata subsp. littoralis, 188, 340, 341, **343**, 344
  - eastwoodiae, 169, 172, 182, 202, 213, **223**, 225, 226
  - exilis, 169, 182, 202, 203, **229**, 230, 373, 377
  - *flava*, 180, 341
  - gouldii, 175, 189, 351, 352, *366*, *367*, **368**
  - graciliflora, 185, 230, 237, 238, *239*, 242, **250**, *252*, 253, 351
  - guadalupensis, 256, 257, **271**, 273, 281, 305
  - guadalupensis subsp. clementina, 174, 185, 255, 267, 272, *273*, *274*, **275**, 283
  - guadalupensis subsp. guadalupensis, 169, 185, **272**, *273*, *274*, 275, 383
  - *hallii*, 292
  - hardhamiae, 185, 255, 281, 286, *296*, *300*, **301**, 383
  - heterochroma, 174, 182, 211, 215, 216, **231**

Camissonia—Continued
hilgardii, 169, 174, 189, *370*, 376, **377**, *379*
hirtella, 186, 255, 257, 271, 279, 281, **282**, *283*, *284*, 286, 290, 291, 294, 297, 298, *301*, 302, 303, 305, 309, 324, 383
ignota, 186, 255, 257, 271, 277, 279, 286, **287**, *288*, *289*, 294, 297, 298, 300, 301, 384
integrifolia, 187, 306, 308, 310, 318, 324, *330*, *331*, 334, 338, 341, **344**, 350
intermedia, 185, 186, 255, 271, 279, 281, 286, 287, 291, **295**, *296*, *297*, 301, 302, 303, 305, 385
kernensis, 306, 307, **308**, *314*
kernensis subsp. gilmanii, 187, 287, *289*, 307, **310**, 321, 324
kernensis subsp. kernensis, 174, 187, 287, *289*, 307, **309**, 310, 311, 312, 318, 324, 338, 345, 350
lacustris, 187, 306, 321, 323, 324, **329**, *330*, *331*, 333, 338, 341, 350
lewisii, 174, 185, 255, 257, 263, *268*, *270*, 271, **275**, 279, 281, 291, 298, 303, 305, 385
luciae, 185, 255, 281, 286, *296*, *300*, **302**, 286
megalantha, 169, 174, 182, **229**, 371
micrantha, 186, 255, 256, 257, 267, 271, *274*, 275, 277, *278*, **279**, 282, 286, 287, 291, 295, 297, 298, 301, 302, 303, 304, 305, 386
minor, 169, 188, 203, 229, 351, 352, **371**, *372*, *374*, 377
multijuga, 171, 174, 184, 202, 204, 205, **207**, 210, 211, 218, 228
munzii, 182, 205, 207, 213, 216, 218, **222**, 232
nevadensis, 169, 172, 188, 351, 352, *355*, **369**, *370*
ovata, 173, 185, 237, **238**, *239*, *240*, 242, 251
pallida, 255, 256, 257, 271, **291**
pallida subsp. hallii, 186, *270*, *288*, **292**, 294, 386
pallida subsp. pallida, 186, *284*, 286, 287, *288*, 290, 291, 292, **293**, 301, 387
palmeri, 169, 185, 237, 238, *239*, 251, **252**, 253, 351
paradoxa, 380

Camissonia—Continued
paradoxa var. *divaricata*, 342
parryi, 169, 172, 182, 203, 209, **227**, 228, 369
parvula, 169, 187, 307, 308, *313*, *314*, 315, 316, **318**, 350
proavita, 169, 186, 255, 257, *274*, **277**, *278*, 281, 291, 297, 298, 387
pterosperma, 173, 174, 189, *372*, 374, **375**
pubens, 166, 174, 187, 307, 308, 310, *313*, *314*, **316**, 319, 338, 345, 350
pusilla, 187, 307, 308, **312**, *313*, *314*, 316, 318, 319, 320
pygmaea, 169, 189, 351, 352, *355*, **366**, *367*, 368
refracta, 169, 174, 176, 188, *297*, 351, **352**, *355*, *355*, 356, 357, 358
robusta, 185, 255, 271, 277, 279, 281, *283*, 286, 298, *300*, **304**, 387
scapoidea, 169, 180, 202, 203, **223**
scapoidea subsp. brachycarpa, 182, 214, 216, **226**
scapoidea subsp. macrocarpa, 169, 175, 182, **225**
scapoidea subsp. scapoidea, 169, 176, 182, 212, 223, **224**, 226
scapoidea subsp. utahensis, 175, 182, **226**
sceptrostigma, 181, 190, *193*, *195*, **196**
sierrae, 306, 323, **326**, 350
sierrae subsp. alticola, 187, *322*, *328*, **329**
sierrae subsp. sierrae, 187, *322*, **327**, *328*, 329
speculicola, **209**, 212
speculicola subsp. hesperia, 169, 175, 184, **210**
speculicola subsp. speculicola, 169, 184, **209**, 210
strigulosa, 169, 188, 306, 308, 310, 317, 318, 324, 325, 326, 329, *331*, 332, **333**, *335*, 338, 339, 341, 344, 345, 346, *347*, 349, 350
subacaulis, 169, 172, 173, 185, 237, 238, *239*, *240*, **242**, 248, 250
tanacetifolia, 172, 174, 176, 237, 238, **244**, 249, 250
tanacetifolia subsp. quadriperforata, 184, 246, **248**
tanacetifolia subsp. tanacetifolia, 184, *239*, *241*, 244, **245**, *246*, 248

- Camissonia—Continued
  - *tenuifolia*, 342
  - walkeri, 176, 182, 184, 203, 205, **210**, 211
  - walkeri subsp. tortilis, 174, 205, 207, 208, **211**, 212
  - walkeri subsp. walkeri, 169, 209, 210, **211**, 212, 222, 225
- Centris rhodopus, 231
- *Chamissonia*—see *Camissonia*
- *Chylisma*—see *Chylismia*
- *Chylismia*, 164, 180, **202**
  - *arenaria*, 236
  - *aurantiaca*, 218
  - *brevipes*, 205
  - *cardiophylla*, 234
  - *clavaeformis*, 217
  - *clavaeformis* var. *cruciformis*, 213
  - *clavaeformis* var. *typica*, 217
  - *cruciformis*, 213
  - *heterochroma*, 231
  - *hirta*, 207
  - *lancifolia*, 214
  - *multijuga*, 207
  - *parryi*, 227
  - *parviflora*, 207
  - *peirsonii*, 219
  - *pterosperma*, 375
  - *scapoidea*, 224
  - *scapoidea* var. *aurantiaca*, 217
  - *scapoidea* var. *seorsa*, 224
  - tenuissima, 227
  - venosa, 207
  - walkeri, 211
- Clarkia, 161, 162, 163, 175, 231, 341, 344, 373, 377, 382
  - tenella, 344
- Cruciferae, 200, 205
- Epilobieae, 351
- *Eulobus*, 164, 165, 189
  - *californicus*, 180, 197
- Gaura, 161, 162, 163, 233, 356, 376
  - angustifolia, 376
  - *decorticans*, 358
  - hexandra subsp. hexandra, 376
  - mutabilis, 233
- Gayophytum, 161, 163, 170, 173, 174, 200, 341, 356, 375, 380
  - humile, 173
  - micranthum, 380
- *Godetia tenuifolia*, 344
- Gongylocarpus, 161, 163, 164, 170, 231
  - fruticulosus, 170
  - rubricaulis, 170
- Hauya, 161, 162, 163, 164
- Heterogaura, 161, 162, 163, 231
- **Holostigma**
  - *alyssoides*, 362
  - *argutum*, 341
  - *bottae*, 264
  - *cheiranthi folium*, 265
  - *heterophyllum*, 341
  - *micranthum*, 279
  - *paradoxum*, 380
  - *spirale*, 265
  - *tenuifolium*, 341
- *Jussiaea subacaulis*, 242
- Ludwigia, 376, 377
  - Sect. Prieurea, 376
  - inclinata, 377
  - *verticillata*, 377
- Oenothera, 161, 162, 163, 164, 165, 231, 356
  - subg. *Chylismia*, 162, 165, 180, 202, 233
  - subg. *Heterostemon*, 237
  - subg. *Primulopsis*, 237
  - subg. *Sphaerostigma*, 235, 305, 350, 375
  - subg. *Taroxia*, 180, 237
  - Sect. *Chylismia*, 202, 374
  - Sect. *Chylismiella*, 374
  - Sect. *Eremothera*, 350
  - Sect. *Euchylismia*, 202, 233
  - Sect. *Eutaraxia*, 237
  - Sect. *Heterostemon*, 237
  - Sect. *Holostigma*, 253
  - Sect. *Lignothera*, 233
  - Sect. *Nematocaulis*, 375
  - Sect. *Sphaerostigma*, 179, 305
  - Sect. *Tetranthera*, 202
  - Sect. *Tetrapteron*, 237
  - *abramsi*, 293
  - *alyssoides*, 352, 362
  - *alyssoides* var. *decorticans*, 358
  - *alyssoides* var. *minutiflora*, 371
  - *alyssoides* var. *typica*, 363
  - *alyssoides* var. *villosa*, 362, 364
  - *andina*, 378
  - *andina* var. *anomala*, 376, 378
  - *andina* var. *hilgardii*, 377
  - *andina* f. *tripetala*, 376, 378
  - *andina* var. *typica*, 378
  - *angelorum*, 192

Oenothera—Continued
arenaria, 236
bistorta, 256, 264, 267
bistorta var. *hallii*, 271, 292
bistorta var. *typica*, 267
bistorta var. *veitchiana*, 267, 271
boothii, 352, 365
boothii subsp. *alyssoides*, 363
boothii subsp. *boothii*, 365
boothii subsp. *condensata*, 362
boothii subsp. *decorticans*, 358
boothii subsp. *desertorum*, 360
boothii subsp. *intermedia*, 364
boothii subsp. *inyoensis*, 360, 361
boothii var. *pygmaea*, 366
boothii subsp. *rutila*, 358, 360
boothii var. *typica*, 364, 365
breviflora, 180, 237, 249
brevipes, 205
brevipes subsp. *arizonica*, 207
brevipes subsp. *brevipes*, 205
brevipes var. *multijuga*, 207
brevipes subsp. *pallidula*, 206
brevipes var. *pallidula*, 206
brevipes race *parryi*, 227
brevipes var. *parviflora*, 207
brevipes var. *scapoidea*, 224
brevipes var. *typica*, 205
californica, 197
campestris, 321
campestris subsp. *campestris*, 321, 329
campestris var. *cruciata*, 345
campestris subsp. *parishii*, 321
cardiophylla, 234
cardiophylla subsp. *cardiophylla*, 234
cardiophylla subsp. *cedrosensis*, 236
cardiophylla var. *longituba*, 236
cardiophylla var. *petiolaris*, 234
cardiophylla subsp. *robusta*, 235
cardiophylla var. *splendens*, 236
cardiophylla var. *typica*, 234
cedrosensis, 236
chamaenerioides var. *torta*, 371
chamissonis, 341
cheiranthifolia, 265
cheiranthifolia var. *contorta*, 345
cheiranthifolia f. *delicatula*, 267
cheiranthifolia var. *nitida*, 167, 265
cheiranthifolia var. *suffruticosa*, 259
cheiranthifolia var. *typica*, 265
chilensis, 342
clavaeformis, 216

Oenothera—Continued
clavaeformis subsp. *aurantiaca*, 218
clavaeformis var. *aurantiaca*, 175, 216, 218
clavaeformis subsp. *citrina*, 213
clavaeformis subsp. *clavaeformis*, 217
clavaeformis subsp. *cruciformis*, 213
clavaeformis var. *cruciformis*, 213, 214
clavaeformis subsp. *funerea*, 216
clavaeformis subsp. *integrior*, 215
clavaeformis subsp. *lancifolia*, 214
clavaeformis var. *peeblesii*, 218
clavaeformis subsp. *peirsonii*, 219
clavaeformis var. *peirsonii*, 219
clavaeformis var. *purpurascens*, 213
clavaeformis subsp. *rubescens*, 221
clavaeformis var. *typica*, 215, 217
clavaeformis subsp. *wigginsii*, 221
clavaeformis subsp. *yumae*, 220
confertiflora, 203
contorta, 166, 307, 339, 345
contorta var. *contorta*, 306, 346, 350
contorta var. *divaricata*, 339, 340, 342
contorta var. *epilobioides*, 306, 307, 329, 333, 339, 340, 342, 346, 350
contorta var. *flexuosa*, 307, 312, 318
contorta var. *pubens*, 307
contorta var. *strigulosa*, 306, 307, 333, 346, 350
contorta var. *typica*, 306, 307, 345, 350
crassifolia, 190
crassifolia var. *leptocarpa*, 197
crassiuscula, 192, 196
cruciata, 321, 323, 329, 332, 346, 350
cruciformis, 213
decorticans, 352, 358
decorticans var. *condensata*, 362
decorticans var. *desertorum*, 360
decorticans var. *intermedia*, 352
decorticans var. *inyoensis*, 352
decorticans var. *rutila*, 352, 358, 361
decorticans var. *typica*, 358
dentata, 179, 306, 307, 321, 332, 333, 339, 340, 341, 346, 350
dentata var. *campestris*, 321, 329, 339, 340, 342
dentata var. *cruciata*, 345
dentata var. *dentata*, 339
dentata var. *gilmanii*, 310
dentata var. *johnstonii*, 307, 310, 321

Oenothera—Continued
- *dentata* var. *parishii*, 321
- *deserti*, 352
- *divaricata*, 205
- *eastwoodiae*, 222
- *erythra*, 356
- *eulobus*, 197
- *exilis*, 202, 229
- *gauraeflora*, 358
- *gauraeflora* race *boothii*, 365
- *gauraeflora* var. *caput-medusae*, 369
- *gauraeflora* var. *hitchcockii*, 363
- *gauraeflora* var. *vermiculata*, 369
- *graciliflora*, 250
- *gracilis*, 165
- *guadalupensis*, 272
- *guadalupensis* subsp. *clementina*, 275
- *guadalupensis* subsp. *guadalupensis*, 272
- *hallii*, 292
- *heterantha*, 237, 242
- *heterantha* var. *taraxacifolia*, 243
- *heterochroma*, 231
- *heterochroma* subsp. *heterochroma*, 232
- *heterochroma* var. *megalantha*, 229
- *heterochroma* subsp. *monoensis*, 232
- *heterochroma* var. *monoensis*, 232
- *heterochroma* var. *typica*, 231
- *heterophylla*, 267, 342
- *hilgardi*, 377
- *hirta*, 257, 279
- *hirta* var. *exfoliata*, 271, 293
- *hirta* var. *hirta*, 281
- *hirta* var. *ignota*, 287, 290, 298
- *hirta* var. *jonesii*, 282, 295, 298, 302
- *hirta* var. *jonesii* f. *reedii*, 282
- *hirta* var. *typica*, 275, 277, 279, 295, 298
- *hirtella*, 256, 282
- *hyssopifolia*, 344
- *ignota*, 287, 298
- *kernensis*, 309
- *kernensis* subsp. *gilmanii*, 310
- *kernensis* subsp. *kernensis*, 309
- *kernensis* subsp. *mojavensis*, 310, 311
- *leptocarpa*, 197
- *megalantha*, 229
- *micrantha*, 256, 257, 275, 277, 279, 295, 302, 304, 305, 380
- *micrantha* var. *abramsii*, 293

Oenothera—Continued
- *micrantha* var. *acuminata*, 339, 340, 342
- *micrantha* var. *exfoliata*, 293
- *micrantha* var. *hirtella*, 282
- *micrantha* var. *ignota*, 287, 290, 381
- *micrantha* var. *jonesii*, 282, 286
- *micrantha* var. *reedii*, 282
- *minor*, 371
- *minor* var. *cusickii*, 371, 373
- *minor* var. *typica*, 371
- *minutiflora*, 342
- *multijuga*, 207
- *multijuga* var. *orientalis*, 211
- *multijuga* var. *parviflora*, 207, 211
- *multijuga* var. *typica*, 207
- *munzii*, 222
- *nevadensis*, 369
- *nitida*, 265, 266, 382
- *nuttallii*, 245
- *ovata*, 238
- *pallida*, 256
- *pallidula*, 206
- *palmeri*, 252
- *parryi*, 227
- *parryi* f. *tenuissima*, 227
- parviflora, 207
- *parvula*, 318
- *phlebophylla*, 207
- *primuloidea*, 238, 243
- *pterosperma*, 375
- *pubens*, 316
- *pygmaea*, 366
- *rutila*, 358, 360
- *scapoidea*, 180, 224
- *scapoidea* var. *aurantiaca*, 217
- *scapoidea* subsp. *brachycarpa*, 226
- *scapoidea* var. *clavaeformis*, 216
- *scapoidea* var. *eastwoodae*, 222
- *scapoidea* subsp. *macrocarpa*, 225
- *scapoidea* var. *parryi*, 227
- *scapoidea* var. *purpurascens*, 215
- *scapoidea* subsp. *scapoidea*, 224
- *scapoidea* var. *seorsa*, 224
- *scapoidea* var. *tortilis*, 211
- *scapoidea* var. *typica*, 224
- *scapoidea* subsp. *utahensis*, 226
- *sceptrostigma*, 196
- *speculicola* subsp. *hesperia*, 210
- *speculicola* subsp. *speculicola*, 209
- *spiralis*, 265
- *spiralis* f. *arcuata*, 257
- *spiralis* f. *clypeata*, 257

Oenothera—Continued
  spiralis var. *linearis*, 259
  spiralis var. *nitida*, 265
  spiralis f. *viridescens*, 259
  spiralis var. *viridescens*, 259
  strigulosa, 333
  strigulosa var. *epilobioides*, 333
  subacaulis, 243
  subacaulis var. *taraxacifolia*, 243
  tanacetifolia, 245
  tenuifolia, 341
  tenuissima, 227, 228
  torulosa, 308, 344
  torulosa f. *chilensis*, 342
  torulosa f. *cruciata*, 345
  torulosa race *helianthemiflora*, 321
  torulosa f. *mixta*, 345
  torulosa f. *permixta*, 321
  utahensis, 363
  virescens, 259
  viridescens, 259
  walkeri, 211
  walkeri subsp. *tortilis*, 211
  watsonii, 207
Onagraceae, 161, 277, 341, 351, 377, 382
Onagreae, 161, 162, 163, 164, 170, 175, 231, 233, 247, 373, 375, 382
Onothera—See *Oenothera*
Polygonaceae, 165
Salpingia, 162
Sphaerostigma, 164, 179, 264
  acuminatum, 342
  alyssoides, 362
  alyssoides var. *macrophyllum*, 363
  alyssoides var. *minutiflorum*, 371
  andinum, 378
  andinum var. *hilgardii*, 377
  andinum var. *minutum*, 380
  angelorum, 192
  arenicola, 256, 282
  bistortum, 267, 271
  bistortum var. *reedii*, 282
  bistortum var. *veitchianum*, 267
  boothii, 365
  boothii var. *pygmaeum*, 366
  campestre, 321
  campestre var. *helianthemiflorum*, 321
  campestre var. *minus* ("minor"), 345
  campestre var. *mixtum*, 345
  campestre var. *parishii*, 321
  chamaenerioides, 356
  chamissonis, 341
  cheiranthifolium, 265

Polygonaceae—Continued
  contortum, 345
  contortum var. *flexuosum*, 318
  contortum var. *greenei*, 333
  contortum var. *pubens*, 316
  decorticans, 358
  dentata subsp. *campestris*, *321*
  dentatum, 307, 342
  deserti, 352
  divaricatum, 342
  erythrum, 356
  filiforme, 318
  flexuosum, 318
  gauraeflorum, 358
  hallii, 256, 292
  heterophyllum, 342
  hilgardi, 377
  hirtellum, 256, 282
  hirtellum var. *montanum*, 282
  hirtum, 279
  hitchcockii, 363
  implexum, 363
  lemmoni, 365
  macrophyllum, 363
  micranthum, 256, 279
  micranthum var. *exfoliatum*, 293
  micranthum var. *jonesii*, 282
  minus ("*minor*"), 371
  nelsonii, 371
  nevadense, 369
  nitidum, 265
  orthocarpum, 316
  pallidum, 256, 293
  paradoxum, 380
  parvulum, 318
  pterospermum, 375
  pubens, 316
  ramosissimum, 242
  refractum, 352
  rutilum, 358
  senex, 365
  spirale, 265, 381
  spirale var. *clypeatum*, 258
  spirale var. *viridescens*, 259
  strigulosum, 333, 334
  tenuifolium, 342, 343
  tortum, 371
  tortum var. *eastwoodae*, 371
  tortuosa, 369
  utahense, 363
  veitchianum, 267, 381
  viridescens, 259

Stenosiphon, 161, 162, 163

Taraxia, 164, 180, 237

  breviflora, 249

  graciliflora, 250

  heterantha, 243

  heterantha var. *taraxacifolia*, 243

  longiflora, 245

  ovata, 238

Taraxia—Continued

  palmeri, 252

  subacaulis, 243

  tanacetifolia, 245

  taraxacifolia, 243

  tikurana, 245

Xylonagra, 161, 163, 170

U.S. GOVERNMENT PRINTING OFFICE : 1968—O-295-855